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**Intermountain
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Ecology and Management of Larix Forests: A Look Ahead

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Proceedings of an International Symposium

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Intermountain Research Station
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Ogden, UT 84401

Ecology and Management of Larix Forests: A Look Ahead

Proceedings of an International Symposium

Whitefish, Montana, U.S.A.
October 5-9, 1992

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Kathy J. McDonald

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PREFACE

This proceedings is a product of the first comprehensive and international examination of Larix species of the world. It reports most of the papers and posters that were presented at the International Symposium "Ecology and Management of Larix Forests: A Look Ahead," held October 5-9, 1992, at Grouse Mountain Lodge, Whitefish, Montana, U.S.A.

Larix species are key components of many cold-temperate forests in North America, Europe, and Asia. Although there is not total agreement on the number of different species, 10 species of Larix are generally recognized, with three in North America and seven in Eurasia. Numerous varieties and hybrids of Larix are also recognized. These species developed over some 35 million years, and during that time some species became extinct. All Larix species share essentially the same major characteristics, the most obvious being coniferous, deciduous, and seral in nature. Their beauty, much of it associated with seasonal hues of light green in the spring and bright yellow in the fall, make them unique in coniferous forests. They occur over extensive areas and transcend international boundaries in the Northern Hemisphere.

How did this symposium come about? A steady increase in demand for current information about temperate coniferous forests brought this idea to the forefront. Several symposia and workshops, usually species oriented, have begun to address these information needs in the Western United States and Canada. The original intent of this Larix symposium was to ferret the best information available for western larch (*L. occidentalis*), a very important species in the Western United States and Canada. To do this we formed a planning committee who concluded that western larch should be featured, but other Larix species of the world should also be included. We then contacted colleagues in North America, Europe, and Asia, and the planning proceeded.

The charter of this international symposium was to explore the ecology and management of Larix worldwide and to feature the latest information on western larch and its associated resources. The symposium included technical indoor sessions with over 100 papers and posters, highlighted by field tours to Coram Experimental Forest, Miller Creek Demonstration Forest, Glacier National Park, Flathead and Lolo National Forests, and to British Columbia and Alberta, Canada. The program was designed for natural resource managers, research scientists, educators, specialists in ecology, wildlife habitat, hydrology, soils, esthetics, fire, insects and disease, geneticists, silviculturists, and others interested in Larix forests including seeds and seedlings, nursery, genetics, stand culture, growth, nutrients, associated vegetation, fire, insects and disease, animals, hydrology, and esthetics.

This symposium culminated over 2 years of planning by a dedicated and innovative committee composed of researchers, managers, and educators from the United States and Canada:

Forest Service, U.S. Department of Agriculture	Intermountain Research Station	Wyman C. Schmidt, Chair Bozeman, Montana, U.S.A.
		Raymond C. Shearer Missoula, Montana, U.S.A.
	National Forest Systems	Ronald Hamilton Ogden, Utah, U.S.A.
		Walter Knapp Portland, Oregon, U.S.A.
		John R. Naumann Missoula, Montana, U.S.A.
University of Montana	Continuing Education	Gerry T. Baertsch Missoula, Montana, U.S.A.
	School of Forestry	Robert D. Pfister Missoula, Montana, U.S.A.
British Columbia Ministry of Forests	Kalamalaka Research Station	Barry Jaquish Vernon, British Columbia, Canada

Some 340 scientists, natural resource managers, and educators from 17 countries participated in the symposium. Participants, such as those from Russia, represented vast forests of Larix, while others, such as Iceland, sought information about species of Larix that might be suitable for afforesting some of their almost treeless landscapes. A dedication of the International Larix Arboretum in Hungry Horse, Montana, U.S.A.; associated with Coram Experimental Forest, highlighted the global cooperation that made this symposium such a success. Small seedlings grown from seeds provided by scientists from around the world were planted by representatives from nine countries.

Without the sponsorship of the following organizations this gathering would not have been possible:

Forest Service, U.S. Department of Agriculture

- Northern Region
- Intermountain Region
- Pacific Northwest Region
- Intermountain Research Station

National Park Service, U.S. Department of the Interior

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International Union of Forestry Research Organizations (IUFRO):

- S1.05-00 Stand Establishment, Treatment, and Amelioration
- S1.05.03 Treatment of Young Stands
- S1.05.06 Multiple-Use Silviculture
- S2.02-07 Larch Provenances and Breeding

We also acknowledge the many other individuals and groups who helped out in so many ways by providing guides for field tours, spouse tours, facilities, and vehicles. We particularly thank the Flathead National Forest and Glacier National Park for moral and logistical support during the planning and conduct of the symposium. Special thanks are due the Salish-Kootenai Tribe for their opening ceremonies and hosting of a Native American festival evening.

Kathy McDonald of the Intermountain Research Station processed the manuscripts and did nearly all of the typing for the myriad of letters, notices, electronic mail, and other matters of communication. Gerry Baertsch and Clare Kelly of the University of Montana developed all the brochures, handled the mailings, and covered all the registration and logistical arrangements. Louise Kingsbury, Intermountain Research Station, edited the manuscripts for the symposium and supervised the final layout and publications processes. All did a tremendous job, and we owe them many thanks.

The world faces many environmental and resource challenges. Many of these challenges in temperate forests of the Northern Hemisphere provide significant tangible and intangible resources for the economic, ecological, and social well-being of the world. Larch forests comprise a large proportion of these vast temperate forests, and we need to utilize the best information available to manage them. That is what this symposium was all about—making the best Larix information available. We can learn much from each other, and the international scope of this symposium is a major step in that direction.

Wyman C. Schmidt, Ph.D.
Symposium Chair
Intermountain Research Station
Forest Service
U.S. Department of Agriculture

VORREDE AUSZUG

Dieser Bericht ist ein Ergebnis der ersten internationalen Tagung über die Lärchenarten der Welt. Er enthält die meisten der Beiträge und Poster, die während des Internationalen Symposiums “Ecology and Management of Larix Forests: A Look Ahead” vorgestellt wurden. Das Symposium fand vom 5. - 9. Oktober 1992 im Grouse Mountain Lodge in Whitefish (Montana, U.S.A.) statt.

Lärchen bilden in vielen kalt-temperierten Wäldern Nordamerikas, Europas und Asiens die Hauptbaumart. Hinsichtlich der Gesamtzahl der Lärchenarten besteht keine einhellige Meinung. Im allgemeinen geht man jedoch von 10 Arten aus. Davon sind drei in Nordamerika und sieben in Eurasien beheimatet. Hinzu kommen zahlreiche Varietäten und Hybriden. Alle Arten weisen dieselben Hauptmerkmale auf. Sie gehören zu den Koniferen, sind laubwerfend und charakteristisch für bestimmte Sukzessionsstadien. Ihr hoher ästhetischer Reiz, der vor allem von ihrer mit der Jahreszeit wechselnden Färbung vom hellen Grün im Frühjahr zum kräftigen Gelb im Herbst ausgeht, macht sie in den Nadelwäldern zu einer einzigartigen Erscheinung. Ihre Verbreitung erstreckt sich in der Nordhemisphäre über große Gebiete und internationale Grenzen hinweg.

Wie kam es zu diesem Symposium? Das treibende Moment war der wachsende Bedarf an Informationen über die kalt-temperierten Nadelwälder. Das Planungskomitee schlug vor *Larix occidentalis* zwar in den Mittelpunkt der Veranstaltung zu stellen, aber auch andere Lärchenarten einzubeziehen. Danach wurden Kollegen aus Nordamerika, Europa und Asien einbezogen und die Planung auf internationaler Ebene fortgesetzt.

Ziel des Symposium war es, Erkenntnisse über die Ökologie und Erfahrungen mit der Bewirtschaftung der Lärche weltweit zusammenzutragen und speziell die neuesten Kenntnisse über *Larix occidentalis* und die von ihr geprägten Ökosysteme zu sammeln. Während des Symposiums wurden über 100 Vorträge gehalten und Poster ausgestellt. Höhepunkte waren die Exkursionen zum Coram Experimental Forest, zum Miller Creek Demonstration Forest, Glacier National Park, Flathead and Lolo National Forest sowie nach British Columbia und

Alberta in Kanada. Das Programm war so zusammengestellt, daß es eine Vielzahl Interessierter aus den verschiedensten Bereichen der Wissenschaft und Praxis ansprach.

An dem Symposium nahmen 340 Wissenschaftler, Waldbauexperten und Unterrichtende aus 17 Ländern teil. Einige Teilnehmer, wie z.B. die Russen, vertraten die Gebiete mit ausgedehnten Lärchewnäldern, andere, wie die Isländer, waren gekommen, um Informationen über Lärchenarten zu bekommen, die man möglicherweise auf ihrer gegenwärtig fast baumlosen Insel anpflanzen könnte. Die Einweihung eines zum Coram Experimental Forest gehörenden Internationalen Larix-Aboretums bildete den Höhepunkt der internationalen Kooperation, die dieses Symposium zu einem großen Erfolg werden ließ. Vertreter von neun Ländern pflanzten hier Lärchensämlinge, welche aus Samen herangezogen worden waren, die man über Wissenschaftler aus aller Welt erhalten hatte.

Wir danken allen Organisationen, die dieses Symposium unterstützt haben. Ohne die Unterstützung durch die nachstehend genannten Organisationen wäre es nicht möglich gewesen, ausreichende Mittel zu bekommen.

Forest Service, U.S. Department of Agriculture

  Northern Region

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  S2.02-07 Larch Provenances and Breeding

Die Welt sieht sich gegenwärtig vielen Herausforderungen durch Umweltprobleme und Ressourcennutzung gegenüber. Viele der temperierten Wälder der Nordhemisphäre stellen wichtige wirtschaftliche und ökologische Ressourcen dar und besitzen weitreichende Wohlfahrtsfunktionen. Lärchenwälder bilden einen großen Teil dieser ausgedehnten temperierten Wälder, und wir brauchen die besten verfügbaren Kenntnisse, um sie zu bewirtschaften. DAS WAR DAS EIGENTLICHE ANLIEGEN DES SYMPOSIUMS-DAS VORHANDENE WISSEN ZUSAMMENZUTRAGEN UND VERFÜGBAR ZU MACHEN. Wir können viel voneinander lernen, und der internationale Rahmen dieses Symposiums ist ein großer Schritt in diese Richtung.

Auszug von Prof. Dr. F.-Karl Holtmeier

THE COMPILERS

Wyman C. Schmidt is Scientist Emeritus, Intermountain Research Station's Research Work Unit on Ecology and Management of Northern Rocky Mountain Forest Ecosystems at the Forestry Sciences Laboratory, Bozeman, Montana, U.S.A. Dr. Schmidt's research has focused on the ecology, regeneration processes, stand development, and related cultural practices in coniferous forests of the Intermountain West. Much of his research has centered on the interrelationships of timber, water, and other resources as well as the interaction of cultural practices with insect pests such as western spruce budworm.

Kathy J. McDonald is Project Secretary and handles the administrative details for Intermountain Research Station's Research Work Unit 4151 at the Forestry Sciences Laboratory, Bozeman, Montana, U.S.A. She has had involvement with numerous other scientific proceedings.

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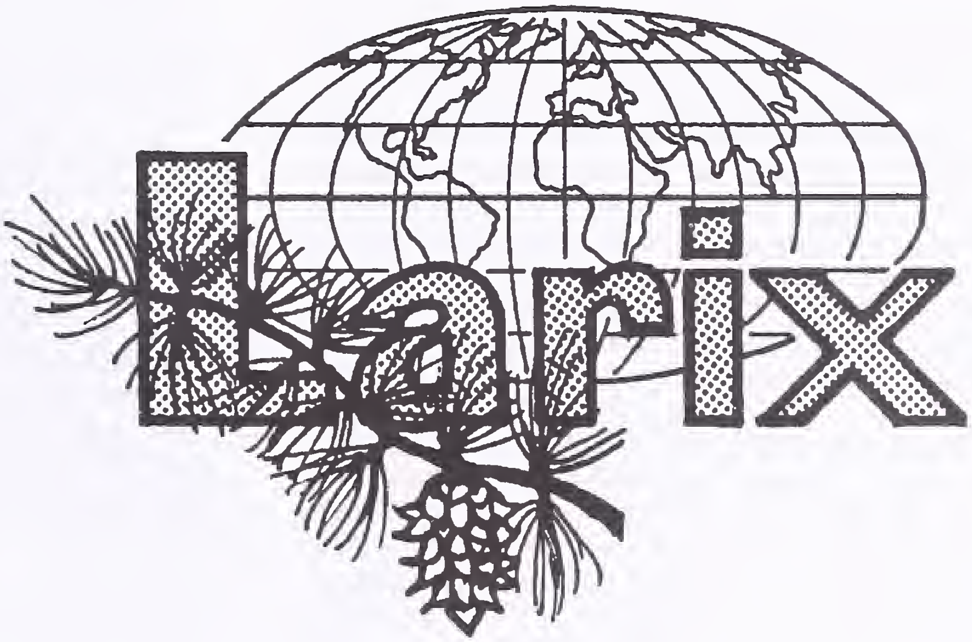
I. Larix Worldwide: An Overview



Keynote Address: International Cooperation in a Global Environment

Jeff M. Sirmon

What an incredible time to be a part of the forestry and natural resources world! A time when technology and science can be focused on the natural world in so many exciting ways. A time when people and institutions are beginning to grapple with the inextricable linkages between the social, economic, and environmental dimensions of sustainability. A time when so many facets of a subject can be synthesized in ways never before imagined.

Just as exciting as the technical and scientific aspects of forestry are the social and geopolitical changes taking place all over the globe. Changes that have profound implications for our interests.

A new world order is emerging and it is, to a large degree, responsible for the collapse of the old system and signifies the awakening to the perils of poverty and pollution. The new order demands attention to problems around us in our world every day. The old order's centerpiece was national security and East/West polarity. The new order shifts to concerns about environment and development that are more real and threatening than ideologies. The new issues revolve around a North/South axis—between the rich developed countries and the poor developing countries.

Human enterprises have quadrupled since World War II—a span within my lifetime—and will quadruple again by the middle of the 21st century. The ability of people to change the face of the earth—through digging, scraping, fishing, logging, building, chemicals, and other tools—affects nature to the degree that nature itself is threatened. There are enough of us that we are currently destroying important parts of the earth's ability to replenish and restore itself.

The post-cold war period—that is, the new world order—seems to be characterized by a need for economic success, environmental security, and international equity. As we explore the meaning of these goals, we find they are undeniably interrelated. The road to Rio for the international Earth Summit in 1992 was paved by people who saw these problems in 1972 when the Bruntland Commission was established. The commission was sponsored by the United Nations with a charge to examine the connection between economic development and the environment and to look at the question of intergenerational equity.

And what an examination it has been. Over these past 20 years while I was doing my part to affect the soil, air, water, forests, and minerals on our domestic forest lands, wise people, thank goodness, asked larger questions: Where are the current trends in industrial production, in energy use, in deforestation, in air pollution, in fishing leading us? What is our world to be like when we add 5 billion more people to this planet with all their animals, machines, and consumption patterns and who are striving for two cars in every garage?

EARTH SUMMIT: PREPARATION AND EXPECTATIONS

The preparation process for Rio was a public education process of unparalleled proportions. The extent of poverty, environmental degradation, pollution, and consumption patterns was described worldwide, over and over. Charges of who is to blame for the bad situation and who should shoulder the burden for changing the trends have had extensive debate. The broad questions of equity, who pays, sovereignty, and so forth, are at least being addressed and in fact form the basis for the commitments from Rio. It is of outstanding significance that the accords that came out of Rio were an absolute and total consensus. Every last paragraph, word, and punctuation mark were by complete consensus of 180 countries.

The Earth Summit in Rio—more properly called the U.N. Conference on Environment and Development (UNCED)—was a watershed event in the affairs of humankind in our attempt to wrestle with the way we conduct our business on this planet. The 180 countries coming together, all struggling with the questions of development, environment, and survival, no one storming away as if these were not appropriate subjects to address. About 40,000 attendees and more than 8,000 journalists. And in the end, 118 heads of state, more than have gathered at any time in history, either in preparing for war or planning for peace. All these people spoke about and made commitments to the social, economic, and environmental basis of sustainability. This event was not insignificant.

The expectations from Rio were high. Expectations for specific treaties on climate change and biodiversity; for a wide-ranging statement of principles of forest conservation and management; for an ambitious Agenda 21 with 900 pages of significant new international commitments to better environmental behavior; and for new financial resources sought by developing countries.

Paper presented at the Symposium on Ecology and Management of Larix Forests: A Look Ahead, Whitefish, MT, U.S.A., October 5-9, 1992.

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WHAT THE EARTH SUMMIT ACHIEVED

Achievement: Framework Convention on Climate Change, in which 154 countries committed to decreasing harmful levels of greenhouse gases, developing national action plans, and increasing scientific research and monitoring.

Achievement: Convention on Biological Diversity, a treaty that addresses the problems of species lost worldwide with a commitment to national plans and conservation strategies. The United States' decision not to sign was a subject of intense controversy and criticism. In public relations terms we never recovered from it. Our decision was not based on opposition to the conservation elements of the agreement, which we support, but rather on our financial and legal concerns about characterizing biotechnology as unsafe and on how to deal with intellectual property rights.

Achievement: The Declaration of Principles on Forestry and the advancement of our "Forests for the Future Initiative." These were in lieu of and by a firm foundation for the President's proposal for a worldwide convention on forests. This initiative promotes sustainable forest use. The United States made forests the top priority for our entire delegation.

Achievement: Agenda 21. Perhaps the most remarkable achievement of the conference, these 900 pages of action plans were adopted by consensus by all 180 countries. The plans provide a blueprint for action for the 21st century to move the world to sustainable development. Agenda 21 addresses issues of protection of the atmosphere and oceans, guidelines for environmental impact statements, toxic release inventories, public participation, community right to know, safe drinking water, and many others. A number of these ideas—such as community right to know, toxic release inventories, and environmental impact statements—were championed by the United States. Agenda 21 is an extraordinarily new consensus on standards by which to measure the performance of governments. No doubt the press, nongovernment groups, and environmental ministries will mine these documents for ideas and will use them to hold governments and industry accountable for their actions for years to come. Just as in the field of human rights, these declarations will be a force to beat recalcitrant governments.

Achievement: The Rio Declaration, or the Earth Charter. This declaration, a kind of "Stockholm Two," outlines principles that blend the perspectives of both developed and developing nations. In a broad sense the declaration embodies the general positive political emphasis that UNCED put on environmental and development needs.

The "spirit" of UNCED was as important as the substance. The conference had far-ranging impacts beyond the individual agreements cited. It significantly heightened the environmental concerns worldwide and in effect was a 14-day crash course in environmental education for governments, heads of state, and citizens worldwide. The North and South Americas, Europe, and Japan received saturating press coverage.

The U.N. conference in RIO marked the arrival of the international environmental issue in terms of trade, energy, technology transfer, bilateral funding, multilateral organizational commitments, and structures. It launched the environment as a major new consideration in foreign policy.

Rio created a compelling rationale for cooperation between the North and South, including funding commitments. It created a new basis for developing countries to make demands on developed countries. As traditional security and strategic claims have waned after the cold war, developing countries have begun to appreciate that they have a new rationale for demanding concessions from richer countries. How they use their forests and burn fossil fuel, or whether they conserve species, all matter to people in developed countries who will pay to influence new policies.

WHAT DOES THIS MEAN FOR FORESTRY?

What does this mean from a scientific standpoint? If we are to have less pollution and more jobs (and that is the bottom line), then there must be an unprecedented transformation to replace technologies deployed today in industries, agriculture, and forestry with ones that meet more exacting environmental criteria. Further still, there must be increases in new technology and changed thinking so that environmental imparities and economic opportunities can go hand in hand.

We must change our attitude about environmental protection from one of mitigating to one of careful planning.

We must change from a command and control system of regulation that fosters adversarial relations between industry regulators and environmentalists. We must move from restrictions to incentives.

What this means for forestry, first and foremost, is that the forestry voice must be more effective in competing for influence in policy and political arenas. Resources must be increased and horizons broadened. One of the strongest criticisms worldwide of forestry professionals is that they are mostly trained in specialist forestry colleges and are not exposed to the breadth of other disciplines that commonly form the grounding of other professionals. How do we prepare foresters to be leaders in resolving cross-sectorial issues? When the major destructive forces to forests are consumptive patterns of the developed world, poverty in the developing world, and population growth worldwide, how do we prepare people to be on the front line in the search for solutions?

I was pleased with the quick action the U.S. Government took following Rio in setting up a high-level policy coordinating group to focus on the implementation of Agenda 21 and other agenda items from Rio. A specific task force has been set up that is cochaired by the Council on Environmental Quality and the State Department. This task force is assisted by representatives from the original negotiating U.S. team in Rio as well as other planning experts from all U.S. Federal agencies that have a part in carrying out the agreements. The Forest Service will examine all of its programs in light of our Rio commitments.

In addition, the United States is committed to the Forests for the Future Initiative, begun in the Bush Administration. We continue to engage other partners of industrialized nations and developing nations in laying the groundwork for the eventual delivery of this initiative.

Other actions prompted by our agreements in Rio or encouraged by the overall atmosphere surrounding UNCED are:

- Make UNCED documents available electronically to all employees of the Forest Service.
- Add an international dimension to the 1995 Resources Planning Act Assessment and Program reflecting the UNCED Secretary General's report on "Conservation and Development of Forests," which is an assessment of the threats to and the conditions of the world's forests.
- Interpret the relationships and response to the agreements from Rio within ongoing programs. Describe how we will put the intent of the Rio agreements in operation.
- Take an active role in promoting the spirit and substance of UNCED with national and international communities of interest.
- Become more focused in our international activities as we seek to arrest deforestation.
- Follow through with quality implementation of the ecosystem management policy in our National Forests.
- Establish the International Institute of Tropical Forestry in Puerto Rico.
- Establish a sister forest program in the Forest Service as a way to facilitate technology transfer.
- Make strong ties to UNCED for the Forests for the Future Initiative projects and programs.

NO HIDING FROM SCRUTINY

Forest Service Chief Dale Robertson, during the Rio conference, announced that the agency would change policy to one of ecosystem management and would abandon clearcutting as a preferred silvicultural tool. The announcement was not solely for domestic audiences. The handwriting is clearly on the wall. Any domestic forestry policy that tends to be at odds with the principles agreed to in Rio will be examined in the international arena. No matter where it occurs in the world, the physical evidence of forest policy, the evidence of pollution, and the evidence of overuse and overexploitation can be communicated worldwide instantly. There will be no hiding from scrutiny by nations and interest groups within many nations.

In domestic debates, discussions of only a narrow part of forestry have unfortunately been interpreted widely as representing our total forest policy. For example, the question of clearcutting in our country is closely associated with the notion of deforestation. The question of subsidies in trade have been linked to our discussions on below-cost timber sales. The debates around spotted owl and other species have been framed in a way as to question our commitment to maintaining biodiversity. Some of our policies in fire management have been associated with excess carbon dioxide emissions.

The fact of worldwide scrutiny poses an important question on how we and the profession of forestry are going to address policies and practices in a way that we can reach resolution and gain support. This fact challenges the leadership in our profession. However, several examples I have observed lead me to believe that we are capable of focusing on resources globally. In preparing for Rio, I was proud of the way our leaders in the pulp and paper industry came together to pledge their commitment to managing lands and natural resources in a quality environment and in fact developed a set of principles to govern their members' behavior. And members of the environmental community are realizing that methods and tactics used domestically in framing environmental issues do not, by and large, fit the situation in developing worlds and that the human factor in finding solutions to environmental questions must be addressed. I hope such examples will be a pattern in the future.

In closing, let me say that for my generation the East-West confrontation was our formative experience. For my children the cold war is only a fading memory. For their future, the North-South cooperation will become a living reality with environmentally sound development as its central concern.

The new world order is demanding a higher priority for our earth's stabilization, for proper care of the oceans, the atmosphere, and the forests. We are one world, and our interdependence is a fact.

Maurice Strong, Director General for UNCED, made the statement that UNCED was the most important conference in the history of humanity. Surely we should heed the direction that comes from such a conference. The actions from our Government and the actions of the Forest Service should be strong and appropriate. We should be aware of and sensitive to the power of expectations that may be released in many different ways throughout the world.

The road from Rio has been surveyed. Now it needs to be paved with deeds and not just good intentions.

Around the World with Larix: an Introduction

Wyman C. Schmidt

Circling the globe at 60° N latitude, one is seldom out of sight of Larix on the extended landmasses of Eurasia and North America. Larch forests essentially encircle the Northern Hemisphere, stretching from eastern Siberia westward across Eurasia (but presently absent in Scandinavia), resuming in eastern North America and westward across the United States and Canada to Alaska, where except for the Bering Sea, they essentially reach our starting point back in Siberia (fig. 1). But along that approximate 20,000-km (12,000-mile) path, larch splits into 10 species and numerous varieties and hybrids. These 10 species occupy a wide variety of ecological conditions and zones ranging from lowland boreal to upper montane to upper subalpine conditions and extend south to 25° latitude at high elevations and north to 75° latitude in the boreal lowlands.

Larches have been in the same general area for a long time. Larch fossils recovered from sediments laid down in the Oligocene to the Holocene eras have been described in North America, Europe, and Asia. More species of larch have already gone extinct than the 10 presently surviving species. Fossil larch have been found in northern Canada, Poland, Russia, Japan, and Alaska, U.S.A. Lepage and Basinger (1991) list many of the fossil species described in the world literature and describe in detail excellent fossil remains of *Larix altoborealis* found in the Canadian Arctic.

All 10 larches are in the genus Larix, a deciduous needleleaf gymnosperm in the family Pinaceae. Although similar in appearance, shade tolerance, and deciduous character, larch species do differ substantially in growth, ability to establish on different substrates, and ability to compete successfully with associated species. Larch's deciduous characteristic clearly distinguishes the genus from evergreen conifers with which it is almost always associated.

Larches are the exception in the characteristically evergreen world of the northern boreal and mountain subalpine forests of the northern hemisphere. They possess morphological and physiological characteristics that distinguish them from their evergreen or deciduous counterparts and likely provide them with unique establishment and survival advantages. But they do well in spite of their differences, especially in adding the diversity that is advantageous to associated flora and fauna. Aesthetically, Larix species have no real match in the evergreen world of temperate forest conifers. Their light green hues in the spring and summer, the gold in the fall, and the absence of foliage in the winter are but a part of the charm that this unique genus adds to its environs.

The 10 most commonly recognized larch species and their general distribution are listed in table 1. In addition to these 10 species there are a large number of subspecies and hybrids where natural ranges of species overlap. Larch taxonomy has had little attention internationally. The last real definitive examination was over 60 years ago by Ostenfeld and Larsen (1930). This is reflected in the lack of total agreement in the international literature about what constitutes a Larix species or a subspecies. It is the age-old taxonomy discussion between the "splitters and the lumpers." Splitting the species into subspecies often makes biological sense at the local or regional level, but in the larger context it makes generalizations difficult. For the purposes of this introduction, generalization to 10 species is in order, but for papers within this proceedings, breakdowns into subspecies and hybrids are described that certainly prove helpful in relating to individual research activities around the world. To more readily illustrate the magnitude of and differences in Larix species distribution, I have divided the northern temperate zone into four geographic areas: North America, Europe, Northern Asia, and Southern Asia (figs. 2, 3, 4, 5). Larix distributions shown here are only approximate and are based on adaptations made from maps and narratives from several sources. Most of the descriptions in the literature are in at least partial, but usually not total, agreement. Good definitive information on exact ranges of the species is just not available in some cases.

Species boundaries in North America are relatively well defined with practically no overlap between *L. laricina*, *L. occidentalis*, and *L. lyallii* (fig. 2). Although *L. occidentalis* and *L. lyallii* occur in much the same geographic area, they are usually elevationally separated by 300 to 500 m. Exceptions to this are noted in this proceedings.

Larix laricina forests are by far the most extensive of the three species in North America, stretching from the east to the west of Canada and into Alaska, U.S.A. Its largely boreal habitat contrasts sharply with that of the upper montane/subalpine habitat of *L. occidentalis*.

Only one species of Larix occurs naturally in Europe. *Larix decidua* most commonly occurs in the subalpine habitat of the Alps, but it also occurs in other areas of central Europe (fig. 3). Different subspecies and varieties are commonly recognized there and are described in this proceedings.

Larix russica (often referred to as *Larix sibirica*) and *L. gmelinii* dominate the Siberian forest landscape in Northern Asia, with *L. russica* to the west and *L. gmelinii* to the east (fig. 4). Their major boundary is contiguous in a generally north-south direction for thousands of kilometers,

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WORLD DISTRIBUTION OF LARIX

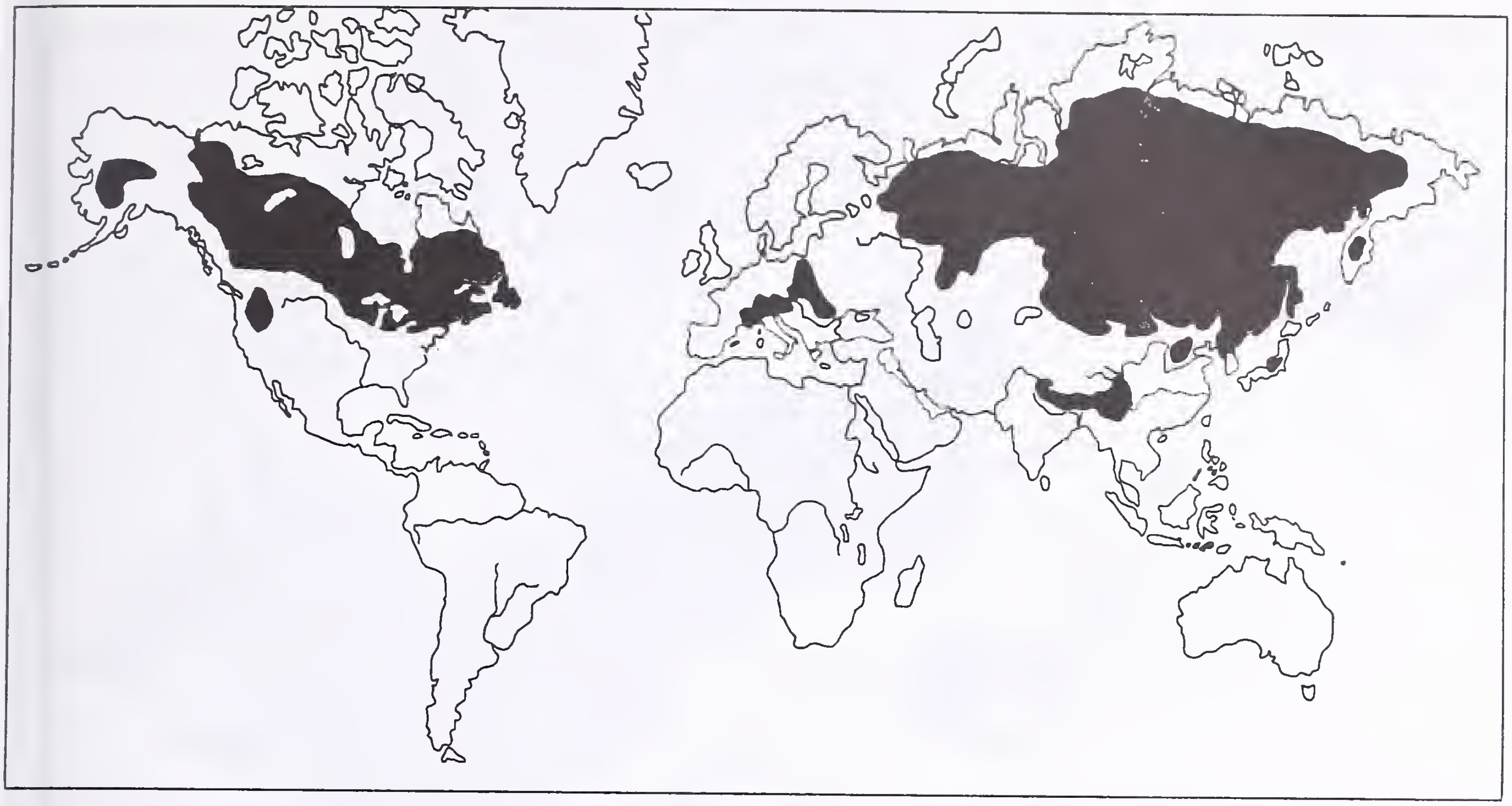

Figure 1—Natural range of the genus Larix throughout the World (adapted from Krüssman 1985).

Table 1—The 10 commonly recognized species of larch with their general location and ecological situation.

Latin name	Common name	General location	Ecological zones
Larix occidentalis	Western larch	Rocky and Cascade Mountains of U.S. and Canada	Upper montane to lower subalpine
Larix lyallii	Alpine larch	Rocky and Cascade Mountains of U.S. and Canada	Upper subalpine to timberline ecotone
Larix laricina	Tamarack	Northeastern and Lake States and Alaska in U.S. and a wide belt completely across Canada	Mainly boreal
Larix russica	Siberian larch	A wide belt in northern Russia and in Mongolia	Boreal to northern timberline
Larix gmelinii (includes *L. dahurica, olgensis, cajanderi,* other subspecies)	Asian larch	Eurasia east of the Siberian larch range	Subalpine to northern timberline
Larix mastersiana	Masters larch	Mountain areas in south China	Upper montane to lower subalpine
Larix griffithiana	Sikkim larch	Himalayas in Nepal, Bhutan, Tibet and south China	High subalpine
Larix potaninii	Chinese larch	Western China	High subalpine
Larix leptolepis	Japanese larch	Honshu, Japan	Subalpine
Larix decidua	European larch	Alps area in France, Switzerland, Austria, Italy, Yugoslavia, Germany with scattered areas in Romania, Czechoslovakia, and Poland	Subalpine

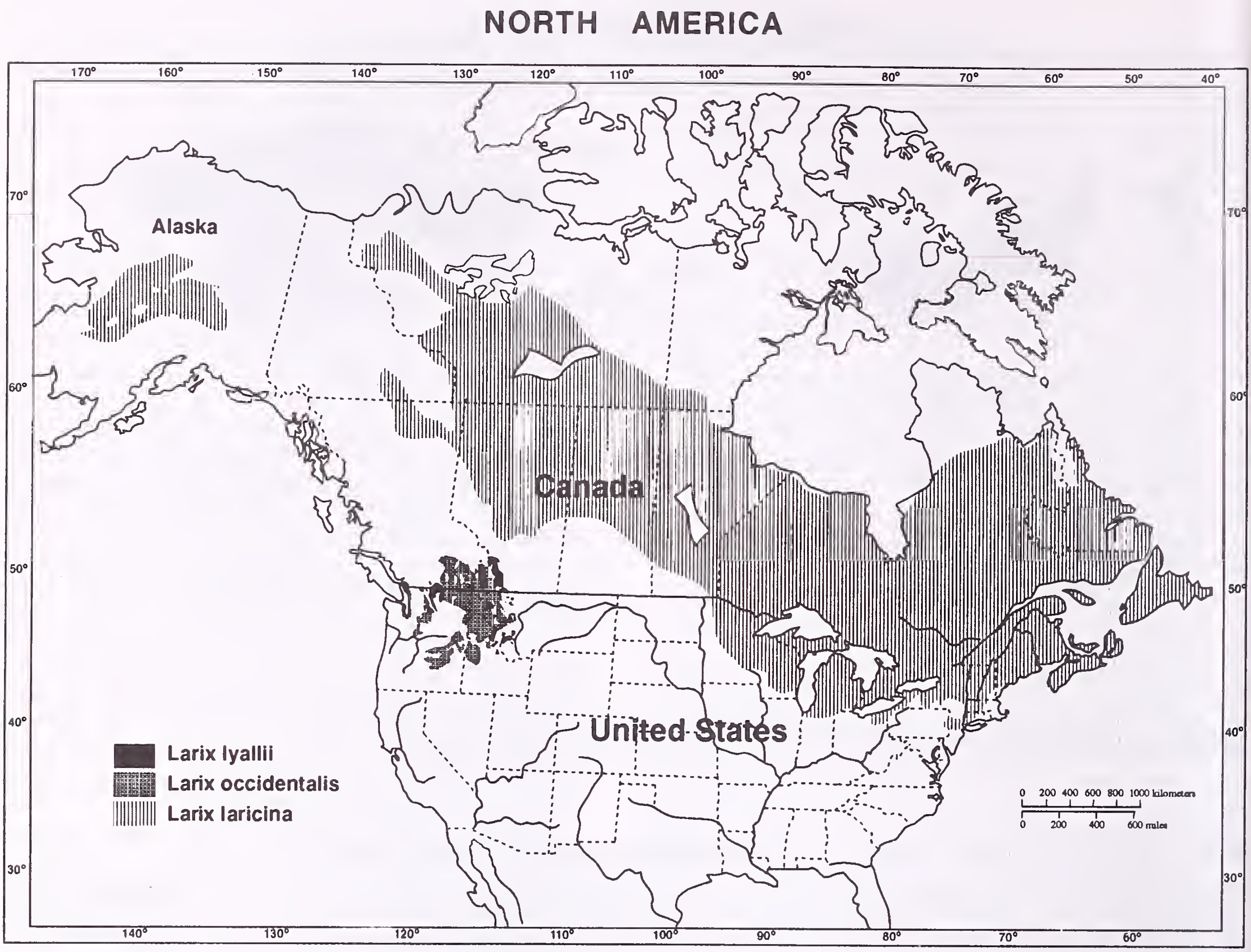

Figure 2—Natural range of Larix species in North America (adapted from Johnston 1990; Arno 1990; Schmidt and Shearer 1990).

and where their boundaries overlap *L.* x *czekanowski* (=*L. russica* x *L. gmelinii*) is often recognized. Within the wide range of *L. gmelinii* there are numerous regionally recognized subspecies or varieties such as *L. cajanderi* in northeastern Siberia, *L. olgensis* on the east coast of Russia and down into Korea, *L. principis-rupprechtii* in northeast China, and *L. kurilensis* and *L. kamtschatica* on Sakhalin Island and Kamchatka. These are described in other papers within the proceedings.

Southern Asia accounts for a wide variety of Larix species, ranging from the montane conditions of *L. mastersiana* in southwestern China to the high elevation forests of *L. griffithiana* in Nepal, Bhutan, and Tibet, and *L. potaninii* in southwestern China to the island environment of *L. leptolepis* on Honshu in Japan (fig. 5). *Larix mastersiana* and *L. leptolepis* are unique, along with *L. lyallii* in North America, in having limited, but important, ranges.

To the casual observer most Larix species look essentially the same, but their cone and needle characteristics and particularly their ecological niches separate them. Some of these characteristics are illustrated in figure 6.

For at least 200 years people have carried seed from one continent to the other in hopes of finding the perfect Larix species for their area. As a result, plantations of introduced Larix can be observed at many locations in the world, particularly in Europe and eastern North America (Krüssman 1985). Genetics research, particularly with hybridization objectives, has been extensive. Some hybrids exhibit superior growth and survival characteristics, and some of that information is presented in this proceedings.

The value of Larix forests for wood products, animal habitats, water production, aesthetics, and other resources is impressive, but the values vary tremendously by species and ecological zones. These forests harbor a wide complement of fauna ranging from the moose to the mouse, the bear to the shrew, and the eagle to the hummingbird, not to mention the vast array of micro flora and fauna, as yet only generally comprehended. Many of these values and ecological principles of this truly international genus are described in this proceedings.

Figure 3—Natural range of Larix species in Europe (adapted from Ostenfeld 1930; Gower and Richards 1990; Holtmeier, this proceedings).

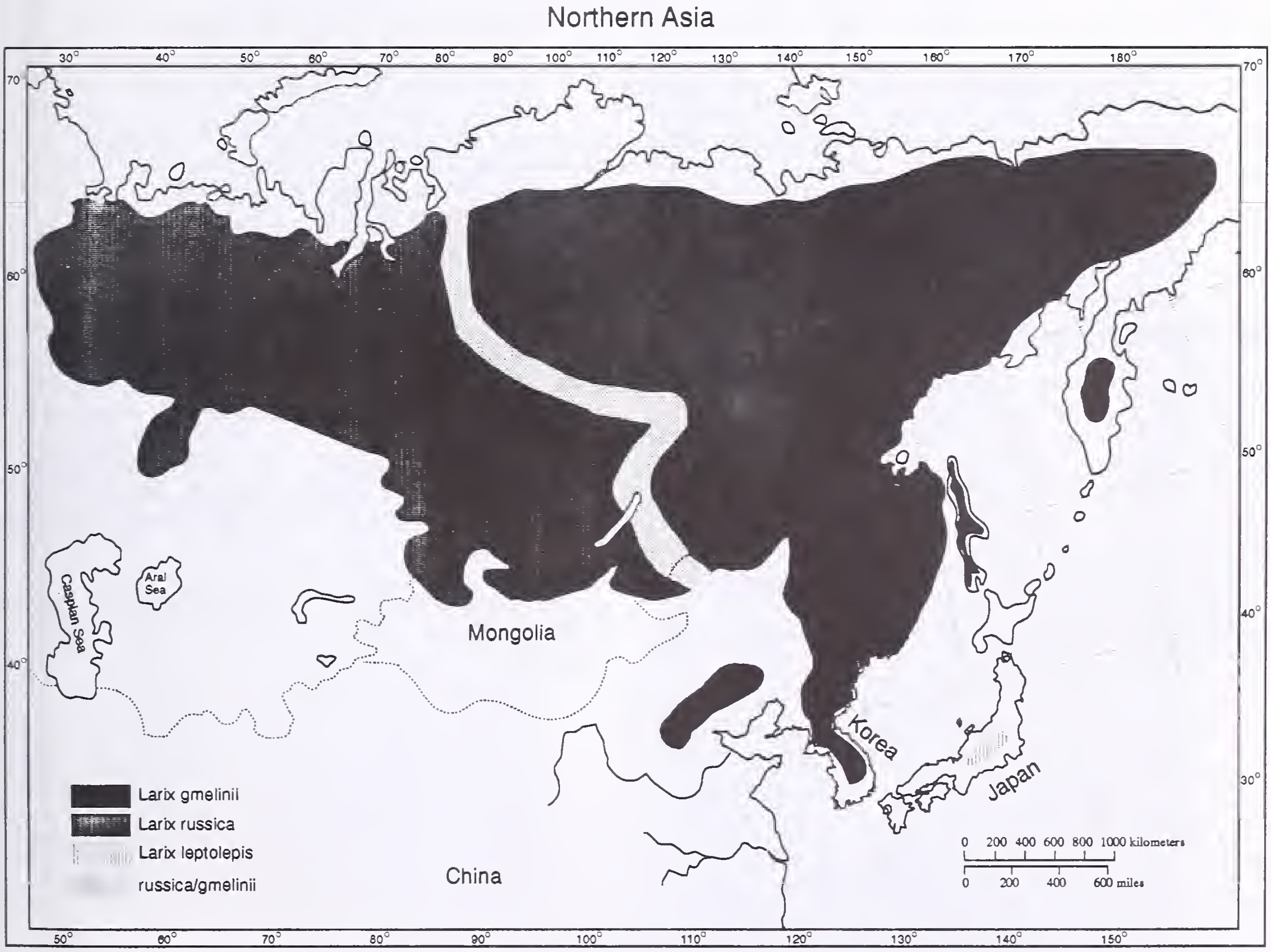

Figure 4—Natural range of Larix species in Northern Asia (adapted from Ostenfeld and Larsen 1930; Gower and Richards 1990; Milyutin and Vishnevetskaia, this proceedings). The area shown as *russica/gmelinii* is often referred to as *L.* x *czekanowski*, and the area in northeast China shown as *L. gmelinii* is often referred to as *L. principis-rupprechtii.*

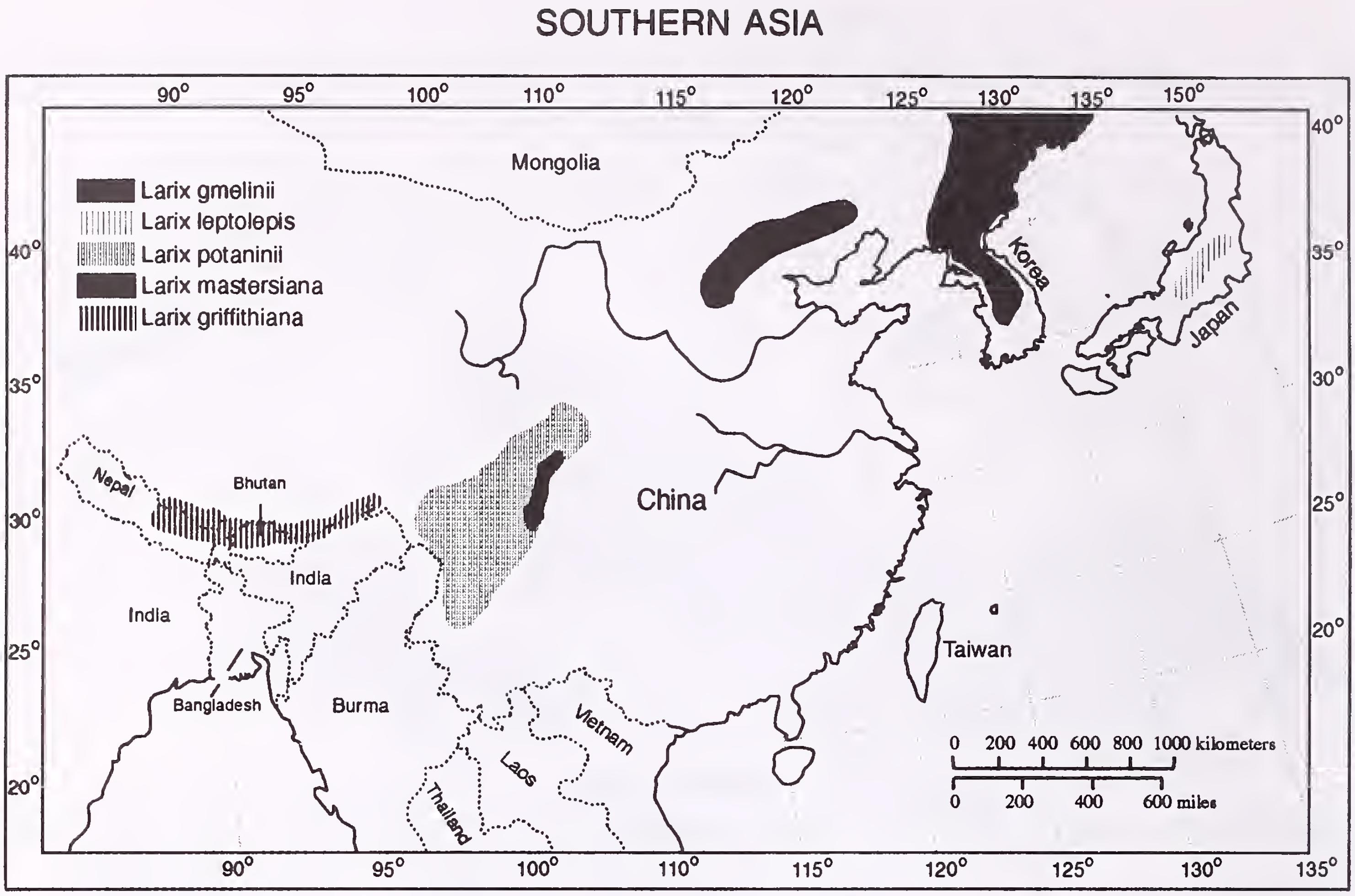

Figure 5—Natural range of Larix species in Southern Asia (adapted from Ostenfeld and Larsen 1930; Gower and Richards 1990; Wang, this proceedings). The area shown as *russica/gmelinii* is often referred to as *L.* x *czekanowski*, and the area in northeast China shown as *L. gmelinii* is often referred to as *L. principis-rupprechtii.*

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Figure 6—This series of photos depicts some of the characteristics of the world's Larix species.

Larix occidentalis

L. occidentalis in a fall landscape scene in western Montana, U.S.A.

A 15-year old *L. occidentalis* in the spacing study on Coram Experimental Forest, Montana, U.S.A.

A 300-year old stand of *L. occidentalis* on Coram Experimental Forest, Montana, U.S.A. Large trees are about 40 m tall and nearly 1 m in diameter.

An ovulate cone of *L. occidentalis* in the early spring.

A late September view of *L. lyallii*, Carlton Ridge, Bitterroot Mountains, Montana, U.S.A.

Ovulate cones and emerging foliage of *L. lyallii* in early spring.

A robust stand of *L. lyallii*, Carlton Ridge, Bitterroot Mountains, Montana, U.S.A.

A planted *L. lyallii* seedling.

A stand of *L. laricina* during the October needle fall period on a lowland in Alberta, Canada.

Larix laricina provenance trial in Alberta, Canada.

A mixed species forest of larch, birch, and pine in the fall season near Lake Baikal in Russia.

A mature forest in the steppe area of Mongolia.

A fall scene in an intermediate-age stand of the subspecies *L. cajanderi*, Yakutia, Russia.

A vigorous young forest of *L. gmelinii* in Korea.

A landscape showing an extensive forest of *L. gmelinii* in Korea.

A young vigorous stand of *L. gmelinii* in northeast China.

A stand of *L. gmelinii* adjoining an agricultural area in northeast China.

Establishing weather instruments in a forest of the subspecies *L. olgensis* in northeast China.

A plantation of *L. gmelinii*, subspecies *olgensis* in northeast China.

Larix mastersiana

A lace-like crown showing the drooping characteristic in a southwest China forest.

A branchlet and cone of *L. mastersiana* in southwest China.

Larix potaninii

Mature cones of *L. potaninii* in southwest China.

Larix leptolepis

A vigorous intermediate age stand in Japan.

A thinned intermediate age stand with a heavy understory in Japan.

Larix decidua

Intermediate age *L. decidua* in a mixed-species stand of spruce and pine near St. Moritz, Switzerland.

The Evolutionary History of the Genus *Larix* (Pinaceae)

Ben A. LePage
James F. Basinger

Abstract—The genus *Larix* Miller, commonly known as the larches or tamaracks, is widely distributed across North America, Asia, and Europe and is a prominent component of the boreal, montane, and subalpine forests. The genus has 10 species: three endemic to North America and seven occurring in Asia and Europe. Living larches appear to form two natural, morphologically distinct groups: the widely distributed short-bracted forms and the geographically more restricted long-bracted forms. Only short-bracted species are represented in the fossil record; the ecologically distinct long-bracted forms as yet lack a fossil record. The fossil record of *Larix* indicates that the genus has long been widely distributed throughout the high latitudes of North America and northeastern Asia but reached Europe only in the last few million years. Phylogenetic relationships of the genus *Larix* have been interpreted.

The larches, deciduous needle-leaved members of the pine family, are common components of the boreal, montane, and subalpine forests of North America, Asia, and Europe. Larches, especially the more broadly distributed boreal species, occupy a wide range of ecological habitats that include early successional forests, open-boreal forests, bogs, treeline (altitudinal and latitudinal), fluvioglacial soils, talus slopes, and moraines (Farjon 1990; Gower and Richards 1990). Larches are well adapted to regions where climate is typically cold and the growing season is short. Deciduousness, intolerance to shade, efficient nitrogen and carbon use, and the ability to become established on poor soils enable larches to become pioneer species in mixed-coniferous forests and the dominant species at treeline (Farjon 1990). Although present knowledge of ecological tolerance, interspecific competition, and silvicultural practices is substantial, relatively little is known about the evolutionary and phytogeographic history of the group.

With the discovery of *Larix altoborealis* LePage & Basinger from early Tertiary deposits on Axel Heiberg Island (fig. 1), the fossil record of the larches was extended with confidence to the Eocene (fig. 2), and the evolutionary history of the genus was reevaluated and reinterpreted (LePage and Basinger 1991a). Although Farjon (1990) allies *Larix* with *Pseudotsuga* and *Cathaya* within the subfamily Laricoideae on the basis of numerous morphological, anatomical, cytological, and physiological characteristics, currently no fossil evidence exists to shed light on the evolutionary origins of the genus *Larix*. Considering the close morphological comparison between fossil and extant larches, it would seem likely that the origin of the group is to be found well before the Eocene and most probably in the Cretaceous.

With recent additions to our knowledge of fossil high-latitude larches, including late Tertiary remains from Ellesmere Island reported here, it is possible to augment the assessments of LePage and Basinger (1991a,b) of larch phylogeny and phytogeography.

DISTRIBUTION OF LIVING SPECIES

Insight into the history of the larches can be gained by study of the distribution of living species. Ten species of *Larix* are recognized by Ostenfeld and Larsen (1930a,b) and Farjon (1990): three species endemic to North America and seven to Asia and Europe (fig. 3). The North American tamarack (*Larix laricina* [DuRoi] K. Koch), and the Asian Dahurian larch (*L. gmelinii* Turczaninow) and Siberian larch (*L. sibirica* Ledebour) are widely distributed as lowland-boreal to subarctic species. The remaining species are restricted geographically and possibly environmentally to mountainous regions (Little 1971; Takhtajan 1986).

Current distribution of larches supports three distinct patterns of displacement. In North America, displacement appears to have occurred east-west across Canada

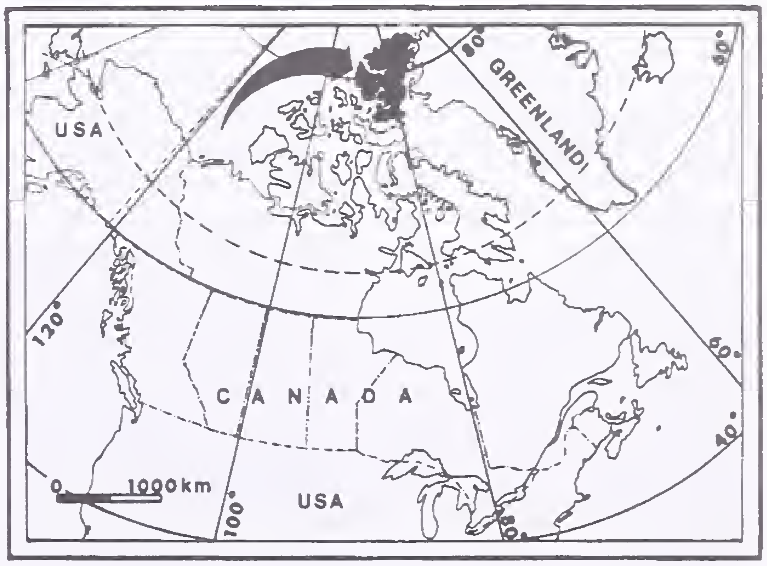

Figure 1—Map of Canada showing the position of Axel Heiberg (small, left) and Ellesmere (large, right) islands.

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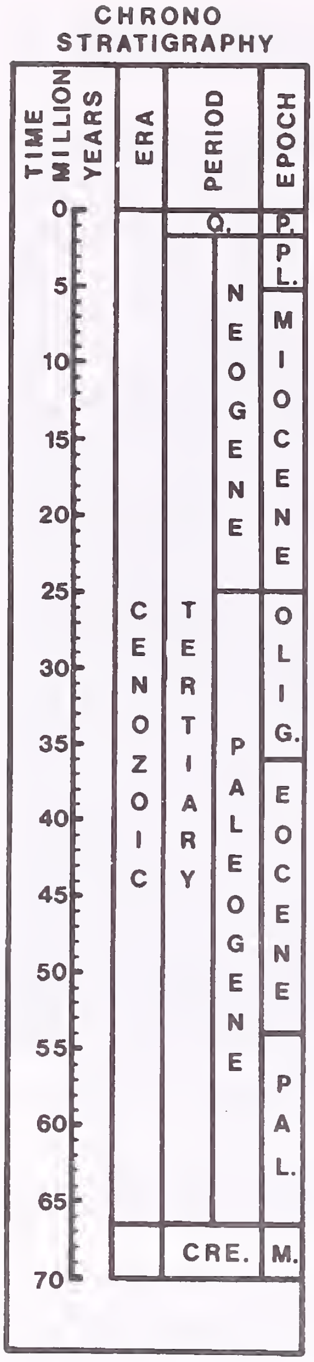

Figure 2—Cenozoic chronostratigraphic chart (after Haq and others 1988). Legend: Q. - Quaternary, P. - Pleistocene, PL. - Pliocene, OLIG. - Oligocene, PAL. - Paleocene, CRE. - Cretaceous, M. - Maastrichtian.

and south along the Western Cordillera. In Asia, two patterns are clearly visible: one extends from northeastern Russia along the eastern coast of Asia and into central China; the other, from northeastern Russia into western Russia and central Europe. These dispersal patterns are referred to as the North American, the Southern Asian, and the Trans-Eurasian (LePage and Basinger 1991b).

In North America, western larch (*L. occidentalis* Nuttall) and alpine larch (*L. lyallii* Parlatore) grow in the montane and subalpine/treeline regions of the Cascade and Rocky Mountains of southern Alberta and British Columbia, northern Washington, western Montana, northeastern Oregon, and Idaho. The distribution of tamarack extends north and east of the Cordillera from northern Alberta to central Alaska, across Canada into Newfoundland, and south into the Great Lakes region of the Northern United States.

Along the Southern Asian route several species are found. Dahurian larch ranges from northeastern Siberia to Korea. Small populations of Kurile larch (L. *gmelinii* var. *olgensis* [Henry] Ostenfeld & Syrach L.), Prince Rupprecht larch (*L. gmelinii* var. *principis-rupprechtii* [Mayr] Ostenfeld & Syrach L.), and Japanese larch (*L. kaempferi* [Lambert] Sargent) grow in the Changbai Mountains of Korea, Taihang Mountains of northeastern China, and subalpine regions of the Japanese Alps in central Honshu, Japan, respectively. Southwest of Korea, small restricted populations of Masters larch (*L. mastersiana* Rehder & Wilson) and Chinese larch (*L. potaninii* Batalin) occur as montane and subalpine species in the mountains north and west of the Sichuan Basin in southwestern China. In the Himalaya Mountains of Tibet and Nepal, Himalayan larch (*L. griffithiana* [Lindley & Gordon] Carrière) grows at high elevations, commonly as a treeline species.

The Trans-Eurasian pattern extends across Russia, where Dahurian larch (east) and Siberian larch (west) occur as prominent components of the boreal forest. The hybrid, *L.* x *czekanowskii* Szafer, occupies the region between the Lena and Yenisei rivers in central Russia, where populations of Dahurian larch and Siberian larch overlap (Farjon 1990; Ostenfeld and Larsen 1930a). Siberian larch occurs as far west as Moscow, while European larch (*L. decidua* Miller) is found as a subalpine species throughout the Alps and Carpathian Mountains of southeastern France, Switzerland, northern Italy, southern Germany, Austria, Czechoslovakia, and northwestern Yugoslavia. The apparent hybrid between Siberian larch and European larch, the Polish larch (*L. decidua* var. *polonica* [Raciborski] Ostenfeld & Syrach L.), is limited to a few hillsides in Poland. This suggests that the distribution of Siberian larch and European larch was much more extensive in the past.

The living larches fall into two morphologically distinct groups. The widespread boreal species (tamarack, Dahurian larch, Siberian larch) and the more restricted Eurasian species (Kurile larch, Prince Rupprecht larch, European larch, and Polish larch) possess short, nonemergent bracts and appear to form a natural group. The remaining species—all restricted to montane and subalpine/treeline regions of western North America, Japan, and southeastern Asia—possess long, exserted bracts and form a second apparently natural group. Although current distribution is instructive, interpretation of phylogenetic relationships and the phytogeographic history of the larches requires evidence from the fossil record.

THE FOSSIL RECORD

Although the fossil record of *Larix* is meager, cones, wood, needles, and pollen have been reported from Tertiary sediments of North America and Eurasia (table 1). The discovery of *Larix altoborealis*, a short-bracted form from Axel Heiberg Island of the Canadian Arctic Archipelago, was the first reliable pre-Oligocene record of *Larix*. It demonstrated that the genus was present, at least in North America, during the Eocene (figs. 4, 5, 8). Reports of *Larix* of Oligocene age (Blokhina 1984, 1985; Dorofeev 1970; Gladenkov and others 1991) and mass burials of

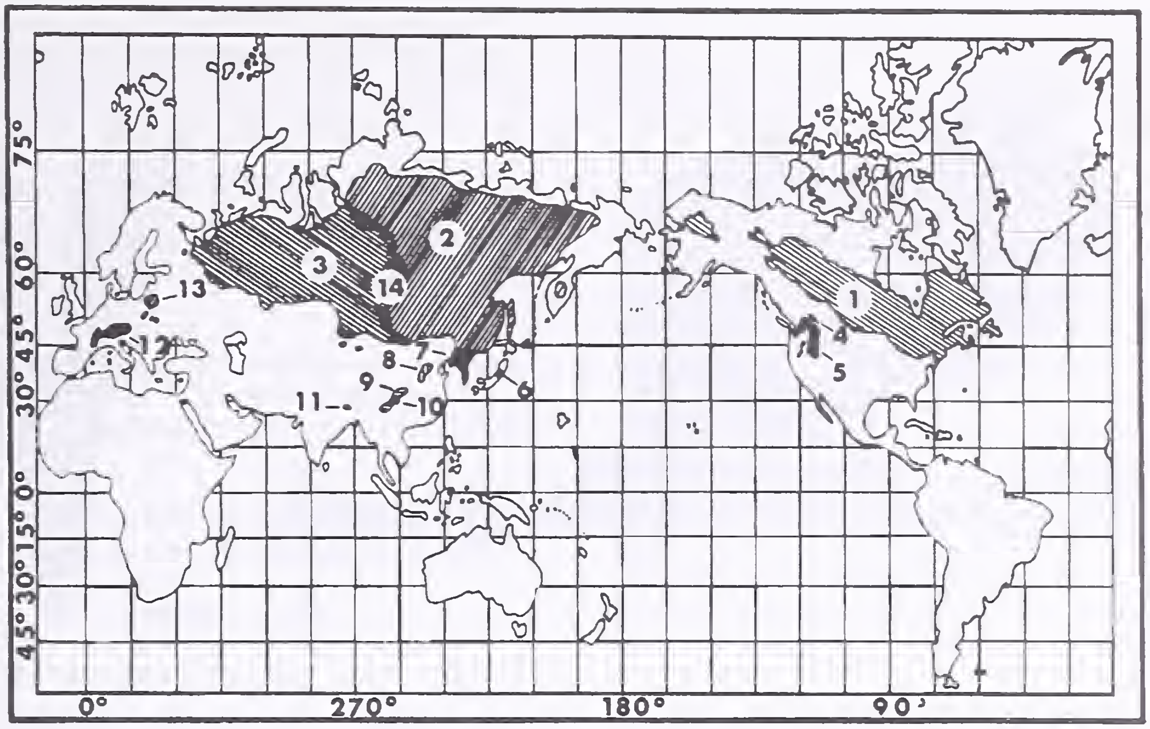

Figure 3—Generalized map of the world showing the global distribution of extant species of *Larix*. Legend of common and scientific names: (1) tamarack (*Larix laricina* [DuRoi] K. Koch); (2) Dahurian larch (*L. gmelinii* Turczaninow); (3) Siberian larch (*L. sibirica* Ledebour); (4) western larch (*L. occidentalis* Nuttall); (5) Alpine larch (*L. lyallii* Parlatore); (6) Japanese larch (*L. kaempferi* [Lambert] Sargent); (7) Kurile larch (*L. gmelinii* var. *olgensis* [Mayr] Ostenfeld & Syrach Larsen); (8) Prince Rupprecht larch (*L. gmelinii* var. *principis-rupprechtii* [Mayr] Ostenfeld & Syrach L.); (9) Chinese larch (*L. potaninii* Batalin); (10) Himalayan larch (*L. griffithiana* [Lindley & Gordon] Carrière); (11) Masters larch (*L. mastersiana* Rehder & Wilson); (12) European larch (*L. decidua* Miller); (13) Polish larch (*L. decidua* var. *polonica* [Raciborski] Ostenfeld & Syrach Larsen); (14) Czekanowski larch (*L.* x *czekanowskii* Szafer). Map modified after LePage and Basinger (1991a) and references therein.

Larix in the Miocene of Russia (Piemenov 1986) demonstrate that *Larix* became a well-established forest constituent in northeastern Russia by the late Oligocene (fig. 10). During the Miocene, larches became widely distributed throughout the high latitudes of North America and Russia, as well as Japan and the Rocky Mountains of Western North America. Larches first appeared in Western Europe, however, only during the Pliocene (fig. 11).

The known fossil record appears to consist entirely of short-bracted species; long-bracted fossils have yet to be found. Dorofeev (1972) proposed that *L. omoloica* Dorofeev was a long-bracted species closely allied to western larch. LePage and Basinger (1991a) disagreed and considered *L. omoloica* to be short-bracted. There was no evidence of an exserted bract provided in either the diagnosis or illustrated material of Dorofeev (1972). Bennike (1990) suggests that *L. groenlandii* Bennike from the 2.0 to 2.5 million-year-old (Pliocene) deposits of Greenland is a long-bracted species, even though none of the recovered cones possessed intact exserted bracts. Cones and needles recovered from the late Neogene (Miocene or Pliocene) of western Ellesmere Island, Canadian Arctic Archipelago (fig. 1), although neither illustrated nor described, have been assigned to *L. groenlandii* by Matthews and Ovenden (1990).

We recovered remains of larches from Neogene deposits in the same general area sampled by Matthews and Ovenden (1990) near Strathcona Fiord, Ellesmere Island (79°29' N., 82°38' W.). We consider our fossils equivalent to theirs and to the fossils described as *L. groenlandii* by Bennike (1990). Examination of our Ellesmere Island cones clearly shows that the bracts are short, commonly half the length of the cone scales, and rarely approach but never exceed the length of the cone scales (figs. 6, 7, 9). Our observations agree with the illustrations and description of the cones provided by Bennike (1990), but we disagree with his interpretation of the bracts. We consider *L. groenlandii* to be a short-bracted species (figs. 6, 7, 9).

Undescribed larch cones, most like those of alpine and Himalayan larch, associated with larchlike seeds and needles from middle to late Eocene deposits in Idaho and Nevada have been collected by D. I. Axelrod (unpublished data, personal communication 1992). If these cones are demonstrated to possess exserted bracts, they would then


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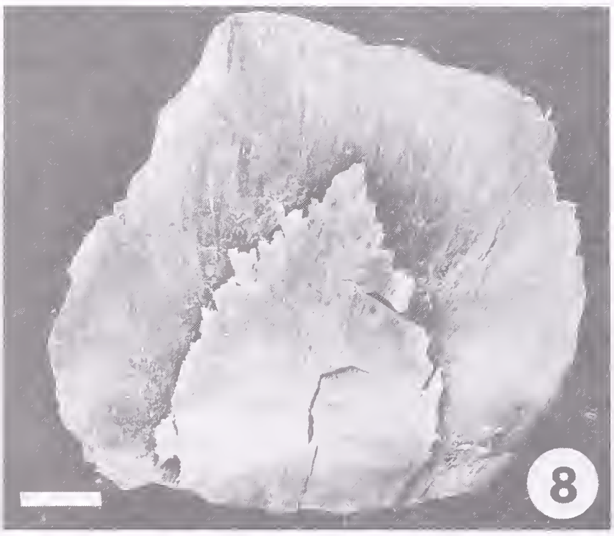
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Figure 4—Cone of *Larix altoborealis* attached to a brachioblast (short shoot) borne on a long shoot. US185-4003. All specimens are housed in the University of Saskatchewan Paleobotanical Collection. Scale = 5.0 mm, except where noted otherwise.

Figure 5—Fascicular needles of *Larix altoborealis*. US185-4001.

Figure 6—A long shoot showing the attachment and arrangement of brachioblasts and cones of *Larix* cf. *L. groenlandii* from Ellesmere Island. US597-5567.

Figure 7—Cone with attached brachioblast of *Larix* cf. *L. groenlandii* from Ellesmere Island. Note that the bracts subtending the cone scales are visible (arrows) and that they are short and not exserted. US597-5568.

Figure 8—SEM photo of *Larix altoborealis* showing a well-preserved, short bract subtending the cone scale. US184-SEM 45. Scale = 1.0 mm.

Figure 9—SEM photo of *Larix* cf. *L. groenlandii* showing a well-preserved, short bract subtending the cone scale. US597-SEM 46. Scale = 1.0 mm.

represent the first occurrence of long-bracted larches and confirm LePage and Basinger's (1991a) idea that the long-bracted species diverged from the short-bracted species early in their evolution.

The general absence of long-bracted larches in the fossil record may reflect their adaptation to alpine habitats, where chance of entry into the fossil record is remote. The distribution of the living larches shows that the short-bracted species commonly occupy habitats at lower altitudes, where chance of preservation is greater.

The fossil record (table 1) indicates that the distribution of *Larix* in time and space correlates with the spread of coniferous vegetation in the circumboreal high latitudes during the mid- to late Tertiary (LePage and Basinger 1991b). Reports of larches from the Pliocene of Greenland (Bennike 1990) and late Neogene of the Canadian Arctic (Fyles 1990; Hills 1975; Matthews and Ovenden 1990, this report) and Alaska (Hopkins and others 1971; C. N. Miller, personal communication 1992) indicate that the larches persisted throughout the North American high latitudes probably until the onset of Pleistocene continental glaciation less than 3 million years ago. The distribution pattern of the fossils further illustrates an apparent absence of *Larix* from Svalbard, Iceland, and Europe during Eocene, Oligocene, and Miocene time.

PHYTOGEOGRAPHY

During the Eocene, three land bridges were available to high-latitude floras and faunas for exchange between North America, Asia, and Europe (fig. 10). The DeGeer Route (McKenna 1972a) was an important land bridge that extended between North America and Fennoscandia (the ancient Scandinavian Peninsula) throughout the Paleocene and Eocene. The Thulian Route, via south Greenland to Europe, is thought to have existed as a series of islands along the Iceland-Faeroe Ridge during the Paleocene and Eocene (Berggren and Schnitker 1983; McKenna 1972a, 1975; Talwani and others 1976; Thiede and Eldholm 1983). The Beringian Route was an effective floral and faunal conduit between North America and Asia from Albian time (about 100 million years ago) to the late Tertiary (Chaney 1940, 1947; Hopkins 1967; McKenna 1972b; Tiffney 1985a,b; Wolfe 1972, 1975).

The North Atlantic routes were apparently functional and available to constituents of high-latitude forests during Eocene time. However, the larches and many of the other plants represented in the early Tertiary of the Canadian north are absent from the Paleocene and Eocene fossil record of western Europe and England (Basinger 1991; Boulter and Kvaček 1989; Chandler 1961-1964, 1978). In fact, taxa such as *Larix*, *Picea*, and *Pseudolarix* do not appear in Europe until the Miocene and Pliocene (Kräusel 1938; Laurent 1908; LePage and Basinger 1991b; Mädler 1939; Reid and Reid 1915; Szafer 1947, 1954). Although the two North Atlantic routes appear to have been available for the exchange of plant and animal taxa, the tropical to subtropical climate of Europe during the Paleocene and Eocene (Collinson 1983) appears to have been an effective floristic filter. When European climate became cooler in Miocene and Pliocene time, the North Atlantic land routes had been destroyed by sea-floor spreading and were no longer available.

The similarity in paleolatitude, climate, and vegetation of the North American High Arctic and Siberian Beringia (Basinger 1991; Chaney 1947; Spicer and others 1987) and the past and present distribution of the short-bracted larches provide good evidence that the larches used the Beringian Route at least as early as the Oligocene (LePage and Basinger 1991b). In addition, the distribution pattern of the living long-bracted forms of Asia and North America indicates that displacement occurred across the Beringian Corridor prior to their climatic exclusion from the high latitudes, and that the current distribution pattern was probably established by the late Tertiary.

TAXONOMIC AND PHYLOGENETIC CONCLUSIONS

Identification of living larches is based on a whole-tree concept. That is, recognition of significant features such as the shape of the tree, the shape and pubescence of new-growth shoots, the morphology of the needles, arrangement of stomates, the form of the bracts, and the size and shape of the cones. However, it is largely on diagnostic features of the seed cones that species description, classification, and identification are based. Nevertheless, problems arise with the use of some cone features for taxonomic purposes. LePage and Basinger (1991a) suggest that intraspecific variability of features such as cone size and shape and details of the cone scale margins may make reliable species determinations difficult.

The bracts subtending the cone scales possess reliable intraspecific morphological consistency and may be considered diagnostic for living larch species, *L. altoborealis* (LePage and Basinger 1991a) and our Ellesmere Island cones. Although most of the fossil cones reported (see table 1) are similar in form to *L. altoborealis* and may

Table 1—Fossil record of the genus *Larix*[1]

Location		Type of fossils				Name
		C	V	W	P[2]	
North America						
1. Axel Heiberg Island	Geodetic Hills "a"	X	X			*Larix altoborealis* LePage & Basinger
	Geodetic Hills "b"	X				*Larix altoborealis* LePage & Basinger
2. Ellesmere Island	Strathcona Fiord	X	X	X		*Larix groenlandii* Bennike
	Makinson Inlet	Unreported				*Larix* sp.
	Isachsen Locality	Unreported				*Larix* sp.
	Wolf Valley	Unreported				*Larix* sp.
3. Meighan Island	Unnamed		X			*Larix* sp.
4. Prince Patrick Island	Green Bay and Duvaney	Unreported				*Larix* sp.
5. Banks Island	Ballast Brook			X		*Laricioxylon occidentaloides* Roy & Hills
	Ballast Brook		X			*Larix* sp.
	Ballast Brook	X				*Larix* cf. *omoloica* Dorof.
	Duck Hawk Bluffs	X				*Larix* cf. *omoloica* Dorof.
	Duck Hawk Bluffs	X	X	X		*Larix* sp.
	Duck Hawk Bluffs	Unreported				*Larix* sp.
	West River	Unreported				*Larix* sp.
	Worth Point			X		*Larix laricina*
6. Devon Island	Haughton Astrobleme	X	X		X	*Larix* sp.
7. Greenland	Kap København	X	X	X		*Larix groenlandii* Bennike
8. Yukon Territory	Bluefish Section		X		X	Larix sp.
	Ch'ijee's Bluff	X	X	X	X	*Larix minuta*, *L.* sp.
	Henderson Bluff	X			X	*Larix minuta*
9. Alaska	Lava Camp Mine	X	X			*Larix minuta*, *L.* sp.
	Cone Bluff, Niguanak	Unreported				*Larix* sp.
	North Slope		X			*Larix* sp.
	Kugruk River, Fish Creek	Unreported				*Larix* sp.
	Lost Chicken Mine	Unreported				*Larix* sp.
10. U.S.A.	Nevada		X			*Larix occidentalis* Nuttall
	Nevada		X			*Larix churchillensis* Axelrod
	Idaho		X			*Larix cassiana* Axelrod
Asia						
11. Russia	Siziman Bay			X		*Laricoxylon jarmolenkoi* Blokhina
	Siziman Bay			X		*Laricoxylon shilkinae* Blokhina
	Primor'ye		X			*Larix primoriensis* Piemenov
	Mammoth Mountain	X				*Larix omoloica* Dorofeev
	Mammoth Mountain	X	X			*Larix* sp. 1, 2
	Botchi River		X			*Larix edelsteinii* Akhmetiev
	Aldan	X				*Larix omoloica* Dorofeev
	Botchi River	X				*Larix schmidtiana* (Palabin) Akhmetiev
	Botchi River	X	X			*Larix* sp. 1, 2
	Korf Bay		X			*Larix preobrajenskyi* Kryshtofovich
	Alexandrovsky Log		X			*Larix* sp.
	Kamchatka	X	X			*Larix* sp. 1- 5
12. Japan	Hokkaido	X				*Larix* sp.
	Onbara		X			*Larix onbaraensis* Tanai & Onoe
Europe						
13. Poland	Krościenko	X				*Larix ligulata* Szafer
	Czorsztyn	X				*Larix europaea* Lam. & DC. *foss.* Geyl. & Kink.
14. Netherlands	Reuver		X			?*Larix europaea* DC.
15. France	Niac		X			*Larix* sp.

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[1] Table modified after LePage and Basinger 1991a.

[2] C = cones, W = wood, V = vegetation (seeds, twigs, and needles), and P = pollen.

Geologic age	Source
Ecoene	LePage and Basinger 1991a
Ecoene	Bustin 1982
Pliocene	Basinger, unpublished; Matthews and Ovenden 1990
Pliocene	Matthews and Ovenden 1990
Pliocene	Matthews and Ovenden 1990
Pleistocene	Matthews and Ovenden 1990
Pliocene	Matthews 1987a, b; Matthews and Ovenden 1990
Miocene	Matthews 1987b; Matthews and Ovenden 1990; Fyles 1990
Miocene	Roy and Hills 1972; Matthews and others 1986
Mio/Pliocene	Matthews 1987b; Matthews and Ovenden 1990
Mio/Pliocene	Matthews and Ovenden 1990
Miocene	Hills 1975; Matthews 1987a; Matthews and Ovenden 1990
Pleistocene	Matthews and others 1986
Miocene	Matthews and Ovenden 1990
Miocene	Matthews and Ovenden 1990
Pleistocene	Kuc 1974; Matthews and others 1986
Miocene	Omar and others 1987
Pliocene	Bennike 1990
Pliocene	Matthews 1987b; Schweger 1987; Matthews and Ovenden 1990
Pliocene	Matthews 1987b; Schweger 1987; Matthews and Ovenden 1990
Pliocene	Schweger 1987
Miocene	Hopkins and others 1971; Matthews 1987b; Matthews and Ovenden 1990
Pliocene	Matthews 1987b; Matthews and Ovenden 1990
Pliocene	Matthews 1987b
Pliocene	Matthews and Ovenden 1990
Pliocene	Matthews and Ovenden 1990
Miocene	Wolfe 1964
Miocene	Axelrod 1991
Miocene	Axelrod 1964
Oligocene	Blokhina 1985
Oligocene	Blokhina 1984
Miocene	Piemenov 1986, 1990
Miocene	Dorofeev 1969
Miocene	Dorofeev 1969
Miocene	Akhmetiev 1973
Miocene	Dorofeev 1972
Miocene	Akhmetiev 1973
Miocene	Akhmetiev 1973
?Miocene	Kryshtofovich 1962
Oligocene	Dorofeev 1970
Oligocene	Gladenkov and others 1991
Pleistocene	Suzuki 1985
Miocene	Tanai and Onoe 1961
Pliocene	Szafer 1947
Pliocene	Szafer 1954
Pliocene	Reid and Reid 1915
Pliocene	Laurent 1908

represent the same clade or species, incomplete descriptions (for example, Dorofeev 1972; Hills 1975; Hopkins and others 1971; Matthews and Ovenden 1990) make it difficult to include this material in the interpretation of systematic relationships among larches.

On the basis of features of the seed cones of both fossil and living larches and past and present distribution patterns, we propose phylogenetic relationships among the larches as indicated in the dendrogram of figure 12. The larches form two long-distinct groups: one possessing short bracts, the other possessing long bracts. As indicated by the dendrogram, we propose a common ancestry prior to Eocene time.

It seems evident that late Tertiary climatic change has isolated members of each group into separate North American and Asian lineages. The distribution and diversity of the Southeast Asian long-bracted species suggest a long evolutionary history and isolation.

The postglacial reestablishment of widespread boreal forests has obscured late Tertiary patterns. Nevertheless, the similarity in cone morphology between *L. altoborealis*, *L. omoloica*, and *L. groenlandii* suggests these taxa probably belonged to a closely related group that was widely distributed in space and in time. The remarkable similarity in cone morphology between *L. groenlandii* and some of the cones of *L. gmelinii* that we have examined suggests that *L. gmelinii* is most closely related to these ancient larches, while *L. laricina*, and perhaps other short-bracted forms, may be more recently derived and a product of Pleistocene glacially induced provincialism.

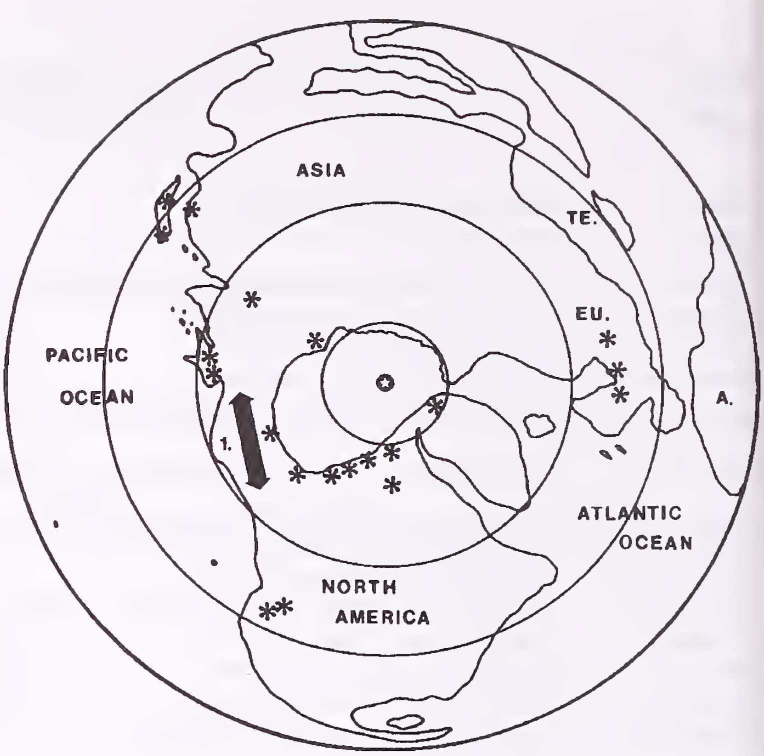

Figure 11—Generalized paleogeographic reconstruction of the Northern Hemisphere for the Neogene showing the distribution of fossil larches and the Beringian Corridor (1). Legend as in figure 10.

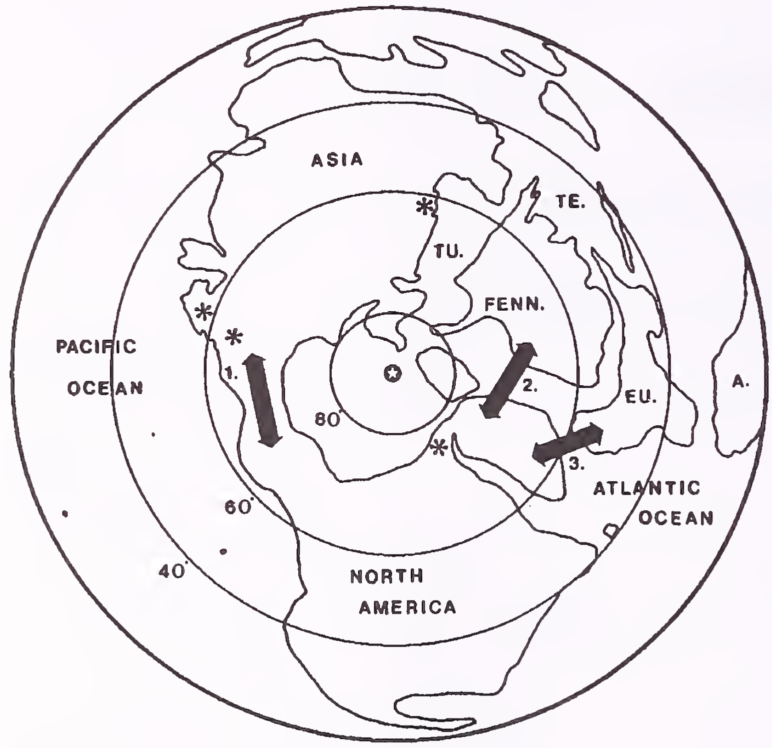

Figure 10—Generalized paleogeographic reconstruction of the Northern Hemisphere for the Paleogene showing the distribution of fossil larches (*), the Beringian Corridor (1), the DeGeer Route (2), and the Thulian Route (3). By the end of the Eocene, the DeGeer and Thulian routes between North America and Europe were broken. Physical continuity between Europe and Asia was established during the Oligocene following regression of the epicontinental sea in the Turgai Strait region. Legend for figures 10 and 11: TU. - Turgai Strait; TE. - Tethys Sea; FENN. - Fennoscandia; EU. - Europe; and A. - Africa. Figures 10 and 11 are modified after LePage and Basinger (1991b) and references therein.

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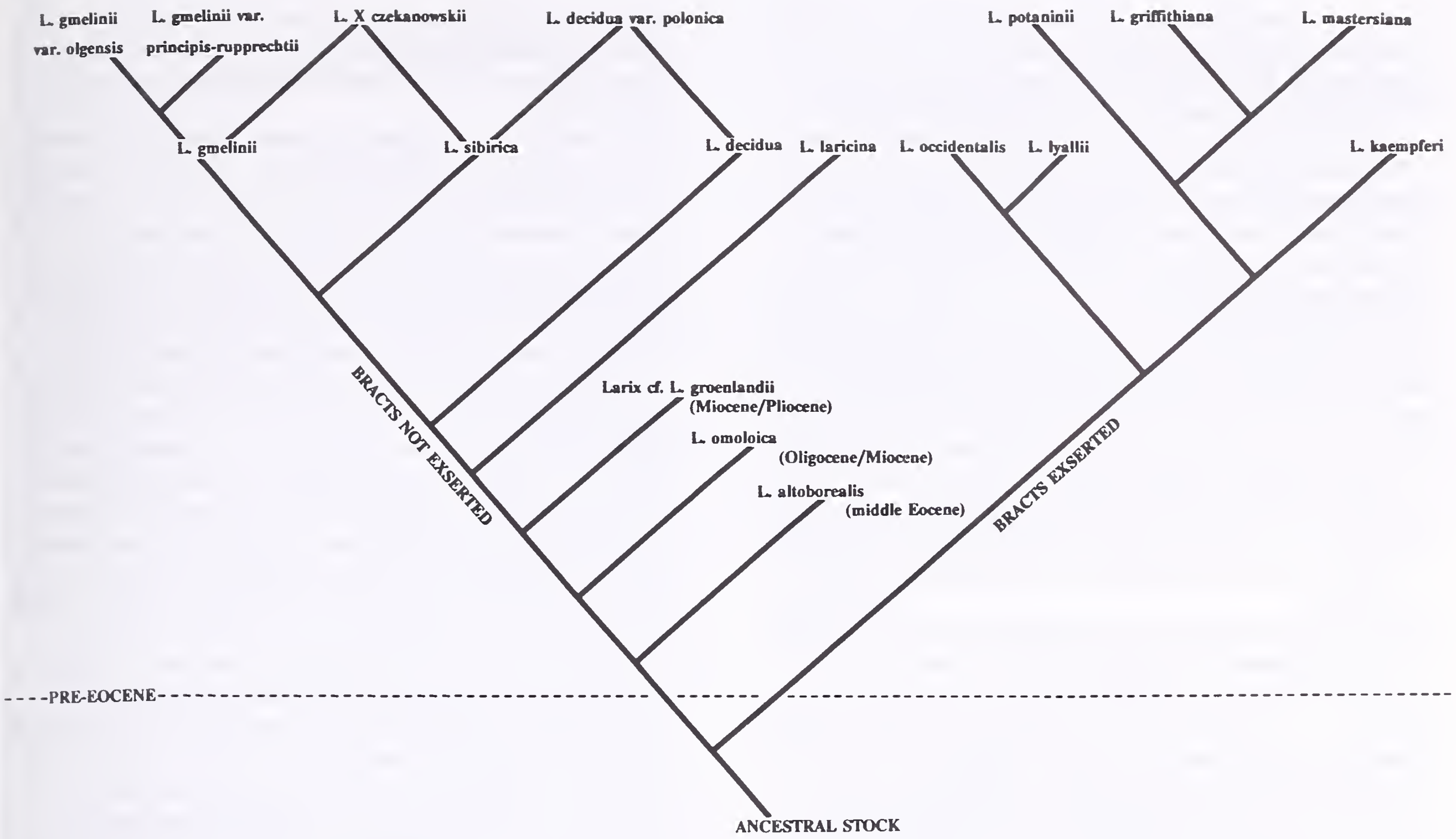

Figure 12—Proposed phylogeny for *Larix*. The larches are divided into two morphologically distinct groups: those species with bracts that are nonexserted and those with bracts exserted. Suggested is an early divergence of short-bracted and long-bracted species. The species within groups are further divided, in part, on the basis of their geographical distribution (that is, North America or Eurasia), external morphological features of cones, the fossil record, and modern distributions (modified after LePage and Basinger 1991a).

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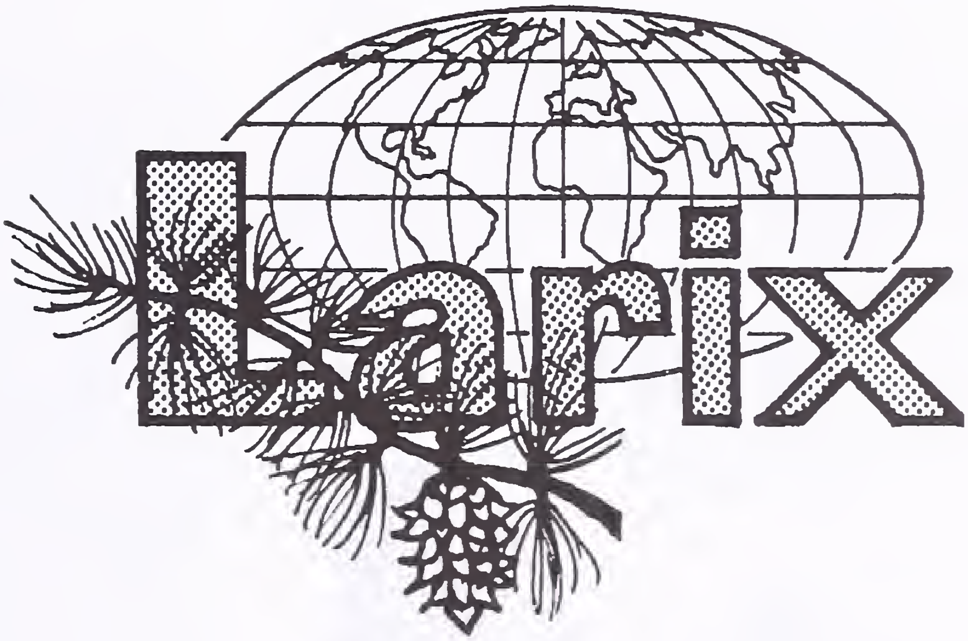
II. Ecology and Management of Larix



Larix occidentalis: a Pioneer of the North American West

Wyman C. Schmidt
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Abstract—Western larch (*Larix occidentalis*) is truly a pioneer in the mountains of the Western United States and Canada. Major disturbances such as fire, harvesting, and seedbed preparations with prescribed fire or scarification provide the most favorable conditions for western larch establishment. Like most seral species, larch regenerates best and grows most rapidly with little or no shade or vegetative competition. Western larch is long-lived, is the largest of the world's larches, and is one of the most productive timber species in the Mountain West of North America. Larch forests respond well to management and are the source of a wide variety of resources such as water, wildlife habitat, wood products, recreation, and esthetics. Insect and disease problems with larch are minimal.

When we in North America think of pioneers, we may picture people in covered wagons heading across the prairies to start a new life. Western larch has similar pioneer characteristics. For thousands of years larch followed the advances and retreats of the glaciers that blanketed the valleys and mountains of much of the inland west of North America.

Glaciation is one of the most dramatic, albeit slow, events shaping the land and leaving in its wake a moonscape of glacial debris largely devoid of flora and fauna. Volcanic fallouts can have much the same effect on the landscape, leaving it mostly bare and receptive to pioneer species especially adapted to those conditions.

Western larch is one of those pioneers in the Mountain West of North America. It establishes before the land is fully occupied by more shade-tolerant competitors. Fire is an integral part of larch ecology following the primary succession. Most fires leave a mosaic of dead and surviving trees and other vegetation in larch forests, providing favorable seedbeds for larch seedling establishment.

MAJOR CHARACTERISTICS OF WESTERN LARCH

Range

Western larch occurs naturally in the Upper Columbia River Basin of Montana, Idaho, Washington, and Oregon in the United States and the province of British Columbia in Canada (fig. 1). On a geologic time scale, it may have had a wider distribution, particularly in relation to the numerous glaciations of the past. Although some western larch have been observed east of the Continental Divide, for all practical purposes larch occurs almost exclusively west of the Continental Divide in the Columbia River drainage.

Climate

The temperature where western larch thrives is relatively cool, averaging 7 °C (45 °F) annually but ranging from 41 °C (106 °F) to –37 °C (–34 °F) (Schmidt and others 1976). Extremes of –46 °C (–50 °F) have been recorded in valleys of Montana where larch occurs. Annual maximum temperatures average 29 °C (84 °F) and minimums –9 °C (15 °F). The May through August growing period averages about 16 °C (60 °F). Frosts can occur any month of the year but the frost-free period usually averages from 60 to 160 days—a big variation from year to year.

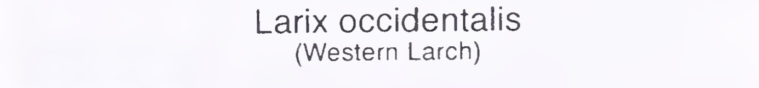

Figure 1—Natural range of western larch.

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The Pacific Ocean strongly influences the inland West and results in a semimaritime climate, particularly west of the Continental Divide where western larch occurs (USDA Forest Service 1965). Most of the precipitation that occurs in the range of western larch comes inland from the Pacific. Annual precipitation averages about 760 mm (30 inches), with 710 mm (28 inches) in the north and 810 mm (32 inches) in the southern part of its range. Extremes recorded in precipitation are 460 mm (18 inches) and 1,270 mm (50 inches). About 20 percent of the precipitation falls during the May through August growing season. As a result, July and August usually have long periods of hot and dry weather with low humidity and high evaporation rates. Lightning storms that start fires are common in late summer. Snow blankets these forests for most of November to April, accounting for over half of the total precipitation.

Soils

Most soils supporting western larch are in the taxonomic orders of Inceptisols and Alfisols with some Spodosols at upper elevations (Schmidt and Shearer 1991). Glaciation and volcanic deposits of ash from the volcanoes of the Cascade Mountains have greatly influenced soil properties of these forests. Loess deposits are common in some areas. Most of the soils where western larch predominates are in the great groups Cryoboralf, Cryochrept, and Cryandept with some in the Eutrobralf and Eutrochrept. Mean annual soil temperatures are 5 °C (41 °F) at 51 cm (20 inches).

Deep, well-drained soils are most suitable for western larch growth. Most of these soils developed over glacial till, alluvium, or colluvium with volcanic ash usually incorporated into the surface horizons.

Western larch, like its relative alpine larch (*Larix lyallii*), has the ability to grow on coarse talus substrates with essentially no soil material near the surface. Larch is superior to its evergreen associates in this regard.

Topography

Western larch grows on steep mountain slopes as well as on flat valleys and gentle topography. On the southern portion of its range larch is conspicuously absent on the hot-dry exposures of south-facing slopes while its light green hues often make up the majority of the tree canopies on the adjacent northern exposures. At the northern limits of its range larch occupies all exposures.

Seed Production

Western larch is monoecious with staminate and ovulate cones distributed throughout the crown. Both are distinguishable from vegetative buds and as a result can be detected in the fall, nearly a year before they mature. As a result, potential cone crops can be measured with some degree of accuracy. Cones mature in late-August and September and their winged seeds are commonly disseminated by warm-dry thermal slope winds (Shearer 1959). As a result, seeds can be distributed uphill by thermal winds generated in the warm valleys and lower slopes. Normally, western larch seeds produced in mature stands are distributed up to about 250 m (820 ft), but major frontal winds can carry seeds much farther—the exact distance is unknown. Most seeds are distributed within 100 m (328 ft) from the seed source (McCaughey and others 1986).

Western larch is one of the best seed producers in the Mountain West with good crops at about 5-year intervals and fair to poor crops in the intervening years. Good crops can occur in succeeding years, but longer periods between good crops are usual. There is a ratio of 1:1 of good and fair to poor crops, so over the longer period about half the years will produce adequate seed for prepared seedbeds. Over 1.2 million seeds per hectare (500,000/acre) have been measured in areas adjacent to timber edges of mature trees (Shearer 1959).

However, in some areas within the range of larch, particularly in western Idaho and central Oregon and Washington, successive poor seed crops that resulted in regeneration failures have been observed. The cause of these seed crop failures has been studied and determined to be due to late season frosts in the spring when staminate and ovulate buds are vulnerable.

Cone production is strongly related to crown size of healthy mature trees, because cones are produced throughout the crown (Shearer 1986). Cones are produced on trees as young as 8 years, but trees do not usually start producing significant amounts of cones until they are over 50 years old. Trees over 500 years old have been observed with heavy cone crops.

Seedling Establishment

Seedling establishment vividly illustrates the pioneering nature of western larch. Assuming a seed source, larch is one of the first conifers to occupy disturbed sites. Historically, glacial retreats and wildfire produced the raw seedbed conditions that favored larch seed germination and seedling survival. At that time nutrients and water are most available, and competition from associated vegetation is at its lowest level. Other species also benefit by those seedbed conditions, but larch both requires and capitalizes on these conditions. High seedling survival and rapid initial development are the result. Larch overtops its associated species in height at this time, and it maintains this height growth advantage for about the first century of its life.

Harvest cutting followed by prescribed burning or some type of site preparation such as scarification also creates the conditions needed for this pioneer species (Shearer 1980). The biological requirements of larch are most effectively met with harvest cuttings such as clearcutting, shelterwood, or seed tree. These, however, have to be accompanied by site preparations such as prescribed burning that prepares a mineral soil seedbed—essentially the same as historically provided by wildfire or other natural phenomena (fig. 2).

Stocking

Western larch commonly overstocks when good seed crops, adequate site preparation, and favorable weather

Figure 2—These 9-year-old western larch in fall color regenerated naturally on an area that had been clearcut and subsequently prescribed burned. Seed from the adjacent larch forest dispersed throughout the harvested area.

the season of germination coincide. Up to 100,000 trees per hectare (40,000/acres) have been observed on some sites (Schmidt 1966). More commonly, natural regeneration is about one-fourth of that, but even this rate of stocking is enough to inhibit growth of individual trees as the young stands develop. Even without mechanical thinning in these young stands, the individual trees will eventually express dominance; however, because of larch shade intolerance, tree mortality will be high. Also, the dominant trees can be severely suppressed in both height and diameter when stocking is heavy.

Composition

Western larch always grows in association with other conifers—up to 10 conifers in the same general area have been observed. Of these, Douglas-fir (*Pseudotsuga menziesii*) and lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*) are the most common associates of larch throughout much of its range. Ponderosa pine (*Pinus ponderosa*) is a common associate on the drier sites, particularly in the southern part of its range.

Larch and lodgepole pine grow fastest in height of any of these associates, with Douglas-fir about half, and Engelmann spruce and subalpine fir about one-fourth the rate of those two species for the initial 30 to 40 years (Schmidt 1969). At about age 50 lodgepole pine slows and larch exceeds it in height.

Western larch and its associates express different levels of shade tolerance with larch the most intolerant of shade, followed by lodgepole pine, Douglas-fir, Engelmann spruce, and subalpine fir.

Seral

Western larch is seral in all forest series and habitat types because of its extreme intolerance of shade. Although some shade is tolerated in the initial germination and first year or two following establishment, larch development is severely restricted by shade after that. Usually it will not survive heavy shading for long periods.

Ecological classifications developed within the range of western larch are based on climax tree and understory species (Pfister and others 1977). Larch is not climax in any of the forest series or habitat types. However, it is a long-lived early successional species in the Douglas-fir, grand fir (*Abies grandis*), western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), and subalpine fir potential climax types. So, larch spans a wide range of moisture and temperature gradients with moisture being limiting at the lower elevations and temperatures limiting at the higher elevations.

Associated Flora and Fauna

Western larch forests typically have rich understories of herbaceous and shrub layers (Pfister and others 1977). For example, on one 40-ha (100-acre) study area, 10 conifer, 21 shrub, and 58 herbeous species were noted (Schmidt 1980). Shrubs included species of *Acer, Alnus, Amelanchier, Physocarpus, Rubus, Symphoricarpos, Vaccinium, Salix*, and others. Herbs included species of *Aralia, Arnica, Calamagrostis, Clintonia, Epilobium, Linnaea, Xerophyllum*, and others. Species composition and density of larch forest understories vary by ecological habitat. They also reflect different productivities of sites.

Larch forests provide food and cover for a wide range of fauna ranging in size from the moose (*Alces alces*) to the deer mouse (*Peromyscus maniculatis*). Some of the most impressive animals such as elk (*Cervus canadensis*), deer (*Odocoilus* sp.), grizzly bear (*Ursus arctos horribilis*) are commonly associated with larch forests. Recent studies of birds and their habitat preferences are shedding light on how management practices can be used to enhance diversity of bird species such as the cavity nesters (McClelland and others 1979; Tobalske 1992). For example, snags of old-growth larch are key habitat for cavity nesting birds (fig. 3).

Insects, Diseases, and Animals

Western larch is relatively free of significant damage from insects and diseases. Although there are many insects and diseases that can adversely affect larch seed production and tree growth, their effects are less pronounced on larch than on the associated species (Schmidt and Shearer 1991). There have been population flareups of several insects such as the larch sawfly (*Pristiphora erichsonii*), larch bud moth (*Zeiraphera improbana*), budworm (*Choristoneura occidentalis*) (Fellin and Schmidt 1967), and larch casebearer (*Coleophora laricella*), but they are usually short-lived and result in little or no mortality. Larch casebearer, a defoliator, was accidentally introduced into western larch forests in the 1950's and soon spread rapidly throughout most of the range of larch, severely reducing growth and threatening larch survival. However, biological control utilizing parasitic insects successfully controlled the larch casebearer to where it is no longer considered a problem—a real success story.

Figure 3—Major fires in western larch nearly always leave some remaining trees to reseed the area. Snags that result from these fires often remain standing for many years—in this case 60 years—providing perch sites for raptors and sites for cavity nesting birds.

Dwarfmistletoe (*Arceuthobium laricis*) is the most significant disease-causing parasite of larch, and it can result in substantial growth reductions where infection levels are high. Proper management practices can largely eliminate dwarfmistletoe infections, but unfortunately such management is often not possible on large areas of public forest lands due to competing uses and values. The most readily apparent disease of larch is a sporadic needle blight (*Hypodermella laricis*) and needlecast (*Meria laricis*), but these are not generally significant problems.

Bear (*Ursus* sp.) occasionally damage and kill young fast-growing larch and can be a problem in managed stands (Schmidt and Gourley 1992). They strip the bark of the lower bole of the tree in search of the sugars that are concentrated in the sap layer in the spring. Seed-eating rodents such as the deer mouse (*Peromyscus maniculatis*) and red squirrel (*Tamiasciurus hudsonicus*) can be a problem some years when the larch seed supply is limited.

Fire

Wildfires in western larch forests can be perceived in the short term as a destructive natural force, burning nearly everything in their path, or they can be perceived in the long term as the force that perpetuates seral species. Without fire or other major disturbance, larch will not successfully regenerate and will eventually be replaced by its shade-tolerant associate species. Regardless of the perspective, wildfires have periodically burned large forest areas in the western forests where larch is the predominate species (Arno 1980; Davis 1980). Wildfires have maintained, or in some cases enhanced, the natural distribution of larch. Because mature larch have thick bark and low resin content, branches that are far above the ground, and foliage of low flammability, some of these old larch usually survive even intense fires—long enough to produce a seed crop to regenerate the receptive seedbeds. Younger seedlings, saplings, and poles of larch have thinner bark and are readily killed by fire.

Many old western larch stands have survived numerous fires. Fire frequencies in the past varied widely in larch forests. On the lower, drier sites of larch, fires of low intensity generally occurred at about 30 to 50 year intervals. On the higher, wetter sites, fires were far less frequent, but when they did occur they were often of stand replacement intensity. Sometimes these old-growth stands also have a small component of older trees, survivors of the stand-replacing wildfire. An old stand of larch near Seeley Lake, Montana, had a tree with 915 growth rings (fig. 4). Some of these old larch have reached up to 2.3 m (90 inches) diameter at breast height and over 45 m (150 ft) in height. More commonly, though, larch matures at 30 to 50 m (100 to 150 ft) tall.

As a result of fire or other major disturbance, young larch stands are usually even aged (Schmidt 1981). To survive, larch must maintain the dominant position in the stand. If overtopped by other trees, larch will grow slowly and will usually die. This characteristic largely dictates

Figure 4—Needle blight on western larch is usually associated with cool-wet springs but it seldom poses any lasting problem.

the choice of stand management practices. Western larch has to be kept in a dominant position in the stand to perform near its potential.

CONCLUSIONS

The key to larch success lies in the regeneration process (fig. 2). Openings in the forest canopy for adequate light, mineral soil seedbeds for optimum seed germination and seedling survival, and reduced competition for light, water, and minerals are the primary elements governing the success of larch establishment and subsequent development. These conditions have historically been met through wildfires, in many cases massive conflagrations. Fire still plays that role in areas such as those designated as wilderness areas.

In areas where management for a variety of resources is practiced, the regeneration requirements for larch and its associated species can be effectively met through harvesting and subsequent preparation of adequate seedbeds. The use of prescribed fire is strongly encouraged for preparing seedbeds, but mechanical site preparation methods are sometimes required.

In some cases, harvest cuttings are precluded or must be greatly modified to meet specific management objectives. Exclusion of some or all of the above silvicultural options will also likely exclude western larch. Ecological requirements dictate that western larch play the pioneer role or it will not play at all.

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Ecological and Geographical Distribution of Larix and Cultivation of Its Major Species in Southwestern China

Wang Shimin
Zhong Shengxian

Abstract—As for the Sect. Multiseriales Patschke of *Larix*, there are one variety and six species in China. This paper presents the suitable ecological environments of the one variety and five species. Those plants, being photophilous, hygrophilous, cold resistant, highly adaptable, fast growing, and with their timber of good quality, are pioneers in the regeneration of the cutover areas on high mountains and reforestation on the waste mountains and slopes in southwestern China. They improve water conservation, protect from soil erosion, and protect regeneration at the upper limit of the subalpine forest in southwestern China.

The plants of Sect. Multiseriales Patschke, one of the two sections of *Larix* in Pinaceae, are tall and deciduous conifers, and are photophilous, hygrophilous, and cold resistant. The deciduous coniferous forests mainly consisting of those plants as edificatoes are usually distributed on the cold mountain ridges or upper slopes. They are often mixed with the plants of *Abies* or *Picea* and form forests in large areas, or scattered along the margins of *Abies* and *Picea* forests, or sometimes form forests mixed with the plants of *Betula* or *Quercus semecarpifolia*. Above the upper limit of those forests are commonly found the alpine shrubs or meadows. They are one of the forest types that are vertically distributed at the highest altitude.

The plants of Sect. Multiseriales Patschke are deciduous. Therefore, sunshine is abundant in the forests, and shrubs, herbs, and grasses are well developed under the forest canopy. On the forest floor there is thick litter, which plays a very important role in water conservation, protection from soil erosion, and maintenance of ecological environment.

The plants of this section are cold resistant and require little on soil conditions. Therefore, they are adapted to a wide range of environmental conditions. They can be found from river valleys up to the coniferous and broadleaved forests at 2,300 to 2,600 m. On the sunny slopes of high mountains they can reach as high as 4,600 to 4,800 m. They can be easily cultivated and grow very fast, so they are considered the ideal pioneers in regeneration of the cutover subalpine forests and afforestation of the waste mountains and slopes in Southwestern China.

The trunks of the plants are tall and erect. Their timbers are hard, tough, light and soft with fine structure and beautiful grains. The timbers are rot resistant and can be used for building, bridge construction, manufacturing of boats and vehicles, and making electric poles, sleepers and pillars, and also as fine material for making furniture and for the woody cellulose industry. Their bark can be used to produce tannin extract and seeds to express oil.

During the growing period, their crowns are light green and very beautiful. They are also the ornamental trees to make the landscapes where they grow much more wonderful.

As for Sect. Multiseriales Patschke there is one variety and six species in China of which one variety and five species occur in Southwestern China. They are:

- *Larix potaninii* Batalin
- *Larix potaninii* var. *macrocarpa* Law
- *Larix mastersiana* Rehd. et Wils
- *Larix griffithiana* (Lindl. et Gord) Hort. ex Carr
- *Larix speciosa* Cheng et Law
- *Larix himalaica* Cheng et L.K. Fu.

ECOLOGICAL AND GEOGRAPHICAL DISTRIBUTION

Figure 1 shows the geographical distribution of the five species.

1. *Larix potaninii*. It is endemic to China and mainly distributed in Aba, Hongyuan, Nanping, Songpan, Pingwu, Maoxian, Lixian, Wenchuan, Xiaojin, Danba, Seda, Luhuo, Daofu, Batang, Kangding, Yajiang, Daocheng, Jiulong, and Muli of western and northwestern Sichuan. It can be also found in Mingxian and Zhouqu in southern Gansu. They are often distributed vertically in the areas of 2,600 to 4,000 m above sea level with the highest at 4,300 m (in Daofu) and lowest at 2,300 m (in Songpan).

The deciduous coniferous forests consisting of *L. potaninii* Batalin often occur on the relatively cold mountain ridges, upper slopes, or upper part of humid river valleys. They are often mixed with *Picea* and *Abies* and form forests. In the forests the annual mean temperature is about 3-6 °C, mean temperature for the coldest month is about –4 to –10 °C and the hottest month 12 to 15 °C, annual accumulated temperature of ≥10 °C is about 500 to 1,600 °C, and annual precipitation is about 800 mm. Mountain brown soil, dark brown soil, and mountain brown podzolic soil are found there. The soil is thick, loose, and fertile, 5 to 10 cm, humus of more than 10 percent, total nitrogen 0.3 to 0.6 percent, active potassium 110 to 230 ppm, active phosphate 20 to 128 ppm, and pH 4.2 to 6.2.

Trees average 20 to 25 m high with diameter breast height of about 20 to 40 cm. The canopy density of the

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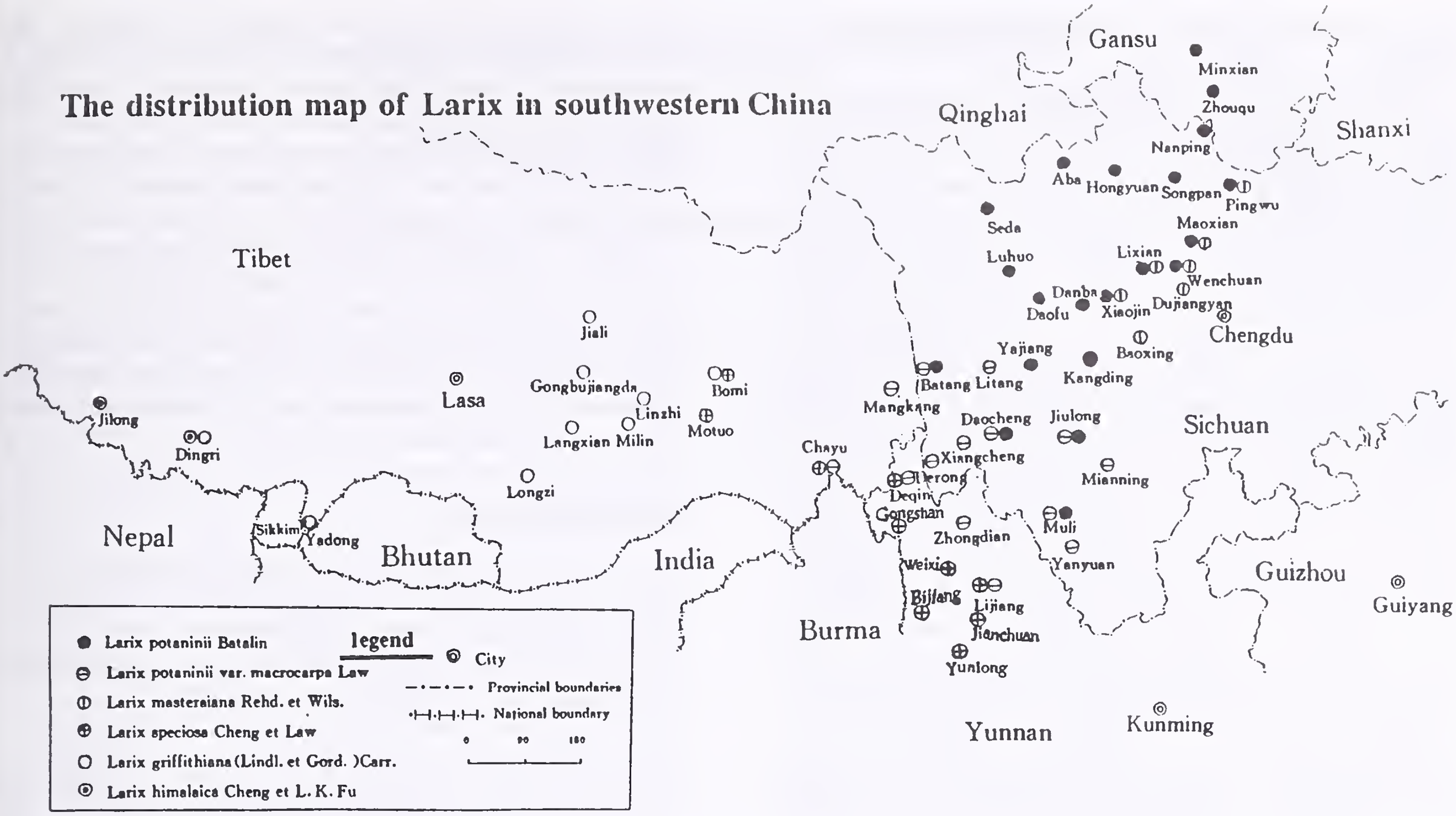

Figure 1—The distribution of *Larix* species in southwestern China.

forests with this species is about 0.4. The understory is dense with cover of about 50 to 70 percent. The understory is mainly composed of various species of Rhododendron and some other plants, such as *Rhododendron agglutinatum, R. dichroanthum, R. yunnanensis, R. litangense, Lyonia villosa, Ribes glaciale, Sorbus rehderiana, S. koehneana, Potentilla fruticose, Spiraea alpina, Cotoneaster microphyllus, Rosa omeiensis,* and *Sinarundinaria chungii.*

2. *Larix potaninii* var. *macrocarpa* Law. This tree is a variety of *L. potaninii* Batalin and endemic to China. It occurs in Batang, Litang, Jiulong, Derong, Xiangcheng, Daocheng, Mianning, Muli, and Yanyuan of southwestern Sichuan, Chayu, and Mangkang of southeastern Tibet, and Deqin, Zhongdian, and Lijiang of northwestern Yunnan. The trees of this variety are distributed at the upper parts of the *Abies*, *Picea* or *Pinus* forests, or mixed with the plants of *Abies* and *Picea*. It occurs at 3,400 to 4,400 m.

Trees of this variety are usually 15 to 20 m high with some as high as 30 m. The diameter breast height is about 30 to 50 cm and the largest 70 to 80 cm. The canopy density of its forests is 0.3 to 0.5. The mountain brown coniferous forest soil and mountain podzolic soil are found there with pH of 4.6 to 5.8. The soil contains 7 to 10 percent organic matter. The annual mean temperature is 3 to 6 °C, mean temperature for the coldest month is –5 to –10 °C and that for the hottest month 10 to 12 °C, annual accumulated temperature of ≥10 °C is 500 to 1,200 °C, and annual precipitation is 600 to 1,000 mm. The understory of the forests mainly consists of *Rhododendron agglutinatum, R. dichroanthum, R. yunnanensis, R. aganiniphum, R. vernicosum, R. trichostomum,* and *R. arizelum*. Some other plants are also found there, such as *Ribes glaciale, Sorbus rehderiana, S. hupehensis, Spiraea alpina,* and *Sinarundinaria chungii.*

3. *Larix mastersiana* Rehd. et Wils. It is endemic to Sichuan, and found in some small areas in Maoxian, Baoxing, Dujiangyan, Wenchuan, Xiaojin, Lixian, and Pingwu. It occurs at 2,300 to 3,200 m with the highest of 3,500 m in Lixian and lowest of 1,650 m in Wenchuan.

The plants of this species are usually scattered along the *Abies*, *Picea*, and *Tsuga* forests or river banks, or mixed with those trees. They are usually 20 to 30 m high with diameter breast height of 30 to 40 cm. The canopy density of the forests is 0.4 to 0.6. The annual mean temperature is 5.8 to 9.1 °C with the mean temperature for the coldest month of –3 to –8 °C and the hottest month 14.6 to 17.6 °C. The annual accumulated temperature of ≥10 °C is about 1,300 to 2,000 °C. The annual precipitation is 700 to 800 mm. Mountain brown soil and dark brown soil are found there with litter of 10 to 20 cm thick. The soil is fertile and loose, and contains 8 to 20 percent of organic matters. Its pH is 4.6 to 5.8.

Understories of these forests are commonly *Rhododendron przewalskii, R. pachytrichum, R. maoense, Sinarundinaria brivipaniculata, S. nitida, Lonicera tangutica, Sorbus rehderiana, S. koehneana, Ribes meyeri* var. *tanguticum, Prunus pilosiscula, Rosa omeiensis,* and so on. The cover averages 60 to 70 percent.

4. *Larix griffithiana* (Lindl. et Gord) Hort. ex Carr. It is endemic to the Himalayan Region of China and mainly occurs in the subalpine areas of 2,800 to 4,100 m in the south and southeast parts of Tibet, such as in Bomi, Linzhi,

Milin, Jiali, Gongbujiangda, Longzi, Dingri, Langxian and Yadong.

This tree is usually found in mixed species forests with *Picea likiangensis* var. *Lizhiensis, P. brachytyla* var. *complanata, Abies spectabilis,* and *A. forrestii.* Sometimes it is also mixed with *Quercus semecarpifolia* and *Betula platyphylla.* Trees are commonly 25 to 30 m high with the tallest of 40 m. The diameter breast height is about 40 to 50 cm and the largest is over 100 cm. The canopy density is 0.4 to 0.6. The annual mean temperature in the forests is 4 to 9 °C, mean temperature for the coldest month is –1 to –6 °C and that for the hottest month is 11 to 16 °C, annual accumulated temperature of ≥10 °C is about 800 to 2,200 °C, and annual precipitation is 600 to 1,000 mm. The litter on the forest ground is about 3 to 10 cm thick. Acid brown and yellow brown soils are deep, loose, and fertile with organic matters of 8 to 28 percent and pH 5 to 6. The understory often found with *Larix griffithiana* is *Lonicera tangutica, L. hispida, Viburnum kansuense, Deutzia purpurescens, Acer caudatum, A. caesium* ssp. *giraldii, Prunus serrulata,* and *Rubus biflorus.* Plant cover averages about 80 percent.

5. *Larix speciosa* Cheng et Law. It is endemic to the Himalayan Region of China, and mainly distributed in Bomi, Motuo, Chayu and the upper mountains along the Yalutsangpo River valleys of Tibet, and in Deqin, Gongshan, Weixi, Lijiang, Bijiang, Jianchuan, and Yunlong of northwestern Yunnan. This species is commonly found between 2,600 to 4,100 m and occurs in small areas at the upper parts of *Picea* or *Abies* forests.

6. *Larix himilaica* Cheng et L.K. Fu. It is also an endemic species to the mountains of China's south side of the Himalayan Ranges, such as in Jilong and Dingri of Tibet. This species is commonly found between 2,800 to 3,700 m.

INTRODUCTION AND CULTIVATION

Since the 1960's, studies have been carried out on the introduction, domestication, and cultivation of some species of Sect. Multiseriales Patschke of *Larix.* In 1967, *L. potaninii* and *L. mastersiana* were planted in an area of about 15 hectares in the Wolong forest region in Wenchuan, Sichuan. By 1978 they grew into dense forests. By then the *L. mastersiana* were about 10 m high. On the average, they grew 1 m in height and 1 cm in diameter annually. In 1959, *Larix potaninii* were artificially regenerated in the Baoxing forest region of Sichuan and in 1972 they averaged 6 m high. Every year they grew about 50 cm in height. The cultivated plants of *L. potaninii* grew three to five times faster than those in natural forests. In addition, *L. principis-rupprechtii* Moyr, *L. sibirica* Ledeb, and *L. kaempferi* (Lamb) Carr were introduced and cultivated in Wolong forest region of Wenchuan, Miyaluo forest region of Lixian, and Liangbei forest region of Sichuan. In the Miyaluo forest region, *L. kaempferi* (Lamb) Carr was regenerated on the cutover area at about 3,300 m, and 99.8 percent survived and are still alive. *Larix kaempferi* (Lamb) Carr was also introduced and cultivated on the mountain areas in northeast China, north China, northwest China, and south China, and the plants grow very well. The oldest introduced trees are now more than 70 years old.

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European Larch in Middle Europe With Special Reference to the Central Alps

Friedrich-Karl Holtmeier

Abstract—As a cultivated tree, European larch (*Larix decidua* Mill. [= *Larix europaea* De Candolle]) is common throughout Middle Europe. Its natural range is in the Alps, Sudetic Mountains, Tatra Mountains, and in the Beskides (southern Polonia). Different varieties of larch peculiar to these regions have developed. Climates characterized by relatively low but late increasing summer temperatures and endangered by late frosts are generally unfavorable for this tree. Continental climates appear to be more suitable to larch. In the Central Alps extensive pure larch forests developed, due mostly to human disturbances, mainly forest pasture.

Compared to the genus *Pinus* (about 90 species) or *Picea* (about 40species), the genus *Larix* is poor in species. Three are native to North America and about nine, with many races and varieties, to Eurasia (Meusel and others 1965). Two species only—*Larix decidua* and *Larix sukaczewii* (syn. *Larix sibirica* Lebdeb. var. *viridifolia*)—are common to Europe. *Larix sukaczewii*, however, only occurs in the northeastern edge of Europe separated by a wide gap from the range of *Larix decidua* and will not be considered here.

High-quality larch timber is used for construction, furniture, paneling, fine veneer, shingles, and many other purposes (Tschermak 1935). It has a high merchantable value but is less important to the economy than beech or oak. Because of its bright autumn colors, larch is of great esthetic value in tourist areas such as the Central Alps.

HABITAT

Native Range of *Larix decidua* and Its Varieties

As a cultivated tree, *Larix decidua* is commonly found throughout Middle Europe. It was introduced to most of that area at first in the middle of the 18thcentury. The natural range, however, is in the Alps, the Sudetic Mountains, and in Polonia. Some smaller occurrences are in the eastern and southern Carpathian Mountains and in the Bihar Mountains (fig.1). Due to the disjunctive distribution pattern, different varieties exhibiting different growth characteristics, morphological peculiarities, and different susceptibility to larch cancer (*Lachnellula* [= *Trichoscythella* = *Dascyphylla*] *willkommii*) have developed. According to their natural ranges they are described as Alpine larch, Sudetic larch, Tatra larch, and Polish larch (Dengler 1971; Leibundgut 1984; Rubner and Reinhold 1953). In the following, the terms "alpine larch" and "subalpine larch" are used. "Alpine" refers to the natural range (Alps) while "subalpine" refers to the altitudinal belt.

Polish larch originally had a wide distribution. However, only a few important occurrences are left. They are between 150 to 600m above sea level.

The natural occurrences of Sudetic larch were considerably restricted by human influence and are actually small. During the 19thcentury other provenances, in particular from Tyrol, were introduced to the area of Sudetic larch. In its natural range Sudetic larch occurs between 300 and 800 m above sea level. It shows good and regular growth and straight shafts. Sudetic larch also is resistant to larch cancer. Because of its relatively great tolerance to shade, it can be more easily cultivated together with spruce and beech, compared to alpine larch.

Tatra larch—also called Carpathian larch—shows a scattered distribution along the Tatra and Fatra Mountains, eastern and southern Carpathian Mountains, and in the Bihar Mountains. In view of its great altitudinal range from about 600 to 1,650m above sea level, the existence of different local races is likely (Leibundgut 1984).

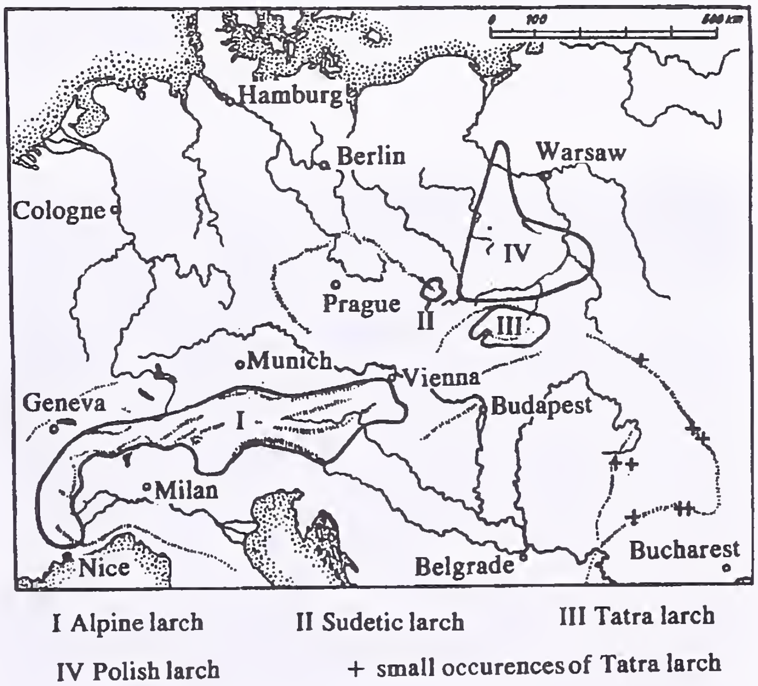

Figure 1—*Larix decidua* and its varieties (except for *Larix sukaczewii*) in Europe (after Rubner and Reinhold 1953, modified).

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Similar to Sudetic larch, Tatra larch seems to be resistant to larch cancer.

Alpine larch is common throughout the Alps (Fenaroli 1936; Mayer 1962; Morandini 1956; Tschermak 1935). All large areas contain larch, and the Alps are the largest continuous distribution area of *Larix decidua* in Middle Europe. This wide distribution, however, cannot be explained by postglacial vegetation history alone, but must partly be attributed to human interferences. In the western and eastern central Alps, larch mainly occurs from the montane belt to tree line (greater than or equal to 1,000 to 2,400m). In the eastern Alps, however, and along the northern and southern rim of the Alps, it is also commonly found at elevations as low as 300 to 500m above sea level (Dengler 1971; Leibundgut 1984; Rubner and Reinhold 1953).

Due to the different local and regional environmental conditions and great altitudinal range (climates, soils) many local varieties have developed (Rubner and Reinhold 1953). Roughly said, the provenances from low and middle elevations (eastern Alps, southern rim of the French and Italian Alps) are characterized by fast growth, straight boles, and high resistance to larch cancer, as also are Tatra and Polish larch (Rubner and Reinhold 1953; Wettstein 1956). On the other hand, larches from the subalpine usually grow slowly and frequently show curved stems. While that growth form might be genetically controlled (Burger 1928), in most cases growth has to be attributed to the influence of snow and soil creep, factors peculiar to mountain slopes (fig.2; see also fig.14). Moreover, there is some evidence that subalpine larches are more susceptible to larch cancer than the provenances from lower elevation, which also are more shade tolerant than subalpine larch. Probably infections by larch cancer are favored by damages caused to the trees by climatic influences such as late frost and mechanical damages, especially at high elevations.

Subalpine larches are also different from lower elevation provenances in phenology. They start annual shoot elongation considerably later and terminate height growth earlier than larches from lower altitudes. In the Inn-Valley and Otz-Valley, Austria, for example, mature larches at timberline flush usually 2 to 2.5months late but turn yellow only 1-month earlier compared to larches at 700m above sea level (Friedel 1967; Tranquillini 1979; Tranquillini and Unterholzner 1968).

Figure 2—Larches turned downslope by snow creep. Prudelvent, Puschlav Valley, Switzerland.

Table 1—Potential frost resistance (°C) of some conifer species during winter at timberline of the northern temperate zone

Species	Needles	Buds	Stem
Europe			
Pinus cembra	−50/−70	−70	−70
Picea abies	−40	?	−40
Larix decidua	—	−35/−50	−45
North America			
Picea engelmannii	−45	−40	−45
Abies lasiocarpa	−50	−45	−40
Pinus aristata	−70	−70	−70
East Asia			
Abies veitchii	−35	−70	−70
Pinus pumila	−70	−70	−70
Larix leptolepis	—	−30	−70

Climate and Soils

Although *Larix decidua* has been cultivated in maritime regions of Europe, where it actually shows good growth in many areas, climates characterized by relatively low and late increasing summer temperatures are generally unfavorable to this tree. While frost-resistant in winter (table1), *Larix decidua* is quite sensitive to frost when flowering and thriving needles. Thus, late frost—common in maritime climates and locations with frequent formation of cold air layers—may become a critical factor in reproduction. Subalpine provenances planted at low altitude may be even more endangered by late frosts because they are already thriving at lower temperatures than low-elevation provenances. On the other hand, low-elevation ecotypes brought to high altitude would thrive too late (higher temperature demand) to fully develop during the short growing season.

The main natural areas of distribution such as Central Alps, southern slopes of the High Tatras, the Sudetic Mountains, and Polonia, are characterized by relatively continental climates that appear to be more suitable to larch. So alpine larch has its ecological optimum in the Swiss Central Alps, in Carinthia, Styria, and in the Wienerwald (Mayer 1962; Rubner and Reinhold 1953; Tschermak 1935). Though different in altitude, these areas are characterized by a warm and sunny growing season. On the other hand, larch also occurs in areas with precipitation as high as 2,000mm, such as the Tessin in the southern Alps. There, however, it is more common at relatively dry and sunny sites (Ozenda 1988). At high elevations, alpine larch grows obviously best on southern and western exposures. Open slopes and convex topography seem to be more favorable than sites characterized by stagnant humid air. Because larch compensates its relatively low amount of needles and its comparatively short growing season (deciduous tree) by high photosynthetic activity (Tranquillini 1979), ventilation—which, besides warmth and high insolation, increases transpiration—is considered to be an important site factor to larch (Rubner and Reinhold 1953; Tschermak 1935). Relative to 100-g needle dry weight, larch transpires about 40percent more than beech (*Fagus sylvatica*) and 800percent more than spruce (*Picea abies*) (Leibundgut 1984).

Larch seems to be relatively indifferent to soil conditions as it grows on silicate substratum as well as on limestone if sufficient soil moisture is provided (high transpiration rate). Best growth is observed on deep, well-ventilated soils, while soils influenced by ground water or stagnant water are unfavorable. Larch is able to adjust its root system to local site conditions. On permeable soils it is able to take up water from great depth (4m and more) by deep-reaching roots.

SILVICS

Larch, in general, is a light-demanding tree, and is not able to thrive light-needles. If too much shaded, needles will atrophy. Thus, under natural conditions larch is a pioneer tree, typical of early stages of forest succession. Pure larch forests only develop if shade-tolerant tree species such as beech (*Fagus sylvatica*), fir (*Abies alba*), or spruce (*Picea abies*) are missing due to natural environmental factors or human interferences. Otherwise larch will be outcompeted. That probably also explains the disjunctive pattern of natural distribution (fig.1).

In cultivated forests outside its natural range, larch is usually mixed with beech and spruce. To grow larch, special management is required to reduce competition of both these shade-tolerant species. On the other hand, beech can easily be grown under larch cover, as larch protects beech seedlings from too intensive insolation and, in contrast to spruce, does not hamper beech crown to develop. Thus, combined management and rotation of both species are possible. Growing larch and spruce together is more difficult. Though larch grows rapidly, it will be passed by spruce after 20 to 30 years and finally be outcompeted. In addition, spruce is the host of *Taeniothrips laricicorus,* which may cause severe damage to larch by sucking sappy bark and needles of young terminal shoots. Shoots will be killed, and after being attacked for several years the upper part of the larch crowns become dry and bushy because lateral branches will now substitute dead apical shoots (Novak and others 1989).

Many other diseases and insects cause injuries to larch. However, they cannot be considered here because a bundle of factors such as provenance, environmental conditions, forest composition and structure, and successional stage, are involved and require too much space for explanation.

LARIX DECIDUA FORESTS IN THE CENTRAL ALPS

In the Central Alps extended pure larch forests are common in the subalpine belt, although shade-intolerant larch cannot successfully compete with *Picea abies* and *Pinus cembra*. Pure larch forests mainly occur on southern exposures and on relatively gentle topography, mainly in the lower part of the mountain slopes just above the valley bottom (figs. 3 and 4). Their existence can only be explained by human interferences.

Under natural conditions, pure larch stands occur on boulder fans, screes, avalanche tracks, and similar sites, where mineral soil is exposed (see also figs. 10 and 11). At advanced successional stages, dense understory vegetation prevents light and wind-dispersed larch seeds from getting into a suitable seedbed. Thus, larch cannot rejuvenate and will gradually become outcompeted by more shade-tolerant species such as *Pinus cembra* (Auer 1947; Holtmeier 1967, 1974, 1990; fig. 8), which would dominate at the final stage of natural forest succession.

However, because of its dark shade-giving crown, *Pinus cembra* prevents the growth of pasture plant communities, and it was systematically eliminated at locations suitable to grazing. Under larch cover, however, good grazing conditions developed. Larch also is less sensitive to grazing than is stone pine. Moreover, larch was favored by forest fires, because it is relatively well protected by its thick cork-like bark and by its ability to replace needles, while stone pine usually is killed by fire. Forest fires were frequent in the past and were used on pastures to get rid of weeds such as dwarfed juniper (*Juniperus nana*) and to keep predators away from grazing cattle and sheep (Holtmeier 1974). Due to such human influences that interrupted natural forest succession in many central alpine areas, larch could spread at the cost of stone pine during history (Auer 1947; Furrer 1955, 1957; Holtmeier 1987; Mayer 1974; Meyer 1955; Moser 1960; Pitschmann and others 1970, 1971; Wendelberger and Hartl 1969).

The cyclic mass outbreaks of the larch bud moth (*Zeiraphera diniana* Gn.) probably increased due to human-induced expansion of pure larch forests. During the gradation peak, growth and seed production of larch become reduced (figs. 5 and 6; see also Campell 1955; Holtmeier 1973, 1974; Nägeli 1969). The most severe damages are to be found mainly at normal sites in the upper montane and up to the middle subalpine belt, especially within the so-called “warm slope zone” (fig. 7). Older trees seem to react more sensitively to defoliation than younger ones. Young trees at timberline or other extreme sites are usually not damaged (Schweingruber 1979). However, what surely is even more important to economy in tourist areas is that the high esthetic value of the larch forests (bright autumn colors, fresh green in spring) is lost during the mass outbreaks of the larch bud moth. Moreover, people feel unpleasant when walking through infested forests because caterpillars rain from the larch trees.

In many central alpine valleys tourism has become the main base of existence, and most of the formerly grazed forests are no longer used. Natural succession is going on again, and under the larch canopy young *Pinus cembra* are growing (fig. 8). This process, however, might be retarded by the larch bud moth, when the larvae feed on the young stone pines in the understory after having defoliated the larch crowns (Baltensweiler 1975; Campell 1955; Holtmeier 1990).

However, in most of these forests, larch will be gradually replaced by stone pine. At those locations where larch should be favored for different reasons (esthetics, timber), special management, such as exposing mineral soil and selective cutting of stone pine, is required (Auer 1947; Campell 1955). Small clearcuts combined with removal of the raw humus layer—carried out when abundant seed

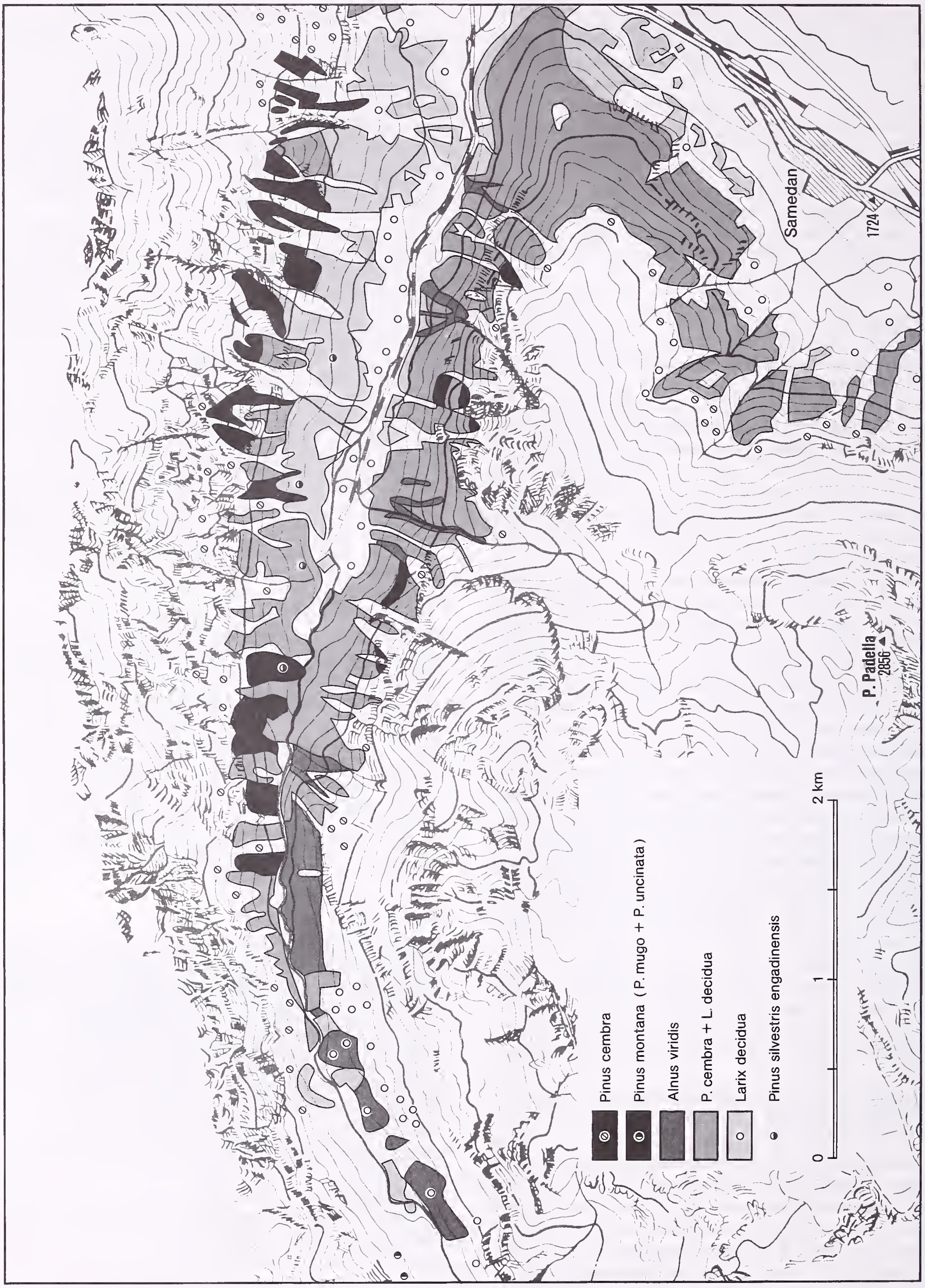
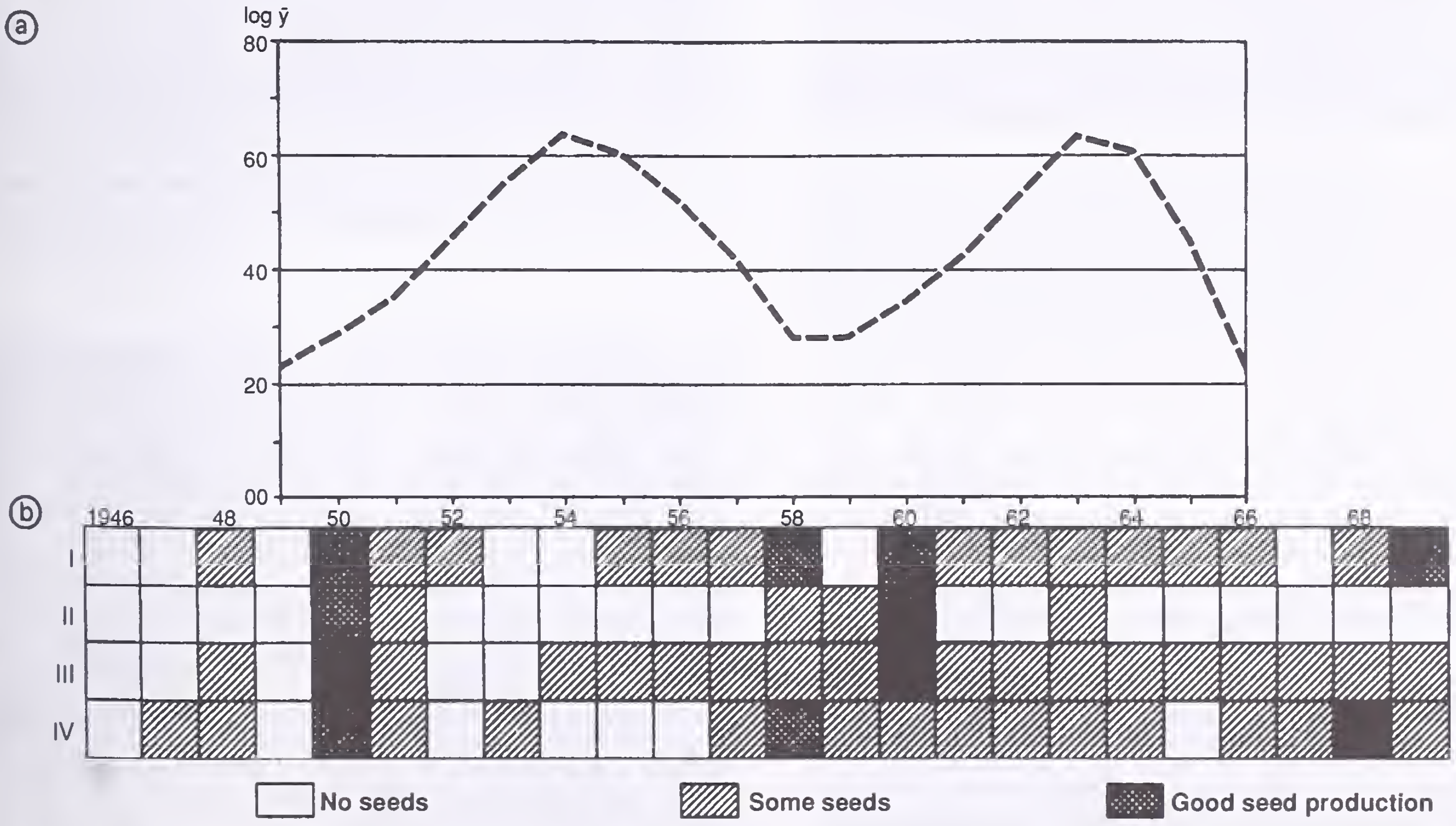


Figure 3—Forest map of the Bever Valley in the Upper Engadine, Switzerland (after Holtmeier 1967, modified).

Figure 4—Larch pasture-forest near Pontresina (Switzerland) at about 1,850 m.



	1946		48		50		52		54		56		58		60		62		64		66		68	
I	□	□	▨	□	■	▨	▨	□	□	▨	▨	▨	■	□	■	▨	▨	▨	▨	▨	▨	□	▨	■
II	□	□	□	□	■	▨	□	□	□	□	□	□	▨	▨	■	□	□	▨	□	□	□	□	□	□
III	□	□	▨	□	■	▨	□	□	▨	▨	▨	▨	▨	▨	■	▨	▨	▨	▨	▨	▨	▨	▨	▨
IV	□	▨	▨	□	■	▨	□	▨	□	□	□	▨	■	▨	▨	▨	▨	▨	▨	□	▨	▨	■	▨

□ No seeds ▨ Some seeds ■ Good seed production

Figure 5—Cyclic gradation of the larch bud moth (*Zeiraphera diniana*) and seed production of some conifers: (a) population growth (after Auer 1947); (b) seed production of I = *Pinus cembra*; II = *Larix decidua*; III = *Pinus sylvestris*; IV = *Picea abies* (after the annual reports of the forest office at Celerina, Upper Engadine).

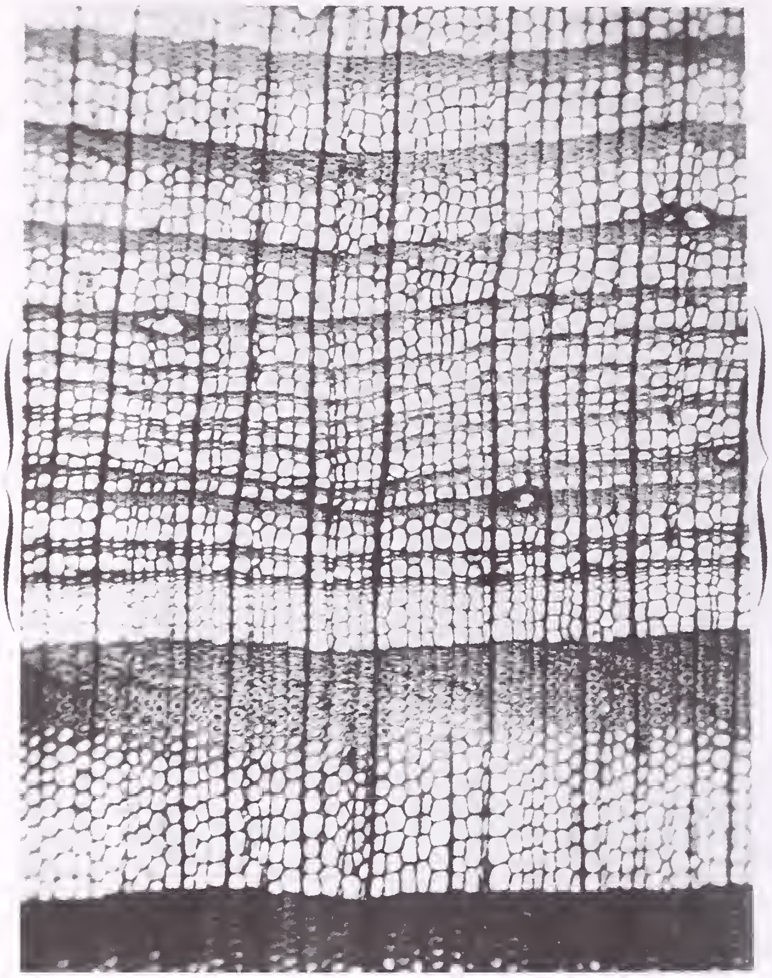


Figure 6—Reduced growth (in brackets) due to attacks of the larch bud moth at the end of the 19th century (from Nägeli 1969).

production is occurring—might be even more favorable to larch regeneration than taking single stems only (Campell 1955).

Above the human-caused present timberline, abandoned or rarely used alpine pastures are invaded by trees. In general stone pine is more successful in resettling these areas than is larch. Stone pine seeds are dispersed by the nutcracker and are usually cached at sites relatively favorable to tree growth (Holtmeier 1990), while larch seeds are wind borne. Wind-mediated seed dispersal is influenced by a bundle of factors such as seed-wing size, seed weight, wind velocity and direction, topography, and plant cover. Thus, in contrast to seed dispersal by the nutcracker, it depends mainly on chance whether wind-borne seeds will reach a suitable seedbed because of the mosaiclike microsite pattern in the timberline ecotone. Many of the microsites are totally unfavorable to germination, establishment of seedlings, and growth of young trees (Holtmeier 1986, 1990; Schönenberger 1985).

However, the most important factor that makes larch less successful in invading the former pastures is the dense dwarf-shrub and grass vegetation that prevents the light larch seeds from getting into a seedbed. At sites where mineral soil has been exposed by erosion or trampling, larch occurs in great numbers (fig. 9). Thus, grazing may be favorable to larch regeneration, provided that after germination of larch seeds cattle will be excluded for a while to

Figure 7—Within the "warm slope zone" the larches have been defoliated by the larch bud moth, while the larches close to timberline and at the valley bottom (cold air layer) were not affected.

allow seedlings and sapling to grow up (Auer 1947). Also, burn areas, clearcuts, avalanche tracks, and forefields of retreating glaciers may rapidly be invaded by larch (figs. 10 and 11). Occasionally, larch also propagates by layering (formation of adventive roots, fig. 12).

Though less resistant to deep freezing temperatures and to desiccation than stone pine, larch is also able to grow at extreme sites (Tranquillini 1979; Schönenberger 1985). Contrary to stone pine, larch will not be affected by snow mold (*Phacidium infestans*) in case of long winter snow cover (fig. 13). Snow creep, however, may be detrimental to larches older than 15 years because about this age the trunk is losing its elasticity. Younger larches, however, may even survive in avalanche tracks because after they are pressed down to the ground by the snow masses they will emerge almost undamaged after melting (fig. 14).

Figure 8—Revived succession after forest pasture has terminated. Stone pines are growing up under the larch canopies.

Figure 9—Larches invading goat pasture ("Il nüd," near Zuoz, Upper Engadine) just after grazing has terminated.

Figure 10—Larches invading an avalanche track on north-exposed slope of Piz Polaschin (Upper Engadine) at 2,050 m.

Figure 11—Larch invading the forefield of the Morteratsch Glacier (Upper Engadine). The area in the foreground became ice-free in the early 1960's.

Figure 12—Larches "migrating" downwind by layering on Pru del vent (Puschlav, Switzerland) at about 2,020 m.

Figure 13—Larch and stone pines (height 180 to 230 cm, about 50 years old) on an abandoned alpine pasture on the northwest-exposed slope of the Upper Engadine at 2,200 m. Stone pines lost needles in their basal parts by snow mold, while larch was damaged by climatic influences above the winter-snow cover.

Figure 14—Larches that could survive for a while in an avalanche track due to their great elasticity (drawing after a photo).

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Larch and Larch Forests of Siberia

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Abstract—Larch is the most widely distributed forest tree species of Siberia and entire Russia. The taxonomy of Siberian larches is vague as the reproductive isolation is weak in larch and all species easily hybridize, which results in varying views on the taxonomy of the Siberian larches. *Larix sibirica* and *L. gmelinii* are considered as the only separate species of larch in Siberia. The morphological, ecological, and forestry features of subspecies and hybrids are also described, including *L. sukaczewii*, *L. cajanderi*, and *L. czekanowskii* .

At the conclusion of the Fifth World Forestry Congress in Seattle, WA, U.S.A., the participants planted trees most typical of their home countries. Russian delegates planted *Larix sibirica* as the national tree.

Larch in Russia grows in forest tundra, taiga, steppe, mountains, plains, and swamps. Larch is the most widely distributed forest tree species of Siberia and entire Russia. The larch forests occupy an area of 268 million ha, which is about 40 percent of all forested area of Russia. Wood volumes are near 25.4 billion m^3, which is more than 34 percent of all Russian volumes.

The taxonomy of Russian larches and particularly the Siberian ones is vague. This is evident because the main species criterion, which is reproductive isolation, is weak in larch, and all species easily hybridize under natural conditions. There are two principal points of view on the taxonomy of the Siberian larch. Prof. N. V. Dylis (1981) maintains that there are three species in Siberia: *Larix sibirica* (Ledeb.), *L. gmelinii* (Rupr.), and the new species *L. sukaczewii* (Dylis) derived from *L. sibirica*. Meanwhile, Prof. E. G. Bobrov (1972a) denies the status of *L. sukaczewii* but distinguishes *L. cajanderi* (Mayr.) as a distinct species from *L. gmelinii*. N. V. Dylis (1981) considers it as a subspecies from *L. gmelinii*.

Our opinion is that there are only two larch species in Siberia: *L. sibirica* and *L. gmelinii*. We reached our conclusion because originally the distinguishing of *L. sukaczewii* as a separate species was based mainly on quantitative features. However, the degree of variability in *L. sukaczewii* and *L. sibirica* is considerable. Some qualitative differences between these two species have also been reported in literature.

QUALITATIVE DIFFERENCES

The *L. sukaczewii* cones are broad-ovate, dark brown color, seed scales are big, wide thick, woody, at top turned inside, and cover scales are not distinct. The *L. sibirica* cones are ovate and oblong-oval, light yellow or yellow brown, seed scales are small, narrow, relatively slender, straight at top and cover scales are well noticeable. However, in some regions, such as the South Urals, these two species look almost the same.

Certainly some differences exist in morphology, ecology, and geographical distribution between *L. sukaczewii* and *L. sibirica*, but these differences are insufficient for identifying *L. sukaczewii* as a separate species.

The identification of *L. cajanderi* as a distinct species is not acceptable either. The morphological differences between *L. cajanderi* and *L. gmelinii* are based primarily on only one characteristic—the angle of deviation of seed scales from the cone axis and its dependent features of cone width and shape. In *L. gmelinii*, seed scale angle from the cone axis is 15° to 45°, and in *L. cajanderi* it is usually 60° to 90° and sometimes up to 110°. Consequently there is a difference in seed dispersal. In *L. gmelinii* it can take months, whereas in *L. cajanderi* it is only a few days. The above morphological features are controlled by ecological conditions unlike the quantitative ones.

Larix gmelinii and *L. cajanderi* do not differ in either qualitative morphological features or quantitative measurements. There is both geographical and ecological isolation between them. *Larix cajanderi* grows in more rigorous conditions than *L. gmelinii*. However, those differences are not evident from morphological and karyological characteristics of these larch species. The differences in these qualitative characteristics are gradual and are probably caused by clinal variation.

All of these factors lead us to conclude that *L. cajanderi* is a subspecies of *L. gmelinii* and not a distinct species. While accepting the fact that there are only two species in Siberia—*L. sibirica* and *L. gmelinii*—we want to briefly characterize *L. sukaczewii* and *L. cajanderi* because these species are often described in Russian botanical and forestry literature.

LARIX SUKACZEWII

The morphological features of *L. sukaczewii* were described earlier. This larch occupies definite limited habitats in the northeastern regions of the European part of Russia, the Urals, and western Siberian regions bordering the Urals (fig. 1[1]). Its stands are a minor component dominated by *Picea obovata*, *Pinus sylvestris*, *Betula pendula*, and *Populus tremula*. *Larix sukaczewii* occupies only 0.1 percent of larch forest areas of Russia.

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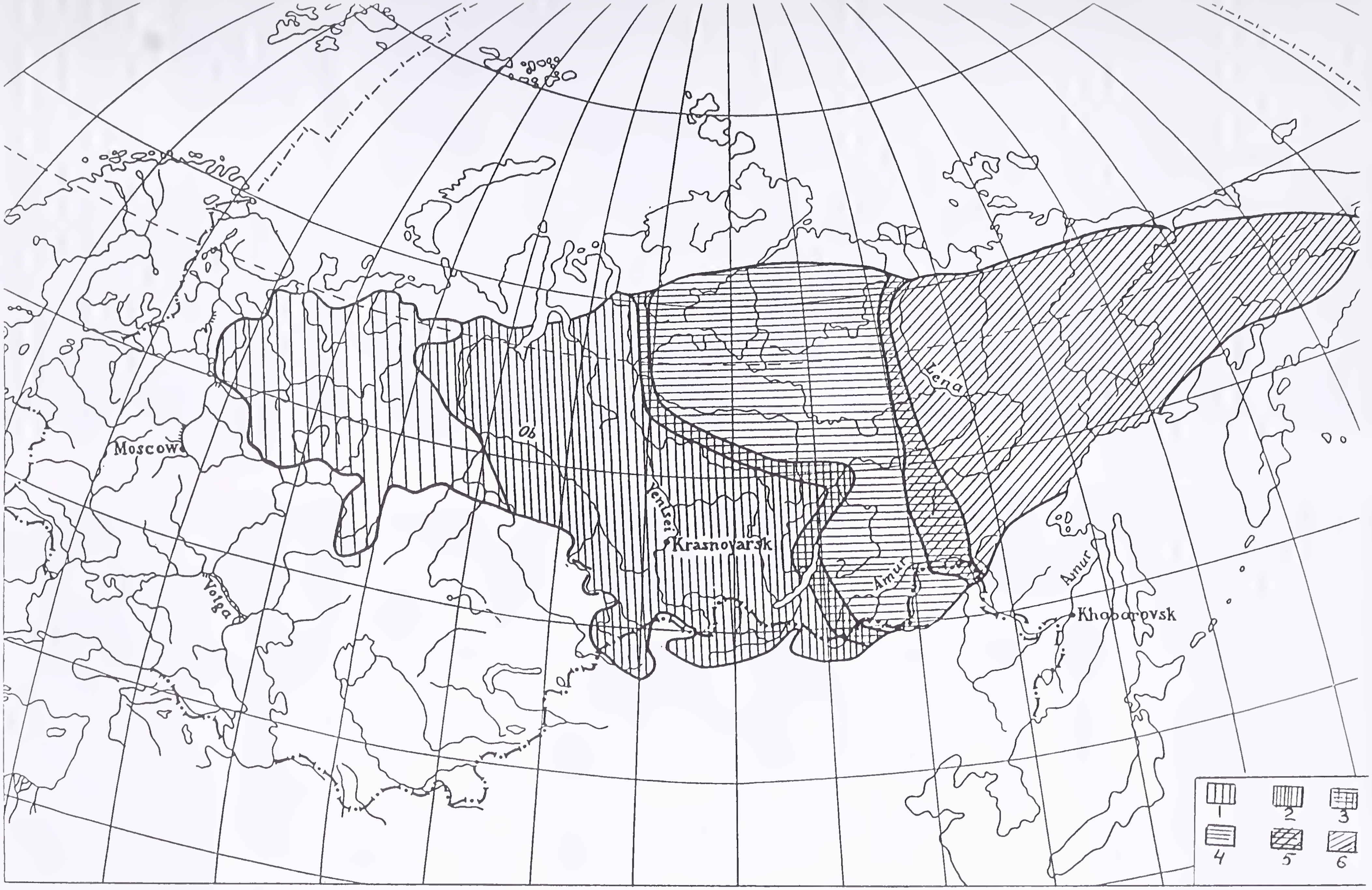

Figure 1—Areas of *Larix* in Siberia.

The *L. sukaczewii* stands are not highly productive (450 to 500 m³/ha), but there are some stands with volumes up to 800 m³/ha. Productivity is limited by competition with other tree species. Those stands of *L. sukaczewii* growing on fertile soils are productive. For example, the famous "Lindulowskaya roscha" stand near St. Petersburg has wood volume of more than 1,500 m³/ha at the age of 216 years, and "Korabelnaya roscha" in Ivanovo district had 1,200 to 1,400 m³/ha at the age of 130 years. The *L. sukaczewii* stands are characterized by a low quality of seeds.

LARIX SIBIRICA

Larix sibirica stands (without *L. sukaczewii*) occupy nearly 14 percent of the larch forest area of Russia. The largest concentration is in the continental mountain regions of southern Siberia (fig. 1[2]), which is characterized by low humidity. *Larix sibirica* is found on sites with colder temperatures when compared to *L. sukaczewii* sites. But in contrast with *L. gmelinii* it is less resistant to cold temperatures. The boundary between *L. sibirica* and *L. gmelinii* coincides with southwestern boundary of the permafrost region.

Larix sibirica has a series of intraspecific hybrids, which may be considered subspecies. Two subspecies—ssp. *rossica* (Sab.) Suk. in the northern and northeastern regions of the European part of Russia, and ssp. *obensis* (Suk.) in the Ob' River basin (except Altai)—were combined to form the distinct species *L. sukaczewii*. Others that have been distinguished are ssp. *altaica* (Szafer) (Suk.) in the Altai area; ssp *jeniseensis* Suk. (Jenisey River basin); ssp. *sayanensis* (Dylis) in the Sayans area; ssp. *polaris* in the upper Lena River basin and regions of Irkutsk Pryangarje; and ssp. *baicalensis* (Dylis) in the southwestern and southeastern Baikal coast. It is also useful to distinguish the ssp. *transbaikalensis* in the western Zabaikalje Mountains.

Larix sibirica grows to 40 m or more in height. The branchlets are often straw yellow. The young cones are red, seldom green, and mature cones are light brown, 10 to 50 mm in length. Cones have eight to 44 scales in three to seven rows. Seed scales are ovate or round, spoon-shaped, and light brown. The scale border is smooth, and the scale length and width are 5 to 17 mm. The brachyblast needles are 5 to 60 mm in length and grow in bundles of 10 to 50. In ideal conditions on mountain slopes and foothills up to altitudes of 1,000 m with well-drained and moist subacid and neutral soils, *L. sibirica* can have wood volumes up to 1,000 m³/ha with average heights of 36 to 38 m and diameters of 45 to 50 cm. Under severe conditions in the northern regions, in swamps and other poor sites, wood volumes in *L. sibirica* stands are only 50 to 80 m³/ha and lower.

LARIX GMELINII

Stands of *L. gmelinii* (without *L. cajanderi*) occupy nearly 35 percent of the larch forest area of Russia. The boundaries of the *L. gmelinii* area are difficult to describe because the species hybridizes with *L. sibirica* in the west and with *L. cajanderi* in the east. Its most northern habitat is on the Taimyr peninsula in the Khatanga River basin, occurring up to 72°40' N. latitude.

Larix gmelinii grows in the northern regions of Krasnoyarsk and Irkutsk districts, including the Putoran Mountains, Nizhnyaya Tunguska, and the higher parts of Podkamennaya Tunguska River basins, and the Vitim River basin. It also grows in the western regions of Yakutia, northern and northeastern parts of Buratia, and the central and eastern regions of Chita districts (fig. 1[4]). In addition, *L. gmelinii* grows in Amur and Khabarovsk regions, where different kinds of larch species and their hybrids were reported, among them *L. cajanderi* and its hybrids *L. olgensis* (A. Henry) and *L. maritima* (Suk.).

In the northern and mountain areas *L. gmelinii* is shrub-like, and sometimes it can have low-lying form. Here, the needles are 5 to 40 mm in length, the brachyblasts grow in bundles of 10 to 50, cones are 5 to 35 mm long, and the seed scales are flat or wavy.

Larix gmelinii is ecologically tolerant. It demands light and grows on recently burned and clearcut areas. It can also grow in forests with a light crown cover. *Larix gmelinii* is highly resistant to low temperatures. It is resistant to spring and fall frosts except when it grows outside its ecological niche.

Unlike all other species, the root system of *L. gmelinii*, including *L. cajanderi*, is often subjected to low temperatures. Frost affects the root systems not only during winter, but also during the growing period in shallow permafrost soils. Commenting on *L. dahurica*, a hybrid of *L. gmelinii* and *L. cajanderi* (fig. 1[5]), Dylis (1981) wrote: "Probably there are no woody species on Earth as tolerant to the high summer thermal gradient between air and soil as *L. dahurica*."

Pozdnyakov (1975) noted: "The most characteristic feature of *L. dahurica* is its location in permafrost region. There are many other woody species in this region, but *L. dahurica* is the best in terms of adaptation to permafrost." The frost negatively affects woody plants because of inhibiting water and nutrient uptake. On the other hand, frost assists in growing season by providing moisture in the soil under the conditions of arid climate or low precipitation or both.

Larix gmelinii is capable of growing on soil with low fertility and grows in a wide range of soils: aridisoils, cold-boggy, stony, acidic, podzolic, and others. However, it is usually characterized by slow growth and low productivity. Its optimal growth is observed on the well-drained soils with relatively deep frost layers.

OTHER SPECIES AND HYBRIDS

Larix cajanderi stands occupy nearly 48 percent of the larch forest area of Russia. It grows in Yakutia (except western regions), in the continental part of Magadan district, in Chucotka, Amur, and Khabarovsk districts (fig. 1[6]), and, according to Professor Bobrov (1972a), in Kamchatka. The morphological and forestry features of *L. cajanderi* were described earlier.

The hybrid forms of *L. gmelinii* and *L. sibirica* occur in the area of interception of these species (fig. 1[3]). This hybrid (*L. czekanowskii* [Szaf.]) possesses features of both species. It is difficult to describe this hybrid because in different populations the number of hybrid forms with the various degree of hybridization varies and depends on the stage of hybridization and ecological and geographical conditions of growth. The frequency of forms genetically similar to *L. sibirica* is higher in the warm and dry habitats, whereas there are more forms similar to *L. gmelinii* in cold and wet conditions.

The ecological and forestry features of *L. czekanowskii* are similar to the parental ones and depend on the number of forms in the stand that resemble either *L. sibirica* or *L. gmelinii* (Kruklis and Milyutin 1977). Some peculiarities of *L. czekanowskii*, according to Bobrov (1972b) are associated with the "introgression of formations," the result of introgressive hybridization of *L. sibirica* and *L. gmelinii.* For example, in some regions of East Zabaikalje, *L. gmelinii* populations with a portion of hybrid forms can occasionally mix with *Abies sibirica*. On the North Baikal coast, *L. sibirica* stands with some hybrids can grow in stands with *Pinus pumila*, which is usually typical for *L. gmelinii* and *L. cajanderi*. Different types of heterosis are often observed in *L. czekanowskii* stands, such as somatic and reproductive.

Some hybrid populations occur in the areas where *L. sukaczewii* and *L. sibirica*, *L. gmelinii,* and *L. cajanderi* intersect, according to current literature. However, this question needs to be clarified because of controversy surrounding the taxonomy of Siberian larches.

The karyological polymorphism of larch species from Siberia have been studied (Kruklis and Milyutin 1977). All investigated larch species—*L. sibirica*, *L. sukaczewii*, *L. gmelinii*, *L. cajanderi*—have similar karyotypes. The highest similarity is observed in two groups of related species: (1) *L. sibirica* and *L. sukaczewii* and (2) *L. gmelinii* and *L. cajanderi*. For the first time, *Larix* with an additional chromosome have been found in *L. gmelinii* populations.

CONCLUDING REMARKS

The tremendous economic significance of larch wood is invaluable in industry and construction. But recently due to the problems in timber floating and processing, larch wood has not been sufficiently used. Larch is often used for shelter belts in the Siberian steppe regions and for landscaping, not only in Siberia, but throughout Russia.

Foresters, not only from Siberia but from other regions of Russia and foreign countries as well, recognize the significance of the Siberian larch. This recognition is explained by high productivity of larch stands both in native and introduced areas. The creation of seed banks from the best larch stands to establish highly productive forest plantations is an important task for Siberian foresters.

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Larix Laricina—Silvics and Genetics

D. P. Fowler
Y. S. Park
J. Loo-Dinkins

Abstract—*Larix laricina* (Du Roi) K. Koch, eastern larch or tamarack, has the broadest range of any *Larix* species. Tamarack attains its best growth on fresh, moderately fertile sites. It can out compete other species on poorly drained or excessively dry sites. Tamarack is closely related to other North American larches. Genetically, it is highly variable at the provenance, stand, and individual tree levels. It is the subject of tree improvement programs in eastern and central Canada. The species can be readily propagated vegetatively.

Larix laricina (Du Roi) K. Koch, (tamarack, American, or eastern larch) is a small- to medium-sized tree, 10 to 20 m in height and 30 to 60 cm in diameter. Under stand conditions, the trunk has little taper and supports a small, conical, open crown with slightly ascending branches. In the far north and on wet soils, the species is often slow-growing and stunted.

Tamarack has a larger natural range than any other North American conifer and a broader range (longitudinal) than any other *Larix* species. Its range (fig. 1) extends from Newfoundland in the east to the central Alaska, which is sometimes referred to as *L. laricina* var. *alaskensis*. The north-south range extends from north of the Arctic Circle (tree line) south through the Lake States and southern New England. Southern outlier populations occur as far south as West Virginia.

Tamarack is one of the fastest growing of the northern conifers (Fowells 1965) and is reported to outgrow other native conifers (Littlefield 1939; MacGillivray 1967; Mead 1978) at least over short rotations. Fowells (1965) indicated growth rates for tamarack to be in the order of 1.8 to 2.4 m^3 (solid wood) per ha per year. Information on plantation-grown tamarack is limited, primarily because the species has not been widely planted. Fowler and others (1988) reported a mean annual increment for 25-year-old, plantation-grown tamarack of 3.4 m^3 per ha per year; approximately a third of that of good Japanese larch growing on the same site.

Tamarack wood is suitable for most solid wood products. It is moderately dense and strong (similar to *Pseudotsuga*), has reasonably good working properties, and can be kiln-dried, pressure treated, glued, and finished successfully (Balatinecz 1986). Wood of young, fast-growing tamarack has acceptable fiber properties for chemical pulping processes, especially kraft. Wood of older trees with a high proportion of heart wood and arabinogalactan content is less desirable, especially for mechanical pulps (Hatton 1986).

SILVICS

A detailed description of the silvics of tamarack is found in Johnston (1990). Only a brief summary will be presented here. Tamarack is an early successional, shade intolerant species. It grows under a wide array of edaphic and climatic conditions. Best growth is attained on fresh, moderately rich soils after fire or other major disturbance. On these sites, it is generally unable to regenerate itself in competition with more shade tolerant species. Tamarack is at an advantage over competing species on excessively wet "bog" sites, where it can persist for several generations. A similar situation can occur on excessively dry sites.

Figure 1—*Larix laricina*: the native range of tamarack (from Johnston 1990).

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As a species, tamarack tolerates extremes of temperature (mean January temperature, –54 to –1 °C) and precipitation (18 to 140 cm) (Roe 1957). The frost-free period ranges from 75 to 180 days.

Tamarack can be found in large pure stands after major disturbances such as fire. In the absence of disturbance it is restricted to sphagnum bogs and swamps or to exposed dry sites. Frequently it is found in association with black spruce (*Picea mariana* [Mill.] B.S.P.) in open muskegs. On better drained soils it is a temporary associate of a large number of species including trembling aspen (*Populus tremuloides* Michx.), white birch (*Betula papyifera* [Marsh]), balsam fir (*Abies balsamea* [L.] Mill.), and white spruce (*Picea glauca* [Moench] Voss).

Reproduction

Tamarack is a relatively precocious species in which both cone and pollen flowers can occur on vigorous open-growth trees as young as 5 to 6 years of age. It is the first of the Pinaceae to flower in the spring (mid to late April in eastern Canada), about 7 to 10 days earlier than Japanese larch (*L. leptolopis* Sieb. and Zucc.) or European larch (*L. decidua* Mill.) and up to a month earlier than native spruces. Flowering often occurs when the ground is still frozen and snow covered.

The cone flowers are distributed over much of the crown, without any well developed separation of the sexes. Tamarack does not produce copious quantities of pollen. Good cone crops are produced at 3- to 6-year intervals, with some cones produced in most years. The small cone flowers develop into small (1 cm long) cones in late summer (late August). Although on average, each cone is capable of producing 30 to 40 seeds, it is more usual to obtain only one to eight full seeds per cone because of inadequate pollination, frost damage, insect feeding, and possibly other causes.

Tamarack is easy to propagate vegetatively via juvenile cuttings (Park and Fowler 1982). For older materials, ranging from ages 3 to 10 years, Morgenstern and others (1984) reported significant variation in rooting percentage among clones, striking dates, and ages, as well as in interactions.

Damaging Factors

A detailed coverage of insects and diseases of importance to tamarack is provided by Pendrel (1986) and Ostaff (1986), respectively. The larch sawfly (*Pristiphora erichsonii* [Hartig]), especially in conjunction with bark beetles, can be devastating to mature and over-mature tamarack. Periodic outbreaks of these insects have resulted in substantial damage to natural stands. The sawfly generally does not result in mortality to young vigorous trees. The larch casebearer (*Coleophora laricella* [Hubner]), may also cause periodic defoliation, but generally not mortality. A number of cone and seed insects contribute to the general poor seed set of tamarack (Amirault and Brown 1986).

Tamarack is highly susceptible to the European larch canker (*Lachnellula willkommii* [Hartig])—probably at least as sensitive as European larch of Austrian provenance. Larch canker was inadvertently introduced into eastern North America in the 1930's, but has failed to become a serious problem except in coastal areas in Maine and the Maritimes region of Canada (Magasi 1983).

The porcupine (*Errithizon dorsatum* [L.]) is undoubtedly the single most damaging agent to plantations of tamarack and other *Larix* species in eastern Canada and the northeastern United States. Porcupines feed on the inner bark, often girdling the trees which results in death or serious deformation.

GENETICS

Larix is more closely related to *Pseudotsuga* than to any other conifer genus (Prager and others 1976). Tamarack can be crossed, but does not cross readily, with any other *Larix* species. Based on species crossability it appears to be more closely related to other North American larches (*L. occidentalis* Nutt. and *L. lyallii* Parl.) than it is to any of the European or Asian species, suggesting a single migration to North America. Crosses of tamarack and *L. decidua*, *L. leptolepis,* and *L. siberica* are possible, but crossability is extremely low.

Tamarack is genetically variable a the provenance, stand, and within-stand levels of variability. At the provenance level, Jeffers (1975), Cech and others (1977, 1983), and Riemenschneider and Jeffers (1980) reported significant differences with respect to height and survival. Based on a study of electrophoretically detectable variation in 36 populations representing much of the range of tamarack, Cheliak and others (1988) suggested that differentiation between provenances is greater than for many other randomly mating tree species. For other diversity measures; i.e., allelic variation, allelic richness, and polymorphism, they reported tamarack to be comparable with other wide-ranging species. Results from a range-wide provenance study using trees from 65 provenances, tested at six locations in the Maritimes region of Canada, indicated significant variability among provenances for 6-year height and stem form. Although relatively small, there were significant provenance x location interactions. Height at age 6 was strongly correlated with latitude ($r = -0.78$) and moderately correlated with longitude ($r = -0.58$) indicating north-south and east-west clinal variation (unpublished data, Forestry Canada-Maritime Region).

At the stand level of variation Rehfeldt (1970) reported significant differences within a single geographic area (Wisconsin). Large differences among stands, within provenances, is also evident from a test of clonally propagated populations of tamarack (Park and Fowler 1982). Evaluation of this test, 9 years from propagation, revealed that there was significant variation in growth traits due to stands within a region (south-central New Brunswick). Furthermore, this variance was greater than the variance due to families within stands. However, the largest component of genetic variation was due to clones within families (unpublished data, Forestry Canada—Maritime Region). Rehfeldt (1970) and Jeffers (1975) also consider tamarack to be highly variable at the intrastand level.

Park and Fowler (1982) studied the structure of a tamarack population in central New Brunswick with respect to relatedness among neighboring trees and inbreeding.

They found the species to be highly variable at the intrapopulation level and demonstrated that trees growing in close proximity to one another were often related. In comparison to other conifer species, tamarack is below average in self-fertility and above average in number of lethal equivalents. Tamarack exhibits relatively large specific combining ability variances for early seedling height.

BREEDING PROGRAMS

Tamarack is not an important reforestation species. Less than 10 million trees are planted annually. However, because of its rapid growth over short rotations, it is recognized to be of potential value, especially to fill identified short-falls in wood supply (Erdle and Wang 1986). Breeding programs for the genetic improvement of tamarack are currently active in Canada (Ontario, Quebec, and the Maritime provinces) and the United States (Maine). Currently all tamarack seed used for reforestation in the Maritimes region of Canada comes from first generation clonal seed orchards.

The breeding strategy for these programs is described in detail by Fowler (1986). A flow chart depicting the breeding strategy is presented in figure 2. Under the program in the Maritime region, 300 plus trees have been selected, on the basis of growth and form, and have been grafted and planted in orchards and breeding gardens. Currently there are approximately 25 ha of producing first-generation orchards. All selected clones are being crossed (polycross) and progeny tested to determine general combining ability and to rogue the orchards. Initially the strategy called for random single pair matings to produce materials for the next generation of selection and breeding. This aspect of the scheme has been postponed until early growth and form data (5 years) are available from the progeny tests and a positive assortative mating scheme can be used.

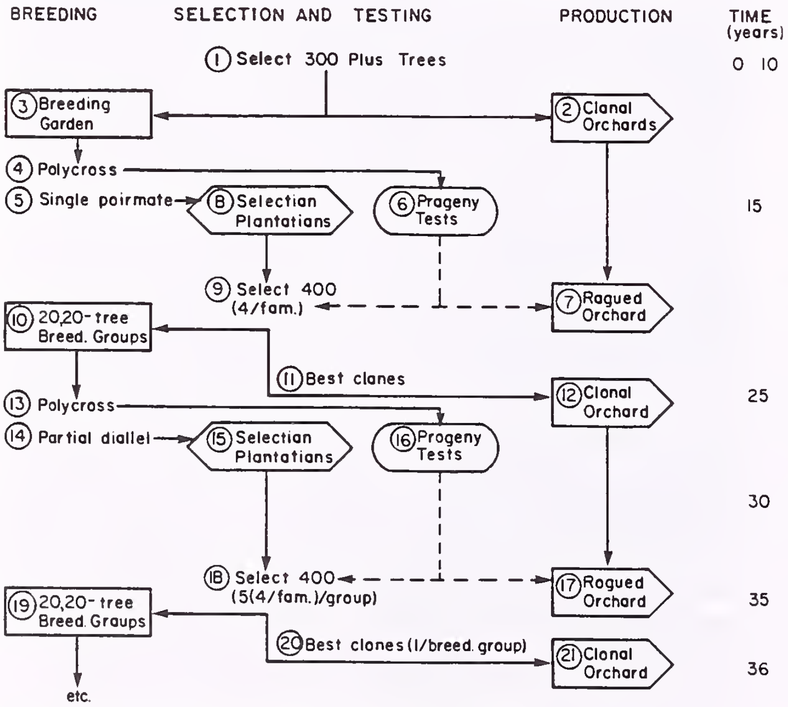

Figure 2—Flow chart for tamarack improvement strategy; New Brunswick Tree Improvement Council program (from Fowler 1986).

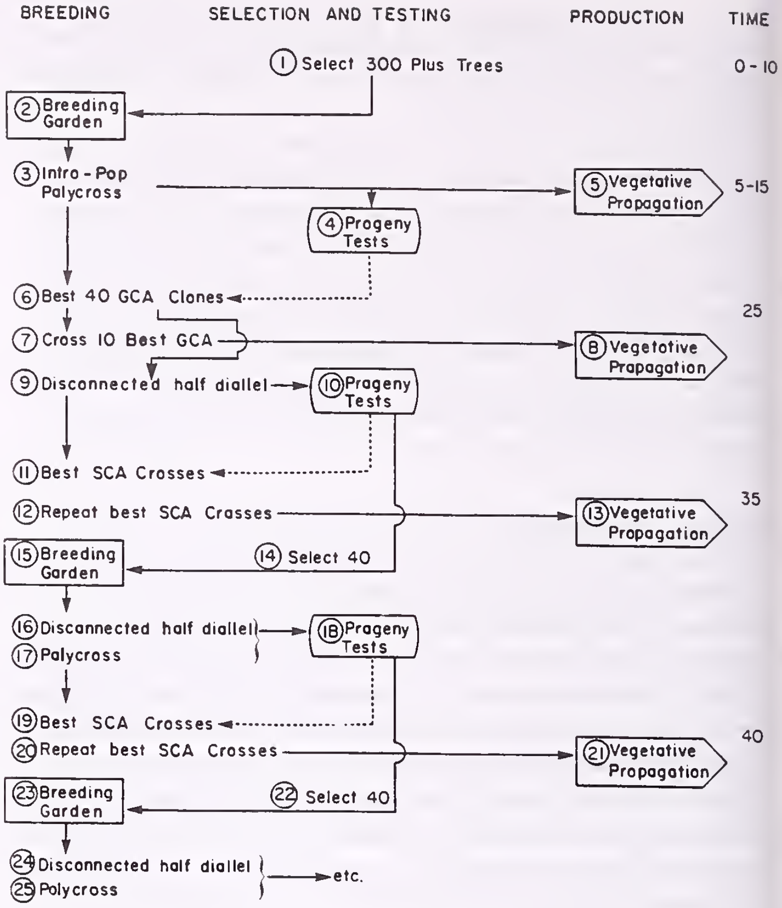

Figure 3—Flow chart for alternative tamarack improvement strategy; mass production using vegetative propagation (from Fowler 1986).

The preceding breeding strategy is designed to capture only general combining ability. There is evidence to suggest that specific combining ability may be important in tamarack (Park and Fowler 1982). Figure 3 outlines a strategy to capture both specific and general combining ability using vegetative propagation to mass produce improved materials.

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Distribution and Management of Japanese Larch

Fukio Takei

Abstract—Japanese larch is native to Japan but has been planted extensively in other parts of the world because of its desirable growth, form, and beauty. Although it has a relatively limited natural range, it has been planted in some areas of Japan for over 150 years. It is shade intolerant and commonly grows with a variety of other tree species. Although insects, disease, and small mammals can cause problems in some areas, Japanese larch is relatively resistant to them.

Japanese larch (*Larix leptolepis*) is a species native to Japan. Its common name in Japan is Karamatsu. The term Japanese larch will be used interchangeably in this paper with Karamatsu. Since the late 19th century, Japanese larch has been successfully transplanted to many European countries, in particular Germany, Holland, Denmark, and England (Schober 1953). Japanese larch has proven to be disease resistant and has a fast growth rate and good stem form compared to its European counterparts.

In Japan, Japanese larch forestation started in the early 1840's in the inland areas of the highland region in Central Japan. In the 1890's it spread widely to the subfrigid zone in the northern part of the Honshu (Tohoku Region) and Hokkaido, due to its inherent cold resistance and high growth rate compared to most important planting species such as Sugi (*Cryptomeria japonica* D. Don) and Hinoki (*Chamaecyparis obtusa* S. and Z.) (Imai 1987).

According to the forestry statistics of Japan (Statistics Bureau 1985), artificial forest areas of Japanese larch are about 1.09 million ha and occupy about 11 percent of total plantation forests, compared to Sugi 4.5 million ha (44 percent) and Hinoki 2.34 million ha (23 percent), making Karamatsu one of the most important planting species in Japan.

DISTRIBUTION OF NATURAL FORESTS OF JAPANESE LARCH

Horizontal distribution of Karamatsu (fig. 1) occupies a small extent of the limited highland region of Central Japan. It is distributed among a small area, ranging from north latitude 35 to 37° to longitude 137 to 140° east.

The northern and the eastern boundary of natural distribution is Mount Umanokamiyama (1,585 m elevation), located at north latitude 38°05' and longitude 139°40' east, near Shiraishi City, at the border between Yamagata Prefecture and Fukushima Prefecture.

The southern limit of Karamatsu natural distribution is located on Mount Tenguishiyama (1,866 m elevation), in the southern parts of South Alps in Central Honshu, at north latitude 35°08'.

Mount Hakusan (2,702 m elevation) is the western boundary. Its location is longitude 136°40' east (Tatewaki and others 1965; Forest Agency 1970).

Vertical distribution of Japanese larch ranges from 900 to 2,800 m above sea level (Forest Agency 1970). Its lowest location is Mount Anzayama in Fukushima Prefecture and the highest is the south side of Mount Fuji (Hayashi 1960).

Vertical distribution of Karamatsu differs from latitude. The higher latitude causes the lower elevation distribution and smaller distribution width (fig. 2). For example, along latitude 35°, we can see larch forests at about 1,000 to 2,800 m elevation, and relatively well-established stands are in the range of 1,200 to 2,500 m. Typical stands of

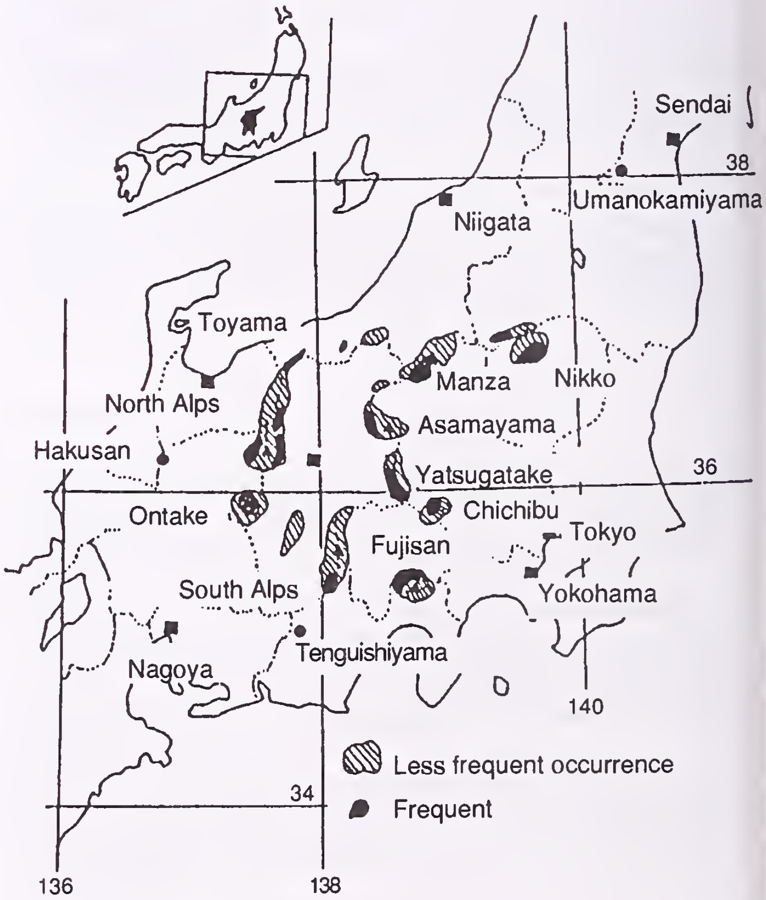

Figure 1—Horizontal distribution of Japanese larch natural forests (Hayashi 1970).

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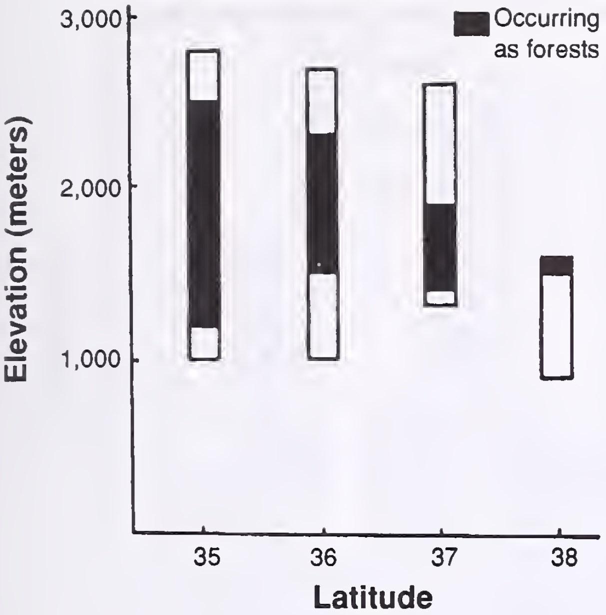

Figure 2—Vertical distribution of Japanese larch (Forest Agency 1970).

this region can be seen on the upper part (1,800 to 2,400 m) of Mount Fuji (3,776 m).

Near latitude 36°, Karamatsu stands are distributed from 1,000 to 2,700 m elevation. Beautiful forests can be seen at Mount Asamayama (1,390 to 1,500 m), Kamikochi (1,540 to 1,620 m), Mount Yatsugatake (1,720 to 1,850 m), Mount Ontakesan (1,600 to 1,650 m), and Mount Kinpuzan (1,360 to 1,750 m).

Along latitude 37°, larch forests can be seen in the width of 1,300 to 2,600 m. Typical stands are Nikko (1,020 to 2,320 m) and Mount Manza (1,800 m).

NATURAL FORESTS AREAS AND STAND VOLUMES

Asada (1981) estimated natural forest areas and their stand volume of Japanese larch at about 6,900 ha and 1.132 million m³, respectively (table 1).

Mine (1954) reported natural forest areas of Karamatsu, about 5,911 ha. According to table 1, South Alps region has the largest areas of Karamatsu, with about 2,300 ha (33 percent of total area). Next, Mount Fuji with about 1,300 ha (20 percent), Yatsugatake with about 1,000 ha (15 percent), and North Alps region with 880 ha (13 percent). For stand volume per hectare, Chichibu has the most, 205 m³/ha, the second is South Alps, with 200 m³/ha, and Ontakesan has 190 m³/ha.

Yatsugatake has the least stocking, 104 m³/ha, Asamayama has 140 m³/ha, and Nikko has 152 m³/ha.

The difference of stand stocking in each region explains the size difference of stands in terms of mean diameter breast height (d.b.h.), mean stand tree height and structural differences, stand density or area occupancy of Karamatsu in the stands.

Table 1—Natural forest area of Japanese larch (Asada 1981)

Location	Forest area		Stand volume
	Hectares	*Percent*	*m³/ha*
South Alps	2,306	33	200.4
Fujisan	1,357	20	139.6
Yatugatake	998	15	104.5
North Alps	877	13	164.2
Chichibu	471	7	205.5
Nikko	412	6	152.3
Asamayama	397	5	140.8
Ontake	84	1	191.0
Total	6,902	100	

STAND COMPOSITION

Stand Age Class Structure

Asaymayama has a large amount of young stands, about 84 percent of total stands in this region. Yatsugatake is second with about 61 percent (fig. 3). In contrast, South Alps has a large number of old stands, about 51 percent of total stands. North Alps has a few young stands, and Mount Fuji has rare old forests.

Mean Diameter and Mean Tree Height

Figure 4 shows the size of Karamatsu natural forests as a mean d.b.h. and mean tree height of some sample stands in each region. According to this figure, Kamikochi forest has the largest, followed by Ontakesan and Nikko. Asaymayama and Mount Fuji have small stands (Forest Agency 1970).

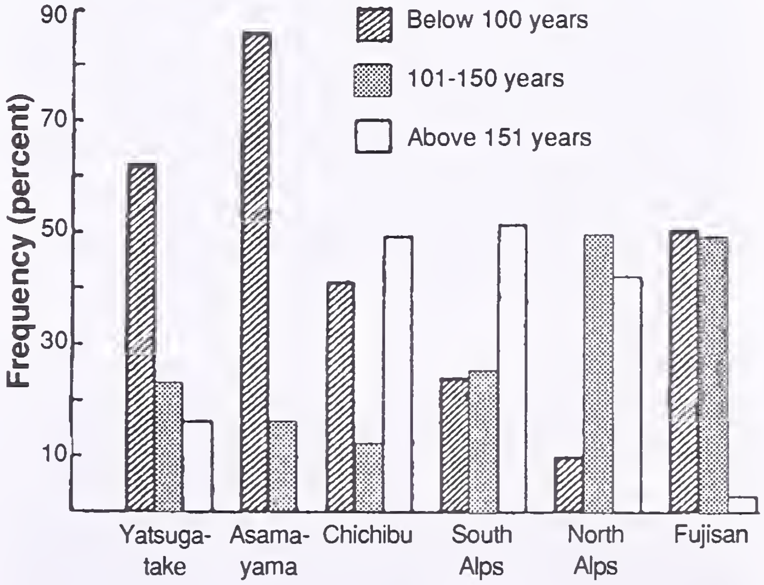

Figure 3—Occurrence ratio of age class stands in natural larch forests (Asada 1981).

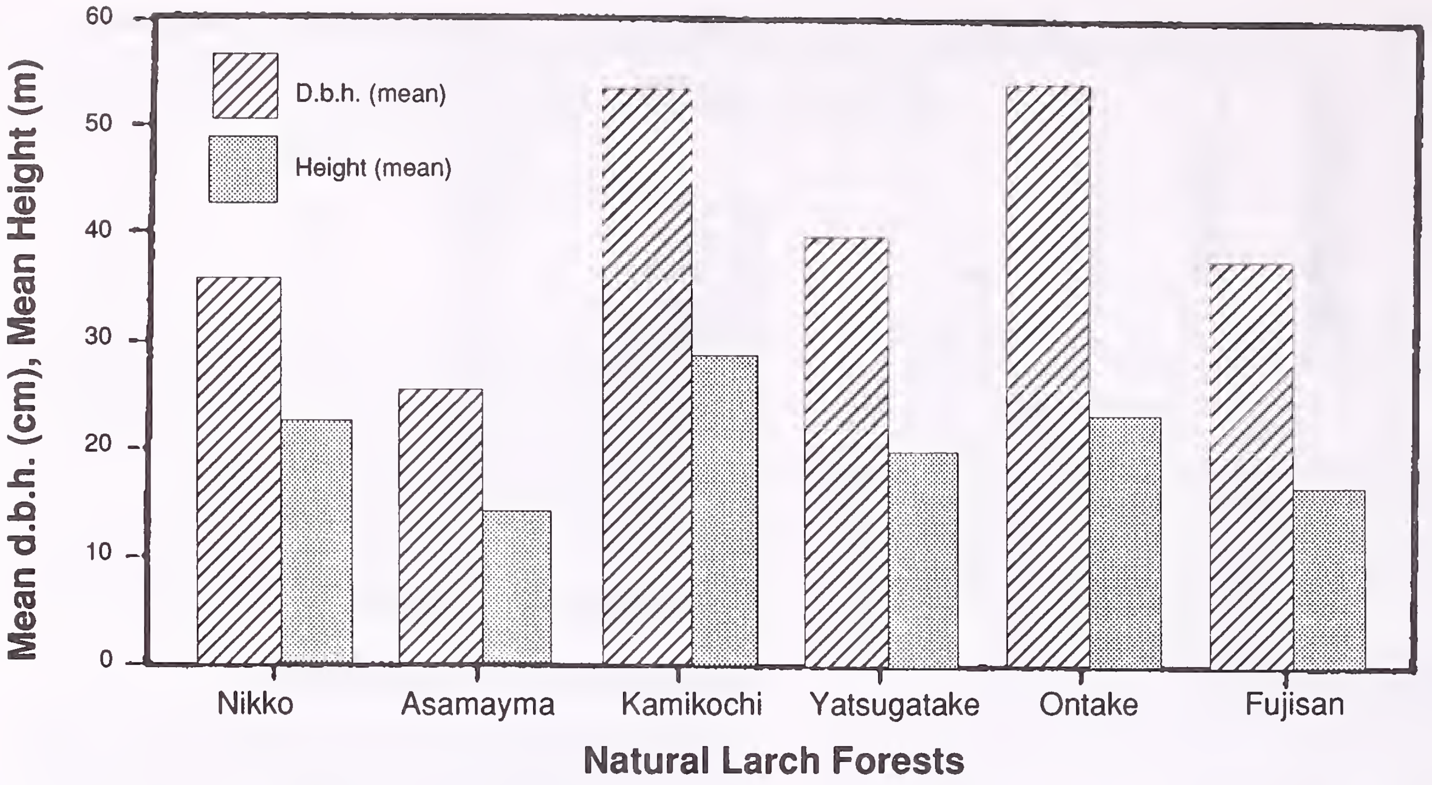

Figure 4—Stand composition of natural larch forests (Asada 1981).

Area Occupancy Ratios and Mixed Tree Species

Area occupancy ratios of larch in some sample stands in each region were classified into three categories: large (more than 50 percent of occupancy ratios), middle (20 to 49 percent), and small (below 19 percent) (Asada 1981).

Karamatsu dominated in the Yatsugatake, Mount Fuji, and Asamayama stands, and showed only a small ratio of larch in the South Alps and Chichibu stands.

Japanese larch grows in admixture in some areas. For example, in Yatsugatake, hardwood species such as Mizunara (*Quercus crispula*) and Shinanoki (*Tillia japonica*) dominated. Larch stands on Mount Fuji mixed mainly with subalpine conifer trees such as Shirabe (*Abies veichii*), Kometsuga (*Tsuga diversifolia*), and Shirabe (*A. veichii*). On the bank of Azusa River in Kamikochi, Shirabe (*A. veichii*), Kometsuga (*Tsuga diversifolia*), Aomoritodomatsu (*A. mariesii*), and Tohi (*Picea jezoensis* var. *hondoensis*), and various species of *Betula* and *Ulmus* commonly occur with larch (Forest Agency 1970).

Stem Form

Stem form data gathered from some sample stands of Japanese larch in each region show that the areas of Nikko and Asamayama have a relatively large number of bent stems of larch. In contrast, larch has straight stems in the Yatsugatake and Mount Fuji areas (Forest Agency 1970) (fig. 5).

ENVIRONMENTAL CONDITIONS IN NATURAL FORESTS

Weather Conditions

The weather conditions of the region where natural forests of Japanese larch occur are generally cool and dry in summer and severely cold in winter. This region has an inland climate in which a large temperature difference can be seen throughout the growing season. Mean temperature of growing summer season (June to August) in this region is cool, 15 to 20 °C, and the winter season (December to February), during the dormancy period, has severe cold, 0 to –6 °C (Forest Agency 1970). Annual mean temperature in this region is estimated about 4 to 6 °C (fig. 6).

In this area, there is usually much rain in the summer season and little rain and dry air in winter. Precipitation in the summer season in this region is about 550 to 1,070 mm, equivalent to one-third of the annual precipitation. Winter rainfall is light (110 to 440 mm), which is about one-tenth of the total annual precipitation.

Soil, Topography, and Geology

Japanese larch generally grows in volcanic regions. It appears as a pioneer tree species on the newly built volcanic immature or landslide deposition soil. These soils are nutrient poor, but they have excellent air permeability (Forest Agency 1970; Schober 1987; Takahashi 1960; Tatewaki and others 1965).

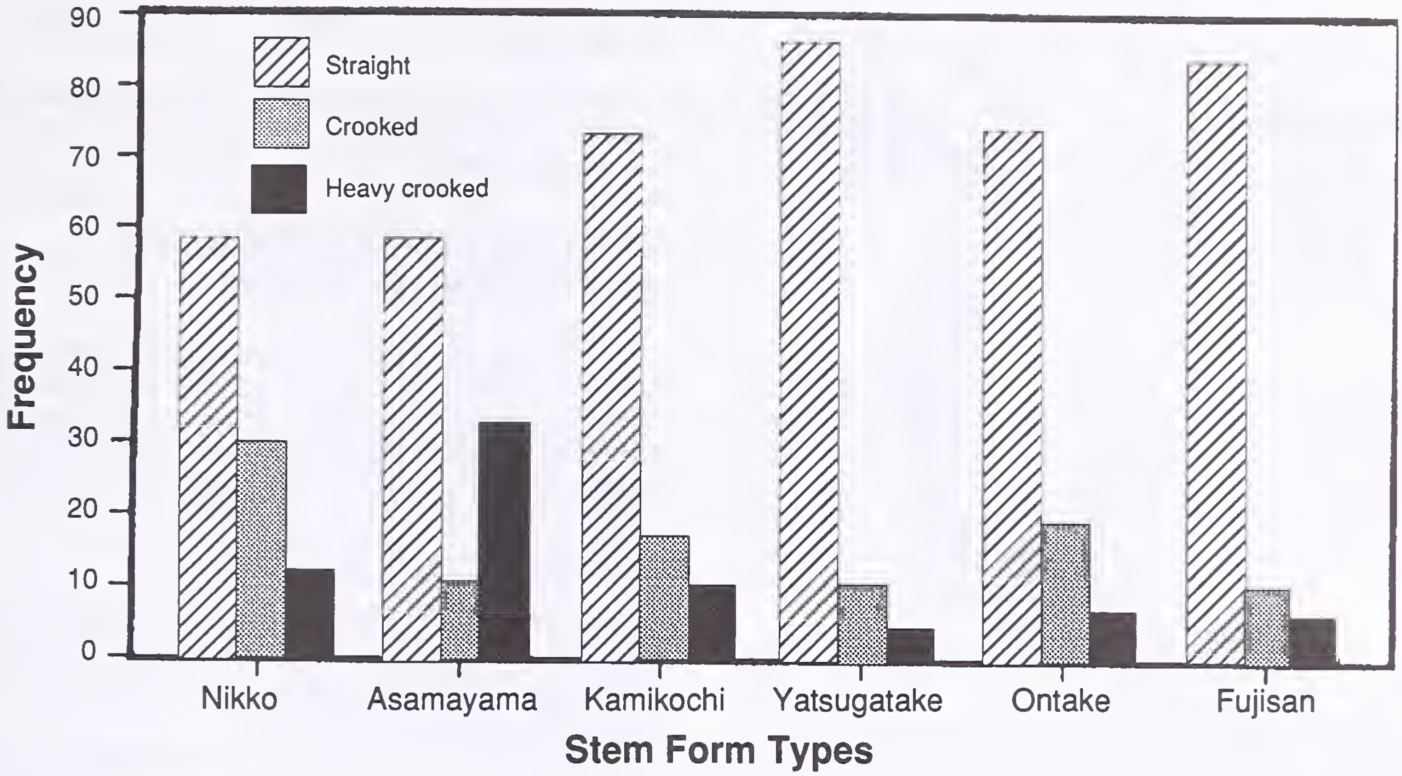

Figure 5—Occurrence ratio of stem form types in natural larch forests (Forest Agency 1970).

Karamatsu grows mainly on the gentle slopes of mountain hillsides or on relatively low ridges and sometimes on the gravel depositions on the bottom of valleys and the gravel-mixed soil of riversides.

The Mount Fuji, Asamayama, Yatsugatake, and Ontakesan areas have beautiful natural larch forests on the volcanic soil, which is composed of pyroxene andesite, andesite, or basalt.

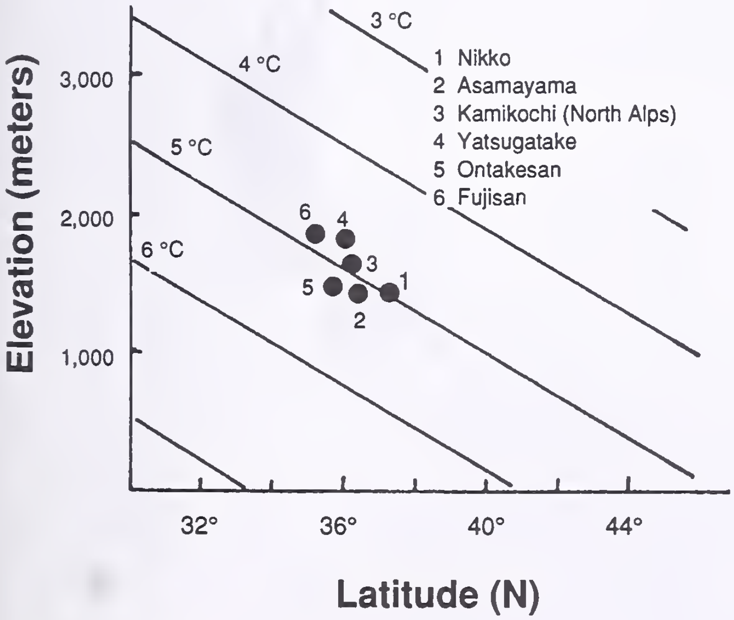

Figure 6—Relationship between elevation, latitude (north), and annual mean temperatures (Forest Agency 1970).

ARTIFICIAL FORESTS OF JAPANESE LARCH

The history of plantation forests of Japanese larch is relatively short, compared to Sugi (Matsui 1969) and Hinoki, which have been the most important planting species in Japan for a long time. The first planting of Karamatsu was made with wild seedlings at Tsumagoi Village in Gunma prefecture around 1880. In the early 1890's, artificial larch forests spread to the subfrigid zone in the northern part of Honshu and Hokkaido. A large amount of artificial forests started at Inland Central Honshu in 1880.

Sugi and Hinoki are important species that grow in relatively warm regions. However, mean annual temperature of Sugi and Hinoki natural stands is 6 to 19 °C (Mashimo 1981) and 6 to 17 °C (Sato 1971), respectively. This is a large difference when compared to Karamatsu stands where the mean annual temperature is 4 to 5 °C.

Japanese larch, which is resistant to cold, was spread to northern Honshu, Hokkaido, and the highland of the southwestern region of Honshu. The mean annual temperature of these regions (mean annual temperature below 10 °C) corresponds to the lower limit of growing temperature of Karamatsu. The upper limit of growing temperature for Karamatsu is 18 to 19 °C (Kato and Matsui 1966) (figs. 7 and 8).

REGIONAL ENVIRONMENT AND GROWTH OF ARTIFICIAL FORESTS

In recent years, there have been many studies aimed at selecting suitable sites for planting Karamatsu. Multivariate analyses have been used to elucidate the relationship between tree growth and environmental conditions.

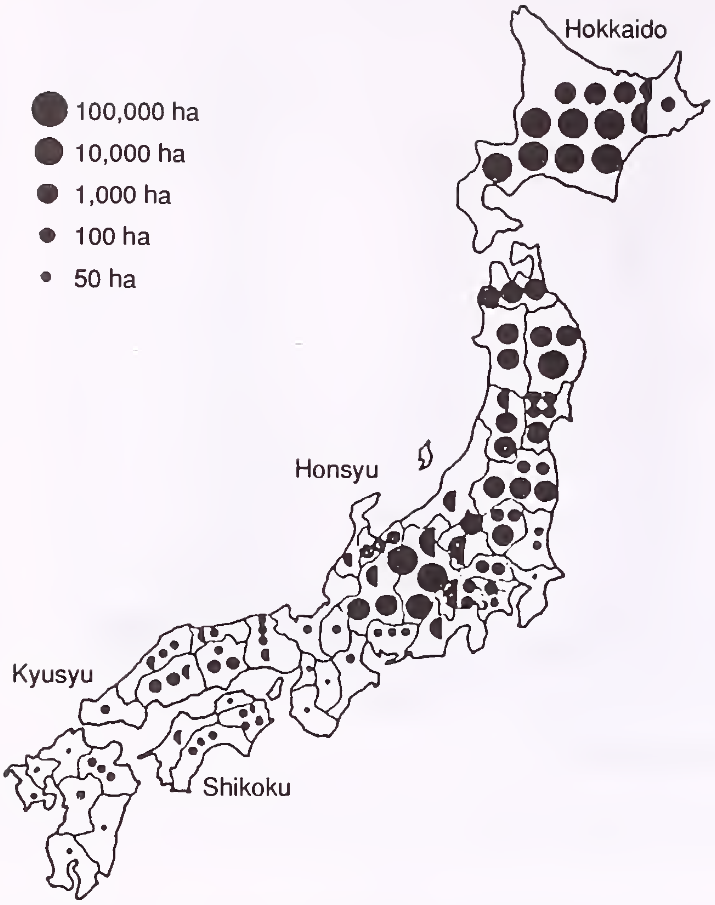

Figure 7—Expanding artificial Japanese larch forests (Mihara 1978).

Results of these analyses clarified that the environmental conditions significant to the growth of Japanese larch are mainly weather conditions, soils, topography, and geology (Kokuzawa 1978).

Weather Conditions

Weather conditions, which include many factors such as temperature, precipitation, and wind and snowfall, are the most important factors for Karamatsu growth. Elevation is also a good indicator of growth of Japanese larch (Kato and Matsui 1966). Table 2 shows the elevational borders of Japanese larch growth (Hayashi 1970).

Soils

Karamatsu grows better on slightly wet soils than on dry soils. Growth is slow on massive structure soils and compact soils. The roots of Japanese larch are biologically aerobic. Consequently, growth of Karamatsu is better on soils that are deeply aerated (Kato 1962; Kato and Matsui 1966).

Topography

Local topography is an important factor for growth of larch. It grows better on the spur than on the summit, and growth is better on concave-shaped slopes than on convex-shaped slopes. There is no relation to azimuth for Japanese larch growth.

Geology

Japanese larch grows better on slate, sandstone, and andesite than on rhyolite, quartzporphyry, granite, or limestone (Mashimo 1981).

TENDING TECHNIQUES OF ARTIFICIAL FORESTS

Artificial forest areas of Japanese larch have reached 1.09 million ha in Japan. Its age class and distribution show that young stands of Japanese larch predominate; for example, forests younger than 30 years account for 89 percent of the total artificial forests (fig. 9).

Planting Stock Numbers

Since long ago, planting numbers per unit area of Karamatsu seedlings has varied from 1,700 to 4,000 trees per hectare, depending mainly on tending practices and timber utilizations (Takei 1978).

In recent years, the decision of planting tree numbers generally depends on silvicultural costs, yarding distance, and wood quality at the time of final cut.

At present, standards for planting seedling numbers are generally 2,000 to 2,500 trees per hectare, and under present conditions, the addition of 1,000 to 1,500 trees is being considered (fig. 10).

Figure 8—Region of annual mean temperature below 10 °C (Mihara 1978).

Table 2—The border elevation of suitable larch growth in different regions

	Hokkaido	Hukushima	Saku region South	Saku region North	Nagano Kiso region	Ina region South	Ina region North
Elevation (m)	700-800 above	1,200 above	1,400 above	1,600 above	1,600 above	1,600 above	1,800 above

Thinning

Thinning practices, including the periods of first thinning, thinning intervals, and the degree of thinning, depend on the timber size and yarding distance at the time of final cut. For example, the current target of the timber size at final cut is for large diameters of 30 to 50 cm. With these diameters, the final yield is 300 to 400 trees per hectare and the final cutting age is 70 to 100 years.

Four to five thinnings are usually planned for Karamatsu stands during a 70- to 100-year rotation. But in practice today, these thinnings usually occur only once or twice in a rotation.

Figure 11 is a stand density control chart that makes it possible to determine quantitatively the relationships between stand density and stand (stem) volume and tree diameter for any given mean height (Takei 1989). These charts have found wide practical application.

Pruning

Until about 20 years ago, the timber utilization of the larch tree, which grows fast, was aimed mainly at low quality timber such as small, civil engineering wood or mine timber. The pruning of larch trees was not practiced because it was said that branches of Karamatsu have a physiological tendency to fall down on their own and make for low-quality woods. But because the utilization of larch wood has advanced and the wood industry has demanded branch-free, good quality timbers, there are now many research projects on larch pruning. These show that adventitious branches can occur on branch-free stems after severe pruning or severe thinning.

TENDING TECHNIQUES

Karamatsu is a shade-intolerant species. It invades burnt-over areas, slide areas, and other sites where the soil has been exposed, regardless of soil properties. It will even grow on dry sites. It also is resistant to cold, and its growth is fast. There are only a few other species that can be planted and grow as successfully as Japanese larch from the northern reaches of the temperate zone to the subfrigid/subalpine zone.

Poor Growth Plantations

Recently, many poorly grown and damaged stands of larch have been seen. These were planted in unsuitable environmental conditions such as poorly aerated and excessively wet soils, high-elevation cold areas, and in areas subject to strong winds.

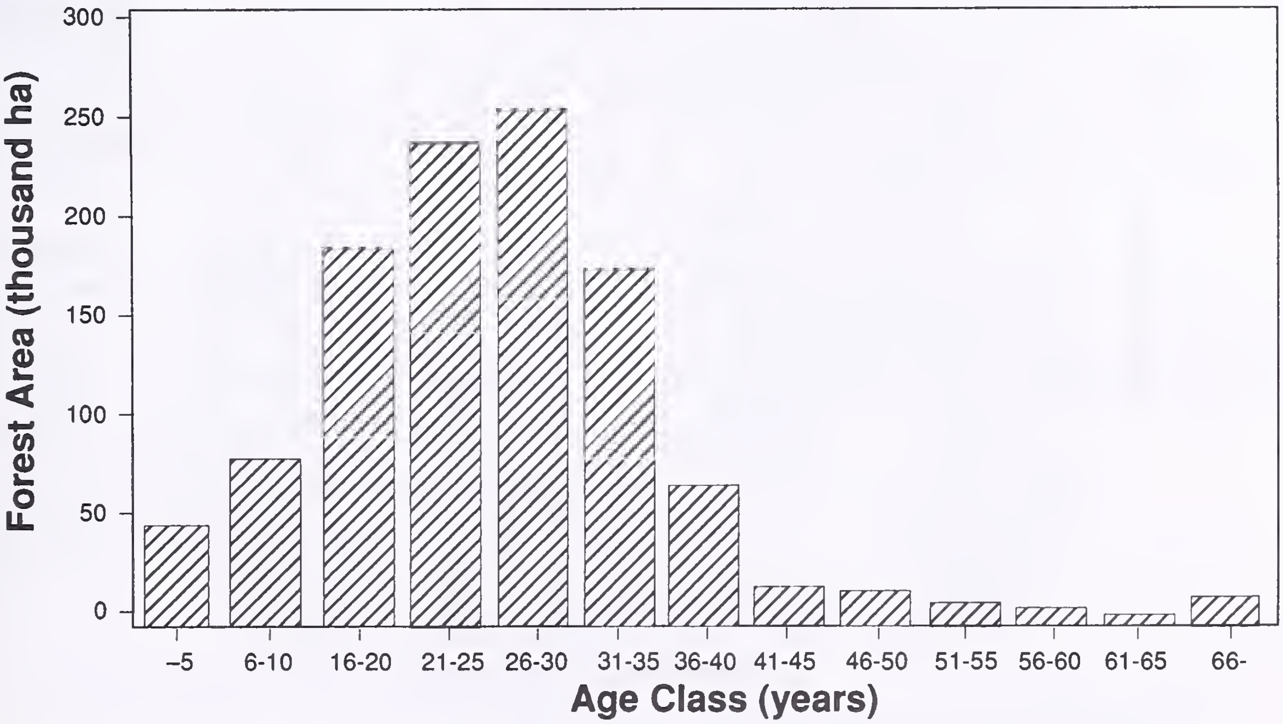

Figure 9—Age class distribution of artificial larch forests.

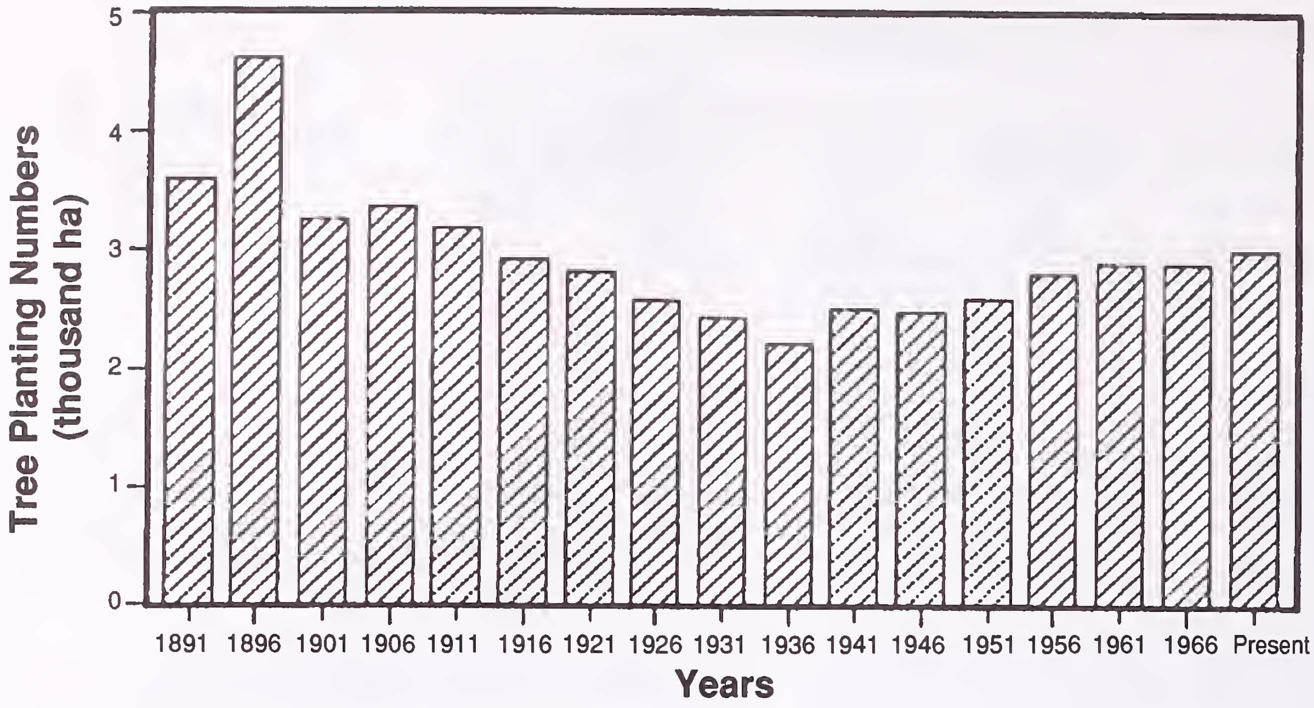

Figure 10—Tree planting numbers with changing times.

Diseases, Insects, and Mammal Damage

Karamatsu is damaged by a relatively large number of diseases and insects (Mihara 1978). The principal diseases are needle cast (*Mycosphaerella lariciIeptolepis* Ito and Sato), shoot blight (*Botryosphaeria laricina* [Sawada] Shang), and root rot (*Fomes* sp.).

Shoot blight disease infects only the current season's shoots and not the shoots from the previous year. Infected shoots are soon killed, tree crowns are deformed into broom shapes, and height growth is checked.

Studies show that the wind during the growing season must be regarded as the most important factor distributing the disease (Ito 1962; Nagano Prefecture 1974; Yokota

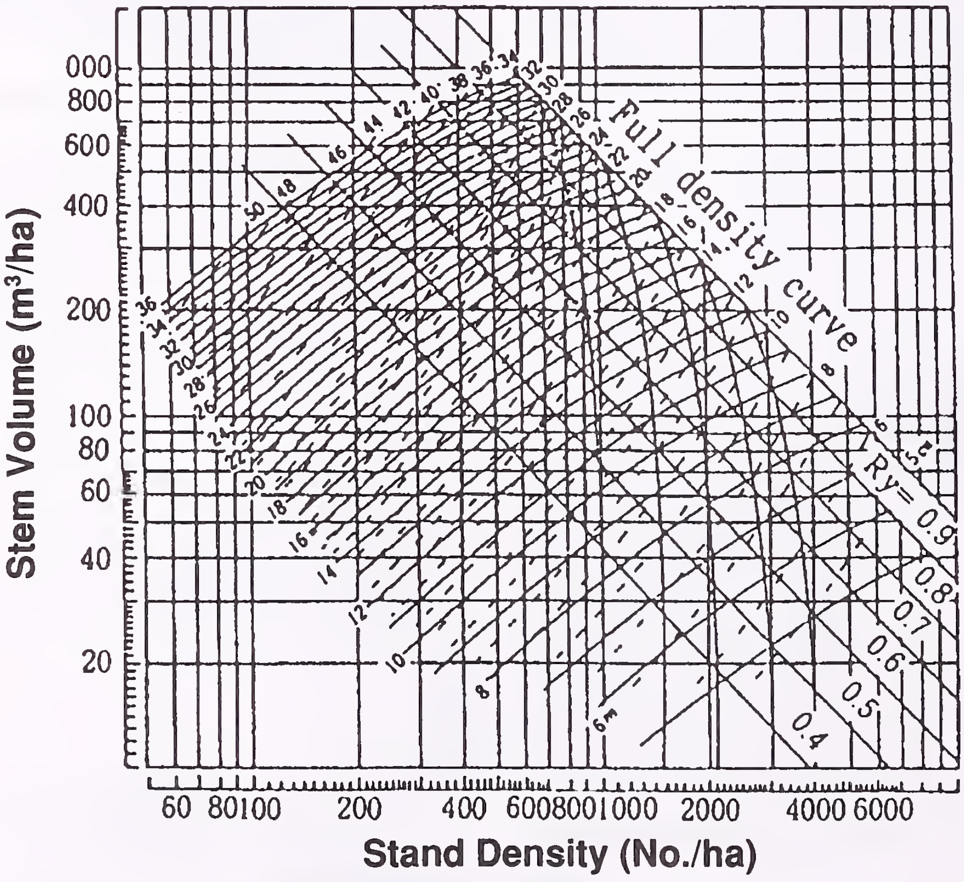

Figure 11—Stand density control chart for artificial larch forests for Nagano Region (Takei 1989).

1966). In Hokkaido, this disease has been widely distributed, especially in the southern part, since 1962. Damaged larch plantations are mainly situated near the seashore, though the disease is spreading to inner parts and eastern parts in Hokkaido.

Areas of damaged plantations amount to an estimated 7,500 ha, with 2,500 ha in northern parts of Honshu (Tohoku region). In 1973, this disease reached about 700 ha in central highland areas. Today, the intensive application of disease preventing chemicals in nurseries, the removal of infected trees from plantations, and the avoidance of planting in areas particularly vulnerable to outbreaks have resulted in no reports of new outbreaks.

Needle cast is found in all larch plantations and causes all leaves of the larch trees to fall. Root rot, which destroys larch roots and lower stems, occurs mainly on the poorly aerated, excessively wet, and massive structure soils (Ito 1962).

The main insect pests include defoliators such as needle spinners, sawflies (*Anoplonyx* sp.), and gypsy moth (*Lymantria dispar* L.).

In Hokkaido, Japanese larch plantations have been damaged by a wild mouse (*Clethrionomys rufocanus bedfordiae*) for a long time.

CONCLUSIONS

For a long time, Japanese larch plantations have been rapidly spreading from the central highlands, where many natural larch forests exist, to the northern parts of Japan, where weather is cold and dry.

Many artificial forests, which exist in different environments, suffered incredible damage due mainly to the lack of judgment concerning the environment. In light of this, we must develop useful judgment techniques about environments and must carefully make larch plantations according to the principle of "the right tree on the right site."

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Ecology and Management of Korean *Larix* spp.

Sung-cheon Hong

Abstract—Two species of *Larix* grow in Korea: *Larix gmelinii* var. *principis-ruprechtii* (Mayr) Pilger (Korean larch) and *L. olgensis* A. Henry (Manchurian larch). By the forest habitat theory, the *Larix* in Korea is not potential climax forest but is seral. South Korea has planted 30 million seedlings annually for the last 5 years, which accounts for about one-third of the plantation timber species. Stand volume attainable at 30 years for a *Larix* stand with site index 16 is 270 m³/ha with a growth of 4.3 percent.

Two species of *Larix* are distributed in the frigid forest zone of Korea. *Larix* spp. are one of the timber species with *Abies*, *Picea*, *Pinus*, *Quercus*, and *Betula* spp. in Korea. We planted 1.8 billion larch seedlings on about 600,000 ha from 1957 to 1990. I would like to report about distribution, ecology, afforestation, and management aspects of Korean *Larix* spp.

DISTRIBUTION AND ECOLOGY

Korea is a peninsula whose total area is about 220,000 km², located at the easternmost of Asia from 33°4' to 43°2' north latitude and from 124°11' to 131°52' east longitude. The forest area of Korea Peninsula covers about 16 million ha, or 73.6 percent of its total area. Meanwhile, in South Korea alone, forest area covers 6,476,000 ha, or about 65 percent of its total area (fig. 1).

Geographically, Korea Peninsula can be divided into three zones according to an isothermal line: subtropical forest region (above average annual temperature 14 °C), temperate forest zone (5 to 14 °C), and frigid forest region (under 5 °C). The temperate forest zone is divided into the south (12 to 14 °C), central (10 to 12 °C), and north temperate forest zone (5 to 10 °C). Figure 2 shows the horizontal distribution zone of Korean forests.

Larix spp. grown in Korea are *Larix olgensis* A. Henry (Manchurian larch) and *L. gmelinii* var. *principis-rupprechtii* (Mayr) Pilger (Korean larch). They are distributed in the subalpine belt of the north temperate zone and frigid region such as Mount Kumkang (above sea level 900 m), Mount Nanglym (1,900 to 2,300 m), Mount Paekdu (500 to 2,300 m), and Huchylyung (1,350 m) (fig. 1).

Some researchers classify Korean larch as *Larix olgensis* A. Henry var. *koreana* Nakai (Kim and others 1988). But its taxonomy remains to be solved in future research.

Korean larch grown in the frigid forest region is between *L. gmelinii* Rupr. and *L. principis-rupprechtii* Mayr in its morphological characteristics. *Larix gmelinii* grows in North China and East Siberia at an elevation between 500 and 1,000 m. *Larix principis-rupprechtii* Mayr grows in China at an elevation between 1,800 and 3,000 m. The number of scales of Korean larch cones ranges from 25 to 40. The end of the cone scale is straight, and the bract does not expose (fig. 3).

Manchurian larch, which grows in the region of Mount Paekdu and North China at elevations between 500 and 1,800 m, has 16 to 40 cone scales. One-year-old branches are covered with red or brown hairs (Zheng 1983).

Korean larch and Manchurian larch are tall, deciduous, shallow-rooted, and shade-intolerant like western larch and Siberian larch (Arno and Hammerly 1987; Borodina 1966). Diameter at breast height can reach about 1 m. Along with *Betula* spp. they are pioneer species after forest fire. They first bear seeds around 15 years. There is a good harvest every 2 to 3 years. Korean larch forms pure forest or mixed forest with evergreen coniferous species such as *Pinus densiflora*, *Abies holophylla*, *Pinus koraiensis*, and *A. nephrolepis,* as well as hardwood species such as *Betula platyphylla* var. *japonica*, *B. ermanii*, *Populus davidiana,* and *P. maximowiczii.* Represented in the shrub layer and herb layer are *Rhododendron parvifoliam*, *Vaccinium ulibioxum*, *Styrax obassia*, *Alnus maximowiczii*, *Magnolia sieboldii*, *Rhododendron mucronulatum*, *Acer pseudo-sieboldianum*, *Syringa reticulata* var. *mandshurica*, *Quercus mongolica*, *Sorbus commixta* and *Lindera obtusiloba* (Lee 1976).

A phytosociology study (Kim 1992) reported *L. olegensis* community on the north slope of Mount Paekdu at elevations between 700 and 1,800 m. Manchurian larch is the dominant tree layer of this community. *Picea jejoensis*, *A. nephrolepis*, *B. ermanii,* and *B. platyphylla* var. *japonica* compose the subtree layer in this community. *Rhododendron aureum*, *Juniperus communis* var. *montana*, *Clintonia udensis*, *Vaccinium vitis-idea*, *Linnaea borealis*, and other species are represented in the shrub and herb layer.

Larix olegensis-Betula ermanii community is also reported as a result of ordination using TWINSPAN (Two-Way INdicator SPecies and ANalysis) and DCCA (Detrended Canonial Correspondence Analysis) (Song 1992). It has been suggested that temperature determines the distribution of Manchurian larch (Song 1992). However, my results (Hong 1989) and the concept of Forest Habitat Type Classification (Pfister and others 1977) suggest that Manchurian larch is not a potential climax forest but is instead a seral forest. Forest fire and artificial

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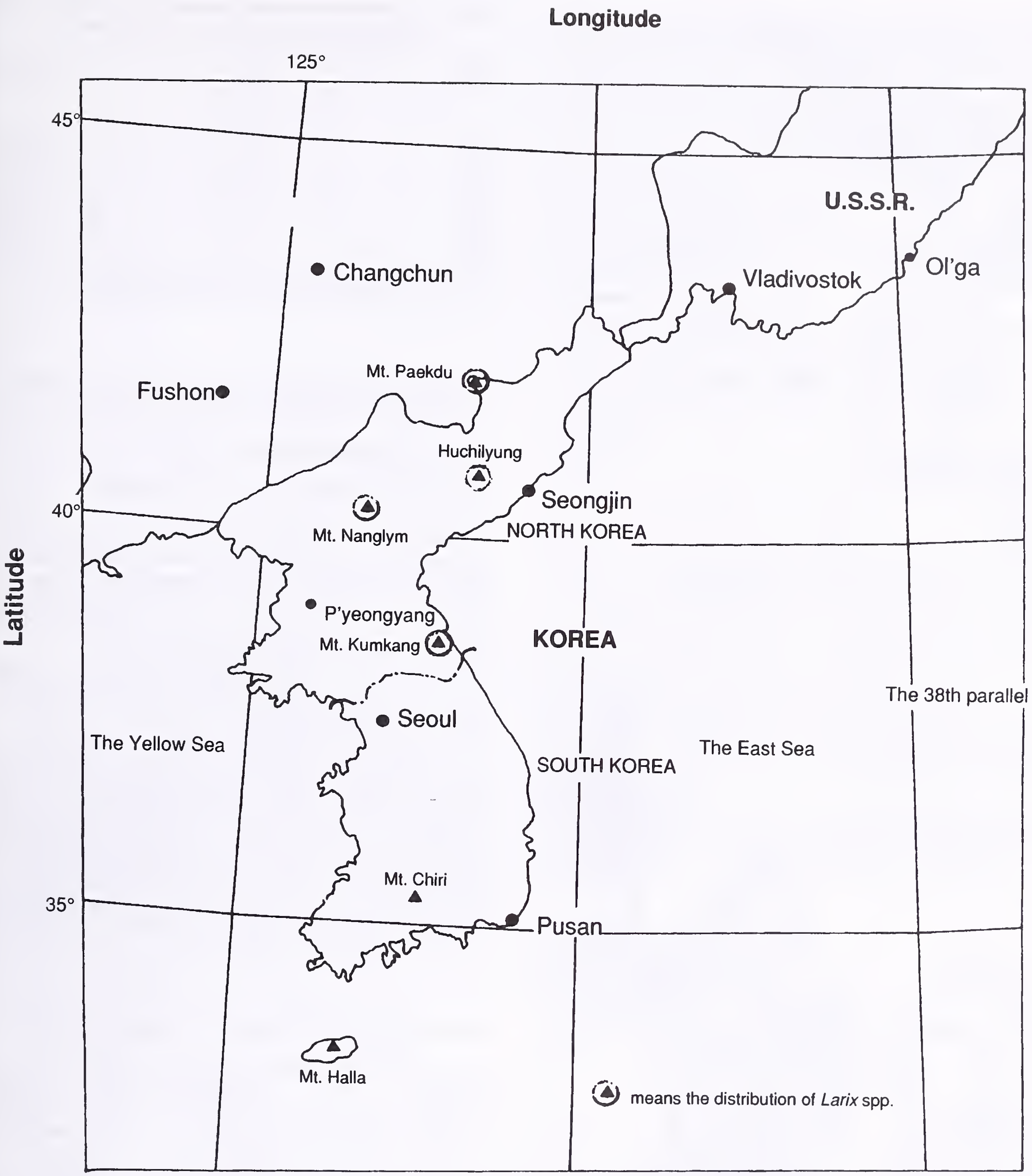

Figure 1—Distribution of *Larix* spp. in Korea (Goode's World Atlas 1982; Forestry Administration, Republic of Korea 1981).

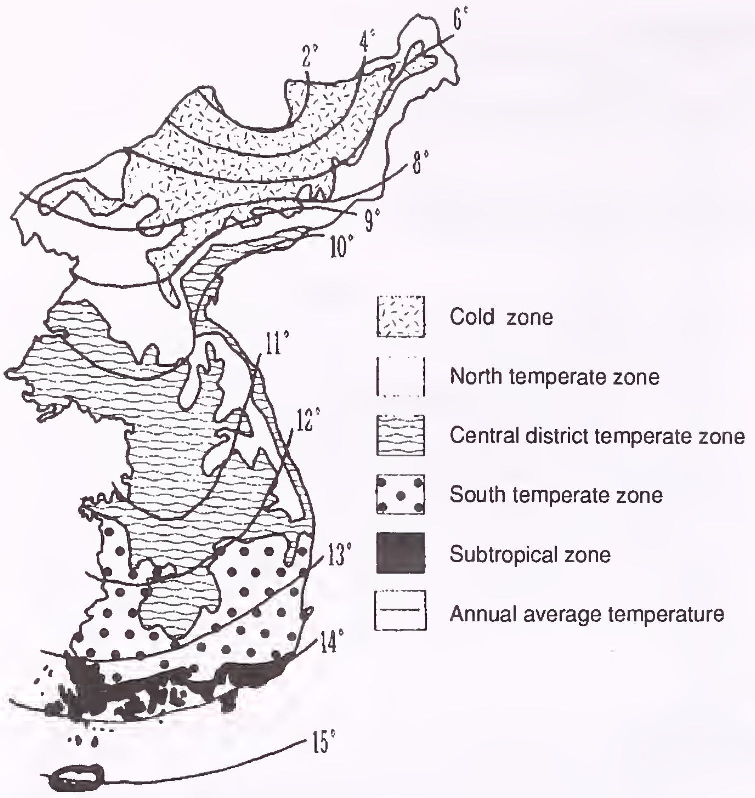

Figure 2—The horizontal distribution of Korean forest (Forestry Administration,Republic of Korea 1981).

Figure 3—Cones of (a) *Larix gmelinii* var. *principis-rupprechtii* (Lee 1976) and (b) *Larix olgensis* (Zheng 1983).

Table 1—Reforestation accomplishment of larch from 1985 to 1990. Unit: area—hectares; number—1,000 stocks[1]

Year	Area	Stocks
	Hectares	
1985	14,084	42,208
1986	11,547	36,011
1987	11,939	36,108
1988	7,416	23,042
1989	4,608	13,889
1990	1,136	3,408

[1] Source: Forestry Administration, Republic of Korea (1991).

behaviors such as logging may have had a great influence on the present distribution of Manchurian larch.

AFFORESTATION AND MANAGEMENT CHARACTER

South Korea started afforestation of *Larix* spp. in the early 1900's. Afforestation on a large scale was started in 1957. We planted 1.8 billion larch seedlings on about 600,000 ha from 1957 to 1990. This number of larch seedlings accounts for about 15 to 16 percent of total seedlings planted during the same period (11.4 billion).

Table 1 shows the areas and the number of larch seedlings planted from 1985 to 1990. Afforestation of larch will continue in the future.

We plant 2- and 3-year-old seedlings at a density of about 3,000 per ha. Intermediate treatments such as fertilization, brush cleaning, pruning, and thinning are carefully followed. Thinning is practiced after about 13, 18, and 26 years of afforestation to improve diameter growth and quality of the lumber. As a thinning method, optimum distance between trees is sometimes adopted. Table 2 shows the remaining number of trees after thinning depending on diameter class.

Table 2—Remaining number of trees after thinning by diameter class[1]

Diameter class	Number of trees	Tree distance
cm	*Per hectare*	*m*
8	2,189	2.1
10	1,782	2.4
12	1,487	2.6
14	1,260	2.8
16	1,090	3.0
18	966	3.2
20	879	3.4
22	791	3.6
24	746	3.7
26	700	3.8
28	663	3.9

[1] Source: Forestry Administration, Republic of Korea (1981).

Table 3—Larch round log price by years[1]

Year	Price in dollars/m^3
1983	81
1984	98
1985	97
1986	97
1987	92
1988	102
1989	112
1990	102

[1] Source: Forestry Administration, Republic of Korea (1991).

Recently, intermediate treatments after afforestation have not been practiced because of high labor wages and low prices of thinning wood. Table 3 shows larch wood price from 1983 to 1990.

The site index of Korean larch (the average height of dominant trees in 20 years) is divided into classes of 10, 12, 14, 16, 18, and 20 m on the basis of the classification curve and classification table. Figure 4 shows the classification curve for site indices of larch. Table 4 shows the site index of larch.

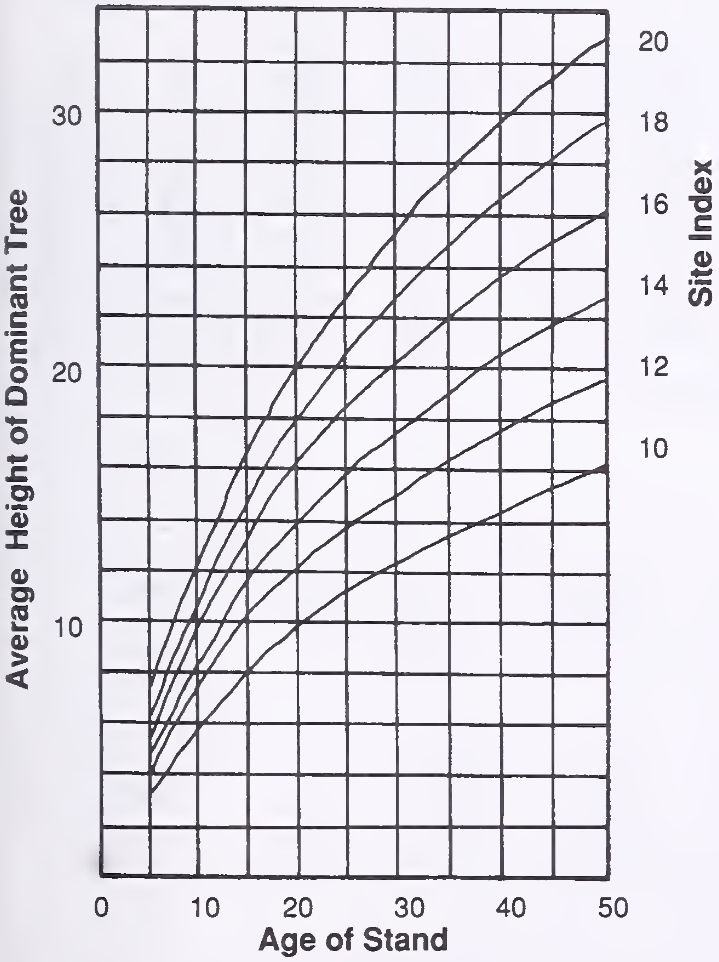

Figure 4—Classification curve of site index in reforestation site of *Larix* spp. (Forestry Adminrationn, Republic of Korea 1981).

In figure 4 and table 4, we find that the volume of larch varies according to the site index. As an example, the volume and height growth of a 30-year-old stand on site index 20 is almost twice as much as those on site index 10. Hence, when we afforest larch, the site quality is one of the most important factors to be considered. Table 5 shows two parts of the yield table of a larch stand, with the older the stand the lower the rate of growth.

In the afforestation area, major diseases are *Mycosphaerella larici-leptolepis* Ito et Sato (a kind of needle cast), *Guignardea laricina* (Swada) Yamamoto et Ito (a kind of shoot blight), and others, but they are not serious.

Diseases occurring in the nursery include *Rhizoctonia solani*, *Fusarium oxysporum*, *Pythium debaryanum*, *Cylindrocladium scoparium* (a kind of damping off), and *Pratylenchus penetrans* (Cobb) Chitwood et Oteifa (a kind of root lesion nematode disease) (Forestry Research Institute 1991).

South Korea has enforced the afforestation of its forest land by means of the powerful afforestation policy and erosion control policy. However, about 80 percent of forest land is occupied by young stands of under 30 years. The average stock volume per hectare is no more than 38.32 m^3 of wood.

Therefore, the domestic timber supply accounts for only 15 percent of Korea's total timber consumption. The remaining 85 percent of timber consumed is imported from various countries. It amounts to $1 billion. Table 6 shows the volume of imported larch wood. With the development of processing technology for larch wood, our import of larch wood may increase. Imported larch wood is used for manufacturing of flooring, boards, building materials, and panels.

Success of Korean larch management in the coming century may heavily depend on the future development of processing technology and reasonable prices for larch wood.

Table 4—The index of site quality of larch[1]

Years of age of stand	Index of site quality 10	12	14	16	18	20
	Meters					
5	3.1	3.8	4.4	5.0	5.7	6.2
10	6.2	7.4	8.7	10.0	11.3	12.3
15	8.4	10.1	11.7	13.4	15.2	16.6
20	10.0	12.0	14.0	16.0	18.0	20.0
25	11.4	13.7	16.0	18.2	20.5	22.8
30	12.6	15.1	17.7	20.0	22.9	25.3
35	13.7	16.5	19.2	22.0	24.8	27.5
40	14.7	17.6	20.6	23.5	26.5	29.2
45	15.6	18.7	21.8	24.9	28.2	31.3
50	16.4	19.7	22.9	26.2	29.8	33.0

[1] Source: Forestry Administration, Republic of Korea (1981).

Table 5—Yield table of larch stand, part 1

		Final yield							
		Average			Per hectare				
Index of site quality	Years of age of stand	D.b.h.	Height	Unit volume	Number of larch	Cross-sectional area	Stem timber volume	Annual increment	Average increment
		cm	*m*	*m²*		*m²*	- - - - - - - - - - - - - -*m³*	- - - - - - - - - - - - -	- - - - - - - - - - - - -
	5	4.4	4.2	0.0047	3,000	6.63	14,146		2.83
	10	8.0	8.0	0.0197	2,101	11.72	41,426	5.46	4.14
	15	11.4	11.0	0.0519	1,538	15.81	79,822	7.68	5.32
	20	14.1	13.3	0.0999	1,219	19.45	121,758	8.39	6.09
14	25	16.7	15.3	0.1552	1,032	22.55	160,146	7.68	6.41
	30	18.7	16.8	0.2127	910	25.13	193,587	6.69	6.45
	35	20.5	18.0	0.2687	831	27.41	223,309	5.94	6.38
	40	21.9	19.0	0.3204	779	29.40	249,569	5.25	6.24
	45	23.0	19.7	0.3633	750	31.17	272,508	4.59	6.06
	50	23.9	20.3	0.3689	732	32.61	292,006	3.90	5.84

Table 5—Yield table of larch stand, part 2[1]

		Thinning yield				Final yield + thinning yield per hectare						
		Average		Per hectare								
Index of site quality	Years of age of stand	D.b.h.	Unit volume	Number	Stem timber volume	Number	Stem timber volume	Annual increment	Average increment	TY of stem timber volume per ha	Rate of TY of T.V. per ha	Rate of increment
		cm	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -	- - - *m³*	- - - - - - - - - -	- - - - - - - - - -	- - - - - - - - - -	- - -	- - - *Percent*	- - -
	5					3,000	14,146		2.83	14,146		
	10	4.0	0.0035	890	3,125	3,000	44,541	6.08	4.45	44,541	7.0	21.7
	15	6.5	0.0128	563	7,206	2,101	87,028	9.12	5.80	90,143	11.4	15.6
	20	8.6	0.0273	319	8,709	1,538	130,467	10.13	6.52	140,788	13.5	10.8
14	25	10.6	0.0474	187	8,864	1,219	169,010	9.45	6.76	188,040	14.8	7.5
	30	12.1	0.0688	122	8,394	1,032	20,.981	8.37	6.73	229,875	15.8	5.4
	35	13.5	0.0920	81	7,452	910	230,761	7.43	6.59	267,049	16.4	4.1
	40	14.6	0.1147	52	5,964	831	255,533	6.44	6.39	299,273	16.6	3.2
	45	15.5	0.1342	29	3,892	779	276,400	5.37	6.14	326,104	16.4	2.3
	50	16.2	0.1513	18	2,723	750	294,729	4.44	5.89	348,325	16.2	1.8

[1] TY: total yield; T.V.: thinning volume. Source: Forestry Administration, Republic of Korea (1981).

Table 6—Volume and price of imported larch, in lumber[1]

	1988		1989		1990		1991	
Country	Volume	Price	Volume	Price	Volume	Price	Volume	Price
	m³	*1,000$*	*m³*	*1,000$*	*m³*	*1,000$*	*m³*	*1,000$*
Japan	142	21	20	6				
America			2,134	238				
New Zealand			24	2	5,717	416		
The rest (USSR)	6,315	434	5,515	513	14,980	1,195	11,143	464
Total	6,547	455	7,693	758	20,697	1,611	11,143	464

[1] Source: Korean Customs Administration, Republic of Korea (1991).

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Larix lyallii: Colonist of Tree-Line and Talus Sites

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Abstract—Alpine larch (*Larix lyallii*) is confined to certain high-mountain ranges of the inland Pacific Northwest in the United States and Canada, where it inhabits cold, rocky subalpine sites and extends upslope to form the timberline. But occasionally alpine larch extends sufficiently low enough to occur with *L. occidentalis*, and they hybridize. Alpine larch has essentially no commercial value but is an important component of diversity. The species provides watershed protection and wildlife habitat and is biologically intriguing and exceptionally picturesque.

Larix lyallii Parl.—known as alpine, subalpine, or Lyall larch—often extends higher up on cool exposures than any other tree, occupying what would otherwise be an alpine tundra habitat. It also forms pure stands on high-elevation boulder piles or coarse talus sites that have no visible finer substrate materials. Alpine larch requires a reliable supply of moisture throughout the brief growing season. Thus, in the drier portions of its range, this species is largely restricted to north-facing slopes and glacial cirque basins. Its distribution is positively correlated with acidic rock types such as granite and quartzite; it is usually absent from basic rocks, such as limestone. Growing on infertile rocklands in a cold, snowy, and windy environment, this species usually remains small and stunted, but in wind-sheltered basins it sometimes grows large. Much of the following description is condensed from Arno (1990), but some new information on reproduction, hybridization, and phenology is included.

NATIVE RANGE

Alpine larch occupies a 195-km long stretch of the northern Cascade Mountains in Washington and southernmost British Columbia. In the Rocky Mountains it extends about 675 km from central Idaho to Banff National Park, AB. The two distributions are separated at their closest points by 200 km in southern British Columbia. This and smaller gaps in the species' distribution generally coincide with an absence of suitable high-mountain habitat. Throughout its range, however, alpine larch is abundant only locally, unlike its widespread evergreen associates subalpine fir (*Abies lasiocarpa*), whitebark pine (*Pinus albicaulis*), and Engelmann spruce (*Picea engelmannii*).

In the Rocky Mountains alpine larch extends from the Salmon River Mountains of central Idaho, latitude 45°30' N. northward to latitude 51°36' N. several kilometers past Lake Louise in Banff National Park, AB. (A fossil larch, probably of this species, was growing about A.D. 1000 to 1250 near the Athabasca Glacier, Columbia Icefield, 90 km northwest of today's northernmost known isolated alpine larch trees [Luckman 1986].) Within this distribution, alpine larch is common in the highest areas of the Bitterroot, Anaconda-Pintler, Whitefish, and Cabinet Ranges of western Montana. It is also found in lesser amounts atop numerous other ranges and peaks in western Montana and northern Idaho (Arno and Habeck 1972). In British Columbia and Alberta, alpine larch is common along the Continental Divide and adjacent ranges and in the Purcell and southern Selkirk Ranges.

In the Cascade Range alpine larch is found principally east of the Cascade Divide and extends from the Wenatchee Mountains (47°25' N.) in central Washington northward to about 21 km inside British Columbia (49°12' N.) Within this limited distribution the species is locally abundant in the Wenatchee, Chelan, and Okanogan Ranges. Arno (these proceedings) provides a detailed range map and discusses factors associated with the species' range limits.

CLIMATE

Alpine larch grows in a cold, snowy, and generally moist climate. The cool growing season, as defined by mean temperatures of more than 6 °C (Baker 1944), lasts about 90 days, and occasional frosts and snowfalls occur during the summer. July mean temperatures range from about 9 to 14 °C. January mean temperatures range from about –14 °C in Alberta to –7 °C in the northern Cascades.

Mean annual precipitation for most alpine larch sites is between 800 and 1,900 mm, the larger amount being more prevalent near the crest of the Cascades. About 75 percent of this precipitation is snow and sleet. In April or May, snowpack typically reaches a maximum depth averaging about 2 m in stands near the Continental Divide and 3 m farther west. The snowpack does not melt away in most stands until early July. Average annual snowfall is probably about 1,000 cm in most stands west of the Continental Divide.

The inland Pacific Northwest often has a droughty period for a few weeks in late summer. Although this drought effect is minor in most alpine larch sites, dry surface soils

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Figure 1—Alpine larch on a snowy, rocky site at the base of a northfacing cliff.

probably prevent seedling establishment in some years. Summer drought may be a factor limiting the species' southern extension (Arno, these proceedings). Northward in the Canadian Rockies, summer precipitation is greater.

Most alpine larch stands annually experience winds reaching hurricane velocity, 117 km/h or more, during thunderstorms or during the passage of frontal systems.

SOILS AND TOPOGRAPHY

Although soil development in alpine larch stands varies, most soils are immature. Generally alpine larch sites have undergone intense alpine glaciation during the Pleistocene and have been deglaciated for less than 12,000 years. Chemical weathering is retarded by the short, cool summer season. Also, nitrogen-fixing and other microbiotic activity that might enrich the soil are apparently restricted by low soil temperatures and high acidity.

Throughout its distribution, alpine larch commonly grows on slopes covered with granite or quartzite talus (boulders) that have not been previously occupied by vascular plants. The species also grows in cracks in massive bedrock. On sites that have appreciable soil development or fine material (including recent moraines), the soils are still rocky and immature.

Throughout the range of alpine larch, pH values were found to be acidic, ranging from 3.9 to 5.7 in the mineral soil (B horizon) (Arno 1970). Such strongly acid, shallow, rocky, and cold soils are extremely infertile. The species grows on several types of geologic substrates but has an affinity for acidic rock types; it is most abundant on granitic and quartzite substrates and absent or scarce on nearby limestone or dolomite (Arno and Habeck 1972; Richards 1981).

Alpine larch achieves its best growth in high cirque basins and near the base of talus slopes where the soils are kept moist through the summer by aerated seep water (fig. 1). It can also tolerate boggy wet-meadow sites having acidic organic soils. The species is most abundant on cool, north-facing slopes and high basins where it forms the uppermost band of forest (fig. 2). It also covers broad ridgetops and grows locally under relatively moist soil conditions on south-facing slopes. In the Canadian Rockies, where summer rainfall is more abundant, it is often found in the timberline zone on south slopes.

In the Montana Bitterroot Range, alpine larch is abundant above 2,290 m on northern exposures. It extends lowest on north-facing talus slopes, free from other competing conifers. But, even when moist, open, boulder-covered slopes extend down the mountainsides to the 1,370-m canyon bottoms, alpine larch rarely colonizes them below 1,980 m.

In the Anaconda-Pintler Range of southwestern Montana, alpine larch forms a narrow band between elevations of about 2,560 and 2,800 m. Northward in the Rockies, the elevation of its timberlines decreases gradually. Stands in northwestern Montana, Alberta, and southeastern British Columbia are generally found between 1,980 and 2,380 m and in the northern Cascades, between 1,830 and 2,290 m.

ECOLOGICAL RELATIONSHIPS

Alpine larch grows in pure stands and also in association with whitebark pine, subalpine fir, and Engelmann spruce near their upper limits. Near the crest of the Cascades, alpine larch is often associated with mountain hemlock (*Tsuga mertensiana*) and subalpine fir.

Four species dominate the undergrowth of most alpine larch stands throughout the Pacific Northwest: grouse whortleberry (*Vaccinium scoparium*), smooth woodrush (*Luzula hitchcockii*), mountain arnica (*Arnica latifolia*), and red mountain heath (*Phyllodoce empetriformis*) (Arno

Figure 2—Alpine larch on talus in a high basin (2,530 m elevation), on Lolo Peak, near Missoula, MT.

1970). But undergrowth beneath larch stands on bogs, recent moraines, alpine tundra, or rockpile sites is often dominated by a variety of other species. Often shrublike (krummholz) subalpine fir and whitebark pine form an undergrowth layer beneath the larch on relatively cold or wind-exposed sites.

Alpine larch is the most shade-intolerant conifer growing at these high-elevation sites and is classed as very intolerant. Its evergreen associates attain their best development in forests below the lower limits of larch. On the better sites where alpine larch grows, subalpine fir is the potential climax dominant and Engelmann spruce often attains large size. Whitebark pine is most abundant on warm exposures and thus tends to complement rather than compete with larch (Arno and Habeck 1972).

Because alpine larch foliage requires higher light intensities than its evergreen associates to maintain active growth through photosynthesis (Richards 1981; Richards and Bliss 1986), it is unable to compete with a vigorous growth of evergreens. Instead, alpine larch owes its existence to its superior hardiness, especially on cool exposures. At the highest elevations alpine larch fills a vacant niche and represents the potential climax. The larch's ability to grow at higher elevations than evergreen conifers on certain sites is partly related to its superior resistance to winter desiccation—dehydration of foliage during warm, sunny periods when the roots are still frozen or chilled (Richards 1981; Richards and Bliss 1986). Winter desiccation in conjunction with lack of summer warmth are evidently primary factors limiting the ascent of tree growth on high mountains (Arno and Hammerly 1984; Tranquillini 1979). Above the limit of trees, the growing season is so short that new growth cannot adequately harden-off, or form a fully developed cuticle, and thus it succumbs to desiccation in winter.

Alpine larch is less vulnerable to winter desiccation than its associated conifers because its leaves are deciduous and its buds are woody and protected (Arno 1970; Richards 1981). Thus, there is little tendency for larch to grow in a shrubby or krummholz form, unlike its evergreen associates. Its deciduous foliage requires a large amount of moisture throughout the summer compared to the evergreens; consequently, it occupies relatively moist sites. Near the upper limit of evergreen conifers, severe climatic conditions allow alpine larch to share climax status with subalpine fir, Engelmann spruce, and whitebark pine. These evergreens often develop in the shelter of a large "patriarch" larch, sometimes growing up through the larch crown as if it were a trellis.

LIFE HISTORY

Cone Initiation and Development—Alpine larch is monoecious; male and female strobili (flowers) are borne separately on short, woody spur shoots scattered among the leaf-bearing spur shoots. Strobili are normally monosporangiate. Buds producing the strobili begin to swell by the end of May, and the wind-dispersed pollen is shed from the small yellowish male strobili in June when there are still several feet of snow on the ground in most stands (Arno 1970; Richards 1981). Female strobili develop into purplish cones 4 to 5 cm long in September. The importance of factors limiting pollination, fertilization, and seed development is unknown.

Seed Production and Dissemination—Seed production in alpine larch has not been well studied, and current knowledge is based mostly on anecdotal information. Arno and Habeck (1972) concluded that seed crops are sporadic and may be dependent on favorable temperatures during cone development. Carlson (1990) found that early in their development, in late May and June, the seed and pollen cones can withstand temperatures of –10 °C and continue to produce viable seed. During 1964 to 1966 and 1989 to 1992, seed and pollen cone production was ubiquitous on Carlton Ridge near Missoula, MT, indicating that given favorable spring weather, pollen and seed crops can occur in successive years. The limits of "favorable" weather are not known, but it seems likely that alpine larch cones can endure weather that would damage cone buds of many other species, including western larch (Schmidt and Shearer 1990). The possible influence of other factors on cone production is unknown. Some of these possible influences include insects, diseases, and weather and growing conditions the previous year.

Buds that produce seed and pollen cones are susceptible to extremely low temperatures during winter. During the first week of February 1989 the Northern Rockies were subjected to a severe Arctic cold wave that caused widespread damage and mortality to both introduced trees and thousands of hectares of native conifers. Higher elevation weather stations in western Montana experienced minimum temperatures of –40 to –45 °C accompanied by high winds. Buds of western larch and interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) were injured or killed. In early spring Carlson (1989) collected alpine larch branches with seed and pollen cone buds. Nearly 100 percent of the collected buds were dead. The only exceptions were live buds on some unusually low crown branches that had been covered by snowdrifts. There was no seed crop that year anywhere in the Bitterroot Range, but a small crop was found farther south at Allan Mountain (see fig. 1 in Arno, these proceedings). There the Arctic front was less severe, with nearby weather stations recording minimum temperatures of about –30 °C. Similar damage was observed by Van der Kamp and Worrall (1990) in buds of several evergreen conifer species in British Columbia during the same cold wave. They did not detect damage in western larch buds. (Alpine larch buds were not observed.) In Montana, vegetative buds of western larch were not killed but were damaged; reproductive buds were killed outright (Carlson 1989).

Based on x-ray analyses, open-pollinated alpine larch seed in 1990 and 1991 were about 30 percent sound, about the same as western larch sampled during that period (Carlson 1993). Reasons for the poor seed set were not studied. More research is needed to define factors such as weather, insects, and diseases that influence seed production of alpine larch.

Phenology—Vegetative buds of alpine larch flush early, when snowpack still covers the ground, about 3 weeks before those of associated subalpine fir and spruce. Presumably the expanding alpine larch leaves have considerable resistance to frost. The onset of larch leaf expansion is associated with a threshold temperature of about 1.5 °C, in contrast to the 5-°C threshold cited for most conifers (Worrall 1993). Alpine larch also has a low heat sum requirement, about 75 degree days, which is about half that of associated subalpine fir and spruce. Observations of bud burst between 1969 and 1992 at Manning Provincial Park, BC, showed that it varied by as much as 6 weeks in May and June and was closely related to the temperature regime (Worrall 1993). In greenhouse experiments, buds burst at the same time in 24-hour days or in complete darkness, and therefore any influence of photoperiod on this process is precluded.

Between 1969 and 1992, the date of occurrence of peak autumn leaf coloration likewise was variable in late September and early October, and correlated with both date of budburst (early flush/early fall) and with temperature in the summer (high temperatures/early fall), suggesting that leaves have a fixed life span that is governed by heat sum. In theory one could use spring and summer temperature as a tool to predict the dates of fall coloration, but this fails when a severe late-summer frost damages the green leaves and they turn dull yellow brown and fail to abscise promptly.

Seedling Development—In contrast to previous work (Richards 1981, Shearer 1961), recent studies show that germination of sound alpine larch seed is not difficult to achieve (Carlson and Ballinger, these proceedings). Carlson (in press) obtained about 40 percent germination of filled alpine larch seed, about the same as western larch. Seeds were placed in leach tubes filled with a peat-based soil and covered with a thin layer (3 mm) of soil. Tubes were thoroughly wet with tap water, covered with clear polyethylene, and placed in a cold room (2 °C) for 30 days. Following the stratification, tubes were placed in a germination room with the temperature maintained at 30 °C under fluorescent lighting. Soil was kept moist with tap water. This procedure, which to some degree may emulate natural conditions, worked well in two successive years with different seed lots.

Although germinated alpine larch seedlings grow reasonably well under artificial conditions, they do not grow tall (Carlson, in press; Carlson and Ballinger, these proceedings). Seedlings attain a height of 3 to 6 cm in 4 months compared to 25 to 35 cm for western larch under the same conditions. In contrast, alpine larch root growth is prolific; the small seedlings filled the growth tubes with roots. This parallels the observations of Richards (1981) on natural seedlings at high elevations.

Alpine larch seedlings germinated under artificial conditions can be successfully outplanted to their natural environment. Carlson and Doolittle (1993) planted containerized seedlings at two locations in the Bitterroot Range south of Missoula, MT. After 1 year, mortality was less than 50 percent. Surviving seedlings had grown 2 to 5 cm in height and appeared healthy. Seedlings planted at a lower elevation, in Missoula at 975 m, did not do as well. Survival was about 25 percent after 1 year, and survivors averaged about 3 cm in height (Carlson and Ballinger, these proceedings). The key to growing this species outside its natural habitat seems to be in maintaining continuously damp soil and negligible competition.

Vegetative Reproduction—Vegetative regeneration of alpine larch does not appear to be a major factor in natural perpetuation of the species (Arno and Habeck 1972). Even where the species assumes shrublike form, we have seldom observed layering. Techniques have been developed to asexually propagate *Larix* spp. from stem cuttings (Edson and others 1991; John 1979). Best success is achieved using cuttings from young trees. These techniques have not been tried with alpine larch but would be of considerable interest.

Growth—Alpine larch is a slow-growing, long-lived tree. Vigorous saplings 1.2 m tall are about 30 to 35 years of age. Dominant trees attain small to moderate dimensions, depending on site conditions, in a typical 400- to 500-year life span (table 1).

Although four to five centuries is a common life span for dominant trees, many individuals attain 700 years, and the oldest are estimated to be about 1,000 years (Arno 1970). Some could be even older (Worrall 1990). Complete ring counts are not possible on the oldest trees because of extensive heart rot. On average sites (high on north-facing slopes) the dominant trees grow 12 to 15 m in height and 30 to 61 cm diameter at breast height (d.b.h.). In most cirque basin sites on granitic or quartzite substrates, dominant trees reach 23 to 29 m tall and 61 to 124 cm d.b.h. The largest recorded alpine larch, in the Washington Cascades, is 201 cm d.b.h. and 29 m tall (American Forestry Association 1988).

When growing in pure stands near or above the limits of evergreen conifers, alpine larch attains only modest height—6 to 14 m—but forms a broad, open, irregular crown composed of long, often crooked branches. Stem analysis (Worrall, these proceedings) indicates that although annual height increments of 10 to 15 cm may occur, average annual growth is about 3 cm, not because leaders are lost, but because the leading bud frequently grows as a spur shoot, often for several consecutive years. This capability, plus the deciduous habit, may be involved in the development of an erect single-stemmed form on high-elevation sites where associated evergreen conifers exist only as low krummholz.

Alpine larch typically grows in open, parklike groves of less than 0.2 ha, interspersed with natural openings of various sizes. Stocking within the small groves is at the rate of 125 to 200 mature trees per hectare (50 to 80/acre) (Arno 1970). Productivity is low—annual yield capability about 0.7 to 1.4 m^3/ha on sites having better than average productivity. Defect is high for all species in alpine larch communities. Essentially no commercial timber harvesting has been done, even in the best developed stands, nor does any seem likely in the future.

Table 1—Average ages for dominant alpine larch of different diameters (Arno 1970)

D.b.h.		Total age Average site	Total age Very good site
cm	*Inches*	*Years*	*Years*
13	5	150	75
25	10	250	125
38	15	350	175
51	20	500	225
99	39	[1]—	450

[1]The largest diameter shown is seldom attained on "average" sites.

Rooting Habit—Alpine larch roots extend deep into fissures in the rocky substrate. Trees are well anchored by a large taproot and large lateral roots and are windfirm. The crown and trunk of old trees may break off in violent winds, but the tree itself is seldom uprooted. Richards (1981) found that alpine larch "seedlings" 16 to 25 years old and only 20 to 40 cm tall had taproots penetrating 40 to 60 cm and laterals descending 20 to 60 cm at about 45° from the horizontal. Mycorrhizal development was found on all trees, but shallow roots had a higher degree of mycorrhizal association than deep roots. *Cenococum graniforme* has been identified as an ectotrophic mycorrhiza of alpine larch (Trappe 1962).

Damaging Agents—Violent winds in alpine larch stands often damage crowns in conjunction with loads of clinging ice or wet snow. Nevertheless, this tree's deciduous habit and supple limbs make it more resistant to wind damage than its associates. Death usually occurs when advanced heart rot has so weakened the bole that high winds break off the trunk. The quinine fungus (*Fcmitopsis officinalis*), which causes brown trunk rot, produces the only conks commonly found on living trunks. This fungus is evidently the source of most heart rot. Other diseases and insects generally cause little damage to alpine larch.

Snow avalanches and snowslides are important sources of damage in many stands, but again this species is better adapted to survive these disturbances than its evergreen associates. Alpine larch poles up to 13 cm thick and 6 m tall can survive annual flattening by snowslides only to straighten again when the snow melts in summer (Arno and Habeck 1972). As larch poles exceed this size, their strong trunks and lack of dense foliage make them resistant to breakage in snowslides. Because of this superior resistance, alpine larch often occupies snowslide sites.

Because this species is usually confined to moist, rocky sites without continuous fuels, even major wind-driven fires usually cause only small patches of mortality in alpine larch stands. Larch and associated whitebark pine often survive low intensity surface fires and retain fire scars as evidence of these events. Conversely, associated subalpine fir is usually killed by any fire. In contrast, fire appears to have had a major influence on alpine larch's distribution along the east slopes of the Continental Divide range in Alberta (Arno 1970). Historically, in the area between latitudes 50°04' and 50°29' N., the east slopes burned in large stand-replacing fires that extended up into the timberline zone. In the southern portion of this area larch survived in rocky sites at timberline and then seeded into and colonized large areas of burns in the highest elevations of the subalpine fir-spruce forest at about 2,050 to 2,200 m. In contrast, along a 16-km segment in the northern portion, extensive replacement fires apparently eliminated larch. Here, larch seldom occupies talus slopes, perhaps because they are limestone.

GENETICS

The genetics of alpine larch are not well understood. We are not aware of any studies dealing specifically with geographic variation of alpine larch. Most of the genetics work has dealt with hybridization between alpine and western larch. Carlson and Blake (1969) first described natural hybrids of western and alpine larch in the Carlton Creek drainage of the Bitterroot Range south of Missoula, MT. They also produced artificial hybrids, using alpine larch as the female parent. Seedlings were produced but died the first summer due to lack of horticultural care. This work was renewed when putative hybrids were described in a sympatric area on the north face of nearby Carlton Ridge (Carlson and others 1990). Natural hybrids can be distinguished based on interpretation of summer and fall foliage color, pubescence of current-year twigs, needle luster, roughness of the bark on 3-year-old branchlets, and general tree form. Variation in combinations of these features on the putative hybrids suggested extensive introgression, implying that the hybrids produce viable seeds. Analyses of several foliar terpenes corroborated conclusions based on morphological features (Carlson and others 1991). To date, 10 locations have been discovered where alpine and western larch are sympatric. Five of these sites have been investigated, and putative hybrids have been found at each one; all are on steep north aspects in canyons of the Bitterroot Range. Additional sympatric sites may exist in the Cabinet Range of northwestern Montana (Arno 1970).

Hybrids were successfully produced through reciprocal crosses in 1990 (Carlson and Ballinger, these proceedings) and 1991 (Carlson 1993). Crossability with alpine larch as the female parent is high; 63 percent of the total seed was sound, and over 70 percent of the sound seed germinated (Carlson, in press). The cross with western larch as the female was less successful, presumably because alpine larch pollen (which develops too late for fertilization with western larch) did not preserve well when it was frozen for nearly a year before pollination. Carlson and Blake (1969) forced alpine larch pollen development with some success, but subsequent attempts have failed. Hybrid seedlings tend to be intermediate in height growth but exceed both parents in stem diameter; they are short and stocky in appearance. Hybrids will be field tested for growth and development in warm-moist and cool-moist habitats.

Putative hybrids previously described produced a bumper cone crop in 1991. Cones and seeds from hybrid trees were collected and compared to alpine and western larch cones. Hybrid seed tended to emulate western larch seed, but cones were intermediate in some features and unique in the degree of exertion of the bract tip. Seeds collected from these cones were viable, and seedlings are now growing and will be studied for growth, development, and chemistry (Carlson 1992).

That alpine and western larch can be crossed with a high degree of success perhaps implies a common ancestry that is relatively recent. Alpine larch evolved characteristics that allow it to survive in cold, moist habitats that are marginal for growth of other trees. In contrast, western larch diverged to become a rapidly growing colonist and competitor on burned sites in warmer and drier habitats. Both grow successfully at the margins of their distributions in open north-facing talus slopes at about 1,800 to 2,000 m in elevation in the Bitterroot Range, the lower limit for alpine larch and the upper limits for western larch. The search for ancestry of these two species should be directed toward studies of DNA. Some work has been done in the genus using chloroplast DNA (Szmidt and others 1987). Paternal inheritance of chloroplast DNA seems to be common in *Larix*.

SPECIAL USES

Alpine larch's primary values seem to be in watershed protection, wildlife habitat, outdoor recreation, and esthetics. The ability of this species to occupy steep north slopes and snow chutes where other trees scarcely grow suggests that it helps to stabilize snow loads and reduces the severity of avalanches (Sudworth 1908). Scientists from several countries (Switzerland, Iceland, Japan, and New Zealand) who are interested in avalanche control or forest establishment on cold sites have obtained alpine larch seed from the Forest Service, U.S. Department of Agriculture.

A diverse assemblage of birds and mammals is associated with alpine larch communities (Arno 1970). Grizzly bears often dig winter dens in alpine larch stands in Banff National Park (Vroom and others 1980). The greatest use of these habitats by most wildlife species is as summer range, when timberline vegetation is succulent, temperatures cool, and water abundant. Mountain goats, bighorn sheep, hoary marmots, pikas, mule deer, elk (wapiti), black and grizzly bears, red squirrels, and snowshoe hares are among the mammals that feed in alpine larch stands. Blue grouse apparently feed heavily on alpine larch needles. The trees provide some concealment and thermal cover in an otherwise open habitat. Woodpeckers, other cavity-nesting birds, and mammals nest in the larger, hollow-trunk trees.

The unusual hardiness of this species, its adaptations to survival in a harsh climate, on rugged topography, and in sterile substrates, make it of special interest for scientific study and for reclamation plantings on high-elevation sites. A recent dendrochronological study of alpine larch concluded that its growth rings are excellent indicators of year-to-year climatic variations, and they may prove useful for reconstructing past climates and for studies of modern climatic change (Colenutt and Luckman 1991).

The natural beauty of alpine larch stands attracts hikers and photographers. The tree's foliage, a translucent bright green in summer, turns lemon yellow and finally golden in September before it falls in October.

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Physical Ecology and Regulation Measurement for Establishment of Fast-Growing and High-Yield Larch Forests in Northeastern China

Yeh-Chu Wang

Abstract—The climate in northeastern China varies considerably because of the vast mountain ranges. *Larix gmelini* and *L. principis-rupprechtii* are spread across these ranges. Artificial and natural regeneration are needed for these species, and cultivation success has been high. Included are five measurements for larch forest management.

We know that energy is the dynamics of life, and water is the source of life. On the earth surface, there is a medium latitudinal zone in which the evaporation per year is greater than the precipitation per year. In China, the northern temperate belt and cold temperate belt are in that latitudal zone. Northern China and northeastern China are all included in the range. The climate is a humid, semihumid, semiarid, and arid pattern from east to west. The aridity in northeastern China is about from 1.5 to 3.4, and from Hebei to Shanxi Provinces, the aridity is around 3.4 to 4.6.

Meanwhile, the continentality in northeastern China is about 65 to 85 percent from south to north; in northern China about 65 to 70 percent from east to west. In this case, the climate is a heat/water synchronous activity pattern, which is good for agriculture and forestry. In the eastern range of northeastern China is the mountainous region where forests in the south and north contain deciduous conifers. The middle part is agricultural land containing the famous chernosem. The western range of northeastern China is the arid region where the south contains dune and the north has the grassland community for husbandry.

Dahurian larch (*Larix gmelini* Rupr.), with height of 30 m and diamter at breast height of 80 cm, is distributed in the Great Xingan Mountains at an altitude of 300 to 1,200 m, from the wetland (swamp) at the bottom to summit areas containing pure forest stands covering about 70 percent of the whole mountains. In the Lesser Xingan Mountain Region, the species can grow to the altitude of 400 to 600 m on gentle slopes and river sides as pure forest stands or mixed with some species of deciduous trees. The species grows well in Heilongjiang, the eastern part of Jilin Province, and the eastern and western part of Liaoning Province.

Larix olgensis Henry (*L. koreana* Nakai), the species, in the initial time of this century was a variety of *L. gmelini* (Dr. Alfred Rehder), but it has been a typical species for a long time. It is distributed along the southern bank of the Songhua River, the Wanda Mountain Range, and the Zhangguangcai Range at an altitude about 500 to 1,200 m. The species also grows in the Changbaishan Range at an altitude about 500 to 1,800 m along river land, valley, and swamp land in pure forests or mixed with some deciduous trees. The larch plantation is already up to 47 degrees north.

Larix principis-rupprechtii Mayr. had been the nomenclature as a variety of *L. gmelini* (Rehder and Wilson), but now it is a typical species and a particular tree in northern China. It grows in the high mountain region in Hebei and Shanxi Province at an altitude about 1,400 to 2,500 m and in the Wutaishan and the Xiaowutaishan Mountains, Hebei, at an altitude 1,600 to 2,800 m. In the Wutaishan and the Guanchenshan in Shanxi Province it grows up to 1,800 m in altitude in pure stands and less than 1,800 m in stands mixed with spruce, picea, poplar, and birch.

Larch mainly is a strong tolerant species to all of the environmental factors: the strong and weak radiant, the high or low air humidity, the deep or shallow soil depth, the more or less soil water content, and the different fertility conditions. Although larch adapts well, the soil must be kept porous for aeration. Thus, the larch forests always distribute along the timber line in altitude and latitude. The maximum height and diameter are, respectively, 30 m and 80 cm for *L. gmelini*, 40 m and 1 m for *L. olgensis*, and 30 m and 1 m for *L. principis-rupprechtii*. They bear small seeds with membranous wing in cones, spreading at maturity. They can germinate when the seed attaches to the mineral soil. Natural regeneration is the best way to establish forests all over the region.

The Great Xingan Mountains are in the cold temperate zone where the temperature difference is large and the coniferous forests occur with several deciduous species. The environmental capacity limits the kinds of animal and plant species, which means the food chain is simple and short. There is no succession stage and no difference between pioneer species and climax species, no lifeform in succession, and no mesophytism at all. The community just fits for itself. Thus, the young seedling can survive under the old growth.

Meanwhile, the slope sites should be kept in natural regeneration, not artificial regeneration, because the soil depth is shallow, 9 to 10 cm or 10 to 15 cm. On the steep slopes artificial regeneration increases erosion. Finally,

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where there is no mineral soil, there is no forest either. Transportation or labor are also difficult in mountains. The soil formation needs a long time, litter decomposes slowly, and nutrients leach rapidly. In the valley or bottom plain, the soil depth increases to 60 to 70 cm. The permafrost layer occurs in island shapes.

Artificial regeneration or natural regeneration or both may be carried on to increase the soil water-holding capacity. In this region, the surface water flow cannot be converted to underground water flow because the conversion mechanism and system of water cycle are not present. Most important to the Great Xingan Mountain Range, the southern slope has smaller capacity to hold the water than the northern slope. This is a serious problem to the fresh water resource for the Nenjiang River in south aspect region.

The Great Xingan Mountains are covered with pure *L. gmelini* forests with a few deciduous species even as *Populus davidiana*, *P. sauveolens*, *Betula platyphylla*, *B. dahurica*, *Quercus mongolica*, and *Alnus mandshurica*. The coniferous forest in this region contains two species, *Pinus sylvestris* var. *mongolica* and *Picea koraiensis*, above 450 m in altitude. Natural regeneration of these two species is much better in the stand, and the former is especially better than the latter. However, the Scotch pine is only about 10 percent in the mixed stand because of its lower tolerance of fire. The Great Xingan Mountains tend to have the most important lightning fires in China.

The damage to larch cones by insects is about 85 to 95 percent. The most persistent insects are *Lassiomma laricicola* Karl, *L. melania melaniola* Fan and *L. infrequence* Ackland. The population of pests and the amount of seeds in larch ecosystem are related in synergism with the coevolution between the community and the environment.

The larch is a kind of fast-growing species in northern China, especially *L. gmelini*, *L. olgensis*, and *L. principis-rupprechtii*. We would like to manage the fast-growing and high-yield plantation forests in the regions because the forest coverage area is only 12.98 percent of our whole country. The *L. gmelini* and *L. olgensis* are the main species for the plantation forests, which have been cultivated in Heilongjiang Province about 60 to 80 percent. The seedling survival rate of *L. olgensis* in Weihe Forest Agency is about 96 percent, and the preservation for 3 years is 95 percent. The average height of 3-year-old seedlings is 244 cm, and the maximum height is 287 cm.

The measurements of the larch forest management are:

1. The hybrid vigor and best provenance to the Olgen larch.
2. Cuttings for plantation instead of seedlings to simplify the productive process (in national nursery of Fangcheng County, Heilongjiang, 1990, the water cultural cuttings of *L. olgensis* were successful, creating about 60,000 seedlings for plantation, and qualification with the conversion percentage of cutting to seedling is 85 percent).
3. Larch species grow fast before 10 to 20 years, and the short rotation for the forest is about 30 to 40 years.
4. Seedling and cutting mixed with soybean and corn crop either in nursery or in plantation.
5. In the nursery stage, HRC (high reserve chemicals—hypogeous root conservation), trace elements, humic acid, chloride choline alkaline, and some nutrients, can be used for root system to increase the growth rate and capacity.

Larix principis-rupprechtii is a best and fast-growing species in northern China, in the mountain area in Hebei Province. The age of plantation stand in the province ranges from 10 to 20 years with an average height growth of 0.6 to 0.7 m per year. The species grows well on the mountain brown soil developed from granite, gneiss, and shale.

III. Scientific Base of *Larix occidentalis*

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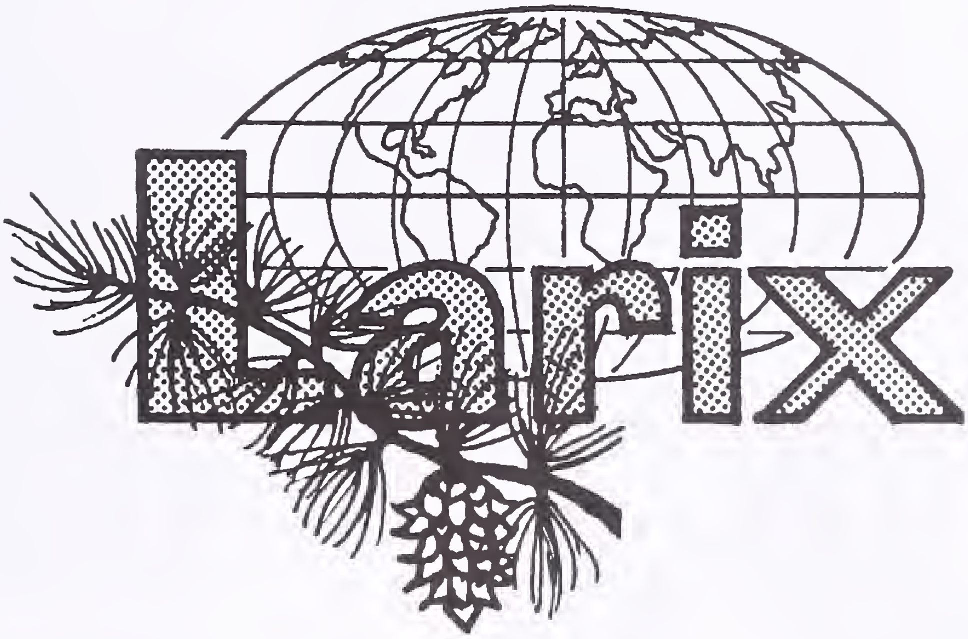

The History of *Larix occidentalis* During the Last 20,000 Years of Environmental Change

Cathy Whitlock

Abstract—During the full-glacial period, tundra, subalpine parkland, and cold steppe were present in the Pacific Northwest. Between 16,000 and 12,000 years ago, the appearance of mesophytic subalpine taxa marks an increase in temperature and effective moisture. After 12,000 years ago, deglaciated regions were colonized first by herb-dominated communities and then by subalpine forests. In the late Holocene, effectively wetter and more equable conditions allowed modern forest communities to develop. The modern range of *Larix* in the Pacific Northwest was established in the last few thousand years.

The restricted and discontinuous range of *Larix occidentalis* in western North America is anomalous when compared to the broad range of many of its forest associates (fig. 1; Little 1971). Present ecological factors are, no doubt, important in maintaining this distribution, but the pattern itself appeals to historical explanations. Either of two biogeographic models seems likely. The range of *Larix* may be a result of vicariance, in which case a once widespread distribution has become restricted because of recent unfavorable conditions. Alternatively, the pattern may be a result of dispersal wherein isolate stands are evidence of range expansion and ameliorating conditions. Although both range contraction and expansion have likely occurred at various times and perhaps even simultaneously, a knowledge of *Larix* history should help disclose the relative importance of these processes in creating the present distribution. The test of either model resides in understanding the factors that have influenced the distribution of *Larix* in the past.

My objectives are to discuss (1) the major changes in climate and environment that have affected the Pacific Northwest during the last 20,000 years, (2) the attendant vegetational responses that have occurred, and (3) the history of *Larix* during this period based on available fossil data. The Pacific Northwest refers to Washington, Oregon, Idaho, northwestern Montana, and southern British Columbia. The timeframe encompasses the events from the height of the last glaciation (about 20 to 16 ka; ka = 1,000 years ago), through the late glacial period of ice recession (about 16 to 10 ka), and into the Holocene interglacial period (10 ka to the present).

Information on past vegetational changes comes from stratigraphic records of fossil pollen and other plant macrofossils preserved in the sediments of lakes and wetlands. Sediment cores taken from such sites yield continuous records that range from the present back to the formation of the lake or wetland. In formerly glaciated areas, including the region where *Larix* now grows, these records extend to the time of ice recession (about 16 to 10 ka). In unglaciated areas, the sedimentary records are often older and contain pollen from plant communities that grew during the glacial maximum (20 to 16 ka). The relationship between modern pollen rain, modern vegetation, and present climate is the basis for reconstructing past vegetation and climate from the fossil pollen record. In the Pacific Northwest, studies of modern pollen rain necessary to establish this relationship have been published for many areas (for example, Barnosky 1981; Heusser 1969, 1973, 1978; Kearney 1983; Mack and Bryant 1974; Mack and others 1978a). Macrofossils (including leaves, needles, and other plant remains) found in association with pollen provide additional paleoecologic information that often pollen alone cannot provide. Macrofossils are also evidence that a particular species grew in the local watershed.

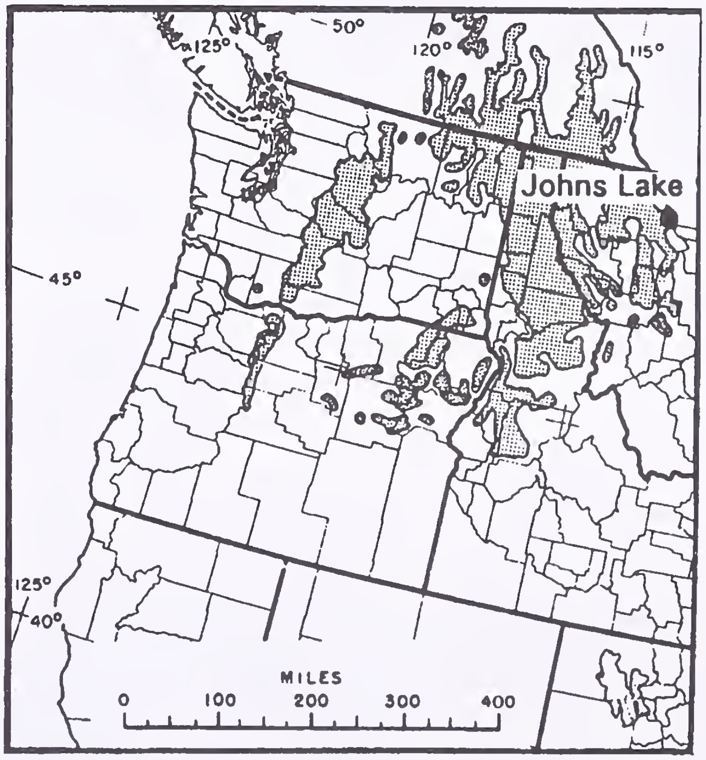

Figure 1—Present-day range of *Larix occidentalis* (after Fowells 1965) and the location of Johns Lake.

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Both radiocarbon dates of organic matter in the core and the presence of ash layers that can be traced to known volcanic eruptions provide a chronologic framework for the vegetational reconstruction. Many Pacific Northwest sites, for example, contain the Mazama ash from the eruption of Mount Mazama in southwestern Oregon about 6.7 to 7 ka (Sarna-Wojcicki and others 1983).

Direct information on the history of *Larix* is scarce. Few pollen records have been studied within its present range (for a listing of sites in the Pacific Northwest, see Baker 1983; Barnosky and others 1987; Mehringer 1985; Thompson and others 1993; Whitlock 1992). Thus, the history must be largely inferred from the response of *Larix* forest associates at other sites in the Pacific Northwest. Also, *Larix* pollen is morphologically similar to that of *Pseudotsuga*; from pollen data alone, one cannot determine whether one or both of the trees were present in the past. Published pollen diagrams often label the pollen spectrum as *Pseudotsuga/Larix* or *Pseudotsuga*-type. Most of this pollen is thought to be *Pseudotsuga* pollen because of the greater importance of Douglas-fir in the forest today (Mack and others 1978b,c,d,e, 1979, 1983). However, this may not be accurate. The pollen of *Pseudotsuga* and presumably *Larix* is not well dispersed. It only appears in modern samples when the tree is abundant in the local watershed. Even in samples from modern Douglas-fir forests, it seldom accounts for more than 10 percent of the pollen rain. *Pseudotsuga/Larix* percentages provide information on their local occurrence more than on their abundance in the regional vegetation. Macrofossils necessary to identify the source of *Pseudotsuga/Larix* pollen have been reported at only one site (see below).

CAUSES OF REGIONAL ENVIRONMENTAL CHANGE

The vegetation history of the last 20,000 years is largely an adjustment of species' ranges in response to a series of changes in the physical environment. The environmental changes result from a hierarchy of controls that determine vegetational responses on different spatial and temporal scales (Bartlein 1988; Whitlock 1992; Whitlock and Bartlein 1993). At the top of the hierarchy, global-scale changes in ice cover, concentration of carbon dioxide in the atmosphere, and solar radiation have caused climatic changes that have affected the entire Northern Hemisphere on time scales of millennia (COHMAP Members 1988). This gross scale of variation accounted for the warming that ushered in the Holocene; it also led to warmer-than-present conditions in the Pacific Northwest during the early Holocene (10 to 6 ka)—the so-called Hypsithermal Period.

Paleoclimatic simulations produced by general circulation models (GCM's) of the atmosphere suggest that two large-scale controls were especially important during the last 20,000 years (Broccoli and Manabe 1987; COHMAP Members 1988) (fig. 2). The first was the Laurentide ice sheet, which at its maximum size covered north-central and northeastern North America. The second control was the changes in the seasonal distribution of solar radiation as a result of variations of the Earth's orbit around the Sun (the Milankovitch cycles). At 9 ka, perihelion (the time when the Earth is closest to the Sun) was in July, unlike today, and at 18 ka when perihelion occurred in January (Kutzbach and Guetter 1986). As a result, solar radiation in summer at middle latitudes of the Northern Hemisphere was greater than present, and winter radiation was less than present between 12 and 6 ka.

These global-scale variations set in motion a series of smaller scale changes, including shifts in atmospheric circulation and variations in the temperature contrasts between land and sea. In turn, these changes led to climatic differences within western North America. Notable outcomes over the last 20,000 years were changes in the seasonal distribution of precipitation (related to the position of the jet stream), the intensity of the northeastern Pacific subtropical high, and the strength of monsoonal flow from the Gulf of California and Gulf of Mexico. As a result, the vegetational history of the Pacific Northwest is different from that of the American Southwest or Great Plains (Barnosky and others 1987; Thompson and others 1993).

Topographic variability in the Pacific Northwest has further modified climate and accounted for mesoscale variations in vegetational history. Precipitation and temperature differences between coastal and interior areas reflect the orographic influence of the Coast Ranges, the Cascade Range, and the Northern Rocky Mountains on the flow of air from the Pacific. While these areas show a common response to the large-scale controls, the specific vegetational history displays considerable intraregional variability. On the smallest spatial scale, substrate, disturbance regime, microclimate, and biology are important in shaping local vegetational patterns. These factors sometimes produce significant site-to-site variations in the fossil record. Their detection, however, requires a comparison of closely spaced sites in contrasting environments.

THE GLACIAL MAXIMUM, 20 TO 16 KA

Paleoclimatic simulations suggest that the Laurentide ice sheet at its maximum size created colder and drier conditions in the Western United States (Barnosky and others 1987; COHMAP Members 1988; Thompson and others 1993; see 18 ka simulation in fig. 2). In the Pacific Northwest, temperatures were lowered by about 5 °C along the coast (Heusser 1977) and by about 10 °C or more in the interior (Mears 1981; Porter and others 1983). Regional aridity was caused by the sheer size of the ice sheet, which split the jet stream over North America and shifted the southern branch south of its present position. The more southerly position of the jet robbed the Northwestern United States of its winter storms, which were funneled into the Southwest. Dry conditions also resulted from a large glacial anticyclone that developed over the ice sheet. Clockwise winds off the ice body generated stronger easterly surface winds in the Pacific Northwest.

In general, vegetational records from the Pacific Northwest suggest that lower treeline lay above its present elevation during the glacial maximum as a result of greater aridity. West of the Cascade Range, lowlands were covered by xerophytic parkland; east of the Cascades, tundra and steppe prevailed in the basins. Upper treeline in the Olympic Mountains and Rocky Mountains was lowered by 600 to 1,000 m (Baker 1983; Heusser 1977), presumably because

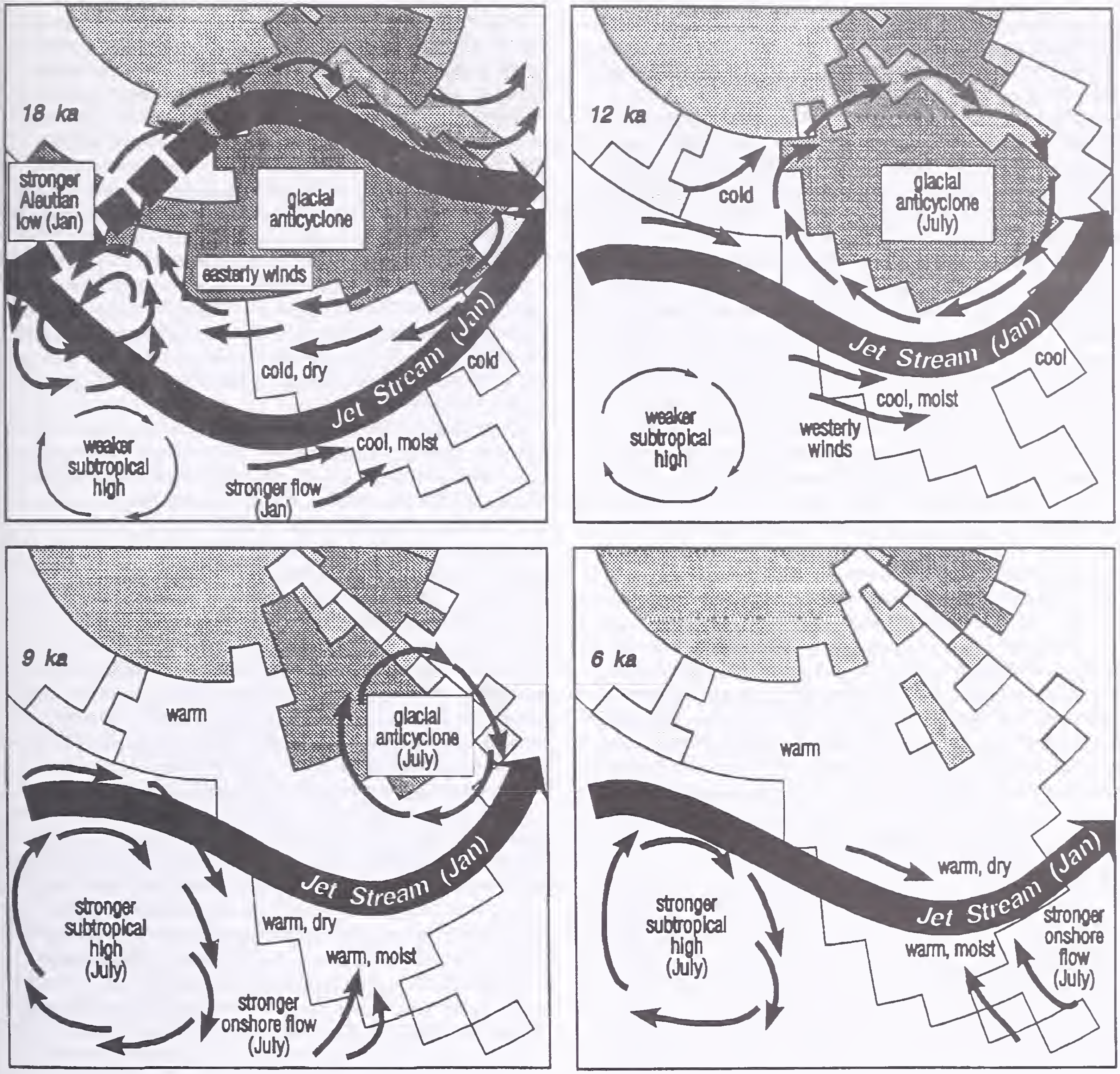

Figure 2—Summary of the major changes in atmospheric circulation during the last 20,000 years (Thompson and others 1993). The maps show the coarse depiction of North America used by the National Center for Atmospheric Research Community Climate Model (COHMAP Members 1988). The stippled area shows the extent of ice sheets and sea ice that serve as boundary conditions for a particular simulation. The thick solid arrow represents the approximate position of January jet stream winds, while the thick broken arrow indicates where the jet stream is weak. Thin arrows represent surface winds.

of lower temperatures and extensive ice cover. Thus, conifers were confined to middle and protected lower elevations, and forest cover was probably discontinuous.

Pollen records that extend to the glacial maximum are available from southwestern Washington, southwestern British Columbia, and the Snake River Plain of Idaho. In the southern Puget Trough of Washington, pollen data between 21 and 16 ka contain high percentages of *Artemisia*, Gramineae, and other herbs, as well as *Picea* and Diploxylon-type pine (Barnosky 1984, 1985b). Needles of *Picea engelmannii* and *Pinus contorta* were found in the sediments of this period. The fossil assemblage most closely resembles modern pollen spectra collected from open subalpine parkland in the Northern Rocky Mountains, which implies that the climate of the Puget Trough was more continental than that of today. This reconstruction is consistent with the model predictions of colder drier conditions related to a more southern position of the jet stream and stronger easterlies from a strengthened glacial anticyclone. Further evidence of the jet stream position comes from paleoenvironmental records from the American Southwest, which show expanded forest and high lake levels during the glacial maxima in areas that are presently arid (Thompson and others 1993).

We lack much information on the ranges of temperate forest taxa during the glacial maximum, but available data argue against significant latitudinal displacements. For example, *Picea sitchensis* was present in the coast range of Oregon, in the area where it grows today (Worona 1993). *Pseudotsuga* and *Alnus rubra* were present in protected habitats in the southern Puget Trough at about 16 ka (Barnosky 1985b). These trees apparently survived in small numbers at a time when the region was largely covered by spruce-pine parkland. *Taxus brevifolia* and *Abies lasiocarpa* macrofossils are reported from the Fraser Lowland of southern British Columbia at 21 to 18 ka (Hicock and others 1982). *Pinus contorta* was probably present in the unglaciated highlands throughout the Pacific Northwest (Barnosky 1985b; Beiswenger 1991). Its proximity and ability to grow on well-drained soils allowed it to colonize deglaciated regions of western Washington at the earliest stages of ice retreat. There is no information on the glacial history of *Larix*, but it too may have survived in the Pacific Northwest during the glacial maxima. Though nearly all of its present range was covered by glacial ice between 20 and 16 ka, it may have survived farther to the west and the south, where the climate was less severe.

THE LATE-GLACIAL PERIOD, 16 TO 10 KA

As the ice sheet shrank in size between about 16 and 12 ka, its effect on the climate of the Northwestern United States became attenuated. In model simulations that incorporate a smaller ice sheet (50 percent of its full size), the jet stream was no longer split and its position in western North America lay over the Pacific Northwest (fig. 2; COHMAP Members 1988). Likewise, the glacial anticyclone was smaller with a smaller ice sheet, and surface easterlies no longer prevailed in the Pacific Northwest. Thus, the model simulations suggest that the climate at 12 ka was warmer than before (although cooler than today), while winter precipitation in the Pacific Northwest increased.

The regional changes that accompanied the transition from the glacial maximum to the late-glacial occurred at different times in different places. In the Pacific Northwest, an increase in moisture and slight warming are recorded between 16 and 15 ka by geomorphic and paleoecologic data. For example, the late-glacial advances of the Juan de Fuca lobe and Puget lobe of the Cordilleran ice sheet have been attributed to increased winter precipitation with the northward shift of the jet about 16 to 15 ka (Hicock and others 1982). Other lobes of the Cordilleran ice sheet may also have reached their maximum limit in the late-glacial period, but the glacial chronology east of the Cascade crest is poorly dated (Clague 1989; Waitt and Thorson 1983).

In the southern Puget Trough, the pollen record shows increased percentages of *Picea, Tsuga mertensiana, Abies,* and *Alnus sinuata*-type (Barnosky 1985b) between about 15 and 11 ka. Needles of *Picea sitchensis, Pinus contorta,* and *Abies* were also recovered in the sediments. The pollen assemblage is similar to modern spectra from subalpine forests in western Washington, where the climate is cool. Climate reconstructions for this period indicate that annual precipitation went from 500 to 1,200 mm and mean annual temperatures rose by 2 to 4 °C (Whitlock and others 1990). Between 11.2 and 10 ka, temperate taxa, including *Pinus, Pseudotsuga, Alnus rubra,* and *Tsuga heterophylla,* appear in the southern Puget Trough and imply further warming. By 10 ka, these taxa dominate the lowland vegetation, and *Picea, Pinus, Tsuga mertensiana, Abies,* and *Alnus sinuata* have shifted their ranges to higher elevations (Barnosky 1985b; Whitlock 1992).

The retreat of alpine glaciers and Cordilleran ice occurred between 16 to 12 ka, based on the oldest radiocarbon dates from lake sediments in these areas (Porter and others 1983; Waitt and Thorson 1983). The early postglacial records in the Okanogan region and Northern Rocky Mountains featured pollen assemblages dominated by Gramineae, *Artemisia,* and other herbs, as well as by *Juniperus*-type, *Betula,* and *Salix.* These taxa suggest that meadow and shrub communities developed in the deglaciated landscapes. *Juniperus communis* (found as macrofossils) apparently grew in areas of poor soil cover and few competitors. *Betula glandulosa* and *Salix* probably occupied riparian settings. Some sites show how high amounts of *Shepherdia canadensis,* which was a successful pioneer species (Mack and others 1978e).

Between about 12 and 10 ka, pollen records from the Okanogan Highlands and Northern Rocky Mountains show increased percentages of *Picea, Abies,* and Haploxylon-type pine (probably *P. albicaulis*) that resemble modern pollen samples from subalpine forests in the eastern Cascade Range and the Northern Rocky Mountains. As in the Puget Trough, the climate was probably warmer than before but cooler than that of today. Diploxylon-type pine and *Pseudotsuga/Larix* appear in the pollen record between 10 and 9.5 ka. Macrofossils identify the source of the pollen as *Pinus contorta, Pseudotsuga,* and *Larix* (inferred to be *L. occidentalis*). These taxa indicate the establishment of temperate conifer forests and provide evidence of further postglacial warming.

THE EARLY HOLOCENE, 10 TO 6 KA

Between 12 and 9 ka, the climatic effects of the ice sheet were replaced by those brought on by the amplification of the seasonal cycle of solar radiation. Model simulations for 9 ka incorporate radiation values that are 8 percent higher then present in summer and 10 percent lower in winter (fig. 2). The direct effects of the radiation anomaly were to increase summer temperatures relative to the present day and decrease winter temperatures (particularly in the interior). In addition, greater summer radiation indirectly caused an enhancement of the northeastern Pacific subtropical high pressure system, which intensified drought in the Pacific Northwest (COHMAP Members 1988; Heusser and others 1985). The radiation anomaly also created greater land/sea contrasts in temperature, which in turn strengthened monsoonal circulation. Areas of the Northern Rocky

Mountains today derive considerable moisture from the Gulf of Mexico, including the region that supports *Larix* (Tang and Reiter 1984). These areas were probably affected by stronger monsoons and experienced wetter-than-present summers and cooler, drier winters (Thompson and others 1993; Whitlock and Bartlein 1993).

Evidence of warm dry conditions in the early Holocene is found throughout the region presently affected by the subtropical high (Barnosky and others 1987; Mathewes 1985). Prairie taxa are registered in southwestern Washington and suggest a northward expansion of the Willamette Valley communities (Barnosky 1985b). Xerophytic taxa, such as *Pseudotsuga* and *Pteridium,* were more abundant in coastal forests (Heusser 1977; Mathewes 1973), and charcoal data suggest more frequent fires in the region (Cwynar 1987). In eastern Washington, the steppe/forest border shifted north of its present position into southern British Columbia, as well as to higher elevations in the Okanogan Highlands and Cascade Range (Alley 1976; Barnosky 1985a; Mack and others 1979). In the Northern Rocky Mountains of Idaho and northwestern Montana, *Pinus contorta* and *Pseudotsuga* were more widespread (Mack and others 1978c, 1983; Mehringer and others 1977), and upper treeline lay above its present elevation, suggesting warmer growing seasons (Kearney and Luckman 1983).

In contrast, the northern part of Yellowstone National Park is a good example of an area that was affected by stronger monsoonal flow and experienced summer conditions wetter than present (Whitlock and Bartlein 1993). In the early Holocene, the region was covered by forests of Haploxylon-type and Diploxylon-type pine (probably *Pinus flexilis* and *P. contorta*), and *Juniperus. Betula glandulosa* was also present. This assemblage implies more mesic conditions than during the late Holocene when open *Pseudotsuga* parkland developed. The climate of northern Yellowstone apparently became drier after 7 ka, as summer monsoons weakened. The present climate regime was established after about 4 ka.

Pollen and macrofossil data from Johns Lake, west of the Continental Divide in Glacier National Park (fig. 1), suggest that low elevations in northwestern Montana also experienced increased summer precipitation in the early Holocene. Johns Lake is an important site, because it provides some specific information on the history of *Larix. Larix* apparently was present in the Johns Lake watershed at the beginning of the Holocene as part of a mixed conifer forest. (The association with *Pseudotsuga* and *Pinus contorta* suggests that the species is *L. occidentalis*). *Larix* did not grow there between about 9.8 and 6.5 ka (fig. 3). The macrofossil record implies that the *Pseudotsuga/Larix* pollen recorded during the early-Holocene interval was from *Pseudotsuga,* which was more common in Northern Rocky Mountain forests at that time. The absence of *Tsuga, Thuja,* and *Taxus,* in addition to *Larix,* further indicates that conditions in northwestern Montana were unfavorable for coastal Northwest taxa.

To discern which elements of the early Holocene climate eliminated *Larix* from Glacier National Park, it is necessary to consider the present ecology of *L. occidentalis* and the likely impact of changes in solar radiation, temperature, and precipitation. *Larix* is less drought tolerant today than its common associates *Pseudotsuga, Pinus contorta,* and *Abies grandis* (Minore 1979). High solar radiation during the growing season is considered a major cause of death (Fowells 1965). In the early Holocene, increased solar radiation in summer would have restricted the range of *Larix. Larix* also grows in cool temperate regions where the average maximum and minimum temperatures are 29 °C and –9 °C (Schmidt and Shearer 1990). In the early Holocene, seasonal changes in solar radiation would have increased the temperature range and created a more continental climate that was less suitable for *Larix*. Furthermore, *Larix* presently grows in moist areas where 80 percent of the precipitation comes from Pacific frontal storms in winter and 20 percent from convectional storms in summer (Schmidt and Shearer 1990). In the early Holocene, greater summer precipitation would have created conditions more analogous to those of the Central and Southern Rocky Mountains today. This change would favor the expansion of *Pseudotsuga* and *Pinus contorta* but not *Larix*. Finally, *Larix* requires fire to become established in natural settings, and fire frequency in northwestern Montana would have been less in the early Holocene as a result of wetter summers.

One can speculate on the range of *L. occidentalis* in the early Holocene. It would have been confined to areas of cool summers, which implies that it lay farther north in British Columbia. The range would have been more coastal than today because of the greater continentality in the Northern Rocky Mountains. A preference for dry summers would also have shifted the range away from the influence of the strengthened monsoons. Fire was more frequent than today in coastal regions of the Pacific Northwest, which would have further promoted *Larix* establishment. Thus, the range of *Larix* in the early Holocene may have been farther north and west in British Columbia and Washington than at present. Perhaps modern outliers of *Larix* in these regions are vicariant remnants of this period.

THE LATE HOLOCENE, 6 KA TO THE PRESENT

In model simulations for 6 ka, summer radiation was still greater than present, although the anomalies were not as great as at 9 ka (COHMAP Members 1988) (fig. 2). Summer temperatures continued to be higher than present, but a weakening of the subtropical high in model simulations suggests that drought was less severe than before. Similarly, lower summer radiation may have reduced summer precipitation in areas affected by the monsoons. As the seasonal cycle of solar radiation has approached the modern in the last 6 ka, the climate has become cooler and wetter in the Pacific Northwest. In eastern Washington, the period between 4.0 and 1.7 ka may have been cooler and moister than today, although the causes of this cooling are unknown.

The overall vegetational changes that occurred in the late Holocene are consistent with the model results. Throughout the Pacific Northwest, pollen sites record an increase in mesophytic taxa starting between 8 and 4 ka. In western Washington and southwestern British Columbia, modern forests composed of *Pseudotsuga, Tsuga, Thuja, Picea,* and *Alnus* were established between 7 and 5 ka (Whitlock 1992), and fires were less frequent than before (Cwynar 1987). In eastern Washington, the area covered by steppe shrank as the ecotone shifted south and to lower elevations

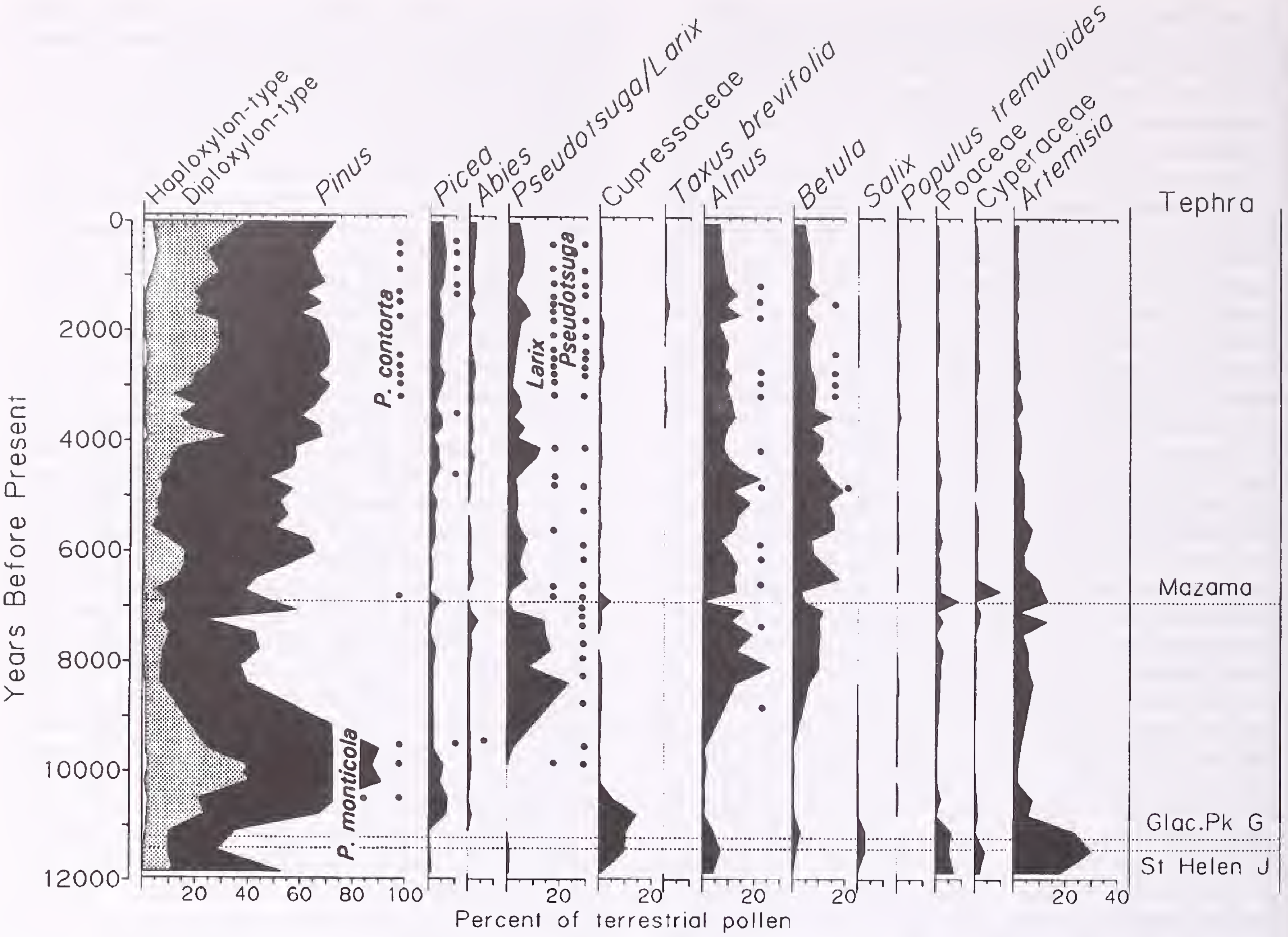

Figure 3—Pollen percentage diagram of Johns Lake, Glacier National Park. Dots mark the stratigraphic position of macrofossils from the cores.

in the Columbia Basin. This transition is abrupt at specific sites, but the timing of the change occurs from 8 to 4 ka (Barnosky 1985a; Mack and others 1978e, 1979; Nickmann and Leopold 1985). Along the flanks of the eastern Cascade Range and in the Okanogan Highlands, *P. ponderosa* forest developed in areas that were earlier covered by steppe (Alley 1976; Mack and others 1978b, d, e, 1979). Increasing percentages of *Pseudotsuga/Larix, Abies, Tsuga, Thuja, Picea,* Haploxylon-type pine, and (in south-central Washington) *Quercus* trace the development of modern vegetational associations as the climate continued to cool. *Tsuga mertensiana, Abies lasiocarpa, Picea engelmannii,* and *Pinus contorta* developed in cool, moist subalpine forests. *Abies grandis, Tsuga heterophylla,* and *Thuja plicata* occupied wet habitats, while *Pinus ponderosa, P. contorta, Pseudotsuga,* and (at low elevations in south-central Washington) *Quercus garryana* were present in xeric sites. *Larix occidentalis* and *Pinus monticola* probably became important as fire seral species.

The evidence of cooling between 4 and 1.7 ka comes from sites in the Sanpoil River valley, the Selkirk Range, and the Kootenai River valley, which feature greater percentages of *Picea* and *Abies* than at present (Mack and others 1978b,c,d, 1983). These pollen taxa are attributed to *P. engelmannii* and *Abies lasiocarpa* or *A. grandis*. Modern associations of *Pinus ponderosa* and Gramineae and, at higher elevations, of *Pseudotsuga* and *Abies grandis* were established after 2.7 ka in the Sanpoil River area. Farther east in northeastern Washington, northern Idaho, and northwestern Montana, modern communities that include *Tsuga heterophylla* appear between 2.4 and 1.7 ka.

Pollen and macrofossil data from Johns Lake offer the best evidence that *Larix* was a component of the mixed conifer forests that developed in the late Holocene. Its prominence at Johns Lake suggests that stand-replacing fires have occurred every 2 to 3 centuries during the last 6.5 ka (Barrett and others 1991). This assertion, however, should be tested by studying fossil charcoal records.

At sites where only pollen data are available, the timing of *Larix* establishment and its subsequent abundance in the vegetation is uncertain. *Pseudotsuga/Larix* pollen is consistently present in the pollen record of the last 7 ka. In the last 2 ka percentages decrease while those of *Tsuga* increase at sites in northeastern Washington, Idaho, and northwestern Montana. These fluctuations in percentages of *Pseudotsuga/Larix* pollen probably are a distorted picture of *Larix* abundance in late-Holocene vegetation that requires verification from macrofossil data. *Larix* grew upslope from most pollen sites, and its contribution to the pollen record was overwhelmed by lowland mesophytic taxa.

CONCLUSIONS

Larix occidentalis has maintained a dynamic equilibrium with the climate and vegetational changes that have occurred in the Pacific Northwest since the glacial maximum. Shifts in its range (although not known in detail) can be explained as a response to a hierarchy of climatic changes ranging from global to local that occurred during this period. The inferred response of *Larix* to these changes suggests that both vicariance and dispersal models of biogeography were involved in shaping the present distribution. For example, range expansions probably occurred during late-glacial warming, when *Larix* and other temperate taxa dispersed from spatially restricted glacial populations. In the early Holocene, the range was restricted and fragmented, as a result of greater insolation, reduced fire frequency, and greater annual temperature range. It is likely that the early-Holocene distribution of *Larix* lay west and north of its present location. As the climate became cooler and more temperate in the late Holocene, the range of *Larix* presumably contracted in the north and west and expanded in the east and south. The present distribution was established only in the last few millennia. Clearly, this reconstruction of the history of *Larix* is speculative. The test of the reconstruction will come from detailed examination of new pollen and macrofossil records in the Pacific Northwest.

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Domestication and Conservation of Genetic Variability in Western Larch

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Abstract—In western larch (*Larix occidentalis*), genetic variability is abundant within and between natural populations. Differentiation among populations involves variety of growth and developmental traits, morphology, and pest resistance. This variation is distributed along geographic and elevational clines of relatively flat slope. Domesticating the wild genetic system requires a strategy that improves economic values while maintaining adaptations to natural environments. While seed transfer in artificial reforestation can be relatively liberal, tree breeding programs that tap the additive genetic variances within populations must also address the strong genetic correlations between growth and other adaptive traits. Appropriate gene conservation measures involve establishing gene pool reserves while natural populations still predominate.

Genetic variation can exist within individuals, among individuals within populations, and among populations. As discussed by Mayr (1970), this variation has been molded by biotic and abiotic environmental effects to produce populations physiologically attuned to only a portion of the environmental gradient occupied by a species. Species, therefore, are composed of local populations, each of which contains adaptively similar, interbreeding trees. As a result, terms such as silvics, ecological requirements, and ecological characteristics that are commonly ascribed to a species reflect the sum total of the genetic variability contained within and among populations. This total constitutes the natural system of genetic variability.

Because genetics is a cornerstone of biology, understanding natural systems of genetic variability is essential to understanding basic concepts in forest biology, such as responses to environmental stress, silvicultural prescriptions and environmental change; inter- and intraspecific interactions; growth and yield; synecological and autecological relationships; and plant geography (see Harper 1977). However, because the characteristics of species are controlled by the system of genetic variability, they can be altered, either purposely or inadvertently. Only by studying genetic responses in relation to environmental gradients can managerial options be developed for conserving those genetic mechanisms that provide adaptation to natural environments.

In western larch, genetic variability is abundant. Some of the variability appears to be neutral and some is adaptive; of the adaptive, some is distributed randomly and some follows systematic patterns across the landscape. The distribution of this variability within and among populations determines the most suitable approaches to management.

GENETIC STRUCTURE OF NATURAL POPULATIONS

It was only a decade ago that the first studies (Rehfeldt 1982) of genetic variation in western larch were completed. These tests involved 2-year-old trees from 82 populations in the Inland Northwest. Seedlings were grown in three common gardens: Moscow, ID, elevation 730 m, average frost-free season 120 days; Benton Flat, Priest River Experimental Forest, ID, elevation 670 m, frost-free season 100 days; and Tarlac, Priest River Experimental Forest, ID, elevation 1,500 m, frost-free period unknown (but short). At these sites, differences among populations were observed in growth, growth rhythm, and freezing damage. Growth rhythm refers to the timing and duration of developmental events in relation to the suitability of the environment for those events to occur (Dietrichson 1964). In plants whose rhythm is attuned to the local environment, developmental events (such as bud burst, bud set, and cold acclimation) occur when environmental conditions are optimal.

Recent work (Rehfeldt 1992b) readily illustrates genetic differences among populations for patterns of shoot elongation (fig. 1). Trees from Lost Valley, a population from a relatively high elevation near the southern edge of the species' distribution in central Idaho, elongated at a relatively slow rate, ceased elongation early, and tended to be short. In contrast, the population from a low elevation (670 m) in the Priest River Valley of northern Idaho elongated at a rapid rate, ceased elongation late, and became tall. A third population from the North Fork of the Flathead River in British Columbia was intermediate.

Genetic differences among populations can be distributed either randomly or systematically across the landscape. While random differences may be important to the adaptation of a local population, systematic patterns invariably correspond to environmental gradients, most likely result from natural selection, and, therefore, are predictable. The early work in western larch (Rehfeldt 1982) related variation among populations to their elevation and geographic location. As a result, the variation could be considered in terms of geographic clines. A cline

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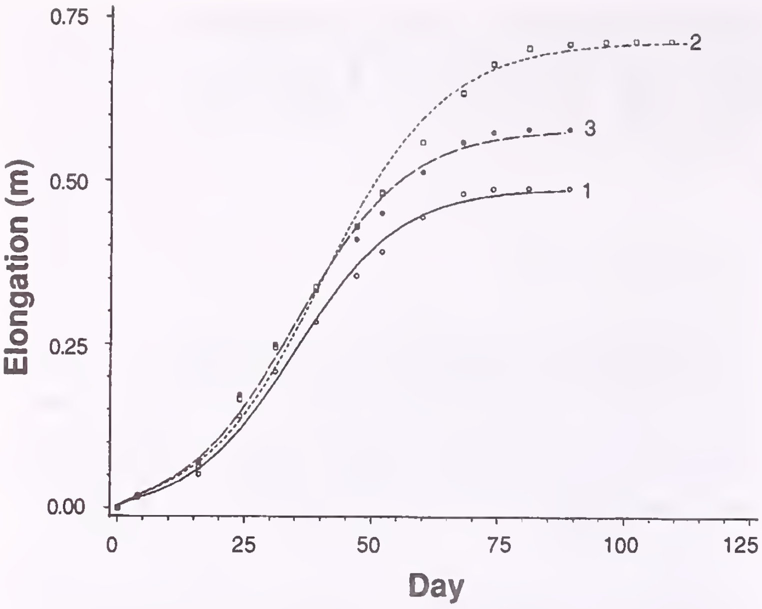

Figure 1—Patterns of shoot growth of 4-year-old trees from three populations growing at the Priest River Experimental Forest. Days are numbered from May 1. 1: Lost Valley, latitude (LT) = 44.95, longitude (LN) = 116.46, elevation (E) = 1,460 m; 2: Priest River, LT = 48.28, LN = 116.88, E = 670 m; 3: North Fork Flathead River, LT = 49.10, LN = 114.48, E = 1,350 m (from Rehfeldt 1992b).

reflects the amount of genetic change along an environmental gradient. The clines were of relatively gentle slope; genetically different populations were separated by relatively large environmental distances.

The clines suggested that populations in the same geographic locality (mountain range or drainage, for instance) that were separated in elevation by about 450 m tended to be genetically different. This elevational cline attributed a high growth potential and low cold hardiness to populations from low elevations. Growth potential refers to an innate ability to produce photosynthate and assimilate wood in the absence of environmental effects (frost injury, drought injury, insects, and diseases) that mask the genotype. As elevation increases, however, the growth potential of populations decreases while cold hardiness increases. The clines therefore, paralleled variation in the length of the frost-free period, a climatic variable that decreases by about 90 days across an elevational interval of 1,000 m (Baker 1944). As a result, western larch populations occupying environments that differ by about 40 days in the mean frost-free period tend to be genetically different. By comparison, similar calculations yield 18 days for Douglas-fir (Rehfeldt 1989), 20 days for lodgepole pine (Rehfeldt 1988), and 35 days for ponderosa pine (Rehfeldt 1991). Elevational clines, however, have not been detected in western pine (Rehfeldt and others 1984).

Geographic variation is depicted in figure 2 as if all populations were from the same elevation. This figure shows that populations from western Montana have the lowest growth potential and highest cold hardiness; toward the west and south, however, the growth potential of populations from comparable elevations increases while hardiness decreases. Although the figure implies that growth potential continues to increase toward the south, few populations were sampled from south of the Salmon River. Recent results (Rehfeldt 1992b), coupled with those involving Douglas-fir (Rehfeldt 1989) and ponderosa pine (Rehfeldt 1991), suggest that the growth potential of western larch should peak in north-central Idaho and from there decrease toward the south.

Like the elevational clines, geographic patterns also are associated with variation in the length of the average frost-free season. At comparable elevations, the frost-free period tends to be about 30 days shorter in western Montana than in northern Idaho (Baker 1944). Consequently, populations from western Montana are better adapted genetically to short frost-free seasons than those from comparable elevations in northern Idaho. Within a given locality, however, populations from low elevation express a high-growth potential that decreases as elevation increases and the frost-free period decreases.

Recent studies tend to corroborate those done by Rehfeldt in 1982 with 2-year-old trees. Joyce (1985) and later Zhang (1990) studied the determinate and indeterminate components of the 2-year and the 8- and 9-year shoots, respectively. In a test of 19 Idaho and Montana populations growing in a common garden in Moscow, ID, differences were detected among populations in the components of shoot growth, but the differences were small. Likewise, genetic differences have been detected among several

Figure 2—Geographic patterns of genetic variation in growth potential expected for populations growing at the same elevation. Zero marks the isopleth with the lowest value; populations from geographic regions separated by two isopleths tend to be genetically different. The base map outlines northern Idaho and encompasses the larch forests of Idaho north of the Salmon River, Washington east of the Columbia River, and Montana west of the Continental Divide (from Rehfeldt 1982).

populations for patterns of shoot elongation (fig. 1), height, and resistance to *Meria* needle cast in tests of 4- and 8-year-old trees (Rehfeldt 1992b). The populations included in these tests, however, were well dispersed both geographically and elevationally; therefore, large differences were expected. Studies of allozymes (Fins and Seeb 1986) generally substantiated low levels of genetic differentiation among populations from the Inland Northwest, although the single population tested from south of the Salmon River (near Lost Valley, fig. 1) seemed to be distinct from populations to the north. All of these results are interpretable in terms of the relatively flat clines that were described by the 2-year results.

In 1981, the Inland Empire Tree Improvement Cooperative established long-term field tests that now can be used to substantiate the 2-year results. The cooperative's program for Montana included 112 populations, all but 10 of which originated from Montana. By using the analytical techniques of Rehfeldt (1989) and the height of 8-year-old trees growing on five sites, geographic and elevational clines were again detected (Rehfeldt 1992c). The elevational cline described by the 8-year results (fig. 3) suggested that populations separated by about 475 m tend to be different genetically, a result that was essentially the same as the early results. Despite the fact that few Idaho populations were sampled, the geographic patterns closely resembled those described by the 2-year data (fig. 2).

Besides corroborating previous results, the cooperative's 8-year data nicely illustrate that populations capable of producing similar phenotypic responses tend to recur across the landscape. For purposes of this paper, it is assumed that similar phenotypic responses reflect genetic similarities. The recurrence of similar genotypes (see Rehfeldt 1991) is illustrated in figure 3 where the elevation ional cline for western larch is plotted for several geographic localities. Populations with a similar growth potential (1.4 m in 8-year height, for instance) can be found at about 600 m in the Kootenai drainage and at about 900 m in the Clearwater. Genetically similar populations tend to recur presumably in association with recurrence of similar environmental conditions. This means that when environmental gradients are multidimensional (occur both geographically and elevationally), genetically similar populations tend to be found at different elevations in different drainages. Or, the same elevation in different drainages can support genetically different populations.

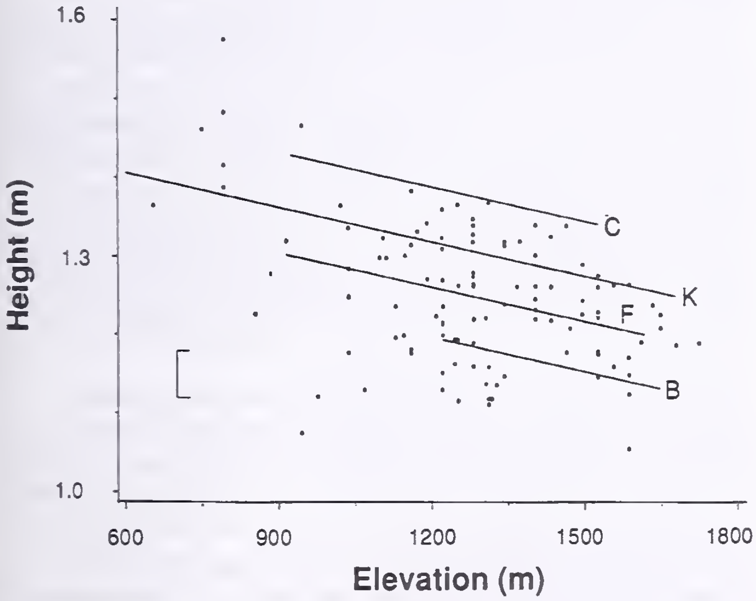

Figure 3—Eight-year height of populations (dots) plotted by elevation of the seed source. Regression lines represent elevational clines for four drainages: C = Clearwater, K = Kootenai, F = Flathead, and B = Blackfoot. The bracket reflects the amount populations must differ before one can be reasonably certain that the differences are real. (Rehfeldt 1992c.)

Even though corroborative, the studies of population differentiation (Rehfeldt 1982) and the cooperative's field tests included many of the same populations; therefore, the results are not completely independent. Consequently, validation of the early work is not complete. In addition, Rehfeldt (1992b) found large differences between three populations for resistance to *Meria* needle cast. In a test in the Priest River Valley, the local population expressed high levels of resistance while two distant populations were decimated. To further validate the early work and to assess the influence of *Meria* on population differentiation, new studies of 143 populations were established by the Intermountain Research Station in 1989 at the Priest River Experimental Forest.

DOMESTICATION

Because forest trees must endure natural biotic and abiotic environmental stresses, strategies for domesticating natural genetic systems must balance the production of improved products against maintaining adaptedness. Without factual information to the contrary, one commonly assumes that the adaptedness of the natural population is near the optimum. Maintaining adaptedness during domestication requires, therefore, that programs be based on the genetic structure of natural populations. However, another view holds that the adaptation of natural populations is more conservative than necessary. According to this view, patterns of genetic variation among natural populations develop from infrequent (every two or three generations) and sporadic (here and there across the landscape) environmental events. As a result, the adaptedness of natural populations lags behind the optimum (see Matyas 1990), and, therefore, the local population is not necessarily optimal (Namkoong 1969). Proponents of this view further assert that mankind, being concerned with single generations (a rotation), can accept greater risks of maladaptation than nature seemingly is willing to take. Even though this argument may be applicable to the forests of the Rocky Mountains, risks have not been defined quantitatively nor are they capable of being defined from the current programs. Until adequate information is available, domestication strategies for western larch should reflect the genetic structure of natural populations.

Domestication programs considered in this paper include seed transfer, tree breeding, and gene conservation. The challenge for each involves managing the resource without irreparably altering adaptive mechanisms.

Seed Transfer

If productivity is to be optimal, planted trees must be adapted to the planting site. Adapted planting stock can be obtained by (1) defining the limits to seed transfer in terms of genetic variation in adaptive traits, and (2) limiting the distance that seeds are transferred from their place of origin. For western larch, seed transfer guidelines have been developed (Rehfeldt 1983) from the patterns of variation discussed earlier. Because clines in adaptive traits are relatively flat, seed transfer can be correspondingly liberal. In general, seeds should be used within ±225 m of the elevation of the seed source. Geographic zones can be as broad as western Montana or northern Idaho.

Such seed transfer guidelines, however, fail to take into consideration the recurrence of similar genotypes across the landscape in association with the recurrence of similar environmental conditions. Recognizing this recurrence allows one even greater flexibility in seed transfer. Although general guidelines are presented by Rehfeldt (1983) for altering the elevation at which seeds are planted as the geographic transfer distance increases, full flexibility requires an expert system such as that developed for ponderosa pine on the Colorado Plateau (Monserud 1990). The expert system, however, requires a model of genetic variation for estimating the degree of recurrence, and such a model will not be available for western larch until current tests are completed by the Intermountain Research Station.

Using guidelines that mirror natural patterns of variation is the most conservative approach to seed zoning. If, however, managers are willing to increase the risks of maladaptation, gains in productivity through provenance transfer seem possible. Unpublished results (Rehfeldt 1992c) of 8-year data of the Inland Empire Tree Improvement Cooperative suggest that the transfer of fast-growing provenances from northern Idaho to northwestern Montana would increase 8-year height 6 to 10 percent. Transfers of broader scale, however, first require long-term field data from which risks can be properly assessed. Although adequate data are not yet available, the possibilities of using provenance transfer to increase productivity with only a nominal increase in risk seem feasible and worthy of exploration.

Tree Breeding

While trees can be selectively bred for traits such as growth, wood quality, disease resistance, or tolerance to environmental stress, current programs with western larch are concentrating on improving growth and productivity. All studies dealing with the quantitative genetics of western larch purport substantial additive genetic variances in morphometric traits (Fins and Rust 1989; Joyce 1985; Rehfeldt 1992b; Zhang 1990). These variances suggest that gains of 18 to 20 percent in juvenile height from a single generation of direct selection are available if breeding is practiced within the seed zones (breeding zones) discussed earlier. Improvement programs hoping to capture these gains are underway in the Inland Northwest and in British Columbia.

While genetic variances in growth are pronounced, so too are genetic variances in adaptive traits such as the cessation and duration of shoot elongation or resistance to *Meria* needle cast (Rehfeldt 1992b). Both the results of Rehfeldt (1992b) and unpublished results (Rehfeldt 1992d), of the Forest Service's early selection trials at Coeur d'Alene, ID, indicate that these adaptive traits have strong genetic correlations with growth traits. As a result, strong direct selection to increase growth will alter adaptational features. On the one hand, a favorable correlation suggests that selection for increased growth potential will be accompanied by an increase in resistance to *Meria* needle cast. But on the other, selecting for increased growth will alter the growth rhythm—bud set will be delayed while the duration of shoot growth is increased. In fact, with regard to growth rhythm, one generation of breeding is expected to be similar to the transfer of unselected provenances from a mild environment to a severe (that is, transferring provenances upward in elevation by about 325 m). To the extent that the growth rhythm of natural populations is optimal, strong selection to increase growth will be accompanied by a deterioration of adaptedness. This also suggests that not all of the gains expected from tree improvement can be realized from direct selection on growth alone.

To overcome adverse genetic correlations such as those linking bud set with growth, breeders must accept lesser expected gains. Two approaches seem feasible: (1) develop restricted selection indices (Lin 1978) that allow gains in growth to be optimized while correlated responses in secondary traits are restricted, or (2) select for the rate (cm/day) of shoot growth instead of the amount of growth. This later approach not only seems suitable for western larch (Rehfeldt 1992b) but also for ponderosa pine (Rehfeldt 1992a), Jack pine (Magnussen and Yeatman 1988) and, possibly loblolly pine (Bridgewater 1990).

Regardless of the technique, controlling the correlated responses requires accepting about one-half of the gains in height expected from direct selection. This means that managers would have to accept gains of 9 to 10 percent instead of 18 to 20 percent in 8-year height. The temptation therefore, will be to augment expected gains by relaxing restrictions on the correlated responses. Relaxing the restrictions, however, increases the risks of maladaptation, and the more the restrictions are relaxed, the more selective breeding within adapted populations resembles provenance transfer.

An alternative to selective breeding, therefore, might be to achieve gains in growth by transferring provenances from slightly milder environments to slightly more severe. While such a program would not alleviate the risks associated with adverse genetic correlations, it would alleviate the costs associated with selective breeding. As long as provenance transfer is supported by long-term field tests (such as those being conducted by the Inland Empire Tree Improvement Cooperative), reasonable gains in growth can be expected with relatively low risk and cost.

Gene Conservation

In western larch, contemporary populations have resulted almost exclusively from natural reproduction. There is, moreover, no evidence suggesting that the natural system of genetic variability has been adulterated by a century of exploitation and management. Consequently, topics in gene conservation center primarily on managerial philosophies that are compatible with the natural system of genetic variability. As long as seed transfer in artificial reforestation is consistent with patterns of genetic variation among natural populations, planting programs not only maintain but also enhance the natural system. A managerial philosophy that embraces basic tenets of forest biology is, in itself, gene conservation.

Tree breeding programs are also a component of the long-term conservation effort. Such programs usually include provenance tests that can be viewed as small reserves of the natural genetic system. Breeding programs, moreover, frequently incorporate several breeding populations within which adaptations to specific environments are maintained.

Nevertheless, there are conservation measures that are appropriate for common species under intensive management. One includes the establishment of gene pool reserves while the natural population still predominates. An ideal format for such a program was described by Wilson (1990) who implemented measures to protect and conserve the native gene pool of Douglas-fir on State lands in coastal Washington. By representing the natural adaptive system, these reserves serve as temporary gene reservoirs for accommodating the unsettled issues of diversity and climate change as they impact forest management.

In addition, even though genetically similar populations tend to recur across the landscape, there are populations deserving special attention—those at either end of a cline in genetic variation. The genotypes contained in these populations tend to be unique, even though the genes themselves may be widespread. In general, silvicultural prescriptions that favor western larch would be appropriate for such populations as they become identified through the testing program.

THE NEAR FUTURE

The last decade has produced a general understanding of the genetic structure of western larch populations. While much of this information has been put into practice, considerably more is required to assure that current programs are biologically sound. Required are:

1. Completion of the studies of genetic variation by the Intermountain Research Station. The primary objective of this program is to develop models of genetic variation for guiding gene resource management in a variable or changing environment.
2. Establishing a series of studies that will provide for assessing genotype-environment interactions, predicting the responses of genotypes along environmental gradients, and forecasting gains in yields from either tree breeding or provenance transfer.
3. Quantitative definition of the risks and gains associated with small-scale provenance transfer. Potential gains from provenance transfer and selective breeding within transferred provenances are higher, but more risky, than from selective breeding.
4. Establishment of gene reserves.

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Reproductive Biology of Larch

John N. Owens

Abstract—The reproductive biology is similar in all larches that have been studied. Cones are normally initiated on short shoots in the summer, and overwinter as preformed buds. Pollination occurs in late winter or early spring of the second year. Fertilization occurs about 6 weeks later, and embryos and cones are mature in late summer. Cone production is periodic, and filled seeds per cone is generally low. Causes of low seed set are thought to be caused by poor pollination and embryo abortion.

The reproductive biology of *Larix* has been described in part for several species and most completely for western larch (*Larix occidentalis* Nutt.). If we assume a reasonable uniformity within the genus, a general description of the reproductive biology can be made. Although the larches are frequent and often abundant producers of cones, they produce relatively few filled seeds per cone. Consequently, low seed production for reforestation is a common concern for all species. This is particularly important in species for which genetic tree improvement programs, seed orchards, or seed production areas have been established. Understanding the reproductive biology is the first essential step for enhancing seed production. The purpose of this technical review is to: review existing knowledge of all aspects of reproductive biology, from cone initiation to seed release; draw attention to those areas in which information is lacking; and suggest areas of useful research. Western larch will be emphasized, but information from other *Larix* species will be heavily drawn upon.

Larix has a reproductive cycle typical of most genera within the Pinaceae. *Larix* is monoecious, bearing both pollen and seed cones. Cone initiation occurs in early summer, almost 1 year before pollination. Pollen- and seed-cone buds are fully developed before winter dormancy. Pollination occurs the next spring and is followed in about 2 months by fertilization. Embryo development is rapid and is completed by late summer when cones mature, dry, open, and shed their seeds (fig. 1).

FREQUENCY OF CONE PRODUCTION AND CONE DISTRIBUTION

In western larch, cones are produced infrequently before age 25. After trees are 40 to 50 years old they generally bear abundant cones for 400 to 500 years (Boe 1958; Fowells 1965). Mature trees have good cone crops on the average every 5 years, but this may range from 1 to 12 years (Roe 1966). Seed cones are often widely scattered throughout the crown, making collection difficult and costly. Cones are relatively small with only a moderate seed potential and few filled seed per cone.

In mature trees, seed- and pollen-cone buds usually arise from a vegetative short (dwarf) shoot apex that is 1 to several years old. Seed cones commonly occur in the upper crown and more distally on branches. Pollen cones commonly occur in the lower crown and more proximally on branches. However, there is considerable overlap in cone positions in both crown and branch. Pollen cones and seed cones frequently intermingle on lower branches. In young trees, seed cones appear first followed within a few years by pollen cones, and seed cones may differentiate from newly initiated axillary buds rather than older short shoots, resulting in mature seed cones being borne on 1-year-old shoots (Powell and others 1984). This is less frequent in mature trees but has been observed in seed orchards and on scions subjected to cone induction treatments.

BUD INITIATION AND DEVELOPMENT

Vegetative Buds and Shoots

To understand and predict the position of cone buds and the method and time of cone initiation, it is necessary to be familiar with vegetative bud and shoot development (fig. 2). The Laricoideae, within the Pinaceae, have both long and short shoots. Lateral branches normally bear a long shoot in the terminal position and one or two in the distal lateral positions. More proximal shoots are commonly short shoots (fig. 3). The dormant long-shoot buds (LSB) are mostly preformed. They bear many brown outer bud scales, and inside of this complex are many basal and some axial leaf primordia (figs. 4, 5). Following dormancy, additional (approximately 30 percent) axial leaf primordia are initiated. After flushing, some axial leaves initiate buds in their axils. Distal buds commonly develop into LSB, and proximal buds develop into short shoot buds (SSB), and the cycle is repeated. The LSB undergoes considerable internode elongation.

The SSB initiates a series of outer bud scales, then a series of basal leaf primordia, the number being characteristic of the species. No axial leaves or axillary buds are initiated, and SSB are completely preformed before winter dormancy (fig. 6). The following spring, leaves elongate and SSB burst, but there is no internode elongation. The apical meristem initiates another series of bud scales followed by leaf primordia to form a bud and thus repeat the cycle.

Larix is more opportunistic in bud and shoot development than most other members of the Pinaceae. Occasionally older LSB convert to SSB, and vice versa. The phenology of LSB and SSB development described above for western larch is shown in figure 2 (Owens and Molder 1979a). Some aspects of shoot, LSB, and SSB development have been described for *L. leptolepis*, Japanese larch

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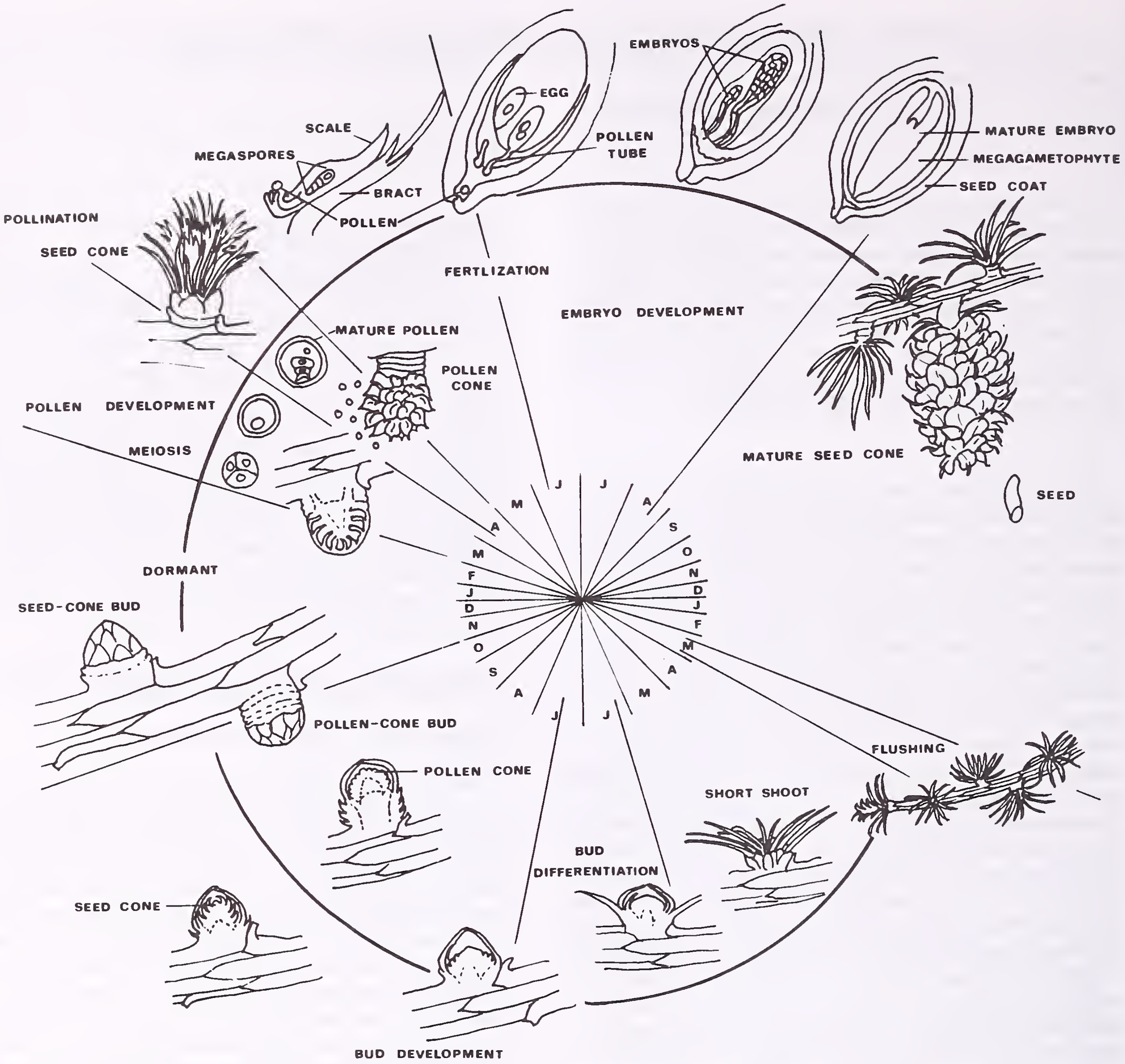


Figure 1—Reproductive cycle of western larch based on a study in south-central British Columbia.

(Fujimoto 1978), *L. decidua*, European larch (Frampton 1960; Fujimoto 1978) and *L. laricina*, tamarack (Kozlowski and Clausen 1966; Remphrey and Powell 1984).

Cone Initiation and Predormancy Development

Both pollen- and seed-cone buds are normally initiated within 1-year or older SSB. After SSB flush in the spring, the apical meristem continues to initiate bud scales for about 3 months. In western larch, bud-scale initiation stops in mid-June, then apices begin to initiate leaf, microsporophyll, or bract primordia (Owens and Molder 1979b). The phenologies of SSB, LSB, pollen- and seed-cone buds are shown in figure 7.

Microsporophylls are initiated for about 2 months followed by the differentiation of two abaxial microsporangia on each microsporophyll (figs. 8-10). Microsporangia form sporogenous cells which, in turn, form pollen-mother cells. The pollen-mother cells begin meiosis and overwinter at the diffuse diplotene stage in western larch (fig. 9) (Owens and Molder 1979b), *L. siberica*, Siberian larch, European and Japanese larch (Ekberg and others 1968; Eriksson 1968). Dormant pollen-cone buds are much larger than SSB and are brown and dome shaped in western larch. The short shoot axis on which each is borne varies in length depending on the age of the short shoot (fig. 11).

Seed-cone buds initiate several basal foliar organs, then bracts and axillary ovuliferous scales during the next 4 months (figs. 12, 14). Two ovule primordia are initiated on the adaxial surface of each ovuliferous scale (fig. 12).

Each ovule forms a large, central megaspore mother cell that does not begin meiosis before winter dormancy. Both pollen- and seed-cone buds become dormant in early fall in western larch (fig. 7) (Owens and Molder 1979b). Dormant seed-cone buds are about the same size and color as pollen-cone buds but are usually more conical (fig. 13) (Owens and Molder 1979b; Roe 1966). The time and method of cone initiation and phenology of cone bud development in other larch species have not been described but are probably quite similar to western larch (Owens and Molder 1979b).

Proliferated seed cones are common in *Larix* (Tosh and Powell 1986). This happens when a seed-cone apex initiates a series of leaf primordia and bud scales after bracts have been initiated. This results in a seed cone with a vegetative long shoot at its apex. Bisporangiate cones are also common, especially in young trees or trees given cone induction treatments. Most bisporangiate cones initiate proximal microsporophylls and distal bracts (Tosh and Powell 1986). Proliferated and bisporangiate cones may partially or fully mature but are usually not abundant enough to be a significant factor in the reproductive biology of *Larix*.

Cone Induction

Cone production has been enhanced in *Larix* as in many other conifers (Owens and Blake 1985). Early experiments demonstrated that bending of horizontal branches downward induced pollen cones to form on upper surfaces of branches (Longman 1961). Spacing in natural stands has enhanced flowering in western larch (Shearer and Schmidt 1987). Girdling has been effective in several species (Bonnet-Masimbert 1982) with and without ammonium nitrate fertilizer (Graham 1986). Exogenously applied gibberellins (GA's) have given few consistent results for larch. GA$_{4/7}$ treatments on 7-year-old seedlings of Japanese and European larch resulted in twofold and eightfold increases in pollen cones and seed cones, respectively (Bonnet-Masimbert 1982). The response was enhanced with girdling. Ross (1991) applied GA$_{4/7}$ (30 mg/mL in 95 percent ethanol) by pulsed stem injection into 30-mm-deep drill holes with double-overlapping stem girdles to 17-year-old western larch. The first treatment was given in May, when long shoots of approximately 85 percent of the trees had flushed. The second treatment was 2 weeks later. New holes were drilled on each treatment

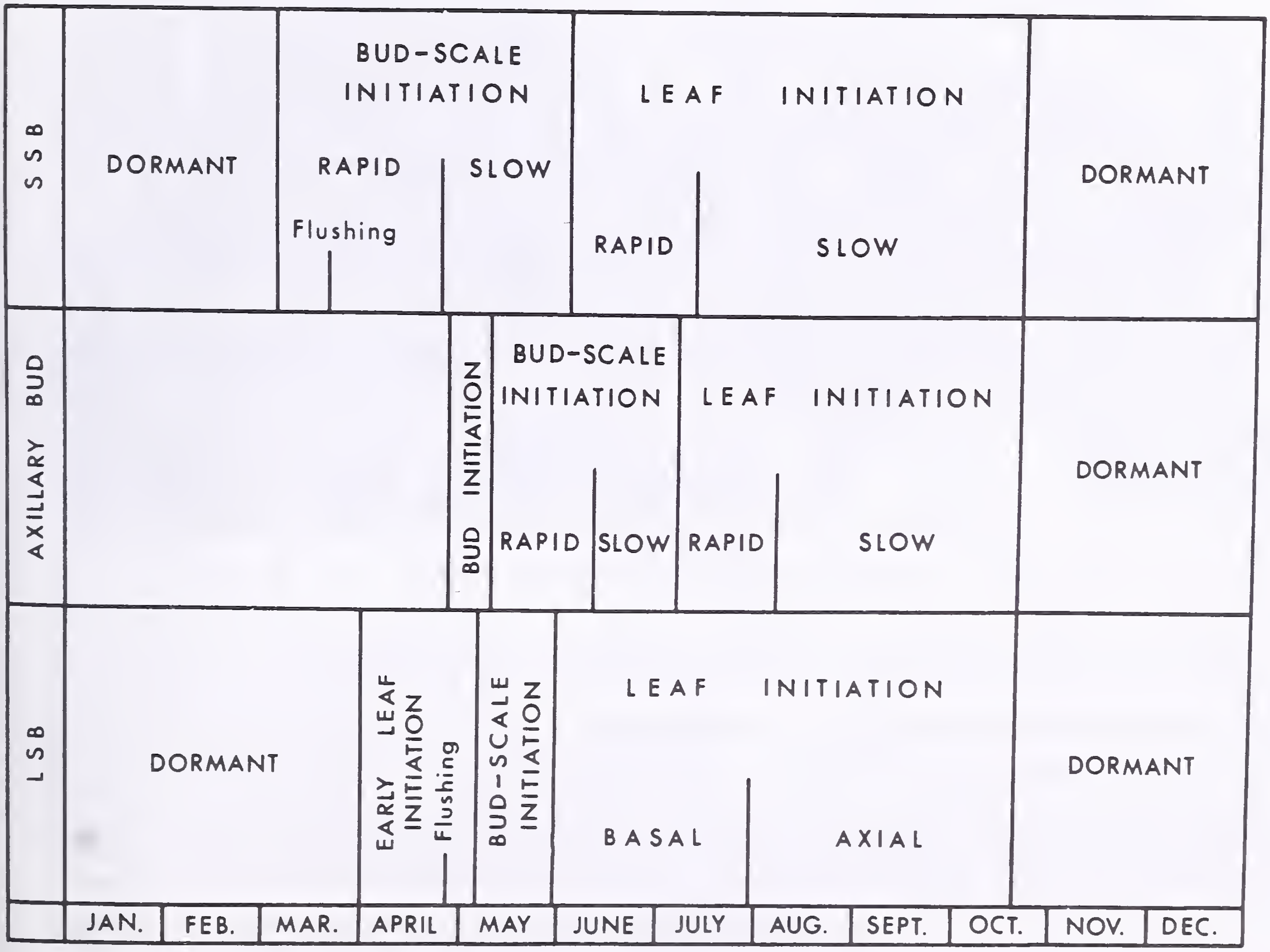
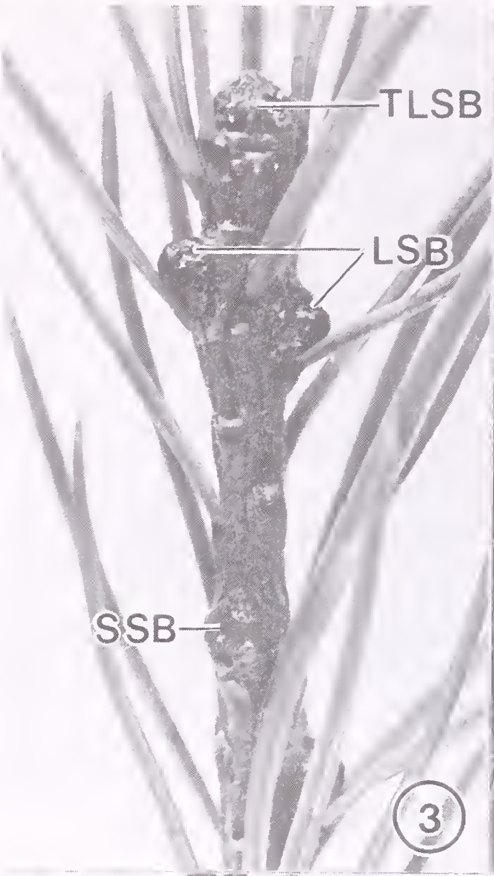
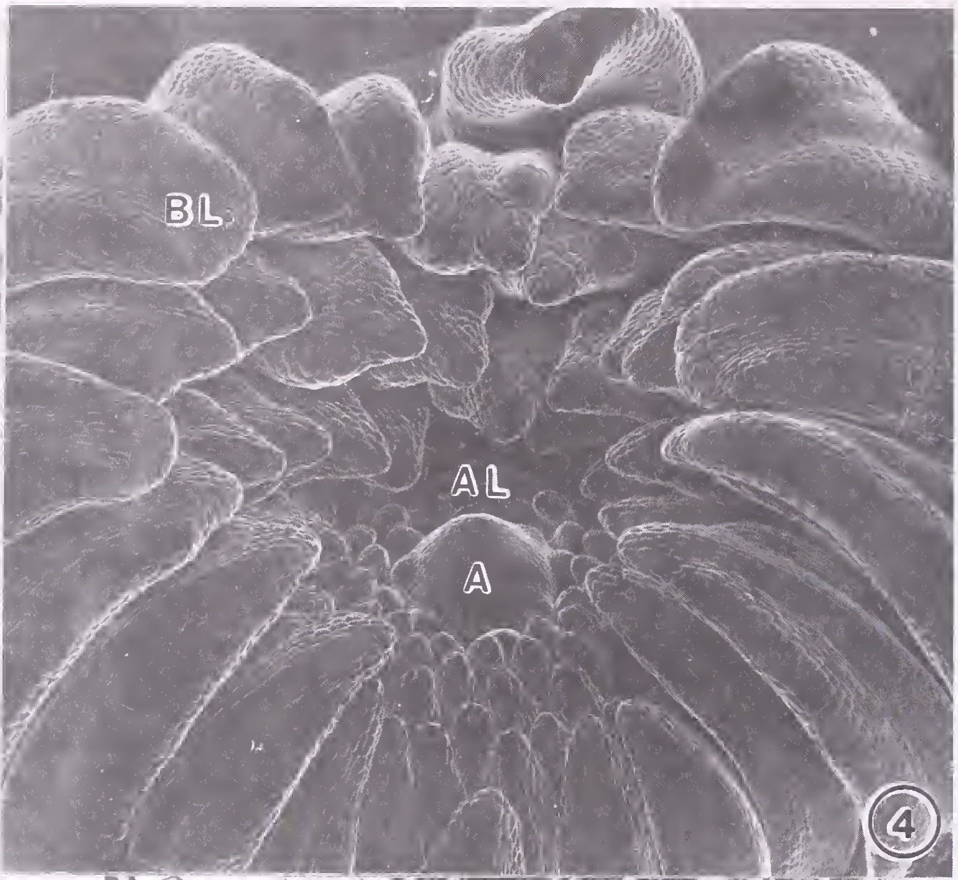
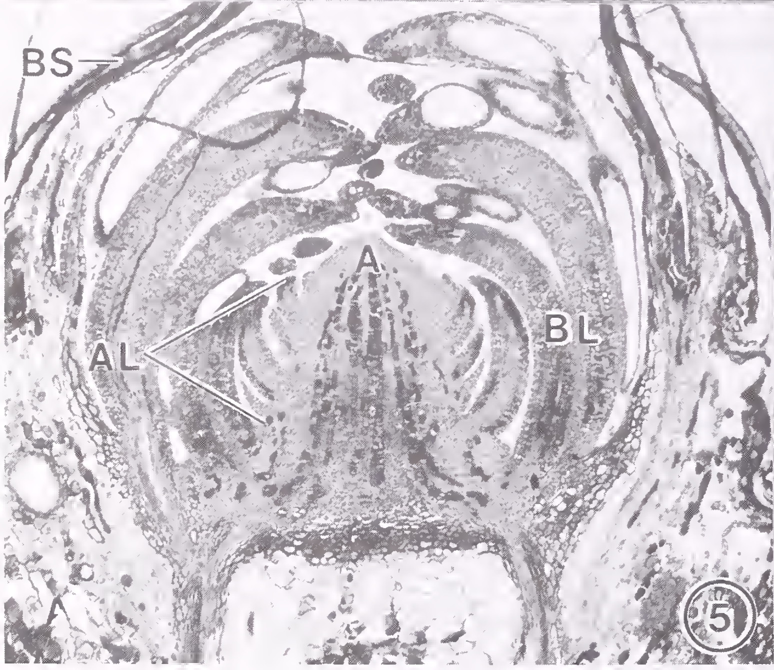


Figure 2—Phenology of vegetative bud development of western larch based on a study in south-central British Columbia (Owens and Molder 1979a).







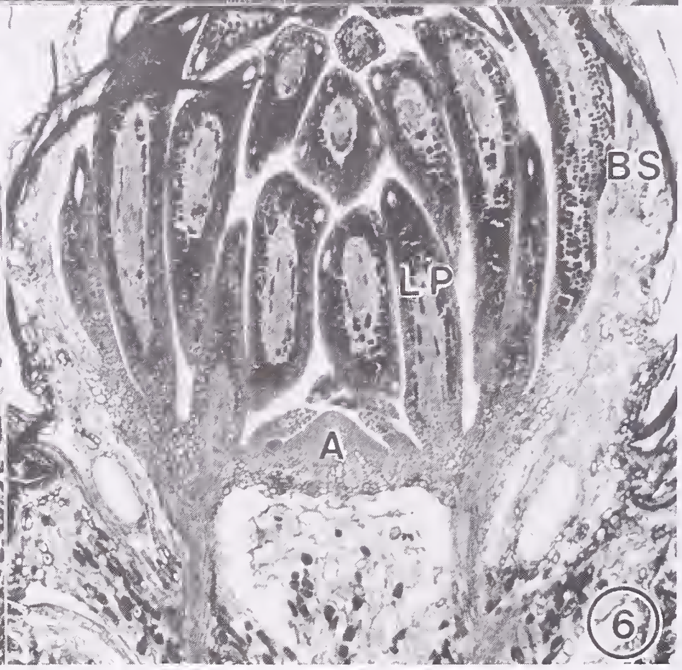


Figure 3—Enlarged distal end of a long shoot showing terminal long shoot bud (TLSB); axillary long shoot buds (LSB), and axillary short shoot buds (SSB). x 4.

Figure 4—Scanning electron micrograph of an unfixed dormant TLSB, with bud scales removed showing the apex (A), large basal (BL), and small axial leaf primordia. x 90.

Figure 5—Median longitudinal section of a dormant LSTB. BS, bud scales. x 35.

Figure 6—Median longitudinal section of a dormant SSB. LP, leaf primordia. x 35.

date. The $GA_{4/7}$ dose was adjusted to tree diameter by varying the number of holes drilled around the stem and the amount of solution injected per hole. Girdling alone did not increase the percentage of trees bearing cones and girdling + $GA_{4/7}$ was not better than $GA_{4/7}$ alone. Both responses were small and provenance specific.

Severe root pruning, resulting from root weevils, stimulated abundant cone production in 3-year-old potted western larch grafts (Ross 1991). Philipson (personal communication) has also obtained flowering in 3-year-old grafts of Japanese and European larch using $GA_{4/7}$, high temperature, and water stress. A followup study demonstrates the effect of these treatments on SSB development and cone bud differentiation (Owens and Philipson, unpublished data). These studies suggest that container orchards may be a viable option in larch. As in other conifers (Owens and Blake 1985), the timing of treatments in larch is important and must be related to bud and shoot phenology rather than calendar date.

Postdormancy Prepollination Development

Dormant cone buds resume development in late winter or early spring (early March in western larch). Pollen mother cells complete meiosis within 1 to 2 weeks followed by several weeks of pollen development and pollen-cone enlargement (fig. 1). *Larix* pollen development is typical of the Pinaceae (fig. 15). The four haploid microspores separate and become round, the outer pollen wall (exine) thickens, and starch accumulates within (fig. 16). The microspore then divides unequally twice, forming two small, lens-shaped prothallial cells and a large antheridial initial. During these divisions, the intine forms within the exine and around the prothallial cells. The antheridial initial divides unequally to form a small generative cell suspended within a large tube cell. The generative cell then divides to form the stalk and body cells (fig. 17). Mature pollen dehydrates to 10 to 15 percent moisture content, which usually causes it to indent. Mature pollen is 60 to 80 μ in diameter,

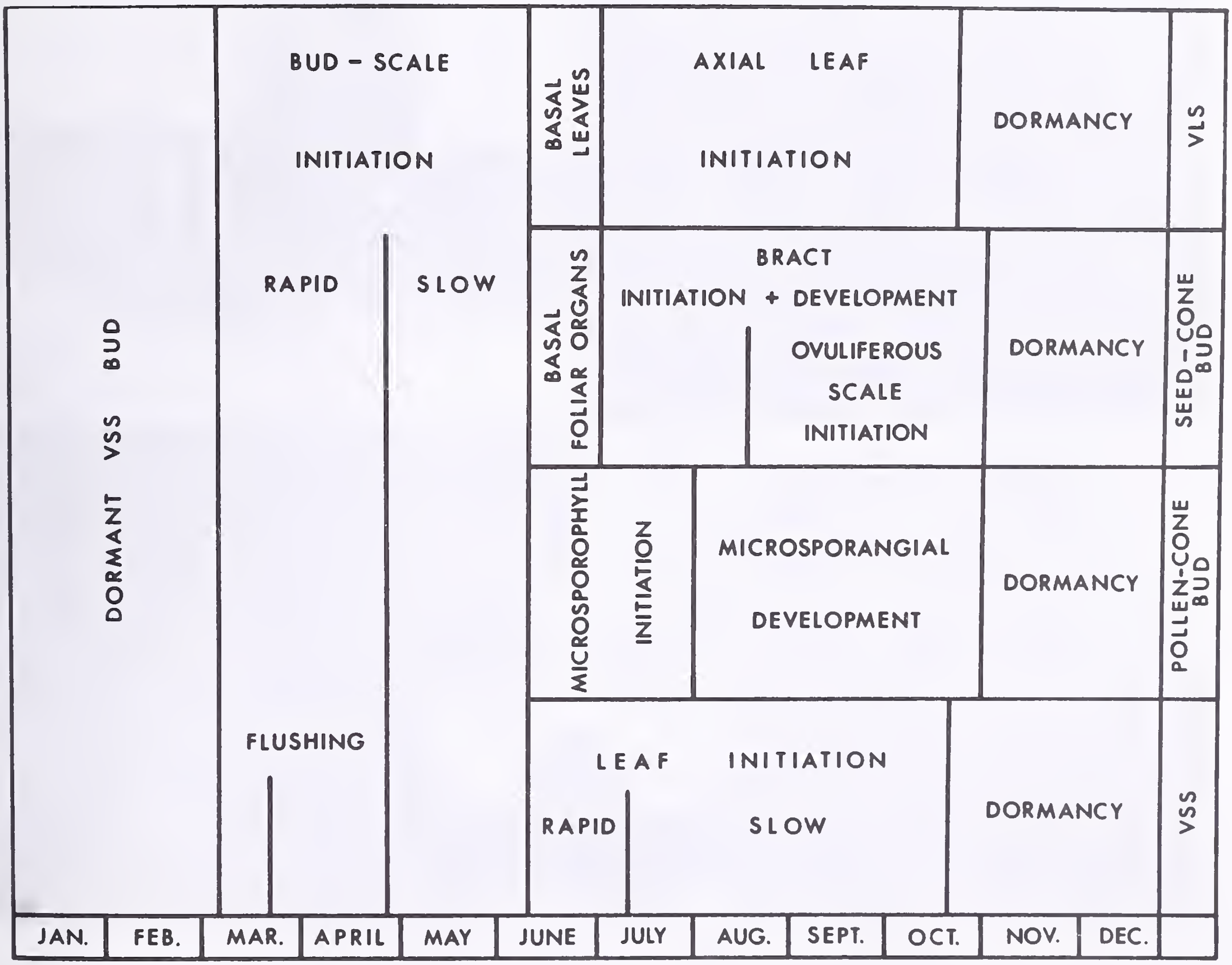
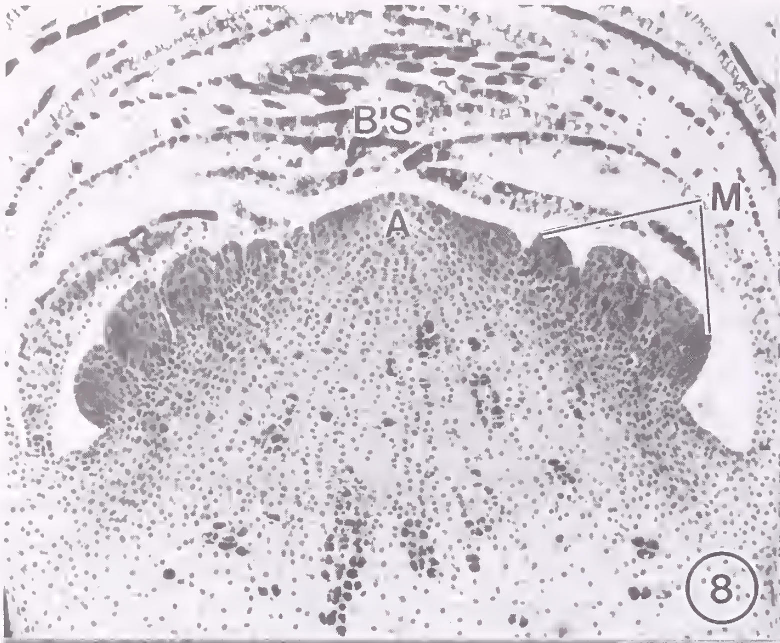


Figure 7—Phenologies of vegetative, pollen- and seed-cone buds of western larch based on a study in south-central British Columbia (Owens and Molder 1979b).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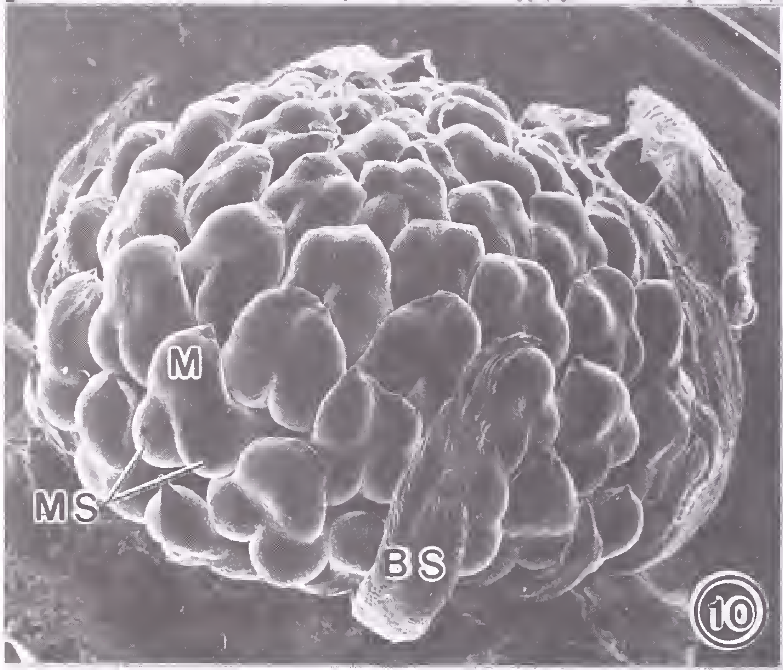
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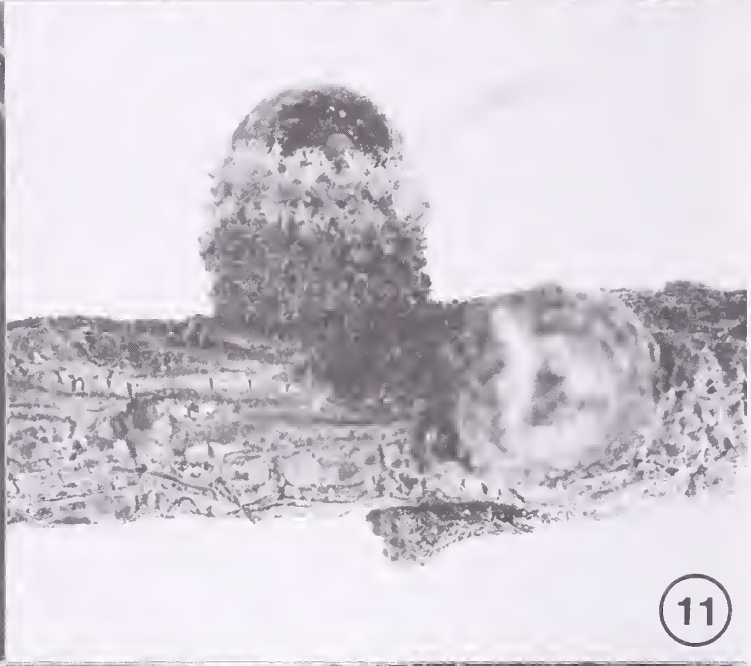
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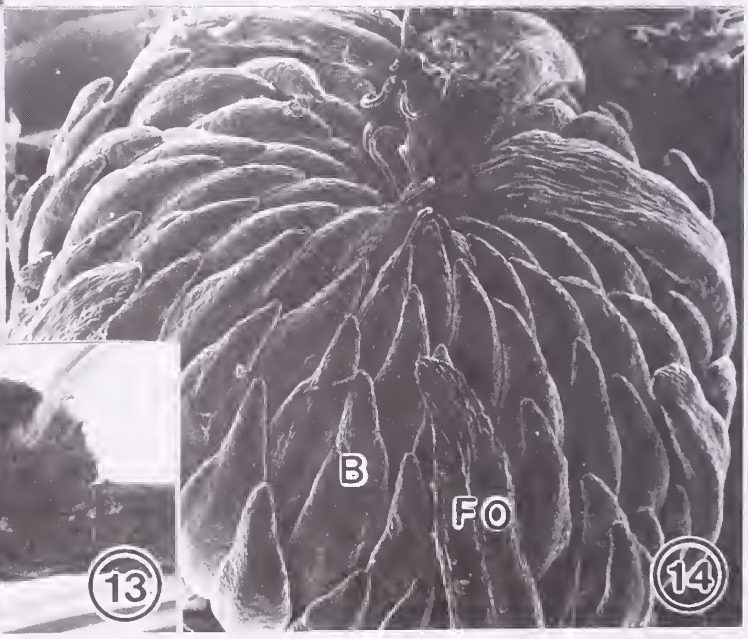
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Figure 8—Median longitudinal section of a pollen-cone bud collected in early July showing bud scales (BS), microsporophylls (M), and apex (A). x 65.

Figure 9—Median longitudinal section of a dormant pollen-cone bud showing microsporophylls (MS) containing pollen mother cells. R, resin canals. x 90.

Figure 10—Scanning electron micrograph of an unfixed dormant pollen-cone bud with nearly all bud-scales removed. x 85.

Figure 11—Dormant pollen-cone bud on 3-year-old shoot. x 5.

Figure 12—Median longitudinal section of a dormant seed-cone bud showing bracts (B), ovuliferous scales (OS), and basal foliar organs (FO). x 100.

Figure 13—Dormant seed-cone bud on a 2-year-old shoot. x 3.

Figure 14—Scanning electron micrograph of an unfixed dormant seed-cone bud. x 100.

lacks wings, and has a smooth exine except for triradiate ridges where the microspores joined (fig. 18).

During meiosis and pollen development, microsporangia swell and pollen cones enlarge and push through the bud scales. Pollen-cone buds commonly begin to flush several weeks before pollen is shed. The pollen-cone axis elongates for about 1 week separating the microsporophylls, which dry, split open, and shed the pollen (fig. 19).

Immediately after dormancy, the seed-cone axis, bracts, and basal foliar organs elongate and cause buds to flush within 2 to 3 weeks (fig. 20). Ovuliferous scales and ovules grow rapidly (fig. 21). The outer layer of the ovule, the integument, elongates to form a tubular micropylar canal and two integument lobes. The adaxial lobe is long, the abaxial lobe remains short, and there is a slitlike micropyle between the lobes. Short stigmatic hairs develop primarily on the adaxial lobe (fig. 22). Within the ovule, the nucellar tissue grows, and the large central megaspore mother cell undergoes meiosis to form a linear tetrad of haploid megaspores. The large inner megaspore remains functional, whereas the outer three degenerate.

The seed-cone axis elongates (figs. 23, 25) widening the spaces between the bracts to allow pollen to pass down to the ovuliferous scales and the receptive ovules.

Pollen- and seed-cone early development have been described in detail for western larch (Owens and Molder 1979c). The cytology and the environmental effects on the phenology of meiosis, microsporogenesis, and pollen development have been as thoroughly studied for *Larix* as for any other conifer (Eriksson 1968; Hall and Brown 1976; Owens and Molder 1979c).

POLLINATION

Pollen is dispersed by wind. Because the number of pollen cones is limited by the number of SSB that can differentiate into pollen cone buds, pollen cone and thus pollen production is not as abundant in *Larix* as in many other conifers. Pollination occurs in early spring, soon after SSB (figs. 19, 20) flush but usually before LSB flush.

The pollination mechanism has been described for western larch (Owens and Molder 1979c), tamarack (Powell and Tosh 1991), and Japanese larch (Villar and others 1984). The following description is for western larch.

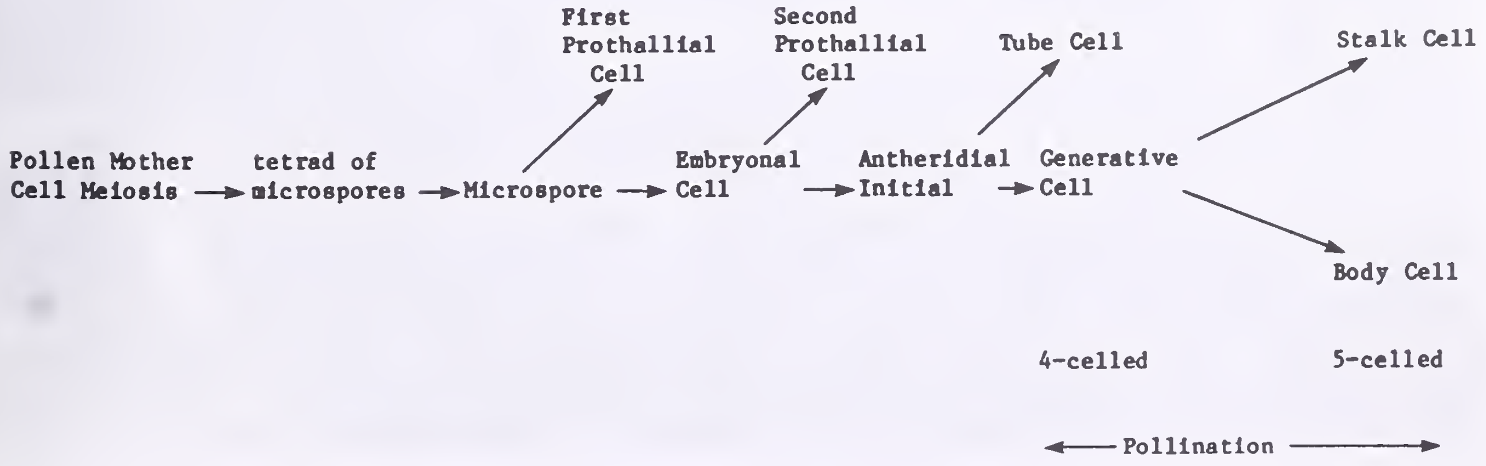
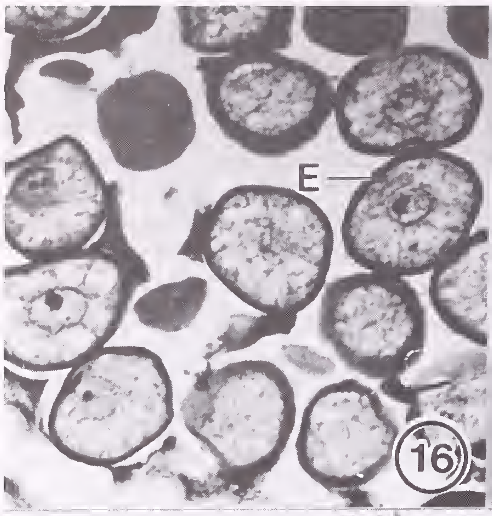


Figure 15—The sequence of cell divisions during pollen development in *Larix* and other Pinaceae (Owens and Blake 1985).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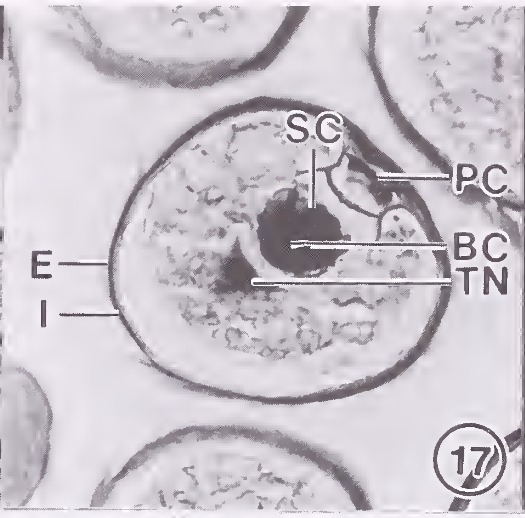
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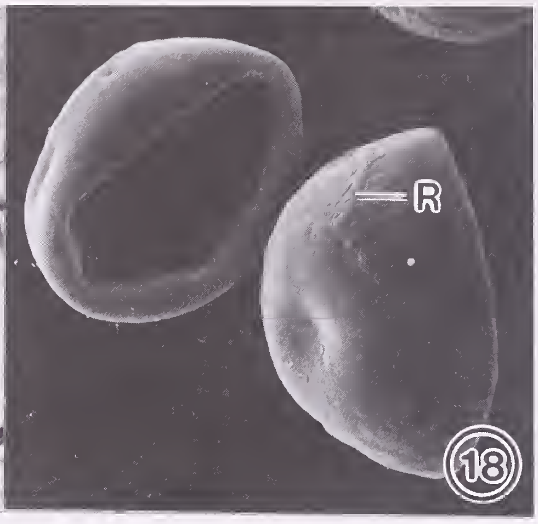
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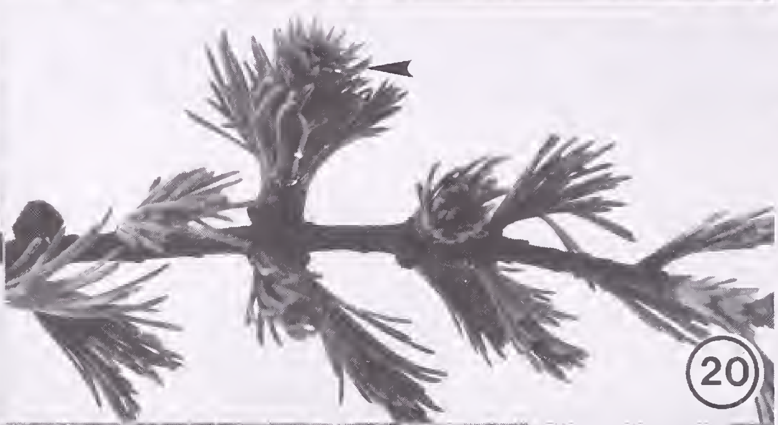
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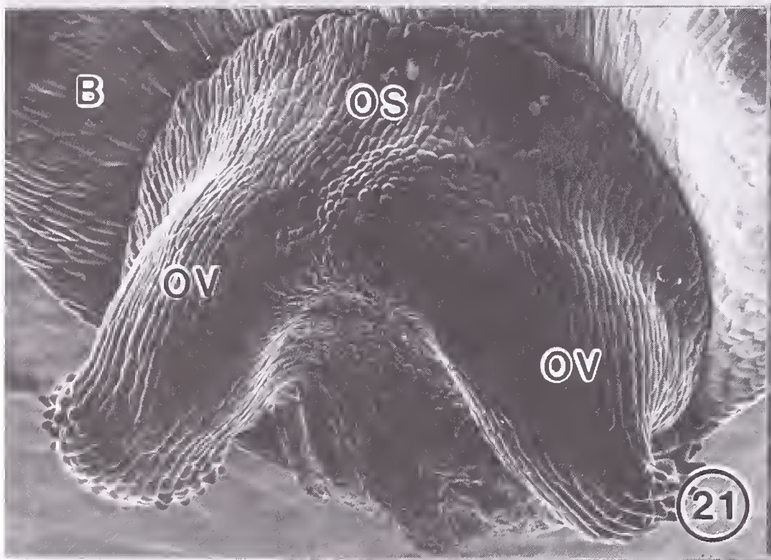
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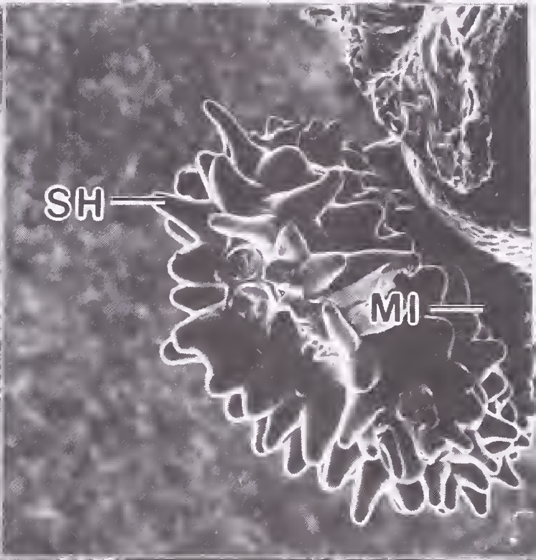
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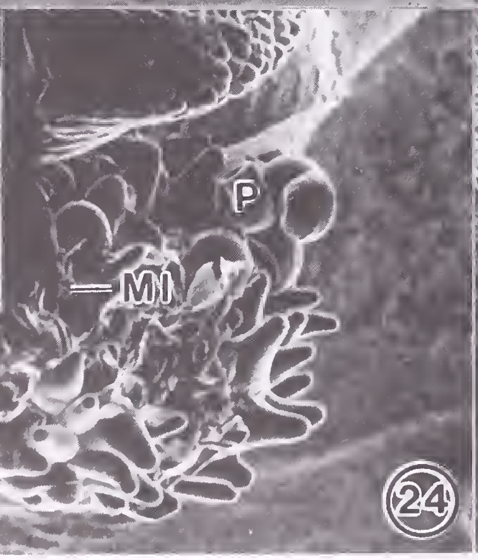
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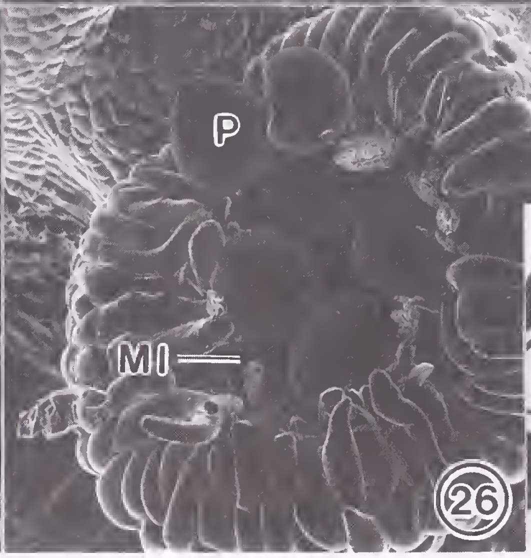
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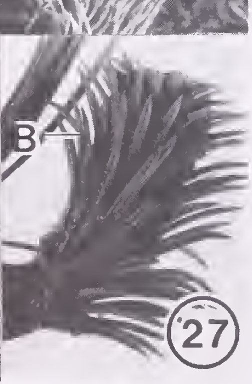
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Figure 16—Section through a microsporangium showing one- and two-cell pollen grains collected in mid-March. E, exine. x 300.

Figure 17—Section of a mature five-cell pollen grain collected in early April showing exine, intine (I), prothallial cells (PC), stalk cell (SC), body cell (BC), and tube nucleus (TN) in the tube cytoplasm. x 1,000.

Figure 18—Scanning electron micrograph of mature, dry, gold coated pollen showing the triradiate scar (R). x 1,000.

Figure 19—Branch at pollination in late April showing a pollen cone (arrowhead). x 1.

Figure 20—Branch at pollination showing a seed cone (arrowhead). x 1.

Figure 21—Scanning electron micrograph of an unfixed ovuliferous scale bearing two ovules before pollination. B, bract. x 130.

Figure 22—Scanning electron micrograph of an unfixed integument tip just before cones are receptive pollination showing the stigmatic hairs (SH) and the slitlike micropyle (MI). x 270.

Figure 23—Emerging prereceptive seed cone. x 1.

Figure 24—Scanning electron micrograph of an unfixed integument tip showing stigmatic hairs with pollen (P) attached from a receptive seed cone. x 270.

Figure 25—Receptive seed cone. x 1.

Figure 26—Scanning electron micrograph of an unfixed integument tip showing pollen being engulfed into the micropyle from a postreceptive seed cone. x 270.

Figure 27—Postreceptive seed cone. x 1.

The integument tips of the ovules form a spiral of large receptive surfaces around and along the length of the cone axis. Stigmatic hairs develop on most of the tips by the time the seed cone is open (figs. 24, 25). Pollen may pass directly to the tip or land on the smooth bracts and be funneled down to the tips.

Pollen collects on the stigmatic hairs over several days (the micropyle is too narrow for pollen to enter directly). The outer cells of the integument tips then elongate, and the hairs around the micropyle collapse. This causes the integument tip to grow inward, carrying pollen attached to stigmatic hairs close to the micropyle into the micropyle (fig. 26) (Owens and Molder 1979c). More peripherally situated pollen may not be engulfed. The integument tips do not discriminate between different types of pollen or other foreign particles; if they fit they can be taken into the ovule. Also, the engulfing process occurs in the absence of pollen.

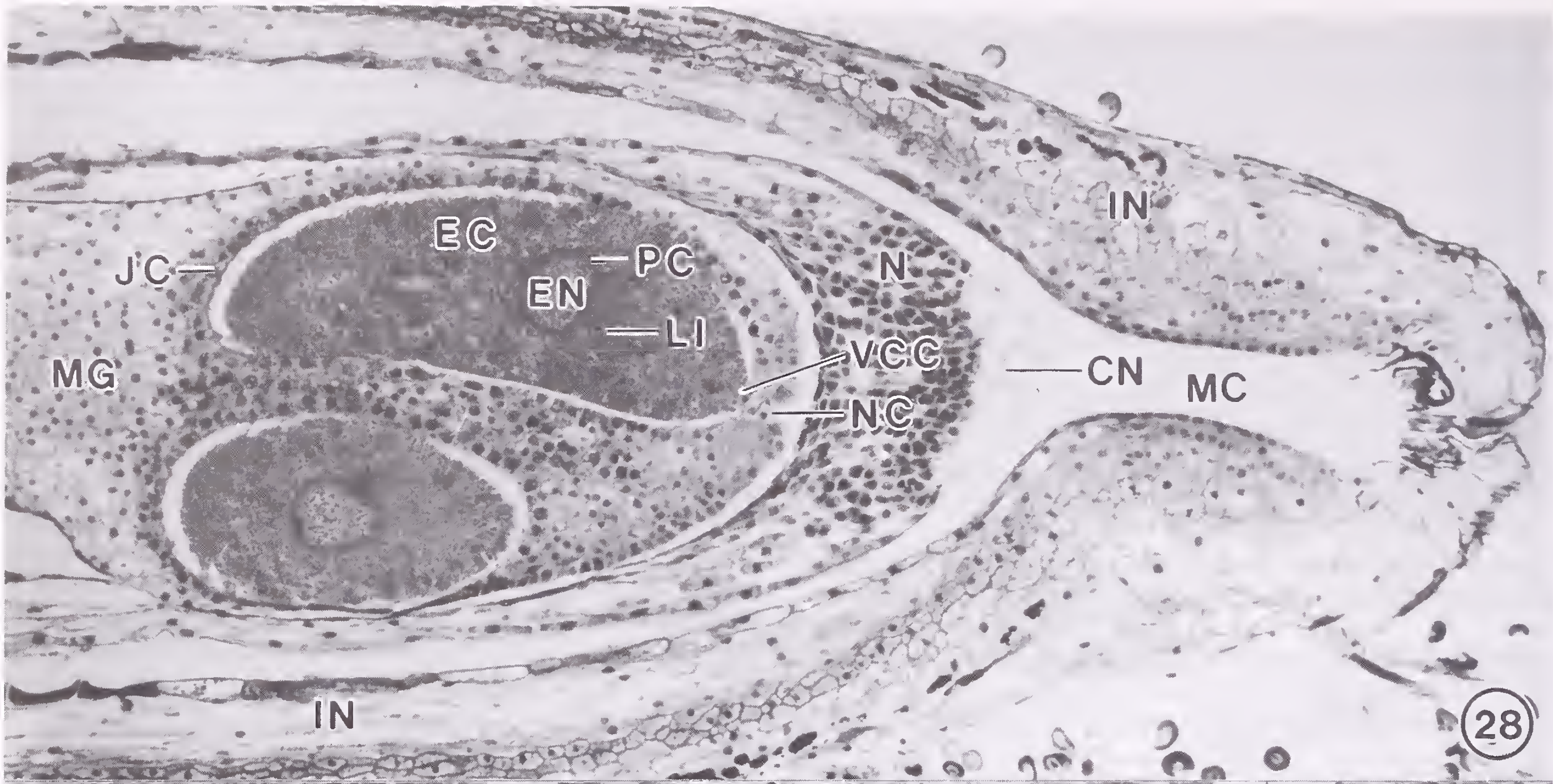
Each cone is receptive for several days in western larch, and maximum receptivity occurs during the 3 to 5 days (fig. 25) after seed-cone buds flush. Cones are no longer receptive once the engulfing process is completed for all ovules or when the scales thicken and seal the cone so that pollen cannot enter (figs. 26, 27). This usually occurs 5 to 7 days after seed-cone buds flush (fig. 1) (Owens and others 1994).

OVULE DEVELOPMENT

The ovule develops rapidly after pollination forming a mature megagametophyte within 6 to 8 weeks (fig. 1). Megagametophyte development is similar in all larch species described thus far and follows the typical Pinaceae pattern. The inner functional megaspore enlarges as the outer three degenerate. The functional megaspore then undergoes free nuclear division. A peripheral layer of cytoplasm containing the haploid nuclei surrounds a large central vacuole. About 1 month after meiosis, cell wall formation begins in the megagametophyte. Anticlinal walls separate all nuclei forming elongate primary prothallial cells. These cells then divide periclinally and the central vacuole becomes filled with isodiametric megagametophyte cells (Owens and Molder 1979c).

Several longer pyramidal cells at the micropylar end of the megagametophyte do not divide but enlarge to form archegonial initials bordered by small jacket cells. Within 1 or 2 weeks, each large archegonial initial divides unequally, producing a small outer primary neck cell and a large inner central cell. The primary neck cell divides anticlinally to form several neck cells. The central cell enlarges and becomes vacuolate. Then about 2 months after pollination, the cell divides unequally to form a small lens-shaped ventral canal cell beneath the neck cells and a large egg cell. The egg nucleus migrates to the center of the egg, its position at fertilization (fig. 28) (Owens and Molder 1979c).

Cytoplasmic changes occur within the developing central and egg cells. Plastids enlarge and engulf large areas of cytoplasm, the plastid stroma becomes reduced and condensed, and lamellae disappear. This process converts all plastids into the large inclusions of the egg (fig. 28; Camefort 1967; Owens and Morris 1990). Tiny cytoplasmic nodules enveloped by crescent-shaped vacuoles form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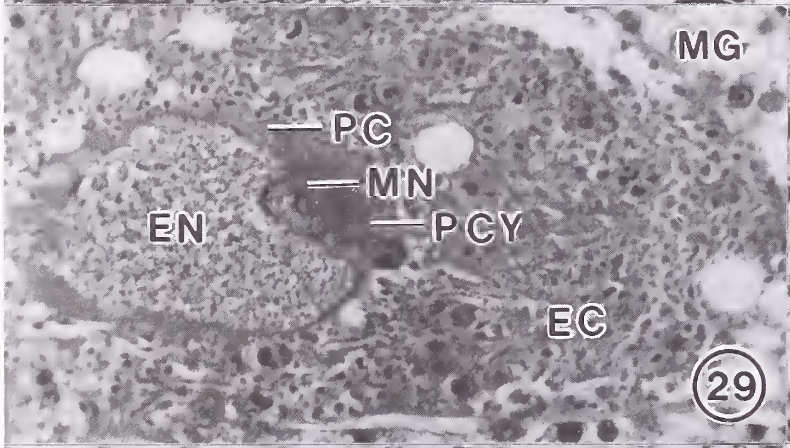
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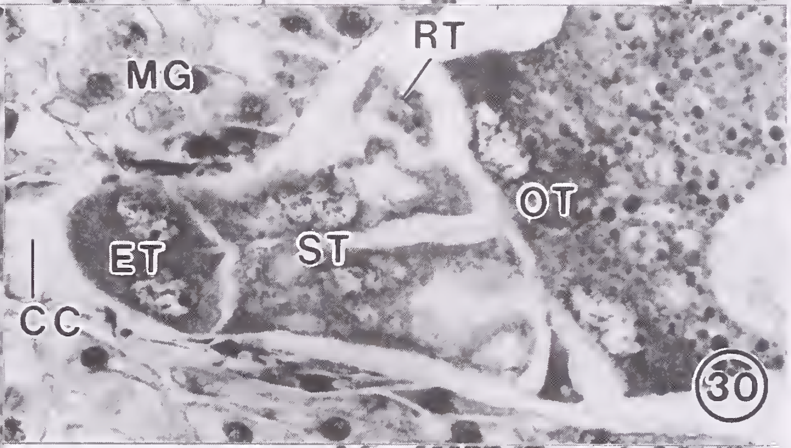
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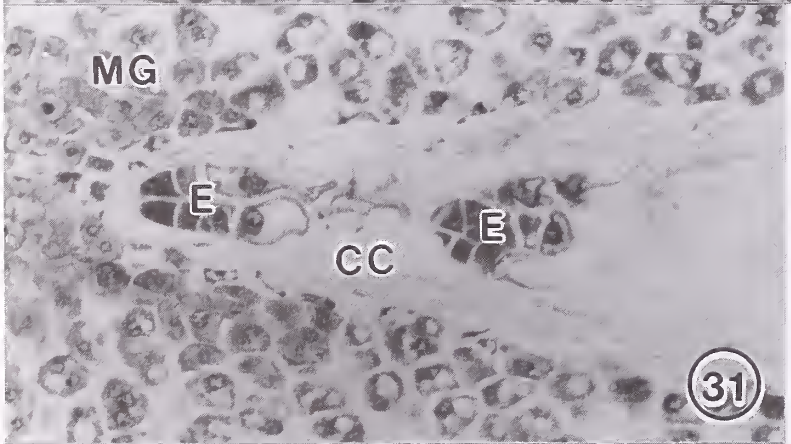
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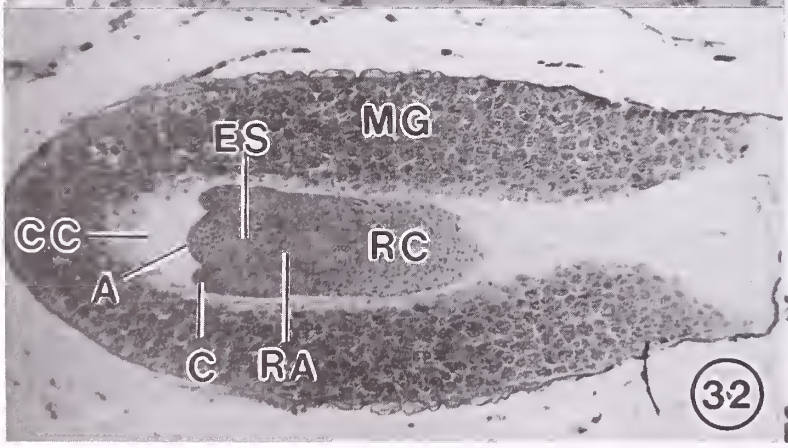
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Figure 28—Median longitudinal section of an ovule collected in mid-June showing integument (IN), micropylar canal (MC), nucellus (N), collapsed nucellar tip cells (CN), megagametophyte (MG), jacket cells (JC), egg cell (EC), egg nucleus (EN), perinuclear cytoplasm (PC), large inclusions (LI), ventral canal cell (VCC), and neck cells (NC). x 50.

Figure 29—Median longitudinal section of an egg cell at fertilization in early June showing the male gamete (MN) entering the egg nucleus and the paternal cytoplasm combining with the maternal perinuclear cytoplasm. x 225.

Figure 30—Median longitudinal section of a four tiered early embryo collected in mid-June showing the embryonal tier (ET), elongating suspensor tier (ST), rosette tier (RT), and open tier (OT). x 340. CC, corrosion cavity. x 340.

Figure 31—Median longitudinal section of a megagametophyte showing two early embryos (E) collected in late June. x 120.

Figure 32—Median longitudinal section of a megagametophyte containing a young embryo collected in mid-July showing the apex (A), cotyledon primordia (C), embryonic stile (ES), root apex (RA), and root cap (RC). x 30.

Figure 33—Median longitudinal section of a megagametophyte and embryo from a mature seed collected in September. EC, embryonic cortex. x 50.

many small inclusions (Singh 1978). Mitochondria become deformed and migrate around the egg nucleus where they, with the dense egg cytoplasm and small organelles, form the perinuclear zone (cytoplasm) (figs. 28, 29; Camefort 1967). The mature egg structure of *Larix* is typical of the Pinaceae (Singh 1978).

The number of archegonia, and thus eggs, per megagametophyte varies among individuals and species: European larch from one to five (Schopf 1943), western larch two to five (Owens and Molder 1979c), but three to four are common numbers in *Larix*. The mature megagametophyte is bounded by a megaspore cell wall, and outside this is the nucellus. The nucellus is attached at its base to the integument, which completely encloses the nucellus (fig. 28).

FERTILIZATION

Pollen taken into the micropylar canal is sealed inside by the closing of the micropyle. Pollen remains in this position for several weeks. There it hydrates, swells, and sheds the exine. In western larch, about 7 weeks after pollination, secretions from the nucellus fill the micropylar canal then recede, drawing the pollen down to the nucellar tip (Owens and others 1994). There the pollen germinates and forms a pollen tube, which penetrates the nucellus. Commonly, several pollen grains are in the micropylar canal, but not all are drawn to the nucellus nor do all germinate. Usually more than one forms a pollen tube. Each pollen tube grows unbranched between the nucellar cells to an archegonium. The large body cell, the tube nucleus, and often the stalk cell pass down the narrow pollen tube within the tube cytoplasm. The body cell settles into a depression (the archegonial chamber) above the neck cells. There the body cell divides to form two large male gametes both surrounded by a common, dense body-cell cytoplasm, rich in plastids and mitochondria. A receptive vacuole forms in the egg cytoplasm, the pollen tube penetrates between neck cells and through the ventral canal cell then bursts, releasing its contents into the egg. The two male gametes and the dense body cell cytoplasm migrate toward the egg nucleus. The leading male gamete fuses with the egg nucleus to form the zygote (fig. 29) and the second male gamete eventually degenerates (Owens and Molder 1979c).

CYTOPLASMIC INHERITANCE

A large amount of the body cell cytoplasm, containing paternal plastids and mitochondria, fuses with the perinuclear cytoplasm. The perinuclear cytoplasm contains deformed maternal mitochondria but lacks plastids. The combined paternal and maternal cytoplasm, the neocytoplasm, surrounds the zygote nucleus and the free nuclei of the proembryo as they migrate to the chalazal end of the archegonium. There the maternal and paternal organelles freely intermingle. In the neocytoplasm, all plastids are paternal in origin (from the body cell), and most mitochondria are of maternal origin (from the perinuclear cytoplasm); whereas, some paternal mitochondria come from the body cell. This pattern of plastid and mitochondrial inheritance has been studied only partially in

European larch (Camefort 1968) but appears to be typical of the pattern found in other Pinaceae that have been studied (Owens and Morris 1991). Recent restriction fragment length polymorphism studies of plastid and mitochondrial DNA support this interpretation of cytoplasmic inheritance in the Pinaceae (Neale and Sederoff 1989).

EMBRYOGENY

One of the most precise and thorough studies of conifer embryogeny is that for European larch (Schopf 1943), which also includes some observation of other larch species and hybrids. Schopf described the sequence of development and origin of tissues present in the mature embryo as well as the theoretical interpretation of this embryogeny. The embryogeny and seed development of western larch have been described less thoroughly (Owens and Molder 1979c) but appear to be identical to European larch. Seed development, emphasizing seed sterility, has been described generally for *Larix* (Hakansson 1960). The following phenology is that of western larch with differences noted for some other species.

Proembryo development begins with free nuclear division of the zygote. Four free nuclei form and migrate within the neocytoplasm to the chalazal end of the archegonium where they form a single tier of nuclei. Mitosis occurs to form eight nuclei followed immediately by transverse then vertical cell walls to form a two-tiered proembryo with four cells per tier. The proximal tier divides transversely to form an open tier and a rosette, or disfunctional suspensor tier (Singh 1978). The distal tier then divides transversely to form the embryo tier and the subjacent suspensor tier. The proembryo stage ends when the suspensor tier elongates and forces the embryo tier out of the archegonium and into the corrosion cavity of the megagametophyte (fig. 30). This occurs about 2 weeks after fertilization in western larch (Owens and Molder 1979c). The corrosion cavity forms through a breakdown of megagametophyte cells in advance of the embryo (figs. 30-32). The suspensor cells elongate and coil, and embryonal tubes are added distally by transverse division of the embryo tier. The suspensor cells and embryonal tubes form a wide, coiled suspensor system. At the distal end, the embryo tier divides to form a small multicellular embryo (fig. 31).

Simple polyembryony commonly occurs when adequate pollen is available. However, by the time the multicellular embryo stage is reached in late June, usually one embryo dominates while the others degenerate (fig. 31). No cleavage polyembryony has been observed in larch, although all four quadrants of the multicellular embryo may not contribute equally to the embryo. This has been referred to as delayed cleavage (Singh 1978) and involves a dominance or overgrowth of one or more quadrants of cells during formation of the multicellular embryo. This is described in detail by Schopf (1943).

Subsequent embryo development is rapid. The multicellular embryo undergoes frequent cell division to form a club-shaped embryo with proximal and distal regions. The proximal region basally adds embryonal tubes to the suspensor and distally adds cells that are forerunners of the rootcap and the root initials. The hemisperical portion above the root initials forms the distal region, which develops into the embryonic shoot axis. About 1 month after fertilization several meristematically active regions arise on the surface of the distal region to form the cotyledon primordia. This leaves a small shoot apical meristem between. Below these, the shoot axis elongates rapidly to form the embryonic stele and cortex (fig. 32) (Owens and Molder 1979c).

The embryonic shoot and root elongate rapidly. By mid-August the embryo is mature and nearly fills the megagametophyte. It is divided into approximately equal thirds: (1) a proximal root cap joined to the suspensor at its base and ending with a distinct root apical meristem above; (2) a central shoot axis with a distinct central stele enclosed by a cortex and terminating in a small mitotically inactive shoot apical meristem; and (3) several cotyledons with distinct procambial strands that are continuous with the stele of the shoot axis (fig. 32).

During seed development the integument differentiates into the seed coat, which consists of a stony middle layer and thinner inner and outer layers. During embryo development, the cells of the megagametophyte and most cells within the embryo become nearly filled with lipid and protein bodies but store relatively little starch except in the root cap and cortex. Dehydration occurs during the last stage of seed development. As a result, the embryo fits more loosely in the corrosion cavity (fig. 33). A seed wing differentiates from the adaxial surface of the ovuliferous scale and is firmly attached to the ovule. An abscission layer begins to develop beneath the ovule and seed wing at fertilization. Developing seeds and seed wings begin to separate from the ovuliferous scale soon after fertilization.

FACTORS REDUCING SEED PRODUCTION

Despite the low production of filled seed in larch, there has been no one comprehensive published study of causes of seed loss in any of the species. Various possible causes of seed loss in European larch were described by Kosinski (1986). Schopf (1943) and Owens and Molder (1979c) attributed much of the seed loss to low levels of pollination that results in no embryos, abortion of the megagametophyte, and empty seeds in several larch species including western larch. Hakansson (1960) also noted a low number of fertilized eggs, presumably due to poor pollination, in European, Japanese, and Siberian larch. Embryo abortion, presumably due to self-inviability, was described for the last three species (Hakasson 1960) and for western larch (Owens and Molder 1979c). Observations were similar in all species. Abortion commonly occurs during early embryo development (fig. 31). Embryo development slows and stops, then the embryo degenerates. Although the megagametophyte then degenerates to varying extents, it has not been determined if embryos abort independent of the megagametophyte or in response to embryo-megagametophyte interactions. Careful study of both embryo and megagametophyte development and accumulation of storage products (lipids, proteins, and starch) in response to selfing and outcrossing must be made to determine the frequency and cause(s) of post-fertilization seed loss. Similarly, the pollination efficiency (percentage of ovules pollinated) and the fertilization efficiency (percentage of eggs fertilized) must be determined to assess other causes of seed loss.

Once the major causes of seed and cone loss are identified and the order of their importance determined, it will be possible to correct some of these causes in seed orchards and seed production areas through cone enhancement, supplemental mass pollination, improved pollination techniques, and selection of parents lacking inherent developmental constraints to seed and cone production.

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Carbon, Nitrogen, and Water Use by Larches and Co-occurring Evergreen Conifers

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Abstract—Larches and evergreen conifers can achieve a similar carbon balance; however, the carbon, nitrogen, and water use efficiency and allocation differ substantially and appear to be intrinsically related to leaf longevity. The net photosynthetic rate (weight basis) is lower for evergreen conifers than larch needles, but evergreen conifers often support two to three times greater foliage mass. The greater water demand by larches may help explain the restriction of larches to more mesic sites.

The expansive boreal and subalpine forests in the Northern Hemisphere are typically characterized by evergreen trees (Wolfe 1979). Larches, deciduous needle-leaf gymnosperms, however, are common components in many subalpine and boreal forests in the Northern Hemisphere. In fact, larches can occur at the northern and altitudinal limit for tree growth where evergreen conifers are absent (Gower and Richards 1990). The widespread occurrence of larches in these harsh environments is an intriguing mystery given the concept that the evergreen habit is more advantageous in harsh environments (Gower and Richards 1990; Mooney 1972; Schulze and others 1977; Waring and Franklin 1979). Larches possess physiological and morphological characteristics that enable them to survive, grow, and reproduce in environments that are commonly dominated by evergreen conifers.

In this paper we compare the major morphological and physiological characteristics that influence the productivity, allocation, and resource use efficiency of larches and co-occurring evergreen conifers. We focus on net primary productivity because it is related to the success of a plant or reproductive output (Harper and White 1974). Thus, from an evolutionary perspective, the leaf habit and morphology that maximizes long-term net primary production in an environment should be favored. To fully understand the natural distribution of larches, we must also understand the reproductive biology and community ecology of larches in relation to sympatric evergreen conifers; these topics are covered by numerous authors in this volume.

We compare leaf and canopy characteristics and resource use efficiency of larches and evergreen conifers. An understanding of these factors can help explain how larches achieve an annual net primary productivity similar to evergreen conifers. We define forest productivity as aboveground net primary productivity (*NPP*), which equals annual biomass increment (*BI*) plus detritus production (*D*), plus biomass consumed by herbivores (*H*). Detritus production refers to the biomass that is produced and shed annually (such as leaf litterfall). Thus:

$$NPP = BI + D + H$$

We use net primary production instead of more forestry-oriented measures of growth, such as board feet or cubic volume, for two reasons. First, biomass allocation to stem growth has a lower priority than to foliage and fine roots (Mooney 1972; Waring and Pitman 1985). Second, foliage and fine roots are responsible for carbon dioxide, water, and nutrient uptakes, which directly influence the competitiveness of a plant.

LEAF CHARACTERISTICS

Although the evergreen habit provides several advantages over the deciduous habit, the winter-deciduous habit precludes the necessity to construct tough foliage. Evergreen conifers must construct a thick cuticle to prevent desiccation and deter herbivory (Baig and Tranquillini 1976). However, because larches must build their entire foliage canopy each spring, it is important that they construct a cheap, disposable leaf. For example, specific leaf area, the amount of leaf area constructed per unit leaf mass, is twofold to threefold greater for larches than evergreen conifers (table 1). In fact, Gower and others (1993) observed a significant inverse relationship between specific leaf area and leaf longevity for European larch and three evergreen conifers.

An appreciation of the importance for larches to construct a cheap, disposable leaf can be gained by calculating the additional biomass that would be necessary for larches to build their same leaf area, but with a specific leaf area comparable to that of an evergreen conifer. For example, larches would have to construct 65 to more than 300 percent more foliage mass to support the same leaf area if they constructed needles similar to evergreen conifers (table 2). Matyssek (1986) also noted the benefit of the large specific leaf area of larch versus evergreen conifer foliage.

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Table 1—Net photosynthesis on an area (Ps area) and mass (Ps mass) basis, leaf nitrogen concentration on a mass basis (Leaf N) and specific leaf area (SLA) data for larchs and sympatric evergreen conifers

Species	Location	Tree age	Ps area	Ps mass	Leaf N	SLA	Source[1]
		Years	*µmol/m²/s*	*nmol/g/s*	*g/kg*	*m²/kg*	
Larix decidua	Bayreuth,	33	4.7	58.8	22.0	12.5	1
L. leptolepis	Germany		4.7	58.8	25.0	12.5	
L. dec. x *lep.*			5.2	65.0	29.0	12.5	
Picea abies			2.8	17.4	16.0	6.2	
Pinus sylvestris			—	—	16.0	—	
Larix decidua	Bayreuth,	30-33	4.0	—	—	11.9	2
L. leptolepis	Germany		4.0	—	—	14.3	
L. dec. x *lep.*			5.0	—	—	8.7	
Picea abies			2.5	—	—	7.6	
Larix decidua	Craigieburn Range,	12	4.8	—	—	—	3
Pinus contorta	New Zealand		3.8	—	—	—	
Pinus mugo			4.5	—	—	—	
Larix decidua	Gif-sur Yvette,	Seedlings	—	170.4	—	—	4
Pinus sylvestris	France (growth chamber study)		—	134.5	—	—	
Larix decidua	Bayreuth,	33	—	—	25.0	10.4	5
L. leptolepis	Germany		—	—	24.0	12.2	
L. dec. x *lep.*			—	—	30.0	11.6	
Larix decidua	Coulee Forest, WI	27	8.9	57.9	31.0	12.3	6
Quercus rubra			12.6	92.3	29.8	9.9	
Pinus strobus			8.5	36.8	21.9	7.4	
Pinus resinosa			11.1	23.6	16.3	5.0	
Picea abies			10.0	19.7	17.8	4.0	
Larix laricina	Slave Lake,	Mature	2.2	—	20.8	—	7
Picea mariana	Alberta, Canada	trees	2.5	—	11.1	—	
Larix laricina	Slave Lake,	24-30	2.2	—	—	—	8
Picea abies	Alberta, Canada		2.7	—	—	—	
Larix laricina	Sarona, WI	Mature	—	—	17.3	—	9
Picea mariana		trees	—	—	10.8	—	
Larix laricina	Slave Lake,	Mature	—	—	15.6	—	10
Picea mariana	Alberta, Canada	trees	—	—	6.7	—	
Larix laricina	Trout Lake, WI	50-60	—	—	—	11.6	6
Picea mariana			—	—	—	3.7	
Larix laricina	Ottawa, Canada	Mature	—	66.5	10.2	—	11
Picea mariana		trees	—	27.3	12.8	—	
Larix leptolepis	Devon,	19	5.8	82.1	—	14.1	12
Picea sitchensis	United Kingdom		8.8	43.6	—	4.9	
Abies grandis			7.1	36.0	—	5.0	
Tsuga heterophylla			6.3	66.3	—	10.5	
Larix lyallii	Ingle Pass, WA	Mature	—	—	21.0	13.3	6
Pinus albicaulis		trees	—	—	11.0	5.1	
Tsuga mertensiana			—	—	12.0	4.6	
Larix occidentalis	Chumstick Mt.,	65-70	—	—	20.0	8.4	13
Pinus contorta	WA		—	—	14.0	4.0	
Pseudotsuga menziesii			—	—	—	4.5	
Larix occidentalis	Blewett Pass, WA	Mature	—	—	17.0	7.6	6
Pinus contorta		trees	—	—	12.0	3.8	

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[1] Source: (1) Matyssek 1986; (2) Schulze and others 1986; (3) Benecke and Havranek 1980; (4) Gowin and others 1980; (5) Matyssek and Schulze 1987; (6) Gower and Richards 1990; (7) MacDonald and Lieffers 1990; (8) Dang and others 1991; (9) Tyrrell and Boerner 1987; (10) Lieffers and MacDonald 1990; (11) Small 1972; (12) Fry and Phillips 1977; (13) Gower 1987.

Table 2—Percent increase in foliage biomass with the SLA of a co-occurring evergreen conifer that must be constructed for larch to support the observed leaf area index

Site and species	Observed LAI	Observed SLA	Percent increase in foliage mass	Source
	m²/m²	*m²/kg*		
Chumstick Mt., WA, U.S.A.				
Larix occidentalis	1.4	8.4	—	Gower and others 1989
Pinus contorta	1.9	3.9	112	Gower and Grier 1989
Coulee Exp. Forest, WI, U.S.A.				Gower and others 1993
Larix decidua	5.1	13.7	—	
Pinus strobus	7.4	7.6	65	
Pinus resinosa	6.2	3.8	262	
Picea abies	10.2	3.3	316	

Leaf nitrogen concentration also influences productivity because net photosynthetic rate is positively correlated to leaf N concentration (Field and Mooney 1986; Gower and others 1993; Reich and others 1991, 1992). In general, leaf N concentration is greater for deciduous than evergreen tree species (Gosz 1981), and larches are no exception. Leaf N concentration of new foliage averages 83 percent greater for larches than co-occurring evergreen conifers (table 1). The difference in leaf N concentration is even greater between larches and evergreen conifers if all age cohorts for evergreen conifers are considered because foliage N concentration commonly decreases with needle age (Son and Gower 1991).

In general, net photosynthetic rate (mass basis) is greater for a deciduous than evergreen species (Chabot and Hicks 1982; Larcher 1983). Net photosynthesis (weight basis) is greater for larches than for evergreen conifers, whereas net photosynthesis on an area basis does not differ consistently between larches and evergreen conifers. The greater specific leaf area and leaf nitrogen concentration of larches than evergreen conifers helps explain the greater net photosynthetic rates (weight basis) for larches (table 1). The maximum net photosynthetic rate of conifers is inversely related to leaf longevity (Gower and others 1993). A similar inverse relationship between leaf longevity and net photosynthesis has been reported for other tree species (Reich and others 1991, 1992), suggesting that this relationship may be universal. The differences in biochemical and morphological leaf characteristics between larches and evergreen conifers explain in part how larches successfully compete with evergreen conifers.

One suggested advantage of evergreens is that they accumulate a significant percentage of their annual carbon budget during the leafless period of deciduous species. While this theory may be correct for evergreens growing in mild climates (Emmingham and Waring 1977; Waring and Franklin 1979), only a small amount of the annual carbon assimilated by evergreens occurs during the leafless period of larches due to adverse effects of the low light levels and extreme air temperature on photosynthesis (Benecke and Havranek 1980; Kloeppel unpublished data; Tranquillini 1979).

CANOPY DYNAMICS AND PRODUCTIVITY

A long-time argument is that the evergreen habit allows evergreens to support a greater foliage mass or area than is supported by deciduous tree species (Schulze and others 1977). Comparison of foliage biomass allometric relationships between larches and co-occurring evergreens suggests that evergreens support a greater foliage mass than larches (fig. 1). Moreover, the difference increases as the leaf longevity of the evergreen conifer increases. However, leaf area does not differ as much, and sometimes does not differ at all, between larches and

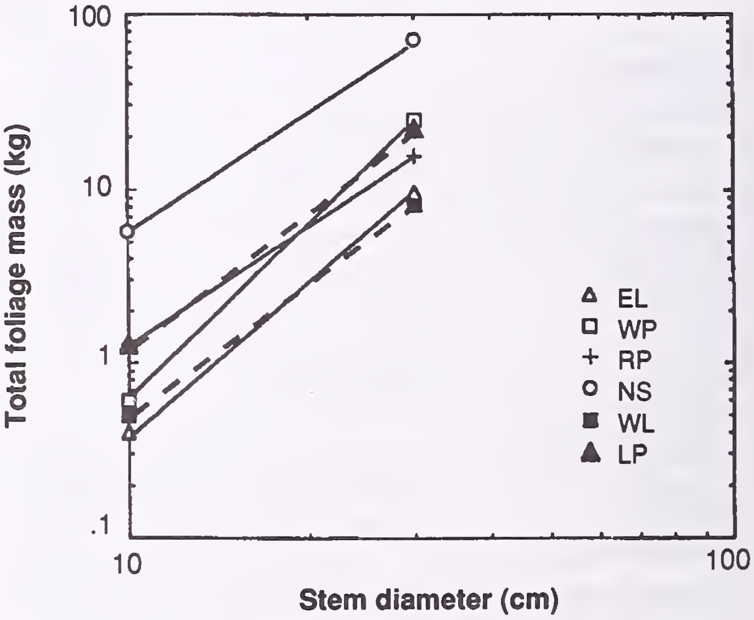

Figure 1—Allometric relationship between total foliage mass (kg) and stem diameter (cm) for larches and co-occurring evergreen conifers. Closed symbols are for western larch (WL) and lodgepole pine (LP) in a natural, mixed stand in Washington (Gower and others 1987) and open symbols are for European larch (EL), white pine (WP), red pine (RP), and Norway spruce (NS) plantations in southwestern Wisconsin (Gower and others 1993).

Table 3—Aboveground net primary production for natural and plantation forests dominated by or containing larch

Location	Species	ANPP	Source[1]
		t/ha/yr	
	Natural Forests		
Idaho, U.S.A. 48°20' N.	*Larix occidentalis* (17)[2] *Pinus monticola* (24) *Thuja plicata* (54)	10.0	1
Idaho, U.S.A. 46°35' N.	*Larix occidentalis* (21) *Pinus monticola* (15) *Abies grandis* (43) *Pseudotsuga menziesii* (19)	7.5	1
Washington, U.S.A. 47°39' N.	*Larix occidentalis* (46) *Pinus contorta* (51)	8.9	2
Washington, U.S.A. 48°30' N.	*Larix occidentalis* *Pinus contorta* *Pseudotsuga menziesii*	8.0	3
	Plantations		
Wisconsin, U.S.A. 43°52' N.	*Larix decidua* (100)	9.3	4
	Pinus resinosa (100)	6.1	
	Pinus strobus (100)	9.3	
	Picea abies (100)	12.0	
Japan 39°45' N.	*Larix leptolepis* (100)	12.7	5, 6
Japan 43°13' N.	*Larix leptolepis* (100)	14.7	7

[1] Source: (1) Hanley 1976; (2) Gower and Grier 1989; (3) Gower 1987; (4) Gower and others 1993; (5) Satoo 1970; (6) Satoo 1977; (7) Satoo 1973.

[2] Percent basal area of stand for species with basal area greater than 5 percent.

co-occurring evergreen conifers because the specific leaf area is much greater for larches than for sympatric evergreen conifers (table 1) (Gower and others 1987, Gower and Richards 1990). However, photosynthesis (weight basis) is greater for larches than evergreen conifers, illustrating an important ecological tradeoff between the deciduous and evergreen habit.

Stem and aboveground net primary production values for larch forests range from 7.5 to 14.7 tons per ha per year (table 3). Stem wood net primary production rates were similar for larch and evergreen conifers, whereas stem wood net primary production rates tend to be greater for evergreen conifers than for broad-leaved deciduous species (Assmann 1970). For example, aboveground net primary production rates did not differ between western larch and lodgepole pine in a natural, mixed stand in the Washington Cascades (Gower and others 1989). Gower and others (1993) estimated that the aboveground net primary production (tons/ha/year) did not differ significantly among European larch (9.2), white pine (9.3), and Norway spruce (12.1), but that all three species had a significantly greater production than red pine (6.0). Matyssek (1986) reported that larch hybrids had a similar or greater net primary production rate than a similar-diameter Norway spruce tree. However, Tranquillini (1979) reported that the annual net primary production was greater for stone pine (*Pinus cembra*) than for European larch. Based on the few data available, it appears that the carbon allocation to foliage versus wood production does not differ consistently between larches and evergreen conifers (fig. 2), despite the marked differences in proportion of foliage versus woody biomass for larches and evergreen conifers.

The similar net primary production rates for larches and co-occurring evergreen conifers, when grown in common gardens or in natural mixed stands, clearly indicate that species with different leaf longevities can achieve a similar net primary production rate, despite the fact that evergreen conifers support threefold to fivefold greater foliage mass. The decoupling of the relationship between net primary production and foliage mass is related in part to a production efficiency (aboveground net primary production/foliage mass) that is greater for larches than for evergreen conifers (Gower and others 1989, 1993). A similar inverse relationship between production efficiency and leaf longevity has been reported for a wide variety of tree species (Reich and others 1992). The greater production efficiency of larches can be attributed in part to the greater maximum net photosynthetic rates and better illumination of the canopy of larch than evergreen conifers (Gower and Norman 1991).

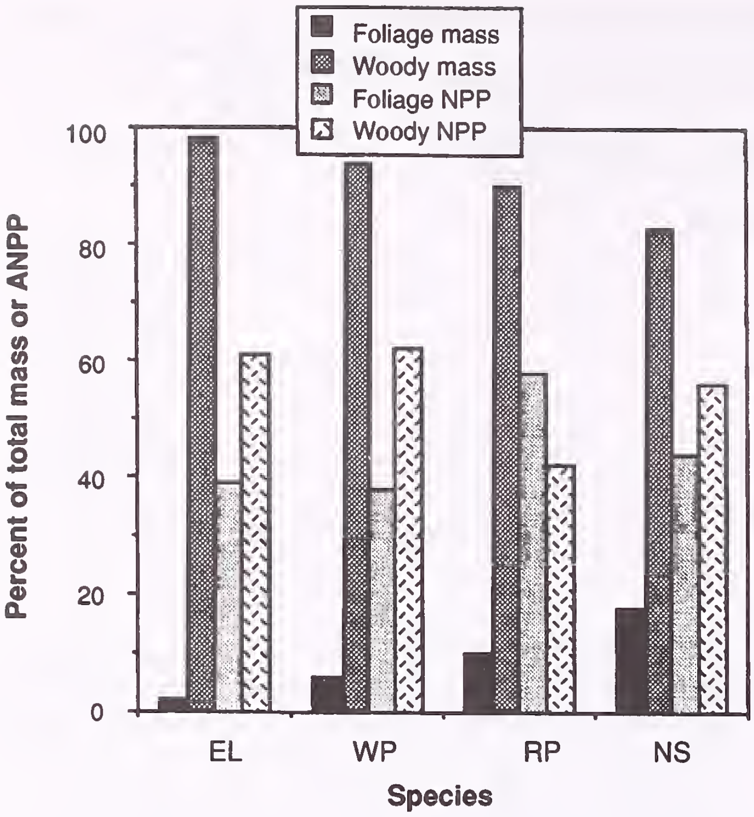

Figure 2—Foliage and woody (stem plus branches) mass or production as a percentage of the total aboveground mass or net primary production, respectively. Data are for European larch (EL), white pine (WP), red pine (RP) and Norway spruce (NS) in Gower and others (1993).

Because larches are shade intolerant (Fry and Phillips 1977), high levels of incident light are required to maintain high photosynthetic rates. If larches do not maintain high photosynthetic rates, the productivity of larches is substantially smaller than that of evergreen conifers (Matyssek 1986). In fully stocked stands where trees compete for light, larches maximize the illumination of their canopies in two ways. First, larches allocate a greater amount of carbon to height growth, relative to diameter growth, compared to evergreen conifers, thereby maintaining their canopy above that of the canopy of competing evergreen conifers (Gower and Richards 1990, Vogel and others 1994). This allocation pattern provides a more dominant canopy position with greater light interception.

Second, results from theoretical models that simulate radiation penetration through forest canopies suggest that a large height to radius crown ratio (such as conical crown of larches) increases radiation interception, especially at higher latitudes where the angle of incident radiation is lower (Oker-Blom and Kellomaki 1983). Tree crowns with a ratio of 1 or lower (such as the crown of broad-leaved deciduous trees) also intercept a large amount of radiation, but trees with this architecture are unable to support the ice and snow load typical of larch environment. Consequently, the conical canopy architecture of larches provides a more favorable carbon balance than that of a more rounded crown of broad-leaved deciduous trees in northern latitudes where larches occur.

NUTRIENT USE EFFICIENCY

Efficient use of nitrogen by larches is particularly important because nitrogen availability is low in subalpine and boreal forests (Cole 1981). Nitrogen use is also important because it is an essential element in RuBP carboxylase, an enzyme associated with photosynthesis. In fact, net photosynthesis is often positively correlated to leaf N concentration (Field and Mooney 1986; Gower and others 1993; Reich and others 1991, 1992).

In general terms, nitrogen use efficiency refers to the amount of biomass produced per unit of nitrogen invested (for example, nitrogen content). However, different working definitions of nutrient use efficiency can refer to periods varying from seconds to a year or to spatial scales ranging from the leaf to the stand level. Foliage nitrogen concentrations are much greater for larches than evergreen conifers (table 1). The high foliage nitrogen concentration explains, at least in part, the greater maximum net photosynthetic rate of larches than that of evergreen conifers. Moreover, potential photosynthetic nitrogen use efficiency, or the instantaneous carbon gained per unit of foliage nitrogen, is positively correlated to foliage nitrogen concentration (Field and Mooney 1986; Reich and others 1992) and is inversely related to leaf longevity (Reich and others 1991, 1992). Gower and others (1993) observed an inverse relationship between potential photosynthetic nitrogen use efficiency and leaf longevity for larch and four other tree species planted in adjacent plantations.

Larches also effectively retranslocate nitrogen from senescing foliage, thereby minimizing the loss of nitrogen from the tree and further increasing nitrogen use efficiency. Chabot and Hicks (1982) and Chapin and Kedrowski (1983) reported that evergreen conifers and broadleaf deciduous trees retranslocate nitrogen with similar efficiency. Larches, however, appear to retranslocate N more efficiently than broadleaf deciduous or needle-leaf evergreen conifers (table 4). In fact, we do not know of another tree genera that retranslocates nitrogen as efficiently as *Larix*. Because larches retranslocate a similar percentage of nitrogen from foliage when grown on infertile or fertile

Table 4—Percent foliage nitrogen retranslocation by larches

Species	Percent N retranslocated Range	Percent N retranslocated Mean	Source[1]
L. decidua	70-84	78	1, 2, 3
L. eurolepis	—	81	4
L. laricina	48-80	70	5, 6, 7, 8
L. leptolepis	66-70	70	1
L. lyallii	81-86	84	9
L. occidentalis	82-90	86	9, 10
All *Larix*	66-90	78	11
Broadleaf deciduous	21-75	52	6
Evergreen conifers	41-74	58	6

[1] Source: (1) Matyssek 1986; (2) Schueller 1978; (3) Son and Gower 1991; (4) Carlyle and Malcolm 1986; (5) Bares and Wali 1979; (6) Chapin and Kedrowski 1983; (7) Tilton 1977; (8) Tyrrell and Boerner 1987; (9) Gower and others 1989; (10) Cole 1981; (11) this study.

soils, we speculate that this trait is under strong genetic control.

The greater instantaneous nitrogen use efficiency at the leaf level and greater withdrawal of nitrogen from senescing foliage exhibited by larches compared to evergreen conifers explains, in part, why stand level annual nitrogen use efficiency is greater for larches than for evergreen conifers (Gower and others 1989; Son and Gower 1991). The efficient use of N from senescing foliage appears to be particularly beneficial to larches because of the adverse effect of cold soil temperature on soil nitrogen availability and the greater annual nitrogen requirement of deciduous than evergreen trees (Gosz 1981; Son and Gower 1991).

WATER USE EFFICIENCY

In most trees, carbon gain and water loss are tightly linked because CO_2 and water vapor enter and leave the foliage, respectively, through stomata. Consequently, efficient use of water (such as greater carbon accumulation per unit water transpired) may increase net primary production if water is limiting. Efficient use of water is particularly important in subalpine and boreal environments where winter desiccation is believed to be a primary factor controlling alpine timberline (Tranquillini 1979).

One advantage of the winter-deciduous habit of larch is that winter desiccation and abrasion of foliage are avoided. Hadley and Smith (1986) reported that more than 75percent of the needles of Englemann spruce (*Picea englemannii*) were shed prematurely due to winter desiccation. It is interesting to note that subalpine larch seedlings retain their needles during the winter if deep snow protects the seedling from blowing ice crystals and desiccating winds (Richards 1985). Despite the winter deciduous habit of larches, they still must protect their buds because they contain the next year's foliage. Richards and Bliss (1986) found that lethal desiccation of buds was 50percent less for alpine larch than sympatric evergreen conifers growing in the Canadian Rockies; the greater avoidance of bud desiccation can be explained by the physical isolation of the bud from the stem by the crown. The crown forms between the bud and stem late in the season and contributes to the resistance to freezing damage by allowing ice crystals to form outside the bud.

Although the winter-deciduous habit of larches reduces winter desiccation, larches use water less efficiently than evergreen conifers during the growing season. For example, Matyssek (1986) reported that for a similar maximum net photosynthetic rate under ambient conditions, European larch, Japanese larch (*L. leptolepis*), and their hybrids all exhibited greater rates of stomatal conductance than did Norway spruce, suggesting that water loss per unit carbon gain was greater for larches than for spruce. Dang and others (1991) reported that water use efficiency was greater for tamarack than for black spruce when soil moisture was high but was greater for black spruce than tamarack when soil moisture was low. Gower and Richards (1990) used $\delta^{13}C$ values for foliage collected from co-occurring larches and evergreen conifers in late growing season to infer relative annual water use efficiencies. They reported that water was used less efficiently by larches than by co-occurring evergreen conifers. The lower water use efficiency of larches than of evergreen conifers may in part explain the absence of larches from xeric sites and their greatest abundance on mesic sites (Arno and Habeck 1972; Schmidt and others 1976).

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Autecology and Synecology of Western Larch

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Abstract—Western larch occupies a limited geographic range in the Northwestern United States and Western Canada and exhibits moderate ecological amplitude within this range. Larch's shade-intolerance relegates it to an exclusively seral successional role. Great longevity and exceptional fire resistance account for its occurrence in late-successional stands. Western larch will likely decrease in abundance compared to historical levels. Effective wildfire suppression and decreased use of clearcut and seed-tree regeneration methods will likely put larch at a competitive disadvantage compared to its associates.

Western larch (*Larix occidentalis*) is a distinctive western conifer due to its brilliant autumn color, rapid growth, and deciduous habit. Larch's properties make it a preferred species for dimension lumber and utility poles, and a favorite among western woodcutters for firewood. This species has also picked up a myriad of common names over the years, including hackmatack, larch, western larch, great western larch, Montana larch, Oregon larch, red American larch, tamarack, western tamarack, and British Columbia tamarack (Green 1933).

TAXONOMY

Western larch is genetically distinct from all other species occurring within its range, with one exception. Western larch occasionally hybridizes with subalpine larch (*Larix lyallii*) where the elevational ranges of the two species overlap (Carlson and others 1990). Hybrid vigor resulting from crossing other larch species has already been exploited. Carlson and others (1990) hypothesize that a *L. occidentalis* x *L. lyallii* hybrid retaining the rapid growth characteristic of the former along with the cold-hardiness of the latter would have considerable management potential.

HABITAT

Distribution

Western larch occupies a limited geographic range in four States (Montana, Idaho, Oregon, and Washington) and two Provinces (British Columbia and Alberta). This species is found in a zone roughly east of the Cascades in Washington, north of the Salmon River in Idaho, west of the Continental Divide in Montana, and south of the 52nd parallel in interior British Columbia and extreme western Alberta. However, Eliot (1938) reported western larch on the west side of the Cascades south of Mount Hood in Oregon; Fiedler (1968) observed larch about 10 miles east of the Continental Divide in northwest Montana; and Lloyd and others (1992) reported an isolated stand of larch approximately 60 miles north and west of its previously documented northern limits in British Columbia.

Western larch is limited by drought at the lower end of its elevational range, and by cold temperatures at higher elevations. In the United States, western larch ranges as low as 2,000 ft in northern Idaho and extreme northwestern Montana, and as high as 6,500 ft (Habeck 1967) to 7,000 ft (Sudworth 1918; Larsen 1930) in western-central Montana and central Idaho. Larch occurs almost exclusively on north and east aspects as it approaches the southern (dry) end of its range; however, it can occur on all aspects on moister sites and in the northern portion of its range.

Climate

Western larch occurs in moderate environments relative to the breadth of climatic conditions within its geographic range. Table 1 depicts the range of climatic parameters associated with the forest habitat type series (United States) and biogeoclimatic units (Canada) within which larch occurs.

Soils

Western larch is typically found on deep, well-drained soils that have developed from glacial till or colluvium parent materials. These soils commonly have volcanic ash incorporated into the surface horizon. The greatest deposition of volcanic ash typically occurs on north to east aspects (Nimlos and Zuuring 1982)—aspects favored by western larch. In the United States, larch most commonly occurs on soils classified within the Alfisol or Inceptisol (and less frequently, Spodosol) soil orders. Embry (1960) found that growth performance of western larch in Montana was significantly related to effective soil depth. However, Pearcy (1965) could find no physiographic or soil factors to predict larch site index in the Swan Valley of western Montana. Spitzner and Stark (1982) investigated differential larch growth rates on andic soils overlaying glacial tills in northwestern Montana. Larch grew better on rapidly drained sites than on otherwise similar sites with slow subsoil percolation. Spitzner and Stark (1982) hypothesize that nutrient deficiencies resulting from a restricted rooting zone on the poorly drained sites limited growth more than moisture

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Table 1—Climatic profile of forest habitat type series (United States) and biogeoclimatic zones (Canada) where western larch occurs.

Habitat type series Biogeoclimatic zone		DF IDF	GF MS	WC/WH ICH	ES/AF ESSF
Mean Annual Precip.	(in)	17-50			
	(cm)	37-57	50-68	57-113	70-85
Mean Growing Season Prec.	(in)	6			
	(cm)	18-27	20-29	21-37	20-32
Mean Annual Snowfall	(in)	103			
	(cm)	120-350	193-450	130-560	200-620
Mean Annual Temperature	(F)	45			
	(C)	4.0-7.5	2.5-4.0	2.5-7.8	1.0-2.5
Frost–free Conditions	(season)	60-160			
	(days/yr)	40-140	35-80	50-170	40-70

Adapted from Schmidt and others (1976) and Goetz (1983)

stress on the well drained sites. General characteristics of soils supporting western larch are shown in table 2.

SYNECOLOGY

Ecological Amplitude

Western larch exhibits moderate ecological amplitude within its restricted geographical range; it does not occur on very warm or dry sites, nor on cold or wet ones.

Western larch occurs as a seral species in 24 of the 64 forest habitat types in Montana (Pfister and others 1977), in 30 of the 41 habitat types in northern Idaho (Cooper and others 1987), and in 11 of 21 habitat types in eastern Washington (Daubenmire and Daubenmire 1968) (table 3).

Associated Tree Species

Western larch is found in four major forest types in the United States and Canada—Douglas-fir, montane spruce/grand fir, interior cedar/hemlock, and Engelmann spruce/subalpine fir. Primary associates of western larch in the Douglas-fir type are Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), ponderosa pine (*Pinus ponderosa*), and lodgepole pine (*Pinus contorta*). Grand fir (*Abies grandis*), Douglas-fir, Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), and lodgepole pine commonly co-occur with larch in the grand fir type in the United States; ponderosa pine and paper birch (*Betula papyrifera*) are occasional co-occurrents. Douglas-fir and white spruce (*Picea glauca*) are primary associates of western larch in the montane spruce type in Canada. Major associates of larch in the cedar/hemlock type are western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), Douglas-fir, Engelmann spruce, subalpine fir, and grand fir. Minor associates in this type include lodgepole pine, western white pine (*Pinus monticola*), and paper birch. Engelmann spruce, subalpine fir, Douglas-fir, and lodgepole pine are common companions of larch in the Engelmann spruce/subalpine fir type, while western white pine and whitebark pine (*Pinus albicaulis*) are occasional associates.

Table 2—Primary characteristics of soils supporting western larch in the United States and Canada.

	United States	Canada
Parent Material	Glacial tills, colluvium Tertiary alluviums Volcanic intrusives	Morainal and colluvial Glacial fluvial (minor)
Development	Inceptisols Alfisols (Spodosols)	Dystric Brunisols Humo-Ferric Podzols Brunisolic Gray Luvisol
Texture	Gravelly loam to silt loam surface soils; silt loam to clay subsoils	Fine clay to coarse sandy
pH	4.8-6.1	4.5-5.8 Calcareous (7.5-7.8)
Humus depths	Mean: 1-2 in Range: 1-8 in	Mean: 4-5 cm Range: 1-25 cm

Successional Status

Western larch is the most shade intolerant species within its range, relegating it to an exclusively seral successional role. Larch is an aggressive pioneer in the historically fire-dominated ecosystems within which it occurs. However, larch's longevity—300 to 500 years common, occasionally 700+ years (Franklin and Dyrness 1973), maximum 900+ years (USDA Forest Service 1965)—accounts for its occurrence as relicts in late-successional stands. Western larch traits of low shade tolerance and rapid early height growth are characteristic of early successional species. However, some other attributes of larch, such as relatively advanced age to first seed production (~25 years) and great longevity (700+ years), are more representative of late-successional species based on classical r-K selection theory (Turner 1985). The capability of mature larch to occasionally survive stand replacement wildfires is due to thick bark and the considerable height of the crown base above the ground. Furthermore, defoliation by fire is less traumatic for larch than for other conifers, since it replaces its needles annually anyway (Fischer and Bradley 1987). These attributes, coupled with low seed weight (137,000 seeds/lb; USDA Forest Service 1974), give larch a different strategy than lodgepole pine for regenerating extensive burned areas, but one that is nearly as effective.

Table 3—Occurrence of western larch relative to forest habitat type series in Montana, Idaho, and eastern Washington.

Classification (geographic area and author)	Forest habitat type series	Number of habitat types within series	Number of habitat types with WL
Montana (Pfister and others 1977)	Limber Pine	3	0
	Ponderosa Pine	5	0
	Douglas-fir	14	7
	Engelmann Spruce	8	2
	Grand Fir	3	3
	Western Redcedar	2	2
	Western Hemlock	1	1
	Subalpine Fir	23	9
	Lodgepole Pine	5	0
N. Idaho (Cooper and others 1987)	Ponderosa Pine	4	0
	Douglas-fir	7	4
	Grand Fir	7	7
	Western Redcedar	6	6
	Western Hemlock	4	4
	Mountain Hemlock	4	4
	Subalpine Fir	6	5
	Lodgepole Pine	3	0
E. Washington (Daubenmire and Daubenmire 1968)	Ponderosa Pine	6	0
	Douglas-fir	3	3
	Grand Fir	1	1
	Western Redcedar	3	2
	Western Hemlock	1	1
	Mountain Hemlock	2	2
	Subalpine Fir	4	2
	Whitebark Pine–SAF	1	0

AUTECOLOGY

Silvical Characteristics

Autecological characteristics are important in that they define the ways in which a given species is unique. They also provide insights into a species regeneration habit, successional behavior, management potential, and distributional limitations. Western larch is a rather modal species in terms of most silvical characteristics, with two notable exceptions: it is extremely shade intolerant, and it is highly resistant to fire. Western larch's silvical attributes are listed in relation to its associates in table 4.

Regeneration

Western larch seeds germinate from late April to early June, usually about a week or two earlier than associated species (Shearer 1967). Death of first-year seedlings early in the season is mainly due to biotic factors such as fungi, birds, and rodents, whereas drought is the primary cause of seedling mortality after about mid-July (Schmidt and Shearer 1990).

Western larch is more dependent on a prepared seedbed to regenerate than any of its associates, including lodgepole pine (Fiedler 1990). Successful regeneration of western larch virtually requires mineral soil or burned seedbeds (Shearer 1980; Schmidt and Shearer 1990). The probability of larch stocking after clearcutting has also been found to vary inversely with elevation and percent grass/sedge cover (Fiedler 1990).

Height Growth and Site Index

Western larch exhibits rapid height growth. Fiedler (1990) found larch to outgrow all of its common associates to age 12, with the exception of lodgepole pine (identical). Schmidt and others (1976) reported that western larch and lodgepole pine heights are also similar at age 50, but that larch is taller at age 100 than any other conifer in the Northern Rockies. However, Deitschman and Green (1965) and Steele and Cooper (1986) report that western white pine is taller than larch at age 100 on productive sites—site index >60 (18.3 m), base age 50—in northern Idaho. Mean maximum height of western larch varies from a low of 96 ft, ±10 ft (29.3 m, ±3.0 m) on the *A. lasiocarpa*/*X. tenax* h.t. to a high of 149 ft, ±21 ft (45.4 m ±6.4 m) on the *T. plicata*/*C. uniflora* h.t. (Pfister and others 1977).

In the United States, western larch site index (base age 50) varies from about 50 ft (15.2 m) in the relatively cold, dry habitat types within the subalpine fir series, to about 80 ft (24.4 m) in the warm, moist western redcedar/western hemlock series (Pfister and others 1977; Cooper and others 1987). Mean site index for this species is shown by habitat type series and biogeoclimatic zone in table 5.

Productivity

Western larch, because of its deciduous habit, would appear to be at a growth disadvantage to sympatric evergreen conifers. Furthermore, for trees of a given diameter, larch has much lower foliage biomass than its associates (Brown 1978). However, both larch and its associates have similar aboveground production rates. Gower and Richards (1990) attribute larch's low-carbon-cost, well-illuminated, nitrogen-efficient canopy for carbon allocation rates similar to evergreen conifers. Total cubic volume production of western larch at age 100 varies from about 2,950 ft^3/acre (206 m^3/ha) on low quality sites, to 6,000 ft^3/acre (420 m^3/ha) on medium sites, to 9,600 ft^3/acre (672 m^3/ha) on high quality sites (Schmidt and others 1976).

Pests

While western larch is susceptible to numerous pests, few are lethal to trees of pole size or larger. Primary insect pests include larch casebearer (*Coleophora laricella*), larch sawfly

Table 4—Relative silvical characteristics of western larch and its common coniferous associates.

	Low ——> Moderate ——> High
Shade tolerance	**WL** LP PP WP DF ES GF AF WC WH
Frost tolerance	WH WC GF PP **WL** DF WP AF ES LP
Drought tolerance	WH WC AF ES WP GF **WL** LP DF PP
Fire resistance	WH AF ES WC LP GF WP DF PP **WL**
Excess water tolerance	PP DF **WL** GF WP AF WH ES WC LP

AF	Subalpine fir	PP	Ponderosa pine
DF	Douglas-fir	WC	Western redcedar
ES	Engelmann spruce	WH	Western hemlock
GF	Grand fir	WL	Western larch
LP	Lodgepole pine	WP	Western white pine

Table 5—Mean 50-year site index for western larch in the Northern Rocky Mountains (by forest habitat type series)[1] and British Columbia (by biogeoclimatic zone).

	H.T. series	DF	GF	WC/WH	ES/AF
50-year S.I. (ft)	mean	59	67	71	61
(Northern Rockies)	range	55-74	62-72	62-80	51-67
	BGC zone	**IDF**	**MS**	**ICH**	**ESSF**
50-year S.I. (m)	mean	17	20	23	17
(British Columbia)	range	13-19	16-22	18-26	16-21

[1]Adapted from Pfister and others 1977, and Cooper and others 1987.

(*Pristiphora erichsonii*), and western spruce budworm (*Choristoneura occidentalis*). Casebearer larvae can completely defoliate larch trees in the spring by mining the needles. Continued defoliation reduces radial growth significantly and can cause mortality (Tunnock and others 1969). The impact of casebearer appears to be inversely related to stand density (Denton 1979). The larch sawfly is a periodically significant defoliator of larch. This insect leaves its signature by biting chunks out of needles rather than mining them, but seldom causes mortality (Drooz 1956). The western spruce budworm is particularly damaging to sapling-sized trees. Budworm larvae typically sever the terminal and current-year laterals of young larch (Fellin and Schmidt 1967), damage that reduces height growth and affects form (Schmidt and Fellin 1973). Spruce budworm larvae have also been documented doing damage to larch cones and seeds (Fellin and Shearer 1968). While Douglas-fir bark beetle (*Dendroctonus pseudotsugae*) will attack western larch (Furniss and others 1981), successful brood production in standing live trees has never been documented (Reed and others 1986). Larch's apparent resistance to the Douglas-fir beetle is attributed to its high concentration of 3-carene, a xylem monoterpene that has a significant negative correlation with beetle attack rate.

Major diseases infecting larch include dwarf mistletoe, needle blight, needle cast, and root/stem rots. Trees parasitized by larch dwarf mistletoe (*Arceuthobium laricis*) commonly develop witches brooms, burls, and spike tops. Mistletoe infection reduces growth and increases vulnerability to other damaging agents, but only occasionally causes death (Kimmey and Graham 1960; Pierce 1960). Initial visual symptoms of needle blight (*Hypodermella laricis*) and needle cast (*Meria laricis*) are similar—red needles (Leaphart and Denton 1961). However, needles infected with blight are retained on the tree for a year or more, whereas needles infected with needle cast are typically shed within weeks after infection (Hagle and others 1987). Larch is also susceptible to red ring rot (*Phellinus pini*), schweinitzii root/butt rot (*Phaeolus schweinitzii*), and quinine fungus (*Fomitopsis officinalis*).

DISCUSSION

Bad news—The range of western larch, as with other western tree species, is determined by drought at low elevations and by cold temperatures at high elevations. Within its range, successful perpetuation of this species requires full or nearly full sunlight and mineral soil or burned seedbeds. Historically, these conditions were provided by wildfires. More recently, managers have created favorable conditions for larch regeneration using either clearcut or seed-tree regeneration methods, followed by dozer scarification or broadcast burning. However, changing management direction, especially on publicly owned lands, points to decreased use of clearcut and seed-tree methods, and less severe and complete site preparation. The resulting environmental and seedbed conditions will likely put larch at a competitive disadvantage compared to its associates.

Good news—Two developments related to the geographic distribution of western larch offer promise for expanding the traditionally recognized natural range of this species. The first development is the discovery of a disjunct stand of western larch approximately 60 miles (100 km) north of the previously recognized northern limit of this species in British Columbia. The location, size, age, and density attributes of this isolated population have been documented by Lloyd and others (1992). The apparent vigor and ability of this population to reproduce suggests that management efforts to extend larch northward to this latitude from its existing limits may well be successful.

A second development is the apparently successful planting of western larch at several locations north and west of its traditionally recognized range in British Columbia. Some extended plantings have survived and grown for up to 20 years. The current northern limit of western larch is believed to be determined by cold-temperature disruption of the regeneration process. This limiting factor can be circumvented to some degree using artificial regeneration.

Carlson (1994) has outplanted western larch, subalpine larch, and *L. occidentalis* x *L. lyallii* hybrids at four locations outside their natural ranges in Montana. Early results are promising, particularly for the hybrids. However, survival and adequate growth to mature size will be required before such efforts can be deemed a success.

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Western Larch: Pest-Tolerant Conifer of the Northern Rocky Mountains

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Abstract—Western larch (*Larix occidentalis*) is tolerant to most insects and disease pests found throughout its Northern Rocky Mountain range. Proper silviculture can minimize problems caused by dwarf mistletoe, western spruce budworm, and larch casebearer. Pathogens rarely cause serious damage. Harvesting and management practices that favor shade-tolerant species are the worst enemies of western larch. Management practices that emulate presettlement fire regimes will favor establishment and culture of western larch.

Trees, insects, fungi, and other biotic agents are integral components of forest ecosystems. Microorganisms may damage trees but also are important in the decomposition of plant substrates and contribute significantly to nutrient and water balances in forest ecosystems. They do not always adversely affect trees. Depending on environmental conditions, species composition, and numerous other variables, tree growth may be favored at the expense of insects and microbes. Conversely, insects and microorganisms can predominate at the expense of trees. When insects and diseases seriously impact tree regeneration, growth, and development, they are frequently branded as "pests" and receive serious attention from forest managers, biologists, and often the public. Direct control measures often are undertaken to reduce pest activity. Because susceptibility and vulnerability to insects and diseases vary among tree species, several long-term options using vegetation management may be available to ameliorate pest problems. It is important to forest managers to understand this concept so they can minimize impacts on commodity production while maintaining beneficial ecosystem functions.

Western larch (*Larix occidentalis*) is an important conifer species indigenous to the Northern Rocky Mountains. The species is highly valued as lumber, and is important for esthetic, wildlife, and watershed reasons (Schmidt and others 1976). The purpose of this paper is to review knowledge of important insects, pathogens, and other agents affecting western larch and to discuss silvicultural methods and strategies to reduce their impacts on this valued species.

INSECT PESTS

The most notable insect pests of western larch are defoliators. Western spruce budworm (*Choristoneura occidentalis*) and larch casebearer (*Coleophora laricella*) are the most serious. Larch sawfly (*Pristiphora erichsonii*), larch budmoth (*Zeiraphera griseana*), and larch looper (*Semiothisa sexmaculata*) occasionally reach outbreak levels and cause noticeable defoliation.

Western Spruce Budworm

Western spruce budworm is native to the western Rocky Mountains in the United States and Canada (Johnson and Denton 1975). Its primary hosts are grand fir (*Abies grandis*), subalpine fir (*A. lasiocarpa*), white fir (*A. concolor*), Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), and Engelmann spruce (*Picea engelmannii*). Budworm feeds on and completes its life cycle on these species. Western larch is a secondary host because budworm seldom completes its life cycle on this species, even though feeding damage is occasionally serious. Small larvae are passively dispersed by wind (fall and spring dispersal of first and second instars, respectively) to all conifers, including larch. Western larch flushes 1 to 2 months before other hosts and larvae previously deposited on larch tend to stay and feed temporarily on developing foliage, seed cones, and pollen cones. The insect has a peculiar feeding habit on larch; it mines and severs expanding long shoots (Fellin and Schmidt 1967). When the terminal leader (long shoot) is severed, height growth is reduced and multiple leaders compete for terminal dominance. This forked-top condition lasts only a few years, until one of the laterals becomes dominant and rapid height growth resumes. Number of larvae on larch decrease when other hosts flush (Carlson 1985); reasons for this apparent exodus are not known. Possibly the nutrient value of larch is not as good as the other hosts, and budworms are able to respond to this difference, spin off the larch, and if lucky are deposited on favorable substrate. Perhaps larvae on larch are more vulnerable to predators. We have observed western larch with branches intertwined with Douglas-fir; larvae were abundant on Douglas-fir shoots, but few were found on the larch (Carlson 1985). Some budworms pupate on larch, indicating they

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Figure 1—Western larch survives severe infestation of western spruce budworm.

can complete their life cycle on this species, but indications are that western larch plays a minor role in the population dynamics of western spruce budworm.

Cone and seed production of western larch can be seriously reduced by budworm. Extensive feeding by western spruce budworm on larch cones was observed by Fellin and Shearer (1968). Chrisman and others (1983) reported lower cone production in stands infested by western spruce budworm in Montana. More detailed studies suggested that up to two-thirds of larch seeds were killed by insects (Shearer 1984).

Budworm damage to sapling western larch probably is more extensive when the surrounding forest is composed mainly of primary hosts, or there is abundant other host biomass intermingled with the larch (Carlson and Wulf 1989). Stand conditions that favor and support epidemic budworm populations will generate overwhelming numbers of budworm larvae; in these cases long shoots, including terminal leaders, may be severed or killed. However, western larch is resilient and survives where other species are killed by budworm (fig. 1). Silviculture with an eye for budworm can substantially reduce the hazard to larch. Seral species should be cultured when possible; trees should be optimally spaced for the habitat. A forestwide mosaic of stands, based on ages, sizes, and compositions that resemble those in presettlement times likely would go far in ameliorating budworm problems on western larch.

Larch Casebearer

Larch casebearer was introduced into the Eastern United States in the late 1800's and was first discovered in Idaho in 1957. This insect soon became the most serious insect problem on western larch (Denton 1979). Unlike budworm, casebearer has only one primary host in the Northern Rockies—western larch—but the insect will survive on other conifers when forced to under laboratory conditions (Ramsay and Long 1988) and has been observed successfully feeding on other conifers in the field (Dewey 1993). The larvae are not passively dispersed by wind as are budworm, but tend to remain on the tree where they hatched.

Casebearers quickly built to epidemic populations in the 1960's and spread throughout most of the range of western larch. Although some mortality of larch occurred due to repeated defoliation, the biggest impact in natural, untended stands was reflected in decreased diameter growth (Denton 1979). Thinned stands, although sustaining higher populations of casebearer (Denton 1979), were not significantly impacted (Seidel 1986). However, repeated heavy defoliation of natural stands may predispose trees to mortality by other factors (Tunnock and others 1969). In general, western larch can withstand outbreaks of larch casebearer and show negligible impact.

Two stand attributes influence casebearer populations: stand density and elevation. Adults preferentially select larch on which to lay their eggs. Thus, for a given population, trees in dense stands would tend to have fewer larvae than trees in open stands (Denton 1979). Even though open-grown larch stands had higher densities of larvae, mortality of larvae was higher in the open stands during an unusually cold, wet period (Denton 1979). Trees in open-grown stands probably would recover from defoliation faster than those in dense stands, suggesting that over a period of years, well-spaced stands may incur lower levels of damage than dense stands. Larch casebearer also is influenced by elevation; apparently the insect is more successful at lower elevations (2,000-4,000 ft m.s.l.) and generally does poorly above 5,000 ft m.s.l. Denton (1979), however, in one case observed significant defoliation up to 5,000 ft.

Larch casebearer populations declined dramatically during the late 1970's and early 1980's. Several factors probably contributed to the decline. An aggressive program in which parasites of casebearer were introduced seems to have been effective (Denton 1972; Ryan and others 1987). Native parasites and predators too may have had significant influence. Also, available feeding sites were substantially reduced when larch needle diseases became epidemic. Cold, wet spring weather is known to seriously impact casebearer populations (Denton 1979). Ultimately, a combination of these factors may have caused the population collapse (Kohler and others 1983).

Other Insects

Larch sawfly occasionally causes defoliation of western larch, but impact has been limited to a small decrease in radial increment (Denton 1958; Ross and Sugden 1968). Similarly, larch budmoth and larch looper occasionally reach epidemic status but do not cause significant damage. Information on relations of environmental and stand conditions to populations of these insects is lacking.

The Asian gypsy moth (*Lymantria dispar*) poses a significant risk to western larch if it becomes established on the North American continent (USDA 1991). This defoliator severely weakens infested trees, reduces growth, and increases mortality. It is known to infest more than 250 plant species, including many broadleafs and conifers. Larch logs imported from Siberia and other parts of Asia can carry the insect. Asian gypsy moth was found in 1991 on grain ships docking at western U.S.A. and Canadian ports. An aggressive eradication effort appears to have been successful (Dewey 1993). Asian gypsy moth prefers larch as a host; in the event it gains a foothold, multispecies stands may decrease stand impact caused by this insect; however, it will feed on a variety of conifer and angiosperm hosts (USDA 1991).

PATHOGENS

The most serious disease of western larch is dwarf mistletoe (*Arceuthobium laricis*), an angiosperm parasitic on twigs and stems. Other disease-causing organisms, including larch needlecast (*Hypodermella laricis*), needle blight (*Meria laricis*), root disease (*Armillaria* spp., *Phellinus weirii, Fomitopsis annosus*), and wood rots (*Fomitopsis officinalis, Phellinus pini*, and others) usually do not cause significant damage to larch forests. Larch seedlings in nurseries at times are seriously damaged by *Fusarium* spp. and *Botrytis*.

Dwarf Mistletoe

Larch dwarf mistletoe is distributed throughout the botanical range of western larch (Hawksworth and Weins 1972). All ages of trees are susceptible. The disease spreads mainly by natural expulsion of seed. During late summer, the seeds mature and are expelled with sufficient force (30 m/sec) to carry them up to 16 m from the seed pod. Seeds have a viscous coating and will adhere to whatever object they land on. If they land on a host twig, they can germinate and may penetrate the host tissue. Successful infections will spread in the cortex of the host for about 2 to 5 years before producing aerial shoots.

Larch dwarf mistletoe can cause significant growth loss and some mortality in infected stands (fig. 2). Losses in 10-year basal area growth approached 69 percent in Montana (Pierce 1960). On and Dooling (1969) estimated that severely infected stands on good growing sites in western Montana produced only 20 percent or less of their potential volume. Weir (1916) reported similar impact in the Blue Mountains of Oregon. Severely infected trees are weakened and become susceptible to other insects and diseases.

Figure 2—Dwarf mistletoe is the most serious pest of western larch.

The disease is easily controlled silviculturally (Baranyay and Smith 1972; Dooling 1974). Spread by seeds is mostly downward and lateral, and as noted above, seeds generally do not move more than 16 m laterally. In mature stands ready for a regeneration cut, 2- to 5-acre group selections or small clearcuts in which all the infected overstory is removed will limit volume losses to 20 to 40 percent compared to an uninfected stand; the small cut size allows infection to spread in from the perimeter. Clearcuts of 20 acres will limit losses to 5 to 10 percent of uninfected (Taylor, these proceedings).

Site preparation, preferably by prescribed fire, will ready the area for a new stand of mistletoe-free larch. In immature larch stands lightly infected with dwarf mistletoe, thinning and sanitation are effective options for dealing with the parasite (Baranyay and Smith 1972; Dooling 1974). Although thinning will increase the growth and seed production of mistletoe on infected leave trees, if the infection intensity is less than 2 in the 6-class rating system (Hawksworth 1961) the benefits of thinning on tree growth outweigh the adverse effects of stimulation of the dwarf mistletoe plants. Crop tree thinning of larch in northeastern Oregon decreased dwarf mistletoe impact and significantly increased growth of residual stocking

(Filip and others 1989). Wicker (1983) reported rapid intensification of dwarf mistletoe infection vertically upward in crowns of immature western larch. He suggested, appropriately, that multispecies stands are generally preferable to larch monocultures because not only will stand losses to dwarf mistletoe be decreased, but biodiversity will be enhanced and impact from other insects and diseases will be minimized. Low levels of dwarf mistletoe are not considered a serious problem.

Other Diseases

Larch needle cast and larch needle blight are indigenous diseases of western larch that periodically cause defoliation. Impact is considered minor (Garbutt 1984; Vanderwal 1970) and is generally restricted to growth loss. Successive intense defoliation likely would cause more serious impact (Dubreuil 1982). Needle diseases can seriously damage seedlings and saplings because terminal shoots may be killed. Little is known of relations between stand conditions and disease intensity. Usually the disease appears in epidemic fashion over extensive areas for only one or two seasons, not to be seen again for 10 years or so.

Armillaria root disease, *Phellinus weirii*, and *Fomitopsis annosus*, serious pathogens of most Northern Rocky Mountain conifers, do not often cause serious impact to western larch. McDonald and others (1987a) found that western larch does not support pathogenic *Armillaria*, even though epiphytic rhizomorphs were found on the roots (McDonald and others 1987b). In the most comprehensive work done to date on *Armillaria* (Shaw and Kile 1991), western larch is only rarely listed as a host for the fungus. James and others (1984) list western larch as a host for *Armillaria*, but the authors did not discuss the degree of susceptibility or vulnerability. *Armillaria* was found as an incidental decay fungus in thinned stands in northeastern Oregon; mortality in residual living trees was infrequent (Filip and others 1987). Western larch seedlings were infected by *Armillaria ostoyae* at the same rate as grand fir, Douglas-fir, lodgepole pine (*Pinus contorta* v. *latifolia*), and ponderosa pine (*P. ponderosa*) in a controlled study. Seedlings that received balanced light and nitrogen were less susceptible than stressed seedlings (Entry and others 1991).

Given the low susceptibility of western larch to *Armillaria* and other root diseases, larch should be featured along with other seral conifers in regeneration of sites with root disease within the range of western larch. This strategy will minimize stand susceptibility and vulnerability to the disease and is supported by Williams and others (1986), Hadfield and others (1986), and Hagle and Shaw (1991).

Trunk and heart rots caused by *Fomitopsis officinalis, Phellinus pini, P. weirii*, and species of *Polyporous* are significant mainly in overmature, old western larch. They are not perceived as a serious threat to timber production in managed western larch stands. Trunk and heart rots are important in creating habitat for cavity-nesting birds and other wildlife indigenous to old-growth western larch stands, and contribute to the biodiversity of these communities.

Western larch containerized seedlings in nurseries usually are not seriously affected by soil-borne diseases (James 1985b). Occasionally, however, losses can be substantial. In 1987, severe mortality to containerized western larch occurred at the Forest Service nursery in Coeur d'Alene, ID, U.S.A. Nearly 45 percent of all the seedlings exhibited disease symptoms and 54 percent of all seed and seedlings were infected with *Fusarium* spp.; nearly 27,000 seedlings were lost (James 1987). Environmental conditions may have predisposed the seedlings to the disease. *Meria* needle cast caused serious losses of western larch seedlings at a southwestern Washington nursery (Cooley 1984) and at a nursery in northern Idaho (James 1985a). Multiple cycles of the disease occurred in a single season, and outplanted seedlings did not survive as well as healthy ones. Gray mold (*Botrytis cinerea*), can damage container stock, but proper sanitation and storage conditions will prevent serious problems (Mittal and others 1987).

Western larch is generally well adapted to the climate of the Northern Rocky Mountains. However, seed and cone crops appear to be vulnerable to weather. The single greatest factor causing demise of cone and seed crops appears to be low temperature during conelet development (Shearer and Theroux 1986). Temperatures as low as –9 °C killed up to 100 percent of the developing cones.

IMPACTS INDUCED BY MANAGEMENT

Adverse effects of insects, diseases, and abiotic agents on western larch appear small in comparison to impacts induced by previous forest management. If western larch has an Achilles heel, it is because the species is the most shade-intolerant conifer in the Northern Rocky Mountains; it is always seral in forest succession (Schmidt and others 1976). This shade intolerance has important implications for larch. Historically, the western larch resource was regulated by natural fire. Even-aged western larch forests often followed intense stand-replacing fires in mesic-to-moist habitats. In drier habitats, western larch stands were maintained by frequent surface fires that cleaned out competing shade-tolerant conifers (Antos and Habeck 1981; Habeck and Mutch 1973; Mutch and others 1993). Since the early 1900's, much of the mature western larch resource has been removed by logging; in many cases little thought was given to regenerating the disturbed sites to larch. Often, no site preparation was done, and shade-tolerant conifers such as alpine fir, grand fir, and Douglas-fir quickly took over the site, at the expense of western larch regeneration (fig. 3). Never-harvested larch forests also are seriously threatened because prevention and control of wildfire have been highly successful since the early 1900's. The shade-tolerant conifers seed in well under the canopy of old-growth larch; without fire they proliferate and compete intensely with larch for water and nutrients and undoubtedly cause premature death of the old growth.

Replacement species are nearly always far more susceptible and vulnerable to insects and diseases than western

Figure 3—Selective removal of western larch during harvesting, along with improper preparation of seedbeds, results in compositional shifts of species from western larch/ponderosa pine to Douglas-fir and other shade-tolerant taxa.

Figure 4—Retention seed tree and retention shelterwood silvicultural systems can be used to perpetuate esthetically pleasing, productive, insects- and disease-free western larch stands.

larch. Douglas-fir, alpine fir, and grand fir are primary hosts for western spruce budworm, Douglas-fir tussock moth, and root diseases caused by *Armillaria*, *Fomitopsis*, *Phellinus*, and others. Root disease may occur in conjunction with repeated defoliation by insects; the effect may be more synergistic than additive. Insects and diseases have caused serious damage to these replacement forests in Oregon, Washington, Idaho, and Montana. In the Blue Mountains of Oregon, over 80 percent of many stands in the replacement forest have been seriously impacted by insects and diseases (Mutch and others 1993). Not only has a productive species tolerant to insects and diseases been replaced by less productive, shade-tolerant species, but insects and diseases cause far more serious damage to the replacement forests. These replacement forests also tend to be overstocked with a great deal of vertical structure; they are highly vulnerable to abnormally intense wildfires. We do not know exactly how much area has been converted from larch to fir forests; several hundred thousand acres is an estimate. Forest managers need to make a concerted effort to reestablish larch in habitats where it has been replaced by shade-tolerant conifers. This would be an effective way in which to minimize future insect and disease losses (fig. 4).

CONCLUSIONS

As we have described, western larch has few important insect and disease pests. However, the most serious, long-lasting impact on regeneration and growth of western larch has come not from insects and diseases, but from harvesting and management practices that favored shade-tolerant species and excluded larch following harvest. Little attention was given to good silviculture, where proper site preparation, a good seed source, and planting are necessary to assure regeneration of larch and other seral species.

Sustaining western larch depends on our management strategies. The species does well under the natural ecosystem processes that include fire, insects, and diseases.

Threat to the species comes not from the natural processes operating in the ecosystem, but from human actions and inactions that disrupt natural events. Every effort should be made to culture larch in concert with other seral species. These stands will, over the long run, be the most resistant to insects and diseases and will provide the greatest benefits.

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Larix occidentalis—Fire Ecology and Fire Management

Stephen F. Arno
William C. Fischer

Abstract—Western larch (*Larix occidentalis*) requires disturbance to perpetuate itself. Until the early 1900's fire was the primary disturbance for western larch in the inland Pacific Northwest. More recently, prescribed burning or mechanical scarification have been used to regenerate western larch. Where other kinds of timber management are practiced, and in parks and natural areas where fire is excluded, western larch is declining and could become scarce. Fire management considerations and review guides for prescribed fire are included.

FIRE ECOLOGY

Western larch (*Larix occidentalis*) is a large, long-lived tree of major importance for wildlife habitat and timber production. It is widely distributed in lower and mid-elevation forests of the inland Pacific Northwest, between the crest of the Cascade Range and the Continental Divide in the Rocky Mountains. This region supports extensive natural coniferous forests where western larch is the only major deciduous tree. The climate is generally moist except for long droughty periods during the summer. These are accompanied by occasional dry lightning storms. As a result, fires have burned these forests continually since they developed more than 10,000 years ago, following the last Pleistocene glacial period (fig. 1; Mehringer 1985).

FIRE ADAPTATIONS

Western larch is considered the most fire-resistant tree of the inland Pacific Northwest. Even if trees are killed in crown fires, larch's lightweight winged seed can be dispersed by wind over considerable distances from neighboring stands. Nearly a century ago Forest Service Chief Gifford Pinchot (1899) remarked that western larch's thick, nonresinous bark is an outstanding adaptation for surviving fire. The bark near ground line on large trees is often 15 cm thick, which protects the cambium from lethal heating in all but the most severe surface fires. Young larch trees are often wounded at the base of the stem in a surface fire, but heal and continue to grow for centuries. Some living larch have multiple fire scars that record numerous fires over the past 350 years (Arno 1976; Barrett and others 1991). Interestingly, western larch's close relative, alpine larch (*Larix lyallii*), has thin bark but grows in damp, rocky sites at the highest elevations where it avoids most fires.

Unlike associated evergreen conifers, western larch develops a high, open crown of relatively noncombustible foliage in which the lower branches are self-pruned. This tree is able to tolerate crown scorch and defoliation in a fire and then produce new foliage from heat-resistant woody buds and epicormic branching on the main stem. Some larch trees survive major fires and become seed trees. Even larch that are killed will occasionally contribute to reseeding the burned area. Damp fresh cones may survive in the scorched upper crown where they mature and scatter their light, winged seeds into the burned area. On burned seedbeds western larch seedlings generally outgrow their competitors (Schmidt and Shearer 1990), which is important because larch growth is greatly suppressed in competition with other conifers of equal or larger size.

SUCCESSIONAL RELATIONS AND FIRE REGIMES

Western larch is listed as an important seral or pioneer species in more than half of the forest habitat types (or site types) identified in northern Idaho and western Montana, and it also has a broad distribution in several other areas (Cooper and others 1991; Pfister and others 1977). This species occupies habitat types in the moist portion of the Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) series—that is, where Douglas-fir is the most shade-tolerant species and thus will become dominant in the absence of disturbance. Larch is also a seral species in the spruce (*Picea* spp.), grand fir (*Abies grandis*), western redcedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*) series, and the warmer habitat types in the subalpine fir (*Abies lasiocarpa*) series. Surveys of the indigenous forest in the late 1800's and early 1900's indicated that western larch was an abundant overstory species within most of its environmental range, no doubt covering several million hectares as a major species (Ayres 1900, 1901; Leiberg 1898, 1900; Whitford and Craig 1918). This abundance of a highly shade-intolerant species was linked to the pervasive influence of forest fires.

Several studies have investigated the historic patterns of fire frequency and severity associated with western larch forests (Arno 1976, 1980; Arno and Davis 1980; Arno and Scott, in preparation; Barrett and others 1991; Davis 1980; Freedman and Habeck 1985; Gabriel 1976; Habeck 1990). These patterns can be classified into the following three kinds of fire regimes.

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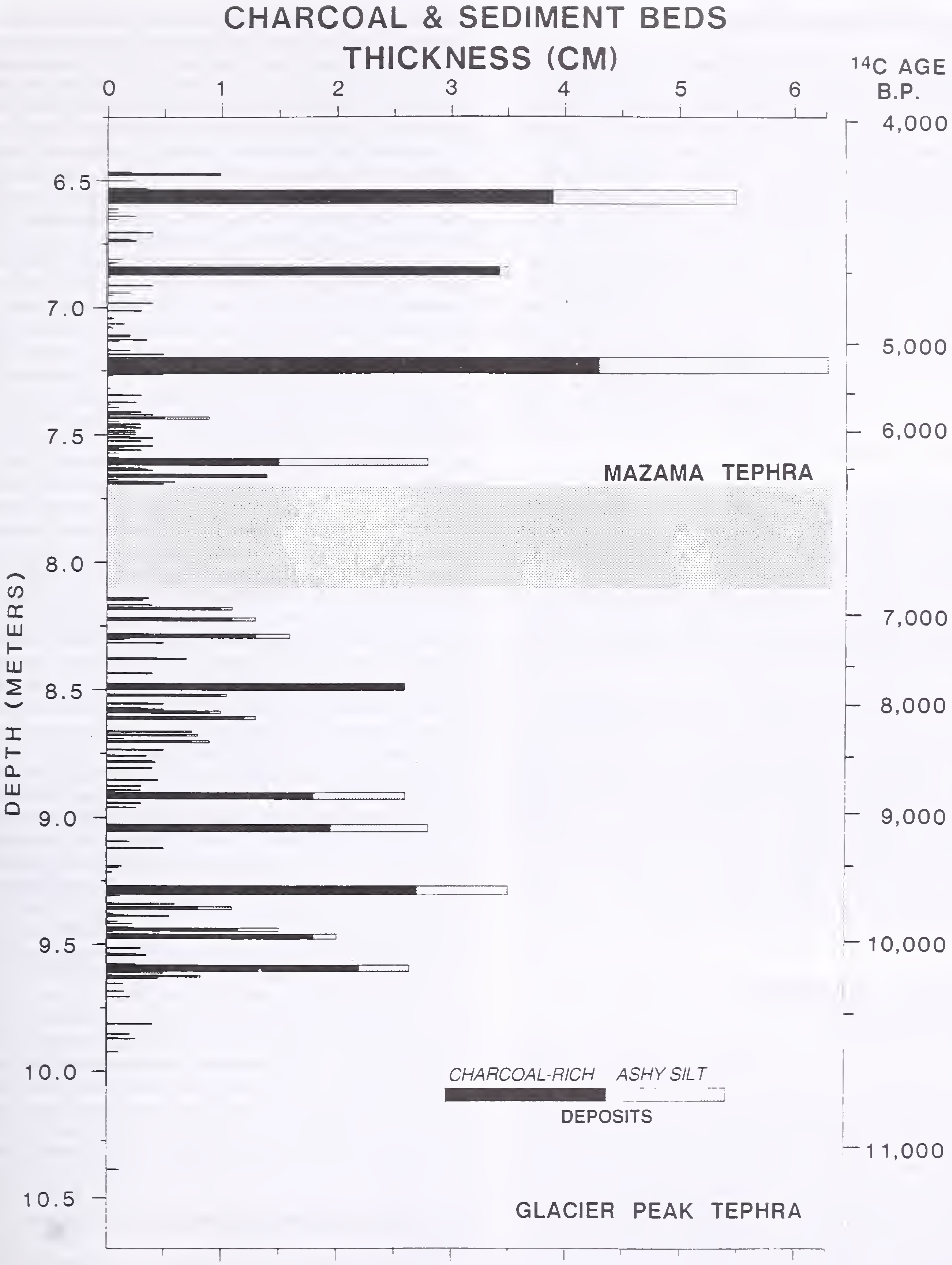

Figure 1—Charcoal layers representing individual forest fires that occurred between 4,000 and 10,500 years ago in a high-elevation western larch forest at Sheep Mountain Bog Research Natural Area, Lolo National Forest, MT. Dark bars are charcoal layers from continuous cores of pond sediments taken by Dr. Peter J. Mehringer, Department of Anthropology, Washington State University, Pullman, WA. Associated light bars represent slope-wash erosional material evidently resulting from a fire.

Frequent Surface Fires

Prior to 1900, warm-dry western larch sites—on Douglas-fir, spruce, or grand fir habitat types—were codominated by open parklike stands of seral larch and ponderosa pine (*Pinus ponderosa* var. *ponderosa*) (Arno 1988; Habeck 1990). These sites burned primarily in frequent surface fires at intervals averaging about 10 to 30 years. Some of these stands also experienced replacement fires at long intervals of 150 to 400 years (Arno and Scott, in preparation; Barrett and others 1991). Ponderosa pine is a long-lived shade-intolerant species that often requires frequent surface fires to perpetuate itself in competition with the shade-tolerant species (Arno and others 1985). Unlike larch and its other associates, ponderosa pine produces leaf litter that is highly combustible. Large quantities of this long-needle pine litter are cast every year, which is conducive to the development and spread of frequent surface fires (Mutch 1970).

Mixed-Severity Fires

Cool-dry larch sites were codominated by seral larch, lodgepole pine (*Pinus contorta* var. *latifolia*), and often Douglas-fir. These sites are on dry subalpine fir (*Abies lasiocarpa*) habitat types and cold-moist Douglas-fir habitat types. They burned at average intervals of about 30 to 75 years in a mixture ranging from nonlethal understory fires to stand-replacing fires. The latter occurred at intervals of about 140 to 240 years in a Glacier National Park, MT, study area (Barrett and others 1991).

Infrequent Stand-Replacement Fires

Moist larch sites were codominated by seral larch, lodgepole pine, Douglas-fir, and Engelmann spruce (*Picea engelmannii*). These sites are found on the wetter grand fir and subalpine fir habitat types as well as the western redcedar and western hemlock habitat types. They burned primarily as stand-replacement fires at mean intervals of 120 to 350 years. Because of larch's high resistance to fire, scattered individuals or groves often survived and served as seed trees.

FIRE MANAGEMENT CONSIDERATIONS

During the past 50 to 80 years fire suppression has significantly changed the role of fire over large areas of the western larch forest type. Suppression is effective in stopping surface fires of low to moderate intensity. Some of these suppressed fires could have become large stand-replacing fires—for instance, when high winds arose (Agee 1990; Arno 1976; Arno and Brown 1991; Barrett and others 1991; Hall 1980). This reduction in fire is generally unfavorable for a fire-adapted seral species such as larch.

Stand-replacing fires favored larch over its competitors because larch was most likely to survive as individual trees. It could also seed into burned areas and outgrow seedlings of the shade-tolerant species. Low-intensity to moderate-intensity fires favored larch by thinning out much of the competition.

When fires are suppressed over a long period, succession advances. Shade-tolerant species increase while seral species fail to regenerate (Arno and others 1985). On many of the sites suitable for larch, foresters have substituted for natural fires by using clearcuts and shelterwood cuts with prescribed burning or mechanical scarification. However, vast areas of the larch sites have had no silvicultural treatment or have had various kinds of partial cutting that removes the overstory trees and allows shade-tolerant conifers to become dominant. In National Parks, wilderness, and other natural areas, fire has generally been suppressed except for the most severe wildfires. For example, during the past 15 years some prescribed natural fires—lightning ignitions allowed to burn under previously designated criteria—have burned a few thousand hectares of the larch type in the Selway-Bitterroot and Bob Marshall Wildernesses.

With fire suppression in partially cut and unharvested stands, dense understories and thickets of shade-tolerant trees develop and the health of all trees declines (Arno and Scott, in preparation; Gast and others 1991; Monnig and Byler 1992; Mutch and others 1993). Dense stands of stagnating trees have now developed over large areas in and adjacent to the western larch type. During the past decade disastrous insect and disease epidemics have swept through a half-million hectares of forests in the Blue Mountains of eastern Oregon, where western larch and ponderosa pine once dominated but have been largely replaced by thickets of shade-tolerant trees. This forest decline is spreading northward into Washington (Gast and others 1991) and eastward into central Idaho (Steele 1993). It is linked to long-term fire suppression and partial cutting that gave rise to stagnant stands of shade-tolerant species in which mortality was hastened by epidemics of several insects and diseases (Gast and others 1991; Mutch and others 1993).

A traditional forestry solution to advanced succession and decadence of forests in the western larch type would be to greatly expand clearcutting and shelterwood harvests with site preparation. This would require extensive road building in roadless areas, would impact watershed values, wildlife habitat, and esthetic concerns, and would no doubt be unacceptable politically. The U.S. Department of Agriculture, Forest Service, and other land management agencies have shown considerable interest in new ecologically based approaches to maintenance of forest health and biological diversity in wildland forests (Overbay 1992). Numerous alternatives involving silviculture and prescribed burning are available for reestablishing an appropriate semblance of the fire process. There is an urgent need to replace fire exclusion with ecologically based management of fire and fuels in a variety of western forest types. If and when land managers make significant progress in restoring and substituting for the fire process, they will surely benefit western larch, which is a consummate fire species.

GUIDES FOR PRESCRIBED FIRE

Because western larch is a seral, fire-dependent tree, the use of prescribed fire is an important part of management to perpetuate the species. Results of research during the past 30 years provide specifications for the use of fire in western larch stands for various silvicultural goals such as fuel reduction, site preparation, regeneration, and vegetation management. Early studies were directed at broadcast burning of clearcut harvest units (Artley and others 1978; Beaufait and others 1977; Boyd and Deitschman 1969; DeByle 1981; Shearer 1975, 1984, 1985, 1989; Steele 1964; Steele and Beaufait 1969). Later work includes understory burning in partial cut stands and in relatively undisturbed forests (Antos and Shearer 1980; Brown and others 1985; Miller 1977; Norum 1975, 1976, 1977).

When there is adequate fuel and when burning is done under dry conditions, the duff is reduced in depth sufficiently to allow larch seedling establishment. Even harvest units with little burned surface regenerate significantly better than unburned units. The amount of bare soil will increase with time on burned but not on unburned units (Shearer 1989).

Timing of prescribed fires to achieve satisfactory site preparation for larch regeneration is critical. Consumption of duff is strongly influenced by moisture content of the duff, especially the lower half (Brown and others 1985; Norum 1977; Shearer 1975). Fires in spring or early summer usually burn only the surface of the duff layer and therefore do not expose mineral soil. Following dry summers, late summer or early fall fires more effectively remove the duff layer and expose adequate mineral soil for larch regeneration. Conditions under which north slopes can be burned to substantially reduce the duff layer usually occur only in August and early September in the larch/Douglas-fir forest type. On warmer aspects there are usually more opportunities to broadcast burn logging slash and provide seedbeds (DeByle 1981).

High-intensity fires over a dry duff layer usually are unnecessary and undesirable. These fires expose a high proportion of mineral soil. If a good seed crop follows, dense overstocking of tree seedlings can result. Moderate-intensity fires in dry duff will usually consume most of the duff and prepare a seedbed that is adequate for larch regeneration. Harsh sites with poor natural regeneration potential can often be successfully planted with larch after burning (DeByle 1981).

Fire will burn most of the duff on a larch-fir forest floor when the duff is at 50 percent water content (by weight). As water content of the duff increases, a decreasing percentage of the duff is consumed (Shearer 1975). When water content exceeds 100 percent in the lower half of the duff layer, fire will not adequately prepare a seedbed (Artley and others 1978). Brown and others (1985) presented numerical relationships of known precision for predicting duff consumption that incorporate results from these forests. These predictive models were designed for easy use by practitioners and apply over a wide range of conditions.

Duff consumption is expressed in three ways: depth reduction, percentage depth reduction, and percentage mineral soil exposed. Each expression is appropriate to evaluating certain prescribed fire objectives. Depth of duff reduction relates to actual amount consumed and smoke production. Percentage duff reduction describes and sets objectives of prescribed fire to leave specified amounts of duff on site. Mineral soil exposure is commonly used to define site preparation needs.

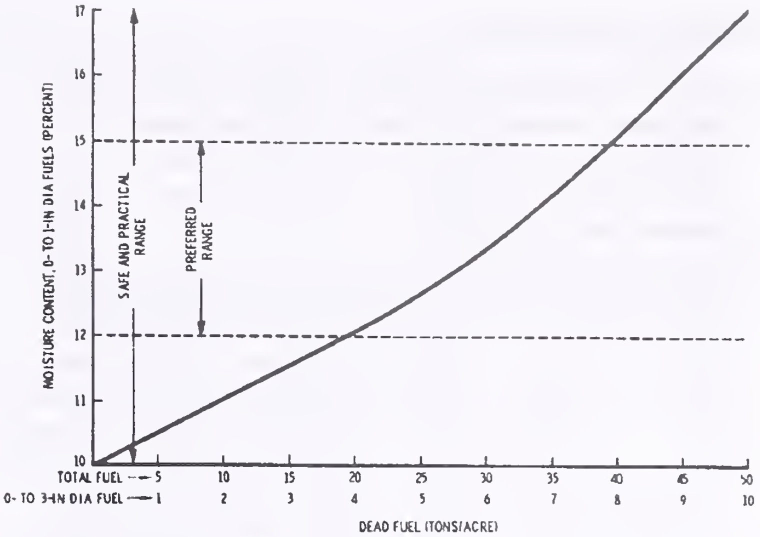

Figure 2—Recommended fuel moistures for safe and practical burning of different surface fuel loads in western larch/Douglas-fir forests.

Safe, effective prescribed fire treatments in partially cut or uncut western larch/Douglas-fir forests can be achieved using properly conducted strip headfires (Kilgore and Curtis 1987) under the correct burning conditions selected for the target fuel complex according to the procedure suggested by Norum (1977). Figure 2 shows the range of burning conditions over which it is possible to burn while still completely controlling the fire. These burning conditions reflect experience in burning under standing timber in a large number of western larch/Douglas-fir stands. The diagonal, curved line gives various sets of fuel moistures and fuel loadings for a spreading fire that is readily controllable and not unduly damaging to overstory trees if other conditions are favorable. Windspeed should be below 10 mi/h, and preferably below 5 mi/h if directly upslope. At 10 percent fuel moisture content, the fire will be fairly intense and will spread readily. At 17 percent moisture content, a continuous bed of fine fuel (preferably cured, needle-bearing slash) is necessary to prevent a ragged fire treatment. This kind of burning is easiest and safest within the preferred range of fuel moisture content shown in figure 2, especially if the heavier fuel loadings are burned at or near the 15 percent level of moisture content and lighter fuel loadings around the 12 percent mark.

The predictive models for duff and woody fuel consumption provided by Brown and others (1985) can be used in conjunction with figure 2 to select burning conditions that best satisfy treatment objectives. Similarly, probable post-fire tree mortality associated with understory burning in western larch stands can be estimated using a procedure described by Reinhardt and Ryan (1988, 1989). The procedure can aid in selecting burning conditions that are compatible with prescription specifications for tree mortality.

Other aids for prescribed burning in forests containing western larch include photo guides for appraising natural and slash fuels (Fischer 1981a,b; Koski and Fischer 1979; Maxwell and Ward 1980; Morgan and Shiplett 1989). Finally, Kilgore and Curtis (1987) released a guide to understory burning in ponderosa pine-larch-fir forests in the Intermountain West. This guide provides burning objectives, example burning prescriptions, and techniques to meet prescriptions including preburn preparation and ignition strategies.

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Spatial and Temporal Relationships in Larix Forests

B. John Losensky

Abstract—Larix forests are a major portion of the Northern Rocky Mountain landscape. This distribution was greatly affected by past fire cycles and fire severity. With the advent of fire exclusion there is an increased risk of major changes in stand composition and a subsequent loss of the larch type. To better assess this potential impact, early surveys and timber examinations were consulted to determine the distribution and structure of larch stands at the turn of the century. This information is presented by county for Idaho and Montana, U.S.A.

In our attempts to maintain the biodiversity of our world new approaches to land management have emerged. One of these methods that is gaining recognition on Federal lands in the United States is the concept of ecosystem management. This approach features a landscape analysis of portions of the forest during the planning process to assure that "all the pieces" of the ecosystem are considered and examples of each are maintained. To do this analysis requires an understanding of the natural communities and the processes that play a role in their development. While the cover type is an important part of the analysis of forested environments, stand age and structure also contribute to environmental diversity and subsequently the number and types of species present. For example maintaining immature stands of ponderosa pine where historically sites were dominated by old growth conditions may exclude certain species. The severity and frequency of processes such as fire also play a major role in the life cycle of most plant species in the Northern Rocky Mountains and therefore must be included in this analysis. At first glance determining natural stand structure may seem fairly simple in the Northern Rocky Mountains when compared to other parts of the country as examples still remain of stands undisturbed by logging. Unfortunately fire protection has had a dramatic impact on stand structure and from a landscape perspective ecosystems have undergone significant change.

This paper attempts to use historical information to help reconstruct a description of our natural stands and in particular the larch-Douglas-fir community that was found in the Northern Rockies at the time of settlement by EuroAmericans in the late 1800's.

METHODS

Data for the analysis were obtained from progress reports published by the Forest Survey Section of the Northern Rocky Mountain Forest and Range Experiment Station between 1938 and 1942 and from the unpublished data from the same survey that are stored as Collection 84 in the Archives section of the Mansfield Library at the University of Montana.

For Idaho the larch-Douglas-fir type (*Larix occidentalis-Pseudotsuga menziesii*) is defined by the Forest Survey as stands containing 10 percent or more of western larch and 75 percent or more of larch and Douglas-fir combined but less than 15 percent white pine (*Pinus monticola*). The area included northern Idaho from the Salmon River to the Canadian boundary. For Montana the larch type is defined as forests in which 50 percent or more of the stand is larch and less than 20 percent is western white pine. The area west of the Continental Divide was covered in the analysis.

Field data were collected between 1932 and 1937 for northern Idaho and western Montana. Data were collected from all land ownerships, and these data were used to portray the percent cover of the vegetation types. By the 1930's appreciable portions of the private land had been harvested which changed the age structure of these stands. The Forest Service lands on the other hand were largely undeveloped. For this reason only the area in Forest Service ownership was used to evaluate the age structure of the various vegetation cover types.

The age structure for the various cover types in Idaho is based wholly on uncut acres while in Montana the data for Forest Service lands included cutover areas. As a result the mature and old growth age classes for ponderosa pine (*Pinus ponderosa*) cover type may be underestimated in western Montana. All cover types in Deerlodge and Silverbow Counties may also be affected as a result of early timber harvest to support mining activity in the Butte-Anaconda area. This area is relatively small and represents less than 2 percent of western Montana.

The 1930's inventory data provided a breakdown of acres of the various cover types by 20-year age increments. These age groups were adjusted to reflect their age in 1900 to better express the natural stand condition. This also helped to eliminate the effect of the 1910 fires. Acres shown as cutover in 1938 were considered to be mature in 1900. Acres shown as burned in 1938 were distributed to the various age classes based on the percentage of the cover type in that class. This was done to better represent the natural fire process where fires burned in all age classes and not just mature stands (Ayres 1901).

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All acres were assumed to remain in the same cover type. While this assumption may be flawed there was no apparent method available to determine the previous cover type. There is also a high likelihood that acres lost to one cover type were offset by gains from another area at the landscape level.

There is always a concern that the vegetation composition or structure at any one point in time may not reflect the "natural" community because of a climatic shift or other major perturbation. This is a valid concern and should temper any analysis of this type. Bog analysis conducted in western Montana suggest relatively uniform climatic conditions for the last 4,000 years (Mehringer 1976). These data would suggest that vegetative communities were somewhat uniform for this time period. Periodic dry periods did result in major fire events (Gabriel 1976) which could change age structure at the multi-drainage level. For this reason average age conditions should be considered at the county or state level so that fire events such as the 1889 fire year do not dominate the age structure.

RESULTS

Distribution

Based on the 1930's inventories the larch-Douglas-fir type represented 13.7percent of the acres in northern Idaho and western Montana. In Idaho the type occupied 9.1 percent and in Montana 17.3 percent (table 1). Bonner, Boundary, Idaho, Kootenai, and Shoshone Counties accounted for 76 percent of the type in Idaho. In Montana

Table 1—Percent area by cover type for all acres by county in northern Idaho and western Montana, 1930's

County	WWP[1]	PP	L-DF	H-WF	DF	ES	LP	WRC	C-WF	SALP	NCF	NF
Northern Idaho												
Benewah	35.3	22.5	12.8	0.6	0.9	0	1.8	1.0	1.7	0.6	5.9	16.9
Bonner	33.4	15.2	21.6	0.2	1.6	0.9	2.5	0.8	0.6	8.1	8.4	6.7
Boundary	24.6	10.0	17.7	0.3	1.2	6.3	5.4	1.2	0.2	21.5	4.5	7.1
Clearwater	49.4	6.5	7.2	1.2	1.8	0.9	5.6	0.6	2.6	9.4	10.6	4.2
Idaho	1.6	13.8	4.2	3.5	12.4	3.6	16.0	0.4	3.2	16.6	7.4	17.3
Kootenai	20.8	24.3	18.8	0.8	4.2	T	2.4	T	0.6	1.3	7.0	19.8
Latah	20.1	20.1	11.9	0.5	0.3	0	0.6	T	1.5	0	2.6	42.4
Shoshone	53.7	3.1	8.4	0.9	4.3	1.9	6.1	0.2	0.5	10.0	9.9	1.0
Nez Perce	0	15.3	2.3	0.3	0.6	0	0.8	0	0	0	1.1	79.6
Lewis	0	22.3	0.8	0	2.7	0	0.2	0	0	0	1.0	73.0
Northern Idaho	22.4	13.0	9.1	1.7	5.9	2.1	8.1	0.4	1.8	10.7	7.3	17.5
Western Montana												
Deerlodge[2]	0	0	0	0	2.5	0.2	24.7	0	0	1.7	19.6	51.3
Flathead	1.0	4.5	21.9	0.1	1.1	4.5	13.5	T	0	16.4	25.8	11.2
Granite[2]	0	4.2	0.3	0	19.2	0.7	34.0	0	0	9.0	6.2	26.4
Lake	1.4	17.6	17.4	0	0.4	4.3	4.3	0.1	0	2.5	8.5	43.5
Lewis and Clark[2]	0	5.6	0	0	15.3	0.9	28.6	0	0	17.3	21.0	11.3
Lincoln	5.2	14.8	35.0	T	1.0	4.2	15.4	0.3	0.2	14.0	6.7	3.2
Mineral	2.5	31.0	25.0	0.2	1.2	0.3	6.9	T	0.2	13.3	17.4	2.0
Missoula	0.2	24.0	22.8	T	5.1	2.7	13.9	T	0	6.1	13.1	12.1
Powell	0	5.5	3.9	0	11.6	0.2	14.1	0	0	16.3	13.0	35.4
Ravalli	0	17.9	0.7	0	9.0	0.3	6.5	0	0	25.5	21.0	19.1
Sanders	6.8	24.5	21.8	0.2	1.7	0.1	3.2	0.1	0.1	7.5	16.1	17.9
Silverbow[2]	0	0	0	0	10.9	0.1	23.8	0	0	0.9	8.9	55.4
Western Montana	2.0	13.7	17.3	0.1	5.1	2.3	13.4	0.1	T	12.9	15.5	17.6
Northern Idaho and Western Montana average percentages												
	11.0	13.4	13.7	0.8	5.5	2.2	11.1	0.2	0.8	11.9	11.9	17.5

[1] Cover type codes: WWP-western white pine (*Pinus monticola*)
PP-ponderosa pine (*Pinus pondersoa*)
L-DF-larch-Douglas-fir (*Larix occidentalis, Pseudotsuga menziesii*)
H-WF-western hemlock-white fir(grand fir) *Tsuga heterophylla, Abies grandis*
DF-Douglas-fir (*Pseudotsuga menziesii*)
ES-Engelmann spruce (*Picea engelmannii*)
LP-lodgepole pine(*Pinus contorta*)
WRC-western redcedar (*Thuja plicata*)
C-WF-western redcedar-white fir (grand fir) *Thuja plicata, Abies grandis*
SALP-alpine (subalpine and alpine forest)
NCF-non commercial forest-rocky, plus deforested cutover, nonstocked burn
NF-non forest-barren, grass, brush, other.

[2] West of the Continental Divide only.

Table 2—Percent of stand volume composed of larch by cover type for counties in northern Idaho and western Montana (all acres), 1930's

County	WWP	PP	L-DF	H-WF	DF	ES	LP	WRC	C-WF	WT. avg[1]
Northern Idaho										
Benewah	21	12	45	21	0	0	6	30	10	23
Bonner	9	10	44	9	8	5	3	2	11	12
Boundary	11	16	53	1	14	5	5	3	10	13
Clearwater	6	8	30	7	2	8	8	3	8	8
Idaho	8	1	43	1	3	3	4	3	2	7
Kootenai	12	10	29	9	6	0	0	0	13	14
Latah	17	17	40	17	9	0	0	0	16	22
Lewis	0	6	39	0	0	0	0	0	0	7
Nez Perce	0	9	32	4	0	0	0	0	0	12
Shoshone	11	12	48	14	3	11	20	10	9	15
Northern Idaho	9	5	41	4	3	6	10	4	6	8
Western Montana										
Deerlodge	0	0	0	0	0	0	0	0	0	0
Flathead	32	22	59	4	3	7	5	12	0	37
Granite	0	0	0	0	0	0	0	0	0	0
Lake	37	22	57	0	9	9	0	18	0	36
Lewis and Clark	0	0	0	0	0	0	0	0	0	0
Lincoln	17	22	67	3	4	11	7	10	4	37
Mineral	7	12	53	0	5	10	10	4	18	20
Missoula	35	19	56	0	3	10	6	12	0	34
Powell	0	8	50	0	1	6	0	0	0	20
Ravalli	0	T	43	0	T	1	0	0	0	1
Sanders	15	16	63	5	2	26	19	11	4	26
Silverbow	0	0	0	0	0	0	0	0	0	0
Western Montana	21	16	61	4	2	9	6	11	7	32
Northern Idaho and Western Montana average percentages										
	10	12	56	4	2	8	7	4	6	17

[1] Percent larch volume weighted by acres of the various cover types.

84 percent of the type occurred in Lincoln, Flathead, Missoula, and Sanders Counties. The most common cover type in Idaho was white pine occupying 22.4 percent of the area followed by nonforest with 17.5 percent with larch-Douglas-fir the fifth most common cover type. In Montana the nonforest type covered 17.6 percent of the area with larch-Douglas-fir the second most common type.

To understand the actual amount of larch that was present at the turn of the century, the volume of larch in the various cover types was compared to the total volume for the types (table 2). Larch was much more common in Montana than Idaho with 32 percent of the total commercial volume composed of larch as compared to about 8 percent for Idaho. Within the larch-Douglas-fir cover type, larch made up 61 percent of the volume in Montana and 41 percent in Idaho. Larch was also a significant part of the white pine and ponderosa pine types in Montana with 20 and 16 percent respectively being composed of larch volume. This was not the case in Idaho where larch volume dropped to 9 percent for the white pine type and 5 percent for the ponderosa pine type. In Idaho larch was most common in the lodgepole pine cover type where it represented 10 percent of the volume. Larch was found in each county in northern Idaho. In western Montana three counties did not contain areas of the cover type. These counties are shown as having zero percent of larch in any of the cover types.

Stand Structure

A measure of stand density for various aged stands was developed by evaluating the volume per acre for sawtimber stands and the stocking density for pole and seedling and sapling stands. In Idaho the average volume for the larch-Douglas-fir type was 9.7 mbf/ac. as compared to 13.5 mbf/ac. for all of the other types. The highest volumes were found on the western redcedar type which averaged 21.6 mbf/ac. and the white pine type at 18.5 mbf/ac. The pattern was similar in Montana with the larch-Douglas-fir type averaging 8.5 mbf/ac. which was the same as the average for all cover types. The larch-Douglas-fir type again was one of the least stocked types with the most volume found in the white pine type with 13.9 mbf/ac. and western redcedar at 13.1 mbf/ac. In reviewing table 3, it can be noted that the larch-Douglas-fir type was one of the lower density types as expressed by board foot volume in both northern Idaho and western Montana.

Stocking level information for the pole and seedling and sapling stands was available only for Idaho (tables 4 and 5). While the mature stands tended to have lower biomass present as indicated by the volume per acre, the younger stands tended to be well stocked. For the pole size stands, the type averaged 72 percent well stocked compared to 63 percent for all other types. Only 7percent of the larch-Douglas-fir type was in the poor stocking class

Table 3—Average board foot volume per acre by cover type for counties in northern Idaho and western Montana (all acres), 1930's

County	WWP	PP	L-DF	H-WF	DF	ES	LP	WRC	C-WF	Avg
Northern Idaho										
Benewah	15.8	10.1	9.2	6.2	5.8	0	7.3	7.4	18.1	12.2
Bonner	15.7	7.2	7.0	9.9	6.2	9.1	6.8	20.2	9.2	12.2
Boundary	16.0	6.8	6.8	10.7	5.5	11.7	8.9	32.9	17.6	12.8
Clearwater	21.5	9.8	9.8	10.4	10.7	15.4	7.8	16.6	13.8	17.9
Idaho	15.1	10.1	11.2	9.8	7.8	11.3	5.6	23.2	10.6	10.1
Kootenai	16.4	8.8	10.4	15.5	7.0	0	5.2	0	7.8	12.7
Latah	15.2	9.1	7.9	7.6	7.8	0	0	6.0	9.1	9.9
Shoshone	17.2	9.8	11.4	11.6	10.7	13.0	6.7	12.8	11.2	15.0
Northern Idaho	18.5	9.6	9.7	10.1	8.3	11.8	6.1	21.6	11.6	13.0
Western Montana										
Deerlodge	0	0	0	0	3.3	4.5	3.4	0	0	3.6
Flathead	12.0	11.0	9.1	9.5	6.6	12.2	4.8	17.0	0	9.7
Granite	0	5.0	7.6	0	5.5	5.5	3.8	0	0	5.2
Lake	11.8	6.7	7.8	0	4.3	7.9	4.0	9.3	0	7.6
Lewis and Clark	0	6.6	0	0	4.8	7.3	3.9	0	0	5.5
Lincoln	16.3	9.8	9.1	9.0	7.0	14.6	5.0	14.2	10.8	10.4
Mineral	10.1	6.1	7.0	0	5.4	12.7	4.8	13.5	7.6	6.7
Missoula	13.0	6.4	7.6	0	5.7	7.9	4.9	8.7	0	7.0
Powell	0	6.1	7.2	0	4.7	7.1	3.3	0	0	5.9
Ravalli	0	7.5	6.1	0	6.0	7.8	3.2	0	0	7.2
Sanders	13.8	8.0	7.5	12.5	6.6	15.4	11.0	13.3	8.3	8.2
Silverbow	0	0	0	0	4.0	0	3.1	0	0	3.3
Western Montana	13.9	7.8	8.5	11.0	5.6	11.6	4.6	13.1	9.7	8.5
Northern Idaho and Western Montana average percentages										
	18.0	8.5	8.8	10.1	7.2	11.7	5.1	20.5	11.6	10.6

as compared to 12 percent for all other types. The averages for all other types are somewhat misleading since they are weighted by values for ponderosa pine (37 percent well and 26 percent poor) and Douglas-fir (50 percent well and 11percent poor). The remaining cover types are similar to the larch-Douglas-fir type.

A similar pattern was found in the seedling and sapling stands with 54percent of the larch-Douglas-fir stands well stocked as compared to 48percent for all other forest types. Poor stocking accounted for 14percent of the larch type compared to 19 percent for all other types. There is more variability between types, however, with the larch-Douglas-fir type about in the middle of the spread.

Patch size and community juxtaposition are also important criteria in understanding ecosystem function. While data are available to make this analysis, they were not in

Table 4—Percent of cover type by stocking class for northern Idaho (all acres), 1930's

	Pole class			Seedling and sapling class		
Cover type	Well	Medium	Poor	Well	Medium	Poor
WWP	81	13	6	45	35	20
PP	36	37	27	37	37	26
L-DF	72	21	7	54	32	14
H-WF	69	17	14	49	32	19
DF	50	39	11	45	34	21
ES	71	22	7	61	29	10
LP	75	22	3	62	27	11
WRC	0	0	0	67	10	23
C-WF	65	27	8	53	17	30
Northern Idaho average percentages						
	65	24	11	50	32	18
Excluding L-DF type						
	63	25	12	48	33	19

Table 5—Percent of larch-Douglas-fir cover type by stocking class for counties in northern Idaho (all acres), 1930's

	Pole class			Seedling and sapling class		
County	Well	Medium	Poor	Well	Medium	Poor
Benewah	52	30	18	18	40	42
Bonner	70	24	6	52	38	10
Boundary	73	22	5	78	18	4
Clearwater	88	11	1	35	43	22
Idaho	91	7	2	75	18	7
Kootenai	65	25	10	38	40	22
Latah	71	21	8	51	27	22
Lewis	99	0	0	45	55	0
Nez Perce	95	5	0	39	61	0
Shoshone	80	14	6	53	31	16
Northern Idaho average percentages						
	72	21	7	54	32	14
All other cover types						
	63	25	12	48	33	19

a form that could be readily evaluated. With the development and application of GIS technology this information should be readily available for future analysis.

Age Structure

An analysis of the age structure suggests some marked differences in stand structure between Montana and Idaho (tables 6 and 7). In Idaho nonstocked areas accounted for 21 percent of the larch-Douglas-fir type which was the same as the average for all other cover types. In Montana 18 percent were nonstocked which is similar to Idaho and slightly higher than the 13 percent for other types in Montana. Seedling and sapling stands occupied about 28 percent of the type in Idaho which is slightly higher than the other cover types (21 percent). In Montana the situation is reversed with about 19 percent of the larch-Douglas-fir type in a seedling-sapling condition as compared to 26 percent for all other types.

When comparing the percentage of area with very young stands (less than 40 years of age) the larch-Douglas-fir type ranks third in Idaho with 49 percent following the lodgepole pine type (76 percent) and the Douglas-fir type (56 percent). In Montana it also ranks third at 37 percent behind the lodgepole pine type (57 percent) and the white pine type (46 percent). The data suggest that young stands were common throughout the two states. This trend is also seen in stands that potentially could have met the Northern Region draft old-growth criteria. Only the age portion of the definition could be evaluated as other components such as tree diameter and number were not available. For this reason the percentages represent the maximum acres that may have met the definition. In Idaho only 20 percent of the larch-Douglas-fir type qualified compared to an average of 26 percent for other cover types. For comparison the potential old growth for the western redcedar type was 81 percent and 52 percent for the hemlock-white fir type. In Montana the percentage is slightly higher for potential old growth (31 percent) for the larch-Douglas-fir type compared to 19 percent for all other types. Cover types with the highest percentage in potential old growth in western Montana were western redcedar (62 percent) and ponderosa pine type (54 percent).

Table 6—Percent acres by age class for larch-Douglas-fir cover type on national forest land for counties in northern Idaho and western Montana, 1900

County	Non-stocked	Seedlings, saplings 1-40	Poles 41-60	Immature 61-100	Mature 101-150	Potential old growth 151+[1]
		Years				
			Northern Idaho			
Benewah	12.3	11.6	2.6	5.2	4.6	63.7
Bonner	30.2	34.8	7.9	3.6	9.3	14.2
Boundary	22.7	33.8	6.8	3.2	9.5	23.9
Clearwater	10.3	24.8	5.2	26.9	24.0	8.8
Idaho	15.7	19.7	3.2	12.6	28.0	20.8
Kootenai	26.7	42.0	5.4	5.2	9.6	11.1
Latah	15.3	8.7	6.3	17.6	10.0	42.1
Shoshone	14.6	24.6	8.1	17.3	14.7	20.6
Northern Idaho	20.7	28.5	6.2	9.7	15.0	19.9
			Western Montana			
Deerlodge	0	0	0	0	0	0
Flathead	8.2	10.5	2.0	4.8	21.8	52.7
Granite	14.7	16.2	27.8	9.6	27.1	4.6
Lake	18.6	13.6	1.3	12.3	15.3	38.9
Lewis and Clark	0	0	0	0	0	0
Lincoln	13.8	27.4	9.2	8.2	15.8	25.6
Mineral	41.0	14.6	7.2	10.6	13.8	12.8
Missoula	0.5	16.8	7.6	8.4	22.3	44.4
Powell	1.9	27.0	1.2	4.9	21.8	43.2
Ravalli	9.7	6.6	8.3	21.2	52.9	1.3
Sanders	39.1	17.9	3.3	5.5	17.7	16.5
Silverbow	0	0	0	0	0	0
Western Montana	18.2	19.1	5.9	7.3	18.2	31.3
		Northern Idaho and Western Montana average percentages				
	18.8	21.4	6.0	7.9	17.4	28.5

[1] Potential old growth minimum age using 1991 Region 1 draft definitions.

	PP, DF, L	LP	Other
Montana	170+	140+	180+
Idaho	150+	120+	160+

Table 7—Percent acres by age class by cover type for national forest land in northern Idaho and western Montana, 1900

Cover type	Non-stocked	Seedlings, saplings 1-40	Poles 41-60	Immature 61-100	Mature 101-150	Potential old growth 151+[1]
		- - - - - - - -	- - - - - - - -	*Years*	- - - - - - - -	- - - - - - - -
			Northern Idaho			
WWP	18.4	21.9	4.2	13.5	12.1	29.8
PP	12.5	8.0	1.7	5.7	26.6	45.5
L-DF	20.7	28.5	6.2	9.7	15.0	19.9
H-WF	3.0	7.1	2.5	7.5	28.5	51.5
DF	39.4	17.3	5.7	12.9	17.6	7.1
ES	11.9	11.2	2.5	10.3	23.0	41.2
LP	31.9	44.5	6.8	9.4	4.0	3.5
WRC	2.5	3.6	1.3	6.2	6.2	80.7
C-WF	21.6	15.3	6.4	13.1	25.1	18.4
Northern Idaho	21.1	22.2	4.6	11.3	15.0	25.8
			Western Montana			
WWP	22.8	23.2	3.8	6.8	22.5	20.8
PP	8.4	9.8	6.2	5.0	16.1	54.4
L-DF	18.2	19.1	5.9	7.3	18.2	31.3
H-WF	1.9	12.6	23.1	0	24.6	37.7
DF	4.8	22.8	8.5	23.5	33.4	6.9
ES	2.8	3.9	1.6	4.8	41.9	45.1
LP	17.5	38.6	11.4	20.5	9.3	2.7
WRC	11.4	10.6	0.7	9.6	5.8	61.8
C-WF	8.6	17.6	27.3	6.9	10.2	29.5
Western Montana	14.6	23.7	7.6	12.6	18.0	23.4
			Northern Idaho and Western Montana average percentages			
	17.4	23.1	6.4	12.0	16.7	24.4

[1] Potential old growth minimum age using 1991 Region 1 draft definitions.

	PP, DF, L	LP	Other
Montana	170+	140+	180+
Idaho	150+	120+	160+

These differences between Montana and Idaho are partly explained by the proportions of the various cover types found in the states. In Idaho types such as western redcedar and hemlock-white fir are more common which have higher proportions of old growth while in Montana the lodgepole pine cover type dominates much of the area which was characterized by young stands. Of interest is the high amount of potential old growth larch-Douglas-fir type in Flathead County (53 percent). This value is exceeded only by Benewah County (64 percent) in Idaho which represents less than 10,000 acres of the type. Missoula (44 percent) and Powell (43 percent) Counties also were major areas of potential old growth. These values are of interest since much of the research for larch has been conducted in Flathead County.

DISCUSSION

Analysis of these historical data on the larch-Douglas-fir cover type brings out a number of interesting points:

- Larch was a more important component of timber stands in western Montana compared to northern Idaho. This is particularly true in the Flathead Valley. Not only was the proportion of larch volume greater in the larch-Douglas-fir type but larch constituted a higher percentage of the volume in most of the other cover types in western Montana.
- While stand density tended to be high in young stands, mature stands were not particularly high in volume. This may be the result of underburns which tended to thin the stand over time.
- The 20 percent nonstocked stands was greater than what might have been expected for a type that is commonly thought to have experienced frequent underburns. For example the ponderosa pine type which typically underburned had only about 10 percent nonstocked areas. This fact plus the relatively low volumes found in mature stands in the larch-Douglas-fir type may suggest a more intense fire cycle with at least portions being of a stand replacement intensity. While a portion of the nonstocked condition could be due to logging this impact would have been more significant on the ponderosa pine cover type.
- The percent of stands that were potentially old growth (26 percent) was lower than anticipated. It was assumed that the type would be similar to ponderosa pine but instead it was more aligned with the white pine type

which is commonly exposed to stand replacement fires. Only two types had less potential old growth: the lodgepole pine type (3 percent) which was expected and the Douglas-fir type (7 percent).

A test of any new analysis procedure is how effectively it addresses the issues of concern. The value of analyzing historical vegetation is to develop an understanding of the natural ecosystem and provide a benchmark or model for ecosystem management today. Using present conditions as a guide will not suffice as many of the natural processes such as fire have been removed or substantially altered. Age structure as well as stand composition have continued to change until the vegetation communities we see today may reflect a condition never before present on the landscape.

While it may not be possible or desirable to return our National Forests to a "natural" condition, using historical data such as these to compare with existing stand conditions and proposed actions will help to reveal potential conflicts and stand components that need consideration to assure that all the pieces are preserved.

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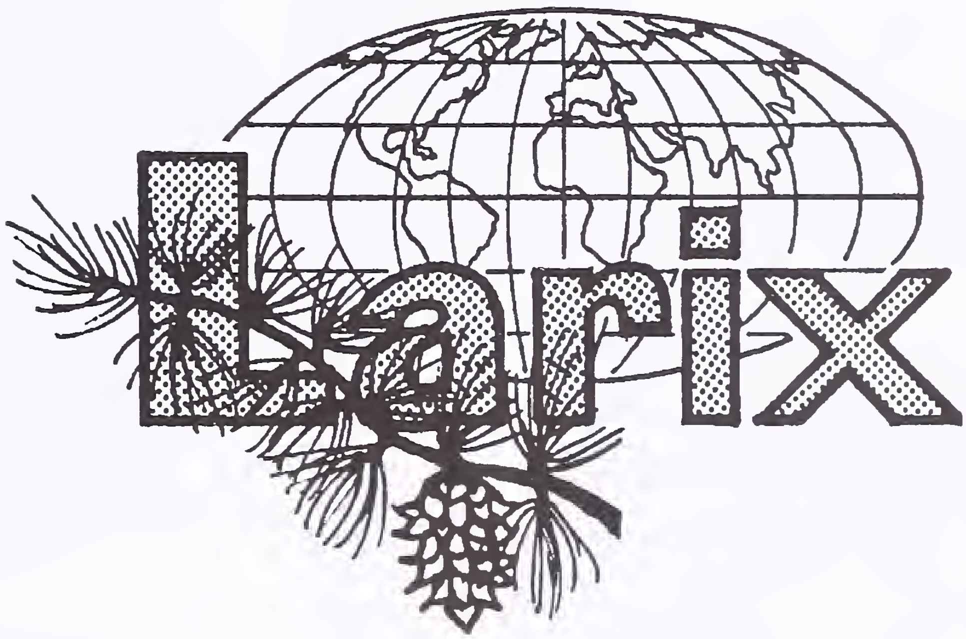
IV. Contemporary Management Issues in North America



Distribution and Volume of Larch Forests in the Western United States

Roger C. Conner
Renee A. O'Brien

Abstract—Two species of larch occur in the Western United States: western larch (*Larix occidentalis*) and alpine larch (*Larix lyallii*). Western larch is more widespread in its distribution and is the predominant tree species on over 2.3 million acres in Idaho, Montana, Oregon, and Washington combined. Larch growing-stock volume amounts to 6.0 billion cubic feet. Recent estimates show net annual growth at over 100 million cubic feet. This represents an average increase in larch inventory volume of 1.7 percent.

The larch resource statistics presented in this paper were derived from two sources: Forest Inventory and Analysis (FIA) and National Forest stand inventories. Larch area, volume, growth, and mortality estimates for lands outside National Forests were based on FIA sample locations established by the Interior West Resource Inventory, Monitoring, and Evaluation Program at the Intermountain Research Station, Forest Service, U.S. Department of Agriculture, and the Inventory and Economics Program at the Pacific Northwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, (USDA 1992a,b). These data were combined with data from National Forest stand inventories to arrive at statewide assessments of the larch resource (Bassett and Oswald 1983; Benson and others 1987; Conner and O'Brien, in preparation; Farrenkopf 1982). English units of measurement were used for these inventories and reports, so this standard is used here.

DISTRIBUTION

The distribution of larch species in the Western United States is limited to four States: Idaho, Montana, Washington, and Oregon. Western larch (*Larix occidentalis*) is found in central and northeastern Washington and Oregon. In Montana, western larch occurs west of the Continental Divide, and in Idaho, from the Salmon River Mountains in the central portion of the State north into British Columbia. The range of alpine larch (*L. lyallii*) is restricted to higher elevations in the mountains of western Montana and northeastern Idaho and to upper elevations in the Cascades of north-central Washington.

Western larch typically occupies cool, moist sites ranging in elevation from 2,000 feet to more than 6,000 feet (USDA 1965). It is most often found on northerly or easterly exposures but does well on all aspects on high-elevation sites (USDA 1990). Most of the larch stands outside the National Forests in Washington and Idaho occurred at elevations of less than 3,500 feet, and at elevations of less than 4,100 feet in Oregon and Montana.

Figure 1 illustrates the extent of the western larch forest type according to Eyre (1980). In addition, each triangle in figure 1 represents an inventory location outside the National Forests where larch is an established component of the stand, but does not necessarily comprise a plurality. Data from FIA locations also indicate that larch is a component of 19 other forest types throughout its Western United States range. Its most frequent associates are Douglas-fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis*), according to inventory data.

AREA AND OWNERSHIP

Based on recent inventories, the total area of the western larch forest type in the United States is estimated to be more than 2.3 million acres (table 1). In terms of area, the larch forest type accounts for just 3 percent of all timberland acres in the four States combined. Nearly 131,000 acres of larch under National Forest management are reserved. Reserved acres, such as those in wilderness areas, are not available for timber harvest. Typically, these areas are not inventoried, so no additional statistics are available. The 2.2 million acres of nonreserved larch are the subject of the remainder of this paper.

Most of the nonreserved larch acres are National Forest land. Combined with the nearly 112,000 acres of other public land, 81 percent of the larch resource is managed by public agencies. The other public owner group includes the Bureau of Land Management, U.S. Department of the Interior, and lands in State, county, and city ownership.

Ownership of the remainder of the larch resource is divided about evenly between two owner groups: forest industry and private. Forest industry lands are the more important in terms of supply of larch for timber products. Industry lands are owned by individuals or companies operating sawmills or other primary wood-processing plants. These lands are managed primarily to supply these plants

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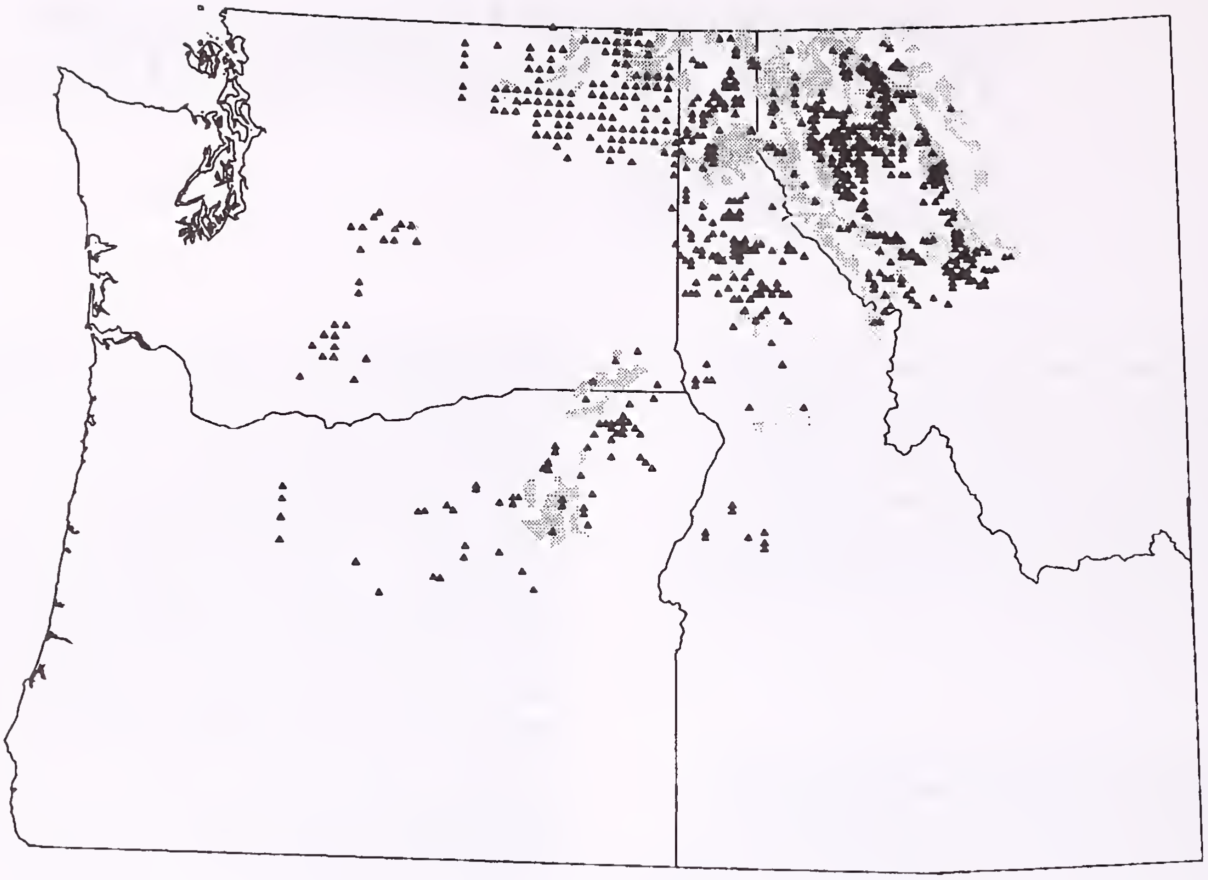

Figure 1—Distribution of FIA locations where western larch is a stand component, overlaid on a larch forest type map (Eyre 1980).

with sawlogs and other raw material. Over 123,000 acres of larch owned by forest industry are in Montana.

The larch in private ownership is owned by farmers and ranchers or located within Indian reservations. Reservation forest land is often managed for the production of timber but is also highly valued for its nontimber attributes. Although intensive management of forest land owned by farmers and ranchers is frequently precluded by small tract size, timber harvest from these lands can contribute substantially to annual removals.

Montana has almost 946,000 acres of the more than 2.2 million acres of nonreserved larch (fig. 2). Another 657,000 acres are in Idaho, about 511,000 acres in Washington, and over 177,000 acres of larch are in Oregon. The distribution by owner within each State closely approximates the overall distribution. The National Forests have the most, ranging from a maximum of about 80 percent of the larch area in Idaho to a minimum 63 percent in Oregon.

Table 1—Total larch forest type area by land class and owner

Owner	Reserved	Nonreserved	Total
	Acres		
National Forest	130,962	1,694,006	1,824,968
Other public	—	111,622	111,622
Private	—	200,673	200,673
Forest industry	—	224,280	224,280
Total	130,962	2,230,581	2,361,543

PRODUCTIVITY

Larch sites have the potential to be very productive. This productive potential is based on the estimated growth of fully stocked, natural stands and can be quantified by classes measured in cubic feet of wood growth per acre per year. By recent inventory estimates, over 1.1 million acres, or half the larch sites, are capable of growing at least 85 cubic feet of wood per acre annually. Another 930,000 acres have the potential to grow from 50 cubic feet to 84 cubic feet per acre annually. Most of the larch sites with the capacity to produce over 85 cubic feet per year are in Idaho and Montana. Generally, productivity over 50 cubic feet per acre per year is considered average for forest sites in these and other Interior West States.

OLD-GROWTH

Recent concern about old-growth prompted an additional screening of larch stand age to determine how much of the resource is in older age classes. Stand age for National Forest land was unavailable, so this analysis was restricted to that portion of the larch forest type area outside the National Forests.

Although stands are no longer classified as old-growth by FIA, stands with an average overstory tree age of at least 100 years are classified as mature. The 100-year age criterion does not necessarily indicate an old-growth condition, but advanced age can serve as a starting point to identify larch stands where recent disturbance, such as timber harvest, may not have occurred.

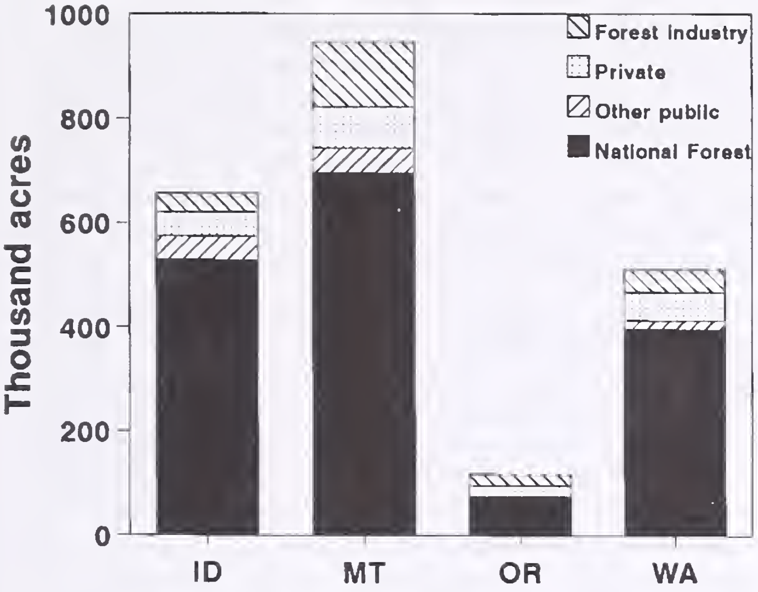

Figure 2—Nonreserved larch forest type area by State and owner.

Less than 95,000 acres of the larch forest type outside the National Forests are classified as mature. This is just 18 percent of the total area of western larch outside National Forest boundaries. In addition, larch trees at least 100 years old were found on fewer than half of the FIA locations distributed over the species' western U.S. range (fig. 3), excluding that portion in the National Forests.

VOLUME

Larch growing-stock volume amounted to more than 6.0 billion cubic feet and accounted for just over 3 percent of the total growing stock in all four States. Most of the larch forest type is in Montana, which is also where most (37 percent) of the total larch growing-stock volume is found. The distribution of larch growing-stock and sawtimber volume by state is:

State	Growing stock	Sawtimber
	Million cubic feet	*Million board feet Scribner*
Idaho	1,422.8	5,322.0
Montana	2,217.4	8,787.0
Oregon	874.0	3,716.6
Washington	1,513.0	5,981.2
Total	6,027.2	23,806.8

By owner group, the National Forests have nearly 3.8 billion cubic feet (fig. 4), or 63 percent of the larch growing-stock volume. Larch growing-stock volume on forest industry lands amounted to 876 million cubic feet; roughly 500 million cubic feet are on other public lands and an equal amount is found on private lands.

The distribution of larch growing-stock volume by diameter class gives an indication of tree size, which is an important consideration in harvesting and utilization.

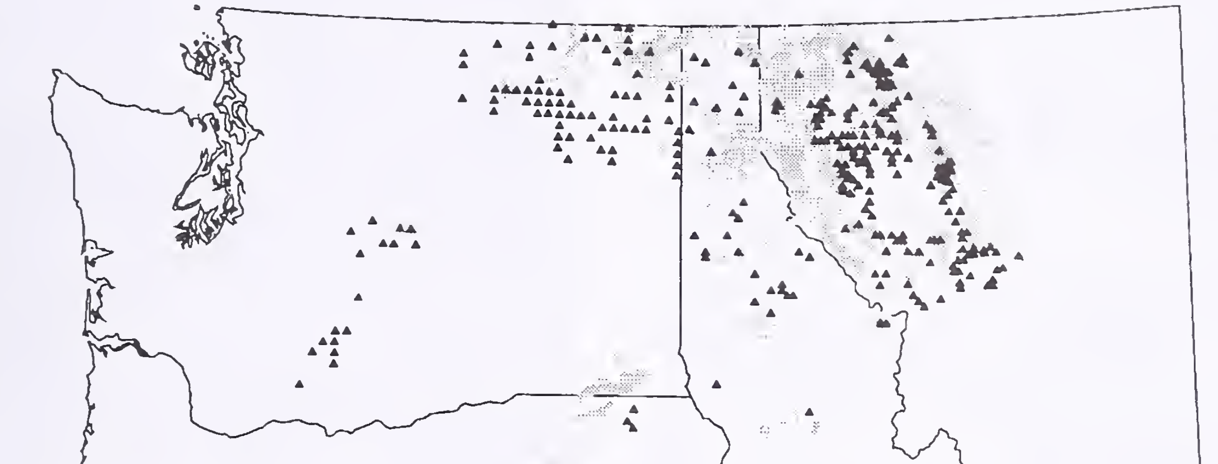

Figure 3—Distribution of FIA locations where larch trees at least 100 years of age were inventoried.

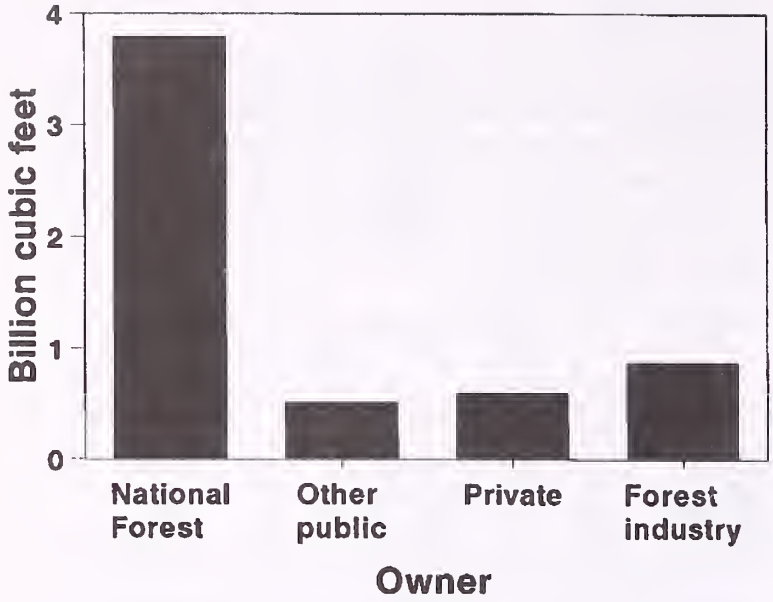

Figure 4—Larch growing-stock volume by owner.

Additional analysis of the data reveals a gradual decline in larch volume within each State in trees greater than 10 inches diameter at breast height (d.b.h.), with a substantial decrease in volume in trees greater than 20 inches d.b.h. More than half of the larch growing-stock volume, about 3.4 billion cubic feet, is in trees with diameters of less than 17.0 inches.

COMPONENTS OF CHANGE

One method of determining change in the larch resource is to estimate growth and mortality and assess their impact on growing-stock inventory. Latest estimates of total growth of larch over the four States amounted to 134.0 million cubic feet (table 2). After deducting for mortality, larch growing stock currently is increasing at a rate of about 1.7 percent annually. These estimates, however, are by no means constant. Mortality losses due to wildfire, insects and disease, and other causes can fluctuate widely from year to year. These in turn affect net annual growth levels. Typically, at least in Montana and Idaho, an average growth rate of between 2 and 3 percent of total inventory is common.

Table 2—Larch growth, mortality, and net change to inventory

	Idaho	Montana	Oregon	Washington	Total
	Million cubic feet				
Total growth	32.0	62.7	6.4	32.9	134.0
Mortality	–6.0	–15.3	–1.7	–10.5	–33.5
Net growth	26.0	47.4	4.7	22.4	100.5
Percent change in larch inventory	1.8	2.1	0.5	1.5	1.7

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Aesthetics of Larch Forests

Larry Blocker

Abstract—Among the nonmarket benefits of *Larix occidentalis* is the wide variety of needle color displays throughout the year: soft green shades across much of the landscape of Idaho and Montana in May and June, followed by darker greens throughout the summer, brilliant yellow shades of fall, and finally the gray of winter. A significant amount of larch is in popular places for people to visit, such as Glacier National Park in northwestern Montana. Larch, particularly in the fall, adds to the recreation and viewing experience of visitors. This paper discusses the role of scenery, variety, and diversity in the management of forested land. Diversity of forested landscapes to meet wildlife needs are examined and compared to the need of diversity for human needs, particularly as diversity relates to the visual environment.

Most of what has been discussed at this symposium is based on science, with many scientific facts and references. I will preface this paper by saying none of what I say is based on scientific data, nor is anything in this paper "factual." That is because the area of aesthetics deals with people and all the complexities and biases associated with being a human being. In this paper, I will discuss the aesthetic considerations of a larch forest. But I will also discuss the Grand Canyon, Chicago, San Francisco, mushrooms, rabbits, elk, camping, and cowboys. By the end of this paper I hope you will see how all of these are related.

The human relationship to environment and identification with that environment is primarily through the visual sense. Introducing the human element to the "science" of managing forests complicates things tremendously. But for public land managers, we have a responsibility to involve the public in the management and decisionmaking for public lands. This is not only supported by law, it is also the right thing to do.

I will first discuss the importance of managing scenery and its contribution to a sense of place, then focus on the aesthetic qualities of western larch (*Larix occidentalis*), and finally, management of scenery as a part of ecosystem management.

MANAGING SCENERY

Alan Gusson, an artist living in New York City, wrote a paper a few years ago titled "Conserving the Magnitude of Uselessness" (Gusson 1979). He points out that a "scene is something we are a part of, to which we relate not as spectators to a play but as players in the event."

This comment has a direct link to the management of the natural—and national and international—resource we call forests. It does not matter whether we are talking about the forests of the Pacific Northwest or Northern Rockies of the United States, or the rainforests in Central America. The theme Gusson's paper and most of what I will be discussing is on the preservation of the sense of place. That sense of place is as important to the inhabitants of a logging community in Oregon, U.S.A., as it is to the indigenous people of a Central American village.

As I discuss aesthetics, I am also referring to the scenic resource or the visual resource. And I refer to this as a "resource" because that is how the public perceives it. We as public land managers have a responsibility to treat scenery as a resource, but beyond that we must treat it as an ecosystem. What exactly is this item we refer to as a scenic resource? Most of us think of scenery as a scenic viewpoint or scenic vista. In this sense, the scenery becomes a background or is relegated to a fixed view from a fixed viewpoint. The landscape, or the aesthetic, offers more than fixed views. It is all views, both seen and seldom seen. It encompasses the biological parts of the landscape such as the animals, both game and nongame, big and small. It also includes large to small plants and fungi, along with everything else that occurs in the world of a forest.

We all know that our landscape has changed tremendously over time due to both natural and human causes. Russel Baker wrote an article in the *New York Times* several years ago that dealt with the subject of a changing American landscape. He asked the question "Has anybody noticed that America is vanishing?" What Baker was referring to was not only the vanishing of the American landscape, but also the vanishing of a sense of place that landscapes are able to convey. He was referring to the endless miles of strip development in many of our major cities. He goes on to say that what is vanishing is the "diversity in the landscapes we inhabit and the places where we live...the capacity of the landscape to evoke memories, to provide us with the direct experience of spaces...and with connections to our own source...." The places we live help give us our identity and are an integral part of our identity. The places we live eventually become a part of us. The longer we stay in an environment, the stronger are the ties to that environment. This is also true for forests where we spend a good part of our leisure hours. They become familiar to us, so changing the forest environment becomes important. That is why the public has become so interested in what we do to their forests.

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AESTHETICS OF WESTERN LARCH

Seldom do we see large expanses of pure larch in the Northern Rockies of North America. It is usually associated with other species such as lodgepole pine or subalpine fir. As stated in one of the handbooks of the Visual Management System used by the Forest Service as a guideline for visual resource management, larch when viewed with other contrasting species such as lodgepole pine, Engelmann spruce, and subalpine fir produces a "rich diversity of form, line, color, and texture." The stand also begins to offer more vertical diversity. These elements of form, line, color, and texture are the same elements used in art and architecture.

Most of the larch forests in northwestern Montana and northern Idaho, U.S.A., are managed for multiple resource values. For those lands within the National Forest System, the decision on which resource values are emphasized are made in Forest Plans. In some cases, the visual resource values are more important than the commodity values. In other cases, the commodity values take precedence. In either case, the management of the visual resource (aesthetics) is given full consideration through an interdisciplinary planning process (USDA Forest Service).

I cannot in this paper cover the details of all possible management regimes necessary to perpetuate the visual characteristics of larch forests. Instead, I would like to expand on the papers by Jack Losensky and Clint Williams. They deal with landscape ecology and the relevance to the management of the visual resource, and even beyond the visual resource to include the entire human habitat.

For some reason, we have relegated the "seen" area of the forest to those important travel routes through the forest, forgetting that the uses of a forest go beyond those corridors. In my mind, the management of these human corridors and recreation sites are similar to the management of wildlife corridors, wildlife linkages, and wildlife habitat in general. If we focus on the concept of human and wildlife needs, how different are the needs for a recreation campsite versus the needs for wildlife habitat? Both humans and wildlife are looking for isolation (vegetative screening between campsites versus hiding cover), and both are looking for thermal cover (canopy versus a warming fire and tent). But we must go beyond these corridors and islands of habitat and look at the entire ecosystem. My point: the human element, whether in the form of viewing a landscape or habitating in it, is a part of the ecosystem of a larch forest, or any other forest or natural resource-dependent area.

AESTHETICS IN ECOSYSTEM MANAGEMENT

Managing the aesthetics (or the wildlife habitat) of a larch forest is only a part of a bigger picture—a picture that includes a strong sense of place that can be sustained ecologically for several generations, perhaps even indefinitely. It involves stewardship of the landscape. As stated in the draft Ecosystem Management Strategy for the Pacific Northwest Region of the Forest Service, "Stewardship means passing the land and resources—including intact forest, riparian, and aquatic functioning ecosystems—to the next generation in as good or better condition than they were found, while also meeting this generation's needs... this includes: 'providing habitat for people which sustain and enhance their physical and mental well-being.'"

Stated in perhaps a less bureaucratic or scientific way in Robert Fulgham's book *Everything I Need to Know in Life, I Learned in Kindergarten,* one of the first things we learned in kindergarten was to hold hands when we cross the street. Relating Fulgham's words regarding our responsibilities as natural resource managers, we must remember to take care of each other, including people now and in the future, the plants, and the animals that inhabit this planet. Basically, that is what stewardship is all about.

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Ownership Patterns

Orville L. Daniels

Abstract—In the United States, National Forest management of commercial timber species, including *Larix,* has been evolving over the last 20 years. The development of sustainable ecosystem management creates management objectives that are much broader than the stand. Ecosystem management considers biodiversity and landscape ecology, which exacerbates the problem created by different management philosophies associated with different land ownerships. The significance of philosophies associated with land ownership within the Lolo National Forest is explored as an example of the current situation.

Discussing something as subjective as "contemporary issues of land ownership" could make any symposium speaker nervous. However, the land ownership issue is important to those of us who manage larch stands, so I am pleased to discuss the issue.

Why is this a contemporary issue when the land ownership pattern in the United States has remained the same for many years? This is a contemporary issue because the last few years have brought major change to land management in this part of the world. The Threatened and Endangered Species Act, new wildlife management objectives by the State of Montana, the western Montana watershed cooperative, development of ecosystem management approaches on National Forests, and a public outcry against forest management practices have pushed us into a spiral of change. When these changes are superimposed over a land ownership that is fragmented such as on the Lolo National Forest in Montana, the management problems are exacerbated. The fragmentation is severe with over one-fifth of the land inside the boundary of the National Forest being privately owned. That then is our situation—a complex ownership pattern and rapid change. I contend that as we move from stand level prescriptions to landscape ecology considerations, a fragmented landscape with differing management objectives will create a difficult situation.

Because land ownership patterns as they affect land management vary a great deal across the United States, I intend to use western Montana and particularly the Lolo National Forest as a case study.

A caveat that I want to make clear is that I intend no judgments of the appropriateness of land management objectives practiced by any landowner. As a public official, my stand is that any land management practice is appropriate as long as it is within the intent of the law. So please take nothing that I say as a criticism. Different objectives are a direct result of private landowner rights.

HISTORY

Historically, timber harvest started in the late 1800's, mostly in the valley bottoms in ponderosa pine and larch types on private lands. This spread to the National Forests where partial cuts were common. This approach continued until the early 1950's when major commercial harvest began on the intermediate elevation lands that included more of the National Forests. At first the National Forests continued to harvest as they had in the valley bottoms, with light cutting and partial removals. Meanwhile, on private lands more clearcuts occurred. So even at this early date differences in land management objectives were evident.

As the National Forests began to recognize that the heavier cuts on private lands and the resulting mineral soil exposure were producing better reproduction and early stand growth, the silviculture treatments and management objectives began to get closer and closer. Around the mid-1960's, harvest practices and postharvest treatment on large corporate holdings and the National Forests were almost identical. A study of aerial photos from that era reflects that on cutover lands the boundaries between the two ownerships were often indistinguishable. Harvest practices, yarding, and postharvest treatments reflects a complete similarity.

In the late 1960's, principally because of visual values or the social unacceptability of large clearcuts, the cooperative relationship and similarity began to erode. By the mid-1970's other values of water quality and wildlife were further splitting the two major landowners. The 1979 Lolo forest plan included strategies for mitigation for the heavier removal and larger units on corporate land holdings. Between that time and 1987 individual harvest units on the National Forest were often deferred or redesigned to take into account the different types of harvest patterns on private land. This remained an internal coordination effort between the Forest Service and the private landowners until 1987 when it became public knowledge that the Lolo National Forest was delaying for 10 years any further harvest in the head of Lolo Creek because of heavy cutting on the private lands. The actual reason for the delay was mostly for wildlife purposes with a lesser reason of water quality protection.

This so-called moratorium catapulted the concern into the public area and became a rallying point for diverse interests. The timber industry appealed the decision, and environmental groups lauded it. The aftermath was an attempt on the part of both corporate landowners and the Forest Service to cooperate more closely on timber harvest scheduling. Although this was a worthy effort, it did not succeed because of radical differences in land management objectives. Corporate objectives were to convert a major part of their holdings to thrifty younger stands at

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an accelerated rate. On the National Forests, even-flow sustained yield, along with other resource needs, controlled the harvest. These differing objectives made cooperation almost impossible.

The next step in this schism between management objectives took place in September 1991 when the Lolo National Forest announced a significantly reduced timber harvest schedule. One reason given for this reduction was the high harvest rates on the 400,000 acres of privately owned forest lands within the National Forest boundary. Other factors also contributed to this reduction. However, different land management objectives on different ownerships were clearly causing change.

PRESENT

This brings us to the present situation, which I consider to be one of uncertainty and transition. There is not a clear vision of where we should be heading, no clear set of common objectives. In fact, we are experimenting with different approaches.

In 1990 the Forest Service started a program called New Perspectives on the National Forests. On the Lolo National Forest that meant we began to change silvicultural prescriptions to be more in tune with the concepts of biodiversity and landscape ecology. After 2 years of that program, we began evolving into a program called ecosystem management. In this program we are looking at large pieces of land to determine the linkages between the component parts and attempting to manage more nearly along natural ecosystem lines. The artificial boundary lines between different ownerships are normally straight lines that do not take into account ecosystems. This is difficult for us.

As an example, part of the ecosystem management program is a greater understanding of fire's role historically in the development of the vegetative patterns on the land. Again those fire patterns are no respecters of ownership boundaries.

Also typical of today's world is the rapid development and even urbanization of the small private land holdings within and adjacent to the National Forest boundary. The owners of these new homes are demanding less and less vegetative disturbance adjacent to their land holdings and are not allowing natural processes to take place on their lands.

Commercial industrial lands are still being managed intensively for fiber production, but the owners are attempting to move into a "new forestry" approach to land management. The early assessment of their cutting patterns is that they are quite different from that on the National Forest. Much of this may be explained by the changing management objective on the National Forest. Simply put, we are no longer attempting to maximize fiber production, but rather are strongly into the concepts of biodiversity and ecosystem management.

FUTURE

The future is not clear. We are in transition, a time of innovation and creativity and differences of approach. No one is able to determine how it will end, if only because we are so dependent on the world economy that we don't know what future land management objectives will be for anyone.

However, some things will probably shape our future. One of the main factors will be the steadily increasing understanding of landscape ecology and biodiversity. We are on the threshold of this subject. Further research and thought about this subject will be necessary to create a changed philosophy for the management of forest lands. Second, increased population coupled with the understanding of ecosystem management and the effects of the world economy will probably change our concept of private property rights. More and more there will be demand that private lands be managed in accordance with the broader social values. This will be an unpopular change but probably is inevitable if we look at current trends. Third, as populations increase and people flee the cities, we will see an increased urbanization of the private lands within the National Forests. This will bring demands for changed patterns of land management practices.

We cannot tell how this will play out, but I'm fairly confident that these three factors will cause further change.

Use and Value of Western Larch as a Commercial Timber Species

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Abstract—Western larch (*Larix occidentalis*) provides a wide variety of primary products that include: lumber, plywood, pulp and paper, particleboard and fiberboard, house logs, poles, pilings and posts, fuelwood, and a water soluble gum used primarily in the pharmaceutical and food processing industries. The annual harvest of western larch is approximately 2.3 million cubic meters. The value of primary products manufactured from western larch exceeds $350 million annually. Harvesting and processing directly employs an estimated 4,000 workers, earning about $140 million annually in labor income. In Montana, U.S.A., western larch provides about 15 percent of the timber processed.

PRODUCTS AND CHARACTERISTICS

Western larch is processed into a number of primary forest products that include

- Lumber
- Plywood
- Pulp and paper
- Particleboard and fiberboard
- House logs
- Poles, pilings and posts
- Fuelwood
- Gum (arabinogalactan)

Lumber

The primary use of western larch is for lumber used in the building or construction industry. Larch is one of the strongest of the softwood species, having straight grain, high specific gravity, and small tight knots. Western larch lumber generally has been and is sold mixed with Douglas-fir (*Pseudotsuga menziesii*), but it does have an identity of its own in some lumber uses.

One special use of larch lumber is as laminated beam stock. If proper drying techniques are used, larch contains a high percentage of superior grades to be used in the tension and compression zones of the laminated beams (Gorman 1992). Also, the reddish brown color of larch is often preferred and can command a premium in a laminated beam.

Higher quality clear lumber finds its way into appearance and factory uses such as interior finish, paneling, window and door trim, or window and door parts. A number of western larch lumber producers in the Inland Region have been targeting some of the appearance and factory grade uses as the supply of clear Douglas-fir lumber from the Pacific Northwest has been reduced due to reduction in the availability of old growth Douglas-fir timber.

Plywood

Western larch is also a preferred species for plywood manufacturing, not only because of its structural properties, but also because it yields large volumes of clear veneers or veneers with small tight knots.

Uses of western larch plywood include standard construction uses such as sheathing, roof decking, and flooring systems as well as patterned siding. Other uses include the manufacture of recreation vehicles, mobile homes, and boats, and the manufacture of carpet strips for stretching and holding carpet. In fact, more than half the carpet strip market in the United States is supplied by Montana producers.

Log Homes

Western larch is a preferred species by a number of log home manufacturers producing homes from larger diameter logs. Its high strength makes it particularly desirable for structural components in log homes.

Firewood

Western larch is a preferred firewood species in the region because of its high specific gravity and resultant high BTU content compared to other softwoods species. Western larch also has relatively straight grain and splits easily.

Other Products

Because of its strength and moderate resistance to decay, western larch has found some use in the production of utility poles and other roundwood products. Some larch is also used to manufacture shakes and shingles.

A water soluble gum (arabinogalactan) is extracted from western larch and marketed under the trade name "Stractan". Stractan is used primarily as a binder in the food, pharmaceutical, cosmetic, and bio-tech industries.

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Residue Related Products

It is important, when examining uses of western larch as a raw material, to look past the point at which the logs are broken down into products, or a great deal of the primary product output will be missed. These other significant products are derived from processing wood fiber residue from sawmills and plywood plants. When logs are broken down into lumber, for example, less than half the wood fiber in the log actually becomes lumber. Much of the remainder, often labeled or mislabeled mill residue, is used as raw material for the pulp and paper industry and for reconstituted board products such as particleboard and medium density fiberboard. Mill residue is also used by facilities producing products such as fuel pellets, electricity, and decorative bark.

Of the 2.25 million cubic meters of logs that sawmills and plywood plants processed annually, about 1.20 million cubic meters actually ended up as finished lumber and plywood. In excess of 0.75 million cubic meters—in the form of chips, planer shavings, and sawdust—was used as raw material to produce pulp and paper, particleboard, and fiberboard.

TIMBER HARVEST AND UTILIZATION

The volume of western larch harvested and processed annually has been about 460 million board feet (MMBF) Scribner or about 2.30 million cubic meters. Of that, 300 MMBF (1.50 million cubic meters) of logs—about 65 percent of the total—were delivered to sawmills and processed into lumber (table 1).

Annually, about one-third of the western larch harvested—150 MMBF (0.75 million cubic meters)—has been processed into plywood.

The remaining 2 to 3 percent of the timber—approximately 10 MMBF (50 thousand cubic meters)—was used to manufacture log homes, roundwood products such as utility poles and posts, shakes and shingles, or was sold as firewood or was chipped at whole log chipping facilities for pulp chips.

SALES VALUE OF WESTERN LARCH PRODUCTS

Average annual sales value of the primary products manufactured from western larch from 1986 through 1990 has been about $365 million in 1990 dollars, f.o.b. the mill manufacturing the product (table 2). Sales value illustrates the importance of the residue sectors. Residue-related products accounted for about $130 million of the annual sales—about 35 percent of the total. Lumber and other sawn products accounted for about 40 percent of the total sales value, or an estimated $150 million per year. Plywood accounted for about $75 million in annual sales, or about 20percent of the total. Other products such as log homes and posts and poles accounted for about $10 million or 3 percent of the total.

Table 1—Annual utilization of western larch.

	Million board feet, scribner	Million cubic meters
Sawmills	300	1.50
Plywood plants	150	0.75
Other	10	0.05
Total	460	2.30

EMPLOYMENT

Approximately 1,400 people are employed annually in harvesting and hauling western larch to mills, and another 2,600 workers are employed at facilities that process larch logs into primary products (table 3). These 4,000 private sector workers directly associated with processing western larch into primary forest products earn an estimated $140 million annually in labor income.

The impact on employment goes beyond the 4,000 workers directly employed in harvesting and processing western larch. Additional employment is generated in other sectors of the economy through the forest products industry's spending and the spending and re-spending of the workers' payrolls.

The primary processing of western larch gives rise to an additional 4,000 to 8,000 jobs in derivative sectors such as retail trade, medical services, and other areas. The total impact measured by employment would be some 8,000 to 12,000 workers and in excess of $300 million in labor income annually. There are also several hundred workers in the various land management agencies managing western larch as a commercial timber species.

Table 2—Average annual sales value of western larch primary products, 1986-1990.

	Millions of 1990 dollars
Lumber	150
Plywood	75
Residue sector (major products: pulp, paper, particleboard, fiberboard)	130
Other	10
Total	365

Table 3—Average annual employment 1986-1990.

Harvesting and processing western larch	Number of workers
Logging	1,400
Sawmills	1,000
Plywood plants	800
Residue-related products	500
Other manufacturing and private sector land management	300
Total	4,000

REGIONAL AND LOCAL ECONOMIC IMPACTS OF WESTERN LARCH

The forest products industry plays an important part in the Inland Northwest Region's economy, and the range of western larch includes some of the most timber-dependent regions of North America. The contiguous region encompassing western Montana and northern Idaho, with the possible exception of southwestern and south-central Oregon, is the most timber-dependent region in the United States, and interior British Columbia is one of the most timber-dependent regions in Canada (Keegan 1992).

As shown in table 4, of the 460 MMBF (2.30 million cubic meters) of western larch processed annually from 1986 to 1990:

- Over 40 percent was processed in Montana
- About 25 percent in British Columbia
- 20 percent in Idaho
- About 5 percent each in eastern Washington and eastern Oregon

Western larch is most important in Montana providing about 15 percent of the timber processed in the state (Keegan and others 1990). In northwestern Montana, it provides about 20 percent of the timber processed in a group of counties where the forest products industry comprises 25 to 50 percent of the counties' economic base (Keegan and others 1990).

Table 4—Average annual volume of western larch processed by state or province, 1986-1990.

	Million board feet, scribner	Million cubic meters
British Columbia	110	0.55
Idaho	90	0.45
Montana	200	1.00
Eastern Washington	30	0.15
Eastern Oregon	30	0.15
Total	460	2.30

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Management Issues of *Larix occidentalis* Forests in British Columbia

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Abstract—In the western larch forests of British Columbia certain management practices fail to recognize the seedbed requirements for western larch regeneration or the important role that fire plays in western larch ecosystems. By failing to provide an appropriate environment for western larch regeneration, these practices threaten to reduce the amount of western larch in the future forests of the Province, unless special steps are taken to promote regeneration of that species.

Western larch is a species with many attributes that make it a valuable component of the forest types of British Columbia. Within its range, it is one of the most rapidly growing species and has few serious pests, which makes it a popular species for management. However, it owes its occurrence to major disturbances that are not being emulated in modern forest management. As a result of the reduction in the use of fire as a management tool and the increasing use of low-impact harvesting and site preparation techniques, inappropriate environments are being created for the natural regeneration of the species. As a result, the percentage of larch in future forests will be much less than at present, unless specific measures are taken to ensure the regeneration of the species.

STATUS OF WESTERN LARCH IN BRITISH COLUMBIA

On a Provincial scale, western larch is a relatively insignificant species. Of the total volume harvested in the Province in 1991 (74,304,000 m^3), western larch comprised a meager 0.6 percent (Anon. 1991). Similarly, of the trees planted in the Province in 1991 (245,596,000), western larch comprised a proportionally meager 0.5 percent. This may be an underestimate of its future significance when the many immature stands of western larch reach maturity. The currently low Provincial profile is reflected in the magnitude of its prominence in other aspects of the Provincial forest resource. For example, a literature search found a number of publications (mostly American) that only included British Columbia in discussions of the range of the species. If these are excluded, the remaining list makes interesting reading, if only for the paucity of its contents. Of the 55 publications identified since 1953 (38 years), 41 (75 percent) dealt with insects and diseases. And 31 percent of these publications dealt with the casebearer (*Coleophora laricella* [Hbn.]) and its parasites. The remaining 14 publications ranged from studies of fume damage through silviculture to wood properties.

Within British Columbia, 75 percent of all larch (standing volume greater than 17.5 cm, all ownerships) occurs in one administrative region, the Nelson Forest Region, in the southeastern corner of the Province (BCFS 1992). There, western larch is still a relatively minor species, representing only about 5 percent of the volume harvested in 1991 and about 4 percent of the trees planted.

OCCURRENCE OF WESTERN LARCH IN BRITISH COLUMBIA

Within its range in British Columbia, western larch is confined to the moist and dry climatic regions. It does not occur in the wet region found generally north of latitude 51. It is also almost completely absent in the very dry climatic region west of the Okanagan River. The eastern limit approximates the Continental Divide.

The range of western larch in British Columbia is thus primarily a reflection of the frequency of wildfire. This range is further modified in the west by the occurrence of excessive summer droughts and in the east, probably, by the occurrence of summer frost events. Both drought and frost will prevent the successful establishment of western larch regeneration. In the north, the natural exclusion from the wet climatic region is probably a reflection of the inability of the species to germinate and compete in a climate where vegetation growth after disturbance is both rapid and vigorous. There is some speculation that the exclusion of western larch from these areas may also be related to the higher natural incidence of needlecast diseases in the wetter climate.

Western larch has not been planted extensively beyond its range but it has been successfully planted as much as 6° north and 4° west of its natural range. It seems to perform well in these locations, at least for the first 10 to 15 years for which data are available. Its current northern natural limit is presumably defined more by the reproductive biology of the species than by identifiable climatic or geological limitations. Similar successful, but less dramatic, extensions into the wetter climatic region tend to confirm that the success of the more northerly plantations is not a coincidence but is probably a reflection of the plasticity of the species. Evidence from some trials suggests that the species has a low temperature limit that is considerably north of its present range (Newsome and others, this proceedings).

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Where in elevation western larch occurs also reflects fire frequency. In the southern portion of its range in British Columbia, it occurs up to 1,600 m. Farther north, as the climate becomes wetter and fire frequency decreases with elevation, the upper elevation of western larch also decreases. There may also be an inverse relationship with snowpack duration.

Pure stands of western larch are rare. More typically, the species occurs in a mixture with a large number of species. The forest cover of the moist climatic region contains large areas of seral stands characterized by great species diversity, in which western larch is one component. In the dry climatic region, western larch occurs in a mixture with Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.). There are also large areas of lodgepole pine (*Pinus contorta* var. *latifolia* Dougl. ex Loud.) that contain Douglas-fir and western larch in variable composition. At the upper elevations, western larch usually occurs as a minor component of the Engelmann spruce (*Picea engelmannii* Parry ex Engelm.)-subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) forests.

Wherever it occurs, western larch grows as fast as if not faster than the other species with which it occurs. In the moister portions of the region, where stand densities are relatively high, tree height is often achieved at the expense of diameter growth, resulting in relatively tall slender individuals. In the drier region, with usually lower stand densities, height growth is often achieved without sacrificing diameter growth. With the possible exception of paper birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides* Michx.), this ability to outgrow all its associated species is the principal basis of what is best described as an affection for western larch by those who manage the species.

ATTITUDES TOWARD WESTERN LARCH

Discussions with foresters who manage western larch in British Columbia reveal the following attitudes. Unlike most other species in British Columbia, western larch is not a readily identifiable forest type and usually occurs as a minor component in many different forest types. Therein lie both its strengths and weaknesses.

Within its range, when compared to the frequency of its occurrence, western larch enjoys a popularity that is disproportionately high. It is highly valued esthetically for its four-season coloration. Its rapid early growth and relatively small number of pests make it a popular species for early achievement of "free growing" status. It produces good quality wood, due to both its high strength properties and its good stem form. In the drier regions, it is highly sought after as firewood, perhaps an unfortunate attribute for a deciduous species. One forester even suggested that we would soon be looking even more to western larch as a source of shake material.

Western larch has occasionally been planted beyond its natural range. Foresters will usually justify such selection by quoting the greater resistance of western larch to Armillaria root rot (*Armillaria ostoyae* [Romagn.] Herink). Curiously, when questioned about the properties and uses of western larch, foresters working within the natural range of western larch will mention this resistance almost as an afterthought. This greater resistance to Armillaria is, however, one reason why western larch is being planted within its range, on otherwise appropriate sites that did not have western larch in the original stand. Many of these are winter or spring ungulate range. Proposals to introduce western larch to the site have occasionally met with opposition from wildlife management agencies. In winter, western larch provides no hiding or thermal cover. As added irony, western larch is also much less attractive as a browse species than its associated conifers in winter and early spring, due to its leafless condition.

Because western larch usually occurs as one component in a number of forest types, the selection of regeneration method frequently causes dichotomous thinking among foresters. Should they plan the regeneration phase for the associated species in the stand, or should they plan the regeneration for western larch? The latter option frequently entails, at least in their minds, a special effort and therefore extra cost.

The regeneration phase of western larch is probably the source of more disappointment and misunderstanding than any other aspect of western larch silviculture. Failure to appreciate the seedbed and environmental requirements for western larch regeneration, and the irregular and somewhat unpredictable nature of western larch seed crops, at least over the majority of its range in British Columbia, have resulted in many larch regeneration failures. These are still occurring, but fortunately the number of successes seem to be increasing.

MANAGEMENT ISSUES

Because of concerns about the regeneration of western larch, I have created a short, rather personal, list of issues on the management of western larch in British Columbia. The first issue is manifest in drier areas where stands of predominantly lodgepole pine are being harvested for mountain pine beetle salvage. A second issue focuses on the ability of the forester to create the necessary seedbed for good western larch regeneration. The third issue looks at the potential impact of nonsilvicultural issues on the environment required by western larch for regeneration.

Western Larch After Mountain Pine Beetle Salvage Harvesting

In the mid-1970's, mountain pine beetles (*Dendroctonus ponderosae* Hopkins) began attacking the large areas of lodgepole pine in the eastern and western portions of western larch's range. Some attacked stands were pure lodgepole pine, but many others were mixed with Douglas-fir, Engelmann spruce, and frequently western larch. It rapidly became evident that to minimize overcutting the annual allowable cut, only the pine should be cut—not the initial practice. The result is large clearcut areas with partially harvested islands. These islands vary in composition and density, from virtually fully stocked stands of Douglas-fir and western larch, to islands that more resemble seed tree cuttings than anything else. This latter situation produces the classical dichotomy.

Faced with a seed tree stand produced by default rather than design, the forester feels challenged to attempt to regenerate western larch naturally, with the frequent result of, at best, natural regeneration of lodgepole pine, and, at worst, planting lodgepole pine. Unfortunately, under this scenario, achieving natural regeneration of western larch is more the exception than the rule.

When natural regeneration of western larch is achieved, it is usually the result of appreciation of the importance of site preparation, and patience. In the majority of cases, the site preparation of choice is mechanical, usually with a bulldozer. Drag scarification has rarely been successful in producing anything other than lodgepole pine regeneration on most of these sites. Disk trenching, while effective as a technique of preparing sites for planting, generally has proved to be ineffective as a method of producing natural regeneration. Apparently, more drastic site preparation than can be obtained with a disk trencher is required to achieve larch natural regeneration on most of these sites.

As with all generalizations, welcome exceptions exist. And the issue here is not the apparent difficulty of obtaining regeneration, but more the effort the forester feels obliged to make when presented with an unplanned seed tree stand.

The irony is that although these sites have a history of relatively frequent fires, and western larch is a species associated with fire, fire is rarely contemplated as a site preparation tool on these sites because of concerns over the low organic matter content of the soil.

When wild fire runs through these same stands, if western larch is a component of the stand, it usually becomes a component of the regeneration. This is often in spite of stem qualities, which normally would not qualify those trees as candidates for a planned seed tree cutting. Frequently, the problem changes from how to get regeneration, to how to reduce excessively high stocking levels to a manageable level.

A final irony is that the postharvest timber volume left in the stand to minimize overcutting is often lost in the reinventory due to too few stems in a large inventory polygon.

New Site Disturbance Guidelines

Among foresters who manage western larch there is a common belief, based on observation, that to get western larch natural regeneration you need aggressive site preparation. It may not be the literal truth, but in the stands where western larch natural regeneration has been achieved, it has usually been achieved as a result of site preparation, either mechanically or by fire. Even planted western larch seems to benefit from an establishment phase with reduced competition from site preparation. While successful plantations can be created on some sites without site preparation, appropriate site preparation usually improves early western larch performance on all sites and can frequently make the difference between acceptable and unacceptable plantation performance.

There is an increasing awareness in British Columbia of the potential impact of harvesting activities on soil properties, and thus on site productivity. This is manifest in the development of site disturbance guidelines that describe the maximum acceptable amount of each of the different types of site disturbance on any site. These guidelines are being extended, with modification, to mechanical site preparation.

One of the disturbance sensitivities included in the guidelines is forest floor displacement. The underlying objective of keeping the forest floor near the seedling has resulted in the most acceptable form of mechanical site preparation being disk trenching, and one of the least acceptable being blade scarification. However, experience has shown that, at least for western larch, disk scarification is not usually effective in preparing sites for natural regeneration and that blade scarification frequently is effective. The proposed guidelines have already resulted in a considerable reduction in the amount of blade scarification. It is too soon to see if the attempts at scarification within the guidelines will result in a lowered regeneration success. Early discussions with foresters who have good success regenerating western larch lead us to expect reduced success. However, successful western larch regeneration should be possible within the guidelines, but much greater operator awareness may be required.

There is limited experience in British Columbia with the use of fire as a site preparation tool for western larch regeneration, and the results are varied. The notable successes are usually associated with high levels of organic matter consumption. Burns with low levels of organic matter consumption have often resulted in inadequate site preparation for western larch and usually have destroyed the pine seed source in the harvesting debris, such that no natural regeneration was achieved. These sites generally require planting.

I am told that the next technique to be the subject of site preparation guidelines is broadcast burning. The use of high-impact burns has already been discouraged. Maybe that will be my next issue because fire is a natural component of western larch ecosystems. Without fire, the future existence of larch on many sites is uncertain.

Visual Quality Objectives

In the lower elevation valleys in the moist climatic region, western larch is a frequent component of a complex seral forest type. In its simplest form the stand structure is often an even-age stratified mixture, with western larch, Douglas-fir, and western white pine (*Pinus monticola* Dougl. ex D. Don) in variable composition, together with other species as a discontinuous A stratum. Western redcedar (*Thuja plicata* Donn ex D. Don) and western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) usually form a more continuous B and C strata. These stands occupy major travel and vacation corridors and significant portions of many domestic watersheds. Many of these stands became established around the turn of the century and thus have had little harvesting activity in them. However, plans for their harvest are now being developed.

A heightened public awareness of forestry activities, increasing public opposition to the use of clearcutting as a harvesting technique, greater concern over the integrity of watersheds, increasing awareness by forest managers of the visual impact of harvesting activities, and a new attitude toward integrated resource management by forest managers have all resulted in a dramatic change in the nature and scale of harvesting proposals in these stands. Among other criteria, the development of visual quality objectives has resulted in the development of harvesting proposals with a low visual impact. In some forest types these modified proposals offer little more than changes in the spatial distribution of harvesting activities, but in this stratified mixture, the potential impact is one of dramatic alteration of the species composition of the mixture.

The introduction of harvesting with a low visual impact to this stratified even-age mixture, will probably result either in the removal of much of the A stratum of which western larch is a component, or the creation of small openings, with minimal site preparation. These treatments will result in either the selective removal of western larch or the preclusion of western larch regeneration through excessive shade and inadequate seedbed preparation. This will mean, at worst, the elimination of western larch from the mixture or, at best, a significant reduction in the percentage of western larch in the stand.

Given the value of western larch as a species, and its significant visual contribution to the forest landscape, this potential reduction has to be regarded as an issue of concern, particularly when more appropriate regeneration techniques are available.

CONCLUSIONS

Reduced or inappropriate site preparation, or the selective removal of the species, may threaten the future of western larch on many sites, but I do not believe that western larch is an endangered species. The issues presented are serious and must be addressed, but they are not insurmountable. Their identification will, I am sure, be followed rapidly by their solution. Western larch is a remarkable species, with a strong, almost fanatical group of "western larch lovers" who seem to go to great lengths to try to promote the species. Larch mania seems to go beyond dispassionate objectivity, and borders almost on the emotional. For this reason, solutions will be found.

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Pest Risks Associated With Importation of Unprocessed Larch Logs From Siberia and the Russian Far East to the United States

Donald J. Goheen
Borys M. Tkacz

Since the late 1980's, a number of American timber companies have shown considerable interest in the possibility of importing raw logs from Siberia and the Russian Far East to the United States. This is viewed as an opportunity to obtain relatively inexpensive but high quality softwood logs for processing here at a time when many American mills, especially in the Pacific Northwest, are facing serious domestic log shortages. Several conifer species have been considered for importation, but most interest has been shown in larch.

In mid-1990, two small test shipments of Siberian logs were brought to Eureka, CA. The Animal and Plant Health Inspection Service (APHIS) of the U.S. Department of Agriculture, and the California Department of Food and Agriculture inspected the test shipments and detected exotic nematodes and Cerambycid borers that they felt might be serious pests. The shipments were fumigated.

The scientific community and the USDA Forest Service were concerned. While we did not oppose free trade and admitted that efforts to locate new sources of raw materials might be worthwhile endeavors, we felt strongly that great caution was needed when considering the possibility of importing unprocessed logs. In our view, destructive forest insects and pathogens have considerable potential to be transported on or in logs that are shipped intercontinentally.

Ample historical evidence shows that exotic insects and pathogens can be introduced into new areas, become established, and have devastating effects. Also, once established, introduced insects and diseases tend to be especially difficult if not impossible to eradicate or control. One has only to consider the well-documented records of European gypsy moth, chestnut blight, Dutch elm disease, white pine blister rust, beech bark disease, larch canker, and Port-Orford-cedar root disease to appreciate just how staggering the economic losses and ecological impacts associated with introduced forest insects and diseases can be.

The forest resource in western North America is vast and tremendously valuable. In addition to timber values, the West has incalculable aesthetic, recreational, wildlife habitat, and watershed values. Introduced insects and diseases could seriously threaten substantial portions of this resource. Nursery stock, ornamental trees, and Christmas tree plantations could be at equally great risk.

In response to such concerns, APHIS imposed a temporary ban on additional Russian log imports until a risk assessment could be done to determine what final regulations should be instituted. Though APHIS bears the responsibility for preventing introduction of exotic pests, the agency has limited experience and expertise with forest trees. Therefore, a joint APHIS/Forest Service team was organized to do the risk assessment of Russian larch logs. We were members of the team. Our objectives were to identify insects and pathogens that might be introduced on unprocessed larch logs from Siberia and the Russian Far East, assess potential for these organisms to colonize logs, survive transit, and subsequently become established on North American tree species, and consider relative potential impacts of these organisms should they become established in the United States.

For our assessment, we relied on an extensive search of the literature and consultation with American plant pathologists, entomologists, and ecologists with knowledge that pertained to the issue. In addition, we visited the Russian Far East and Siberia where we consulted with Russian scientists and foresters and did on-site evaluations of forest stands, timber harvesting operations, log storage areas, and railroad, river, and seaport transportation facilities.

We found that though information on forest insects and diseases from the Russian Far East and Siberia is far from complete, at least 175 phytophagous insects and pathogens that have larch species as hosts have been reported from the region. We concentrated on developing profiles of organisms from this list that either do not yet occur in the United States or that might differ genetically between Russia and the United States.

Six organisms that we feel constitute documentable risk of being introduced on larch logs from Siberia and the Russian Far East are Asian gypsy moth (*Lymantria dispar*), nun moth (*L. monacha*), spruce Ips beetle (*Ips typographus*), xylem-inhabiting nematodes (*Bursaphelenchus* spp.), the larch canker fungus (*Lachnellula willkommii*), and the annosus root disease fungus (*Heterobasidion annosum*). These are by no means the only organisms that might be introduced, but we feel that they are fairly

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representative of the variety of forest insects and pathogens that potentially could enter the United States from Russia.

ASIAN GYPSY MOTH AND NUN MOTH

Asian gypsy moths and the related nun moths are voracious feeders on the foliage of a broad range of trees, shrubs, and herbaceous plants. The resulting defoliation can contribute to substantial growth loss and, in some cases, host death. Asian gypsy moths show some preference for larch, alder, and willow as hosts, and nun moths prefer spruce, larch, and true firs. Both moths are widely distributed and considered to be major pests in Siberia and the Russian Far East. Nun moths do not occur in North America. The gypsy moths that are already established in eastern North America differ from the Asian race in that they originated in Europe, have somewhat different feeding habits, and have flightless females. Female Asian gypsy moths as well as female nun moths are active fliers that are capable of covering distances as great as 10 miles.

Asian gypsy moths and nun moths pass the winter in the egg stage which lasts approximately 9 months. Both species frequently lay their egg masses, each of which may contain up to 1,000 eggs, on the bark of stems and branches of trees, including larch. Egg masses are deposited preferentially in bark crevices and fissures and are very difficult to detect visually. Egg masses are also very tolerant of extremes in temperature and moisture and are attached securely to their substrate.

The potential for occurrence of viable Asian gypsy moth and nun moth egg masses on untreated Russian larch logs transported to the United States would be substantial. This would especially be true at times when epidemics were occurring in the vicinity of Russian transportation routes or seaports (as is currently the case). Given the wide host ranges and the adaptability of these species, colonization potential should be great. The capacity for long distance flight by females imparts an especially dangerous spread potential to Asian gypsy moths and nun moths.

SPRUCE IPS BEETLE

Spruce Ips beetles are found wherever spruce grows on the Eurasian continent. They do not occur in North America. Spruces are their preferred hosts, but they also will infest other conifer species, especially larch and pines. They normally breed in cut logs and windthrown trees but attack numerous standing trees during epidemics. Outbreaks are triggered by population buildups following windstorms, droughts, fires, or other events that weaken or stress substantial numbers of trees. Once started, outbreaks may not subside for some time.

Spruce Ips beetles are strong fliers capable of infesting trees at distances of up to 30 miles from where they emerge. In cool climates, they produce one generation per year, but in warmer areas they may have two or even three generations a year. Host trees are killed by the combined effects of the beetles mining in the inner bark and tissue mortality caused by innoculation of associated stain fungi. Fungal associates of the spruce Ips beetle have been shown to be particularly virulent.

Due to limitations imposed by inclement weather, poor access, rudimentary transportation facilities, and scheduling problems, many Russian logs spend considerable time (often months) in decks, in trains or log rafts, or in log piles at mills or ports. Frequently, logs are in the vicinities of many other logs and often close to forests. Incidence of infestation of logs by bark beetles, including but not limited to the spruce Ips beetle, is extremely high. Beetle eggs, larvae, pupae, and callow adults occurring in galleries under the bark would be very difficult to detect on unprocessed logs. They would be very likely to survive ocean transit. Colonization potential in the United States also should be great. Though spruce Ips beetles could be introduced on larch logs, it is most likely that they would become established and spread in spruce stands should they arrive in North America.

XYLEM-INHABITIING NEMATODE

Several species of xylem-inhabiting nematodes that occur in Siberia and the Russian Far East are not reported from the United States. These include *B. mucronatus* and *B. kolymensis* which have true firs, larch, and pine species as hosts. Xylem-inhabiting nematodes may breed in cut logs, wood chips, weakened trees, and, in some cases, healthy trees. They may occupy wood to considerable depth in logs. They have a tremendous capacity for rapid reproduction, especially under warm conditions. Each female produces about 80 eggs, and the life cycle can be completed in as short a period as 4 days.

In live hosts, the nematodes feed on and kill the epithelial cells in the resin canals hastening tree death. In dead host material, they feed on fungi. They are very well adapted to withstand drying and are capable of surviving without food for long periods of time. Xylem-inhabiting nematodes are vectored to new hosts by woodboring beetles, especially members of the family Cerambycidae.

Because of the Russian practices of leaving logs decked in the forest or in piles at ports or mills, there is an extremely high likelihood that many destined for import would be visited by Cerambycid beetles for feeding and egg laying purposes. Vectors are strong fliers, and vectoring is very efficient. Many logs would almost certainly be contaminated with nematodes. Nematodes and vectors should survive transit easily in unprocessed logs. In fact, *B. mucronatus* and its vector were found on the test shipments that have already arrived from Siberia.

Likelihood of successful colonization of logs, slash, and standing trees around ports of entry is very high and subsequent spread potential also would be substantial. The unknown factor with xylem-inhabiting nematodes is their damage potential. Some xylem-inhabiting nematodes merely breed in already-dead or very severely stressed trees, causing little or no serious damage. This is usually the case when they are in their native habitat. When introduced into new areas, however, there is a possibility of a very different scenario. For example, the pine wood nematode (*B. xylophilus*) which was introduced into Japan from North America has caused devastating losses there. Mortality of 25 percent of all Japanese red and black pines has been attributed to this nematode.

World wide, there is great concern about xylem-inhabiting nematodes. Many European countries have a zero tolerance for nematodes in their log imports.

LARCH CANKER FUNGUS

The larch canker fungus (*L. willkommii*) is native to Asia. It is widely distributed in Siberia and the Russian Far East. It also occurs in Europe where it was probably introduced and in the Northeastern United States and adjacent portions of Canada where it is known to have been introduced, eradicated, and introduced again.

The fungus affects numerous larch species and, in inoculation tests has been shown to be virulent on western larch. There are indications that it also may affect Douglas-fir. Infection results in formation of sunken perennial cankers centered on dead branchlets and dwarf shoots. Cankers often girdle stems, causing branch death or, especially in the case of small trees, whole-tree mortality. *L. willkommii* produces fruiting bodies in cankers which discharge spores when moistened by rain. Spores are dispersed by wind over considerable distances. New infections occur at any time of the year but especially in fall through wounds or dead branchlets. Infection is favored by moist, cool conditions. Where such conditions prevail in Europe and eastern North America, especially in coastal locations, larch canker has caused 50 to 100 percent mortality in larch plantations.

L. willkommii is a good saprophyte that can survive for some time in dead wood and bark. It can occupy wood of logs to considerable depth and could be very difficult to detect.

Given its characteristics, the potential for the larch canker fungus to enter the United States on unprocessed Russian larch logs is extremely high. Climatic conditions on the West Coast should be particularly favorable for *L. willkommii*. However, because the natural range of western larch is east of the Cascade Mountains, wild trees should not be directly exposed to innoculum from import logs unless such logs were transported from the coast to east-side mills. Ornamental larch are grown near ports of entry. They could be infected and serve as bridges to natural stands of western larch. Of course, if the fungus could infect Douglas-fir, colonization potential would be extremely high.

ANNOSUS ROOT DISEASE FUNGUS

The annosus root disease fungus (*H. annosum*) occurs throughout the Northern Hemisphere. It is found in virtually all Russian forests and is considered to be the most damaging tree pathogen in Siberia and the Russian Far East. *H. annosum* is a heterothallic fungus. There are several morphologically identical but genetically different strains of the fungus that are intersterile. These strains differ markedly in pathogenicity and host range. Two strains of *H. annosum* occur in western North America. One primarily affects ponderosa pine on very dry sites and the other affects hemlocks and true firs. Strains of *H. annosum* from eastern Russia have not been studied. Indications are that they may be very different from those currently found in the United States.

H. annosum is spread by wind- or water-borne spores. Sexual fruiting bodies are produced in hollow stumps, root crotches, or the underside of logs and windthrown trees. Spores are released virtually all year long and are carried by the wind for distances of up to 100 miles. Spores that land on freshly cut stump surfaces or fresh wounds germinate and the fungus colonizes the tree or stump. Subsequently, the pathogen can grow via root contacts into surrounding hosts, creating gradually expanding disease foci. Asexual spores of *H. annosum* are produced on damp, decayed wood and are dispersed by water and probably wind. They do not spread as far as sexual spores, but they too are capable of initiating new infections.

H. annosum damages trees in two ways, either by causing outright mortality or by causing progressive butt and stem decay. The fungus can survive for years in colonized wood and can occupy logs to the very center.

Russian logs infected by *H. annosum* would be difficult to detect, especially if they only contained incipient decay. Even logs with conks on them might be missed because of the cryptic appearance and inconspicuous nature of such fruiting bodies. Likelihood of *H. annosum* entering the United States on unprocessed logs from Siberia and the Russian Far East would be high, and initiation of new infections on wounded and cut trees in the vicinity of ports would be very possible.

Consequences of establishment would depend entirely on the characteristics of the Russian strains of the fungus. There might be no increase in damage, there might be increased damage on the same hosts that are already affected by native strains, or tree species currently not affected might be damaged. If a strain of *H. annosum* that damaged either western larch or coastal Douglas-fir was introduced, losses could be particularly severe. Neither of these species are damaged to any degree by native strains of the fungus.

CONCLUSIONS AND RECOMMENDATIONS

In our team's final report (Pest Risk Assessment of the Importation of Larch from Siberia and the Soviet Far East. USDA Forest Service, Miscellaneous Publication No. 1495. September 1991), we concluded that all six representative organisms had considerable potential for colonizing Russian larch logs, surviving on or in logs during transit, becoming established in North American forests, and spreading rapidly once established. Many other organisms, including a substantial number of presently unknown insects and pathogens, probably have similar potentials.

We further indicated that, in our estimation, it is very likely that introduction of some of these pests could have very significant economic, ecological, and social impacts, similar in magnitude to those caused by introduced forest insects and diseases of the past. Because the pathogens are so difficult to detect and often occupy wood to considerable depth in logs, they represent particularly great risks in our view.

We recommended that, to be safe, logs for importation from eastern Russia to the United States should receive mitigating treatments that would eliminate insects and pathogens on the surface, in the bark, and to the center of the wood. In a companion report prepared by APHIS (An Efficiency Review of Control Measures for Potential Pests of Imported Soviet Timber, USDA Animal and Plant Health Inspection Service, Miscellaneous Publication No. 1496. September 1991), possible effective treatments were considered. APHIS is currently in the process of preparing final regulations to be applied to Russian logs. It is to be hoped that these will incorporate the recommendations of the risk assessment.

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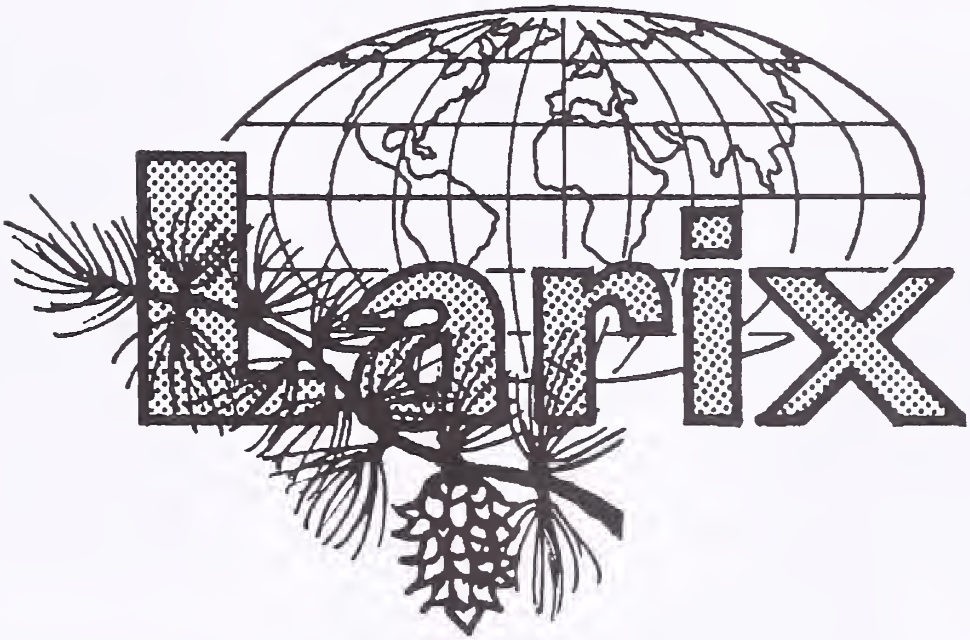

Natural Regeneration After Harvest and Residue Treatment in a Western Larch Forest of Northwestern Montana, U.S.A.

Raymond C. Shearer
Jack A. Schmidt

Editor's Note: This is an abstract of a paper that will be published separately from this proceedings. Inquiries regarding the study and data may be made through the authors at the address listed at the bottom of this column.

Historically, major disturbance, usually wildfire, preceded regeneration of western larch (*Larix occidentalis*) in the forests of the Northern Rocky Mountains. Observation and research show that establishment of western larch and other conifers is enhanced by coupling timber harvest with site preparation that exposes some mineral soil. But regeneration probability decreases, especially for shade-intolerant species such as western larch, when there is little disturbance. This research tracked establishment of natural regeneration as influenced by harvest cutting method and forest residue reduction treatments, including light prescribed fire, on the Coram Experimental Forest located in northwestern Montana, U.S.A.

In 1974, on an east-facing slope, a forest comprised mostly of overstory Inland Douglas-fir (*Pseudotsuga menziesii*) and western larch was harvested using three methods of harvest cutting: a shelterwood, a clearcut, and a set of eight small group selection cuttings, within each of two elevational zones. The lower units lay between 1,195 and 1,390 m and the upper units between 1,341 and 1,615 m. Each shelterwood, clearcut, and set of group selections received four levels of timber and residue utilization. Moist fuels on about half of each area were prescribed burned in September 1975.

The interaction of poor site preparation, low cone production, and high seed mortality initially limited natural regeneration. At the outset of this study in 1974, a serious western spruce budworm (*Choristoneura occidentalis*) outbreak was ongoing in the study area. Budworm larvae killed most potential seed cones of subalpine fir (*Abies lasiocarpa*), Inland Douglas-fir, and Engelmann spruce (*Picea engelmannii*) that year, but larch and western hemlock (*Tsuga heterophylla*) disseminated considerable seed. The budworm population collapsed in 1975, and cone production quickly resumed for Douglas-fir and more slowly for Engelmann spruce and subalpine fir.

Natural regeneration began in 1975; western larch regenerated mostly on soil exposed during yarding of logs, and western hemlock on moist sites, especially near the bottom of the lower elevation units. By 1979, an average of 1,435 seedlings per ha were counted on all units: 808 larch, 571 Douglas-fir, 10 subalpine fir, 15 spruce, 21 hemlock, 5 western redcedar (*Thuja plicata*), and 5 lodgepole pine (*Pinus contorta*). Although the average number of seedlings exploded to 16,494 per ha in 1992, the average number of larch decreased to 649 seedlings. Quick recovery of shrubs and herbs virtually stopped establishment of new larch by the early 1980's.

In contrast, Douglas-fir regenerated prolifically during the 1980's and averaged 15,120 seedlings per ha in 1992. The number of subalpine fir and Engelmann spruce seedlings continued to increase slowly within all units: to 268 subalpine fir per ha and to 175 spruce per ha in 1992. Also, western hemlock and western redcedar increased in numbers to 160 and 36 seedlings per ha in 1992 mostly on the warmer, moister areas of the lower elevation units. Lodgepole and western white pine (*Pinus monticola*) were occasionally represented.

Composition of natural regeneration in 1979 was, in percentage: western larch 59, Douglas-fir 38, and all other species 3. Percentage stocking of 0.0004 ha plots was 16 for western larch, 11 for Douglas-fir, and less than 1 for other species. In 1992, 18 years after treatment, percentage natural regeneration was composed mostly of Douglas-fir at 92, western larch 4, and all other species 4. Percentage stocking was 60 for Douglas-fir, 15 for larch, 6 each for spruce and subalpine fir, 4 for western hemlock, 2 for western white pine, and 1 each for western redcedar and lodgepole pine.

Without subsequent disturbance, the new forest will be dominated by Douglas-fir both in the overstory and understory. Occasional groups or individual western larch will also occur in the overstory, mostly where soil was exposed during logging or where prescribed fire decreased the duff layer. Subalpine fir and Engelmann spruce will slowly increase in the understory throughout the units. Western hemlock and western redcedar will be limited to the warmer, moist areas on the lower elevation units. Occasional lodgepole pine will mature as an overstory tree and may provide a temporary seed source following a future disturbance, especially fire. Because of its greater shade tolerance, the few western white pine will continue in this stand in the overstory and understory unless killed by the white pine blister rust (*Cronartium ribicola*).

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Factors Affecting Establishment of Planted Trees, Including European Larch, Near the Alpine Timberline

Walter Schönenberger
Josef Senn
Ueli Wasem

Abstract—Survival, annual height increment, and type and degree of damage and diseases of some 100,000 European larch (*Larix decidua* Mill.), cembran pine (*Pinus cembra* L.), and mugo pine (*P. uncinata* [Miller] Domin) seedlings were recorded annually after planting in 1975. By 1991, larch survived much better than the two pine species, 73 percent for larch, 38 percent for mugo pine, and 25 percent for cembran pine. Losses of larch resulted from long duration of snow cover in spring and competition with herbaceous vegetation. Larch was less susceptible to parasitic fungi. Height increment of larch was much better on mineral soil than on thick raw humus layers. Dry twig tips on young larch could be ascribed to *Ascocalyx abietina* attack and sometimes to frost.

Afforestation at high altitudes is costly and involves high risk, as frequent failures demonstrate. Because of the slow development of such afforestations it is difficult to understand and to follow the causes and processes that lead to a failure and then to suggest measures to improve success.

In a long-term afforestation experiment we therefore studied the behaviour of young trees under various site conditions with measurements and observations. In addition, extensive environmental investigations and climatic recordings were carried out in the experimental area, in order to understand the differences in diseases, growth, and survival rate between different sites.

The aim of this study is to provide the basis for selective planting suited to site and tree species in order to be more successful with less expense.

STUDY SITE

The Stillberg experimental area lies near Davos, in the central Swiss Alps, at the timberline on a 35 to 40° inclined NE slope at 2,080 to 2,230 m elevation. The slope is an avalanche catchment divided into several "pockets" by spurs (fig. 1). As a result there are four distinct relief types in horizontal succession: spurs, north-slopes, gullies, and east-slopes. The crest above the avalanche starting zone is flatter, as is the avalanche deposition zone at the slope foot.

The mesoclimate of the experimental area has been described by Turner and others (1982, 1988), Schönenberger (1985), and Schönenberger and others (1988). The climatic data from the meteorological station at 2,090 m elevation are:

- annual mean temperature (period 1961-1980): 1.6 °C
- mean temperature of the warmest month (July): 9.1 °C
- of the coldest month (January): –5.5 °C
- annual precipitation (period 1975-1981): 1,053 mm
- the annual mean temperatures vary between 2.2 and 0.7 °C
- the mean July temperatures between 11.3 an 7.6 °C
- there are no frost-free months
- number of frost-days per year: 217
- number of ice days: 80
- the annual maximum snow cover varies between 130 and 210 cm.

The bedrock is silicious. The soils are acid, mostly podsolised, and partly with extremely deep layers of raw humus (Blaser 1980).

The experimental area is dominated by different subalpine dwarf shrub and grass communities.

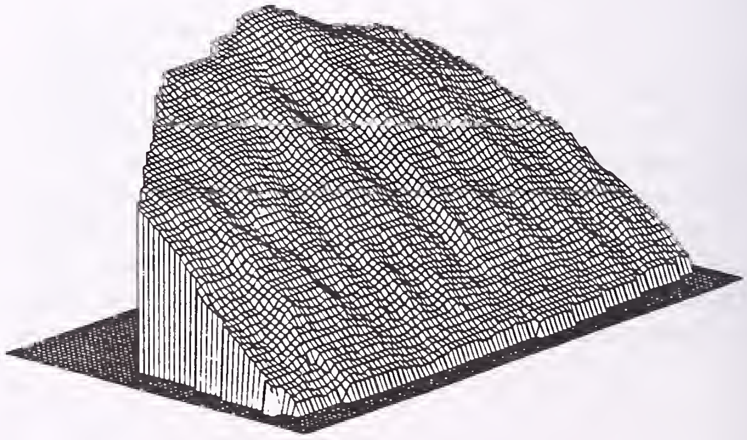

Figure 1—Topographic model of the afforestation area Stillberg. The grid confines the 4,000 square units of the afforestation, each being 3.5 m x 3.5 m and containing 25 trees of the same species, alternatively European larch, cembran pine, and mountain pine.

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MATERIAL AND METHODS

In 1975 about 100,000 young trees of three species (European larch, *Larix decidua* Mill., age 1/0, height 2 cm; cembran pine, *Pinus cembra* L., 4/1, 14 cm; and mugo pine, *Pinus uncinata* [Mill.] Domin, 2/1, 10 cm), were planted at equal distances over an area of 5 hectares. Two months before planting the trees were transplanted into 10 x 10 cm peat pots filled with peat and long-term fertilizer (2 g per liter), so that the root-systems already regenerated before planting.

The afforestation area was divided by a grid of 3.5 x 3.5 m into about 4,000 square units (fig. 1), each unit containing 25 trees of the same species (distance between trees 70 cm). The tree species alternated from one square unit to the next.

Survival of all trees was recorded annually as from 1976 (number of square units with larches = 1,351, with cembran pines = 1,351, and with mountain pines = 1,350). Tree height and mortality causes were assessed annually in a representative sample of 226 square units containing larches, in 228 square units containing cembran pines, and in 228 square units containing mountain pines. Tree height relates to net height, i.e. the frequent loss of apical shoots is taken into account.

The experimental area had been ecologically analyzed (Turner 1980) and mapped prior to planting. For interpretation of the afforestation, results of the following maps are available: vegetation map (Kuoch 1970), soil map (Blaser 1980), map of wind speed (Nägeli 1971), map of global radiation (Turner 1966). The original maps were later superimposed on the afforestation grid and computer-plotted.

According to the vegetation map (fig. 2) the configuration of the plant communities in the terrain has the following pattern: the uppermost part of the area, the crest, is largely covered with the subassociation *Empetro-Vaccinietum cetrarietosum*, and the slope foot with *Rhododendro-Vaccinietum*. In the middle slope a typical correlation of plant communities with relief-type is evident. On the wind-exposed spurs the low-growing, open *Cetrario-Loiseleurietum cladonietosum*, which is rich in lichens, occurs. Towards the north-slopes, but still near the spurs, follows *Empetro-Vaccinietum cetrarietosum* with many lichens. Next is the mossy subassociation *Empetro-Vaccinietum hylocomietosum* on the actual north-slopes with much snow, little solar radiation, and a deep raw humus layer. The avalanche gullies are densely covered with high-growing grass (*Calamagrostietum villosae*). On the adjoining east-slopes ensue the thermophile *Junipero-Arctostaphyletum*, first *juniperetosum*, towards the spurs *callunetosum*.

The plant communities were taken as a basis for the analysis of the afforestation results, because they are excellent site-indicators for the expert. On account of the plant communities the knowledge from the Stillberg experiment can be reliably transferred to other regions.

The map of mean snow disappearance (fig. 3) shows remarkable variation within the area. On spurs and east-facing slopes snow usually disappears first, before the beginning of May in the 10 years average. Snow cover lasts longest, until later than June 20, on the north slopes and on the crest in the uppermost part of the experimental area.

RESULTS AND DISCUSSION

Survival

In 1991, 16 years after planting, 73 percent of the larches were still alive, compared to 25 percent of the cembran pines, and 38 percent of the mugo pines. In all three species, survival was clearly dependent on altitude and local site parameters, and varied enormously within short distances (fig. 4). Losses were highest in the upper part of the area, especially on the crest. Here only larch survived to a

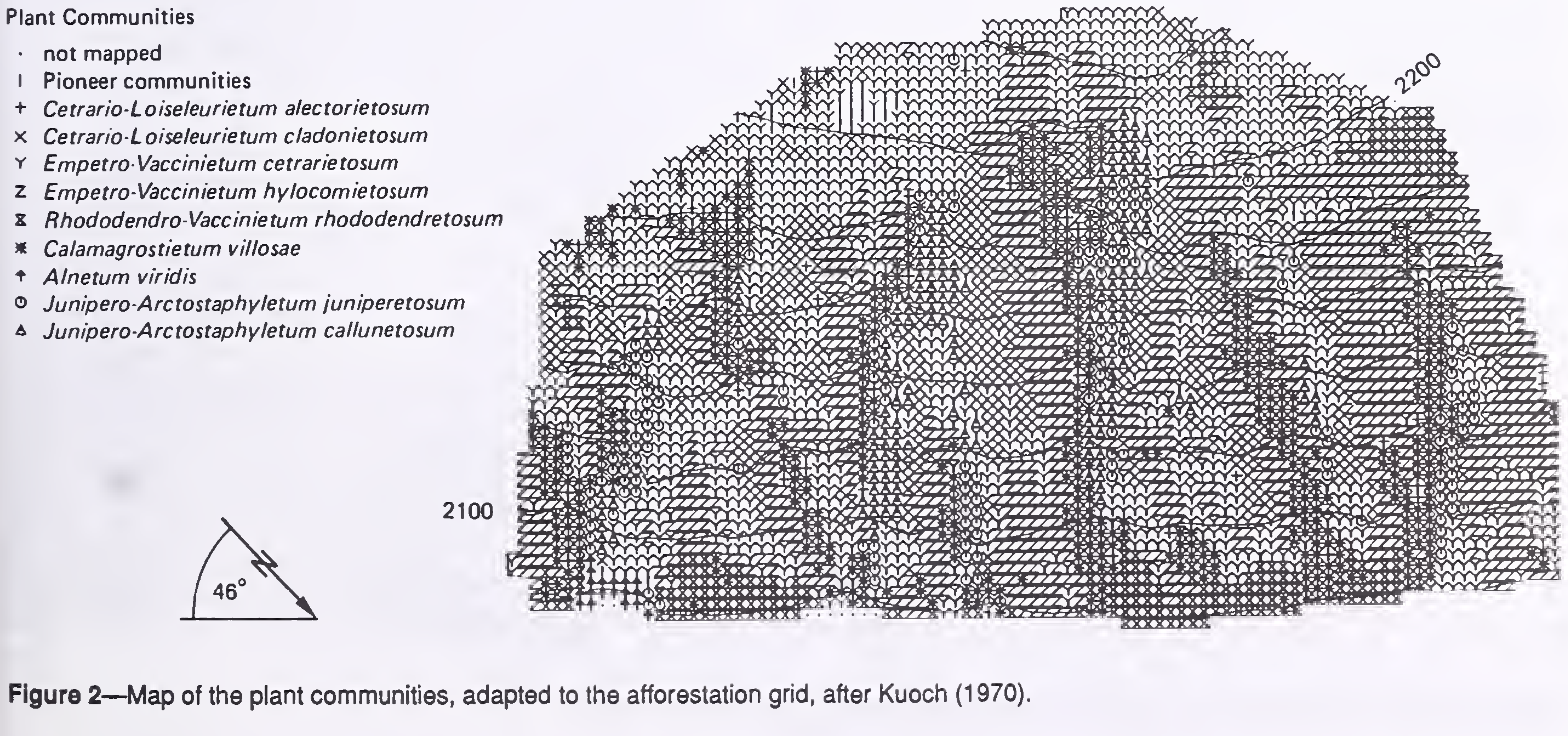

Figure 2—Map of the plant communities, adapted to the afforestation grid, after Kuoch (1970).

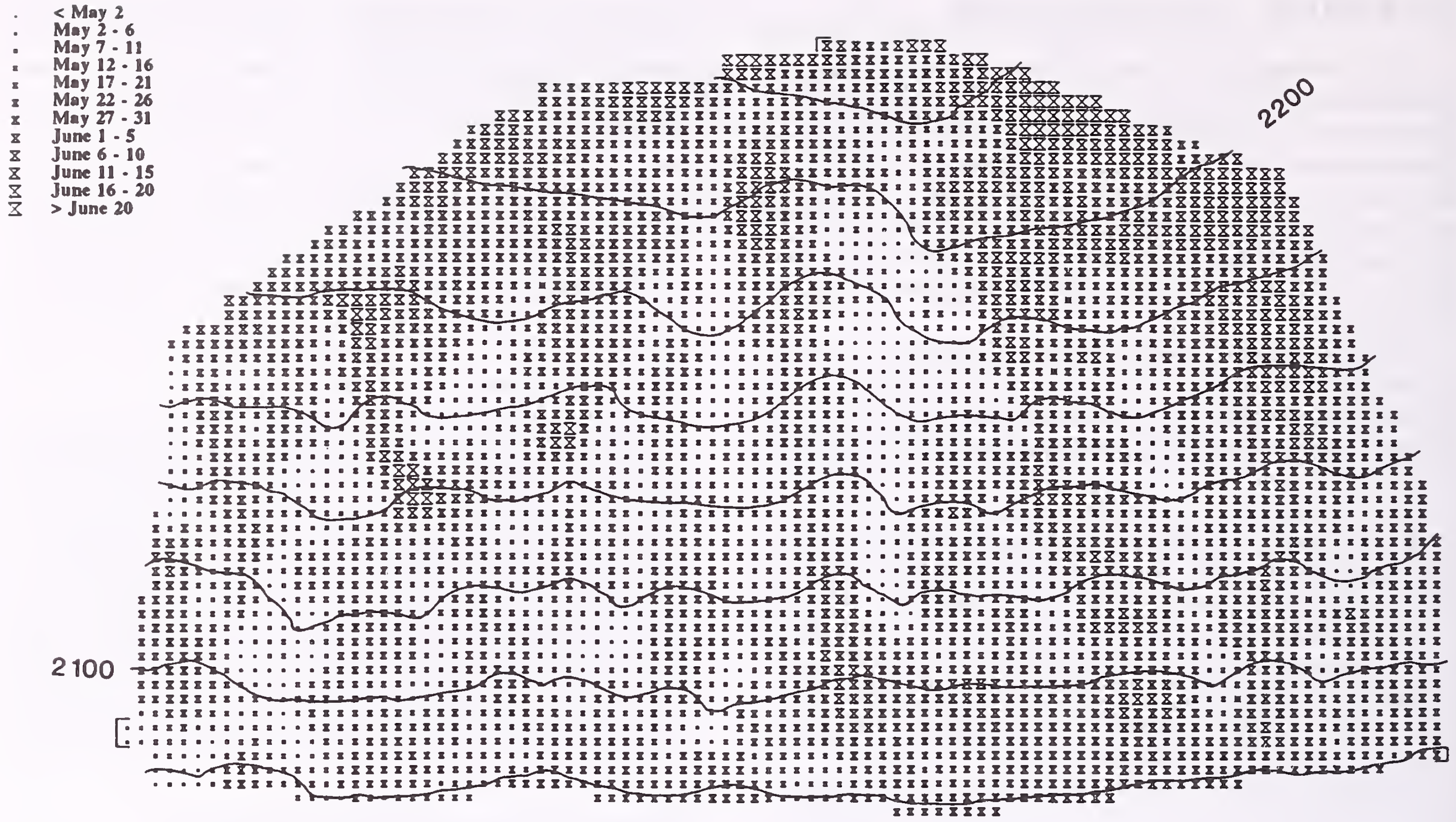

Figure 3—Map of disappearance of snow cover in spring, adapted to the afforestation grid, data based on 10 year average.

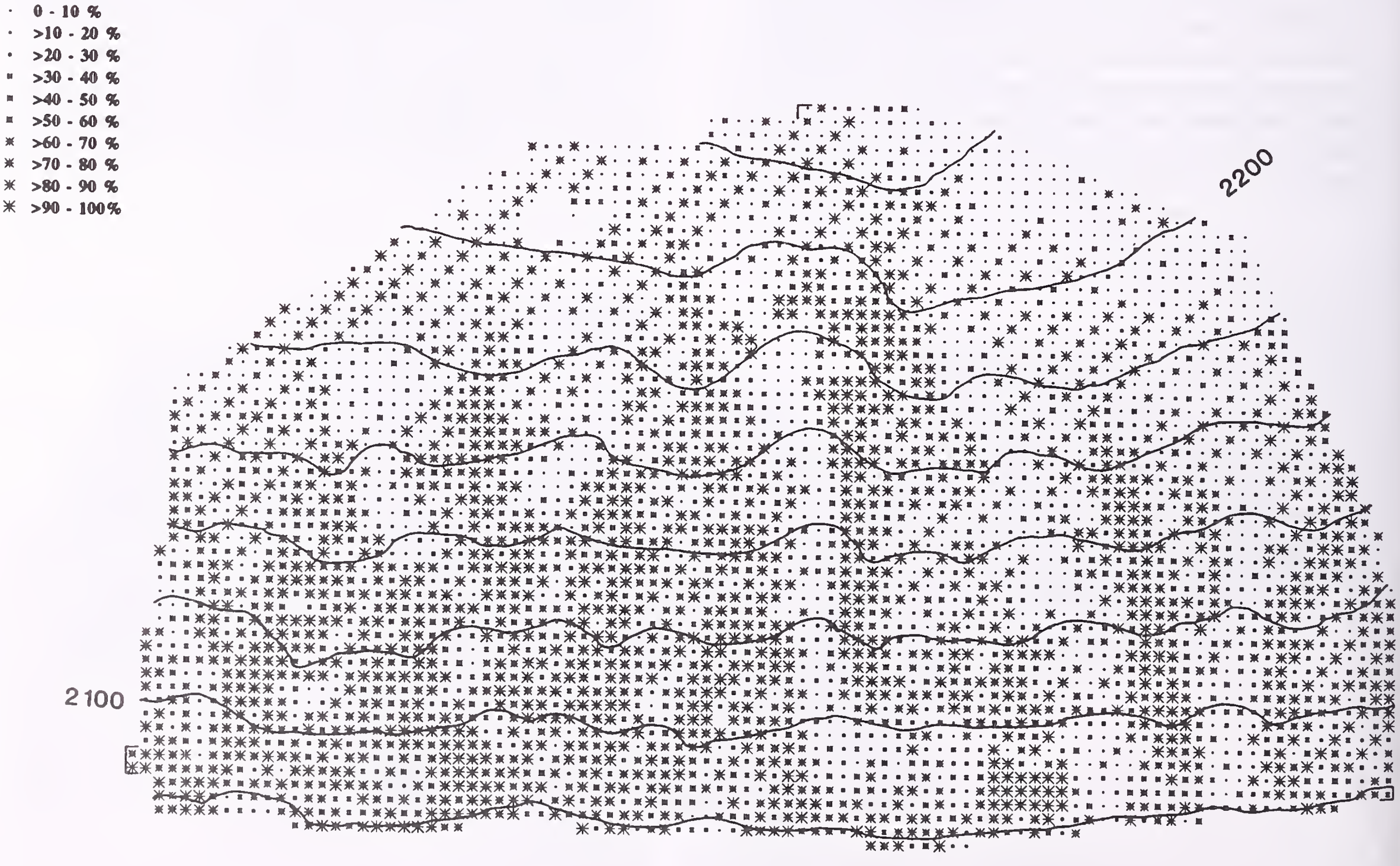

Figure 4—Map of tree survival rate in percentage (number of trees alive in 1991 in a square unit * 100/number of trees planted in 1975). All three tree species shown.

certain extent (demonstrated by the diagonal alignments of square units with good survival). Survival was best on the slope foot. On the undulating middle part of the afforestation area, tree survival was relatively high on east-facing slopes and on spurs. Avalanche gullies were noted for poor survival, which was also reduced on north-slopes.

Development of survival rate varied considerably between and within the tree species according to the site conditions as reflected by the plant communities (fig. 5). The losses of larch were relatively high in the first years but later decreased. Cembran and mugo pine on the other hand suffered few losses at the beginning, but losses increased later. The main reason for the variation in survival between the three species during the first years may be the differences in age and size at the time of planting. The one-year-old larches were on average only 1.9 cm high and therefore less robust and weaker competitors than the three-year-old mountain pines and the five-year-old cembran pines, which were on average 10.4 cm and 13.8 cm high.

Mortality Causes

During the first 16 years, 27 percent of the planted larches died, a proportion that was relatively small compared to the two pine species. In 78 percent of all dead larches no cause for mortality could be recognized. In 8.3 percent of the dead larches, death was assigned to competition with herbaceous vegetation. The parasitic fungus *Ascocalyx abietina* (Lagerb.) [= *Gremmeniella abietina* (Lagerb.) Morelet] was assessed as the mortality cause for 4.2 percent of the larches. Lethal mechanical bark injuries were found in 2.3 percent, and uprooting by snow and soil movements was responsible for another 1.9 percent of the tree losses. Browsing herbivores, particularly chamois (*Rupicapra rupicapra*), contributed 1.1 percent to the total mortality of larch. The last figure, however, may be considerably higher since many of the young trees that disappeared may have been browsed by chamois.

To learn more about the impact of site factors on survival we performed stepwise regression analysis (SAS 1985) with arcsine transformed survival rates of larches (number of trees in a square unit alive in 1991/number of trees planted in 1975) as the dependent variable and the site factors altitude above sea level, slope, radiation, wind velocity, number of snow-free days in winter, avalanche frequency, and date of disappearance of snow cover in spring as the influence variables. Since some of these site factors were not mutually independent the following result should be regarded with caution.

Date of disappearance of snow cover in spring was the most important factor explaining some 23 percent of the total variation in survival of larch. Survival decreased with increasing duration of snow cover in spring. Larch, however, was much more tolerant to long-lasting snow cover in spring than were the two pine species. In 1991 30 percent of the larches were still alive in square units that were snow-covered after June 10, whereas the pines had virtually disappeared at such sites. At sites with late snow disappearance (fig. 3) that can be characterized as

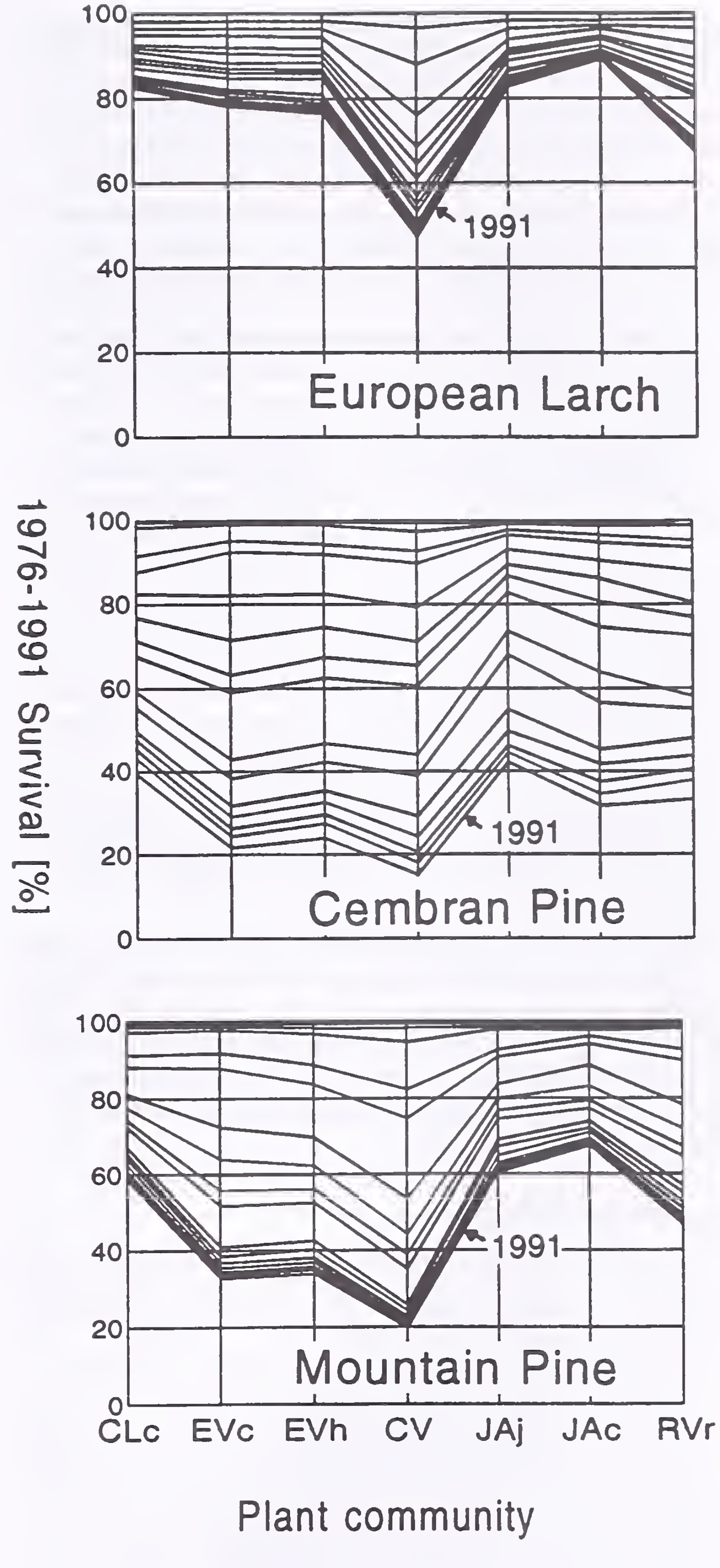

Figure 5—Development of tree survival rates in different plant communities. Each line represents survival of a given year from 1975 (=100 percent) to 1991. Plant communities: CLc = *Cetrario-Loiseloirietum cladonietosum*; EVc = *Empetro-Vaccinietum cetrarietosum*; EVh = *Empetro-Vaccinietum hyloconietosum*; Cv = *Calamagrostrietum villosae*; JAj = *Junipero-Arctostaphyletum juniperetosum*; JAc = *Junipero-Arctostaphyletum callunetosum*; RVr = *Rhododendro-Vaccinietum rhododendretosum.*

Empetro-Vaccinietum and as *Calamagrostietum*, the parasitic fungus *Ascocalyx abietina* was the major mortality cause for pines. The larch, however, was much less susceptible to fungal diseases. Only 1.1 percent of the planted larches were recorded as killed by *Ascocalyx abietina* compared to 53.3 percent of cembran pine. No other fungal disease has been found to have a significant effect on larch mortality. Field assessment of *Ascocalyx* damage in larch, however, has sometimes been difficult since frost damage may have looked very similar. The biggest problem for larch at sites with long-lasting snow cover in spring may be thick layers of raw humus. Low temperatures greatly reduce decomposition and lead to the accumulation of organic material on which European larch grows poorly.

The second important of the site factors we included in the regression analysis of larch mortality was the frequency of avalanches. On sites with frequent avalanches the young larch trees survived less well than on sites with few or no avalanches. The reason for this relationship, however, was not uprooting or stem breakage by the moving snow. Avalanches carried mineral soil into the gullies leading to lush herbaceous vegetation such as *Calamagrostietum* causing strong interspecific competition. At the time of planting, larches were by far the smallest in height compared to the pines and therefore suffered most from competition with herbaceous vegetation. However, once the larch trees survived the first years and managed to establish themselves their further survival was much better than that of the two *Pinus* species.

The impact of the other site factors, global radiation, slope inclination, and wind velocity, on survival of larch was significant, too, explaining between 1 and 2 percent of the total variation. Survival increased with increasing global radiation, slope inclination, and wind velocity, but decreased with increasing altitude and with increasing number of snow-free days in winter.

Height Growth

In 1991 mean height of the larch trees was slightly greater than mean height of cembran pine but significantly lower than that of mountain pine.

Stepwise regression of tree height of larch on the various site factors revealed altitude and global radiation as the two most important factors explaining some 28 and 18 percent of the total variation. Tree height decreased with increasing elevation, and increased with increasing global radiation. Further, wind velocity explained 9 percent, and slope inclination 6 percent of the variation in height. Tree height decreased with increasing wind velocity but increased with increasing slope inclination. No other of the site factors we included in the analysis had any detectable significant impact on height in larch.

Comparing only mean height among the three tree species, however, may lead to wrong conclusions. Variable site conditions caused enormous variation in tree height as well as in survival. Survival rate of larch was about double that of the two *Pinus* species. Larch trees survived well on many sites that allowed only very poor growth, i.e. at the highest altitudes and on the sites longest covered by snow in spring, whereas the two pine species completely disappeared from many of these sites. On such poor sites, however, the total height of larch trees was only a few centimeters after 16 years, which greatly reduced the overall mean height of larch. Mean height of the two pine species on the other hand gained from the absence of values from poor sites. When we compared the sites that allowed vigorous growth, larches were obviously the most successful of the three species, attaining the greatest height and best survival rate.

CONCLUSIONS

The consequences of the results from the Stillberg experimental plantation for afforestation practice are thoroughly discussed in Schönenberger and others (1990).

A good knowledge of the ecology of subalpine habitats is required in order to estimate the prospects of success of afforestations. The slightest irregularities in the terrain give rise to large differences in micro-site, so that favourable and unfavourable sites may lie very close together. Specific threats to particular tree species from fungi, game, insects, climatic extremes, snow movements, and competition on the individual sites must be taken into account. Given these difficulties, it may pay to employ special, more laborious methods of cultivation and planting, e.g. to use potted rather than bare-rooted plants. Cluster arrangement must be preferred to a regular planting pattern, since it allows consideration of micro-site conditions, the establishment of a good surface structure, and the preclusion of uniform stands. Last but not least, the growth conditions in mountainous regions impose appropriate methods of tending for young growth and thickets. As development proceeds only slowly, the thorough documentation of work conducted is especially important to ensure that experiences are not lost.

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Microsite Characteristics and Safe Site Description for Western Larch Germination and Initial Seedling Establishment

Brian P. Oswald
Leon F. Neuenschwander

Abstract—Eight variables were used to describe microsite types and measured before treatment, at postburning treatment, and 1 year later microsite condition. Litter, small vegetation, soil surface roughness, duff, and sticks were significantly affected by burning treatment; shading, moss, and large vegetation were not significantly affected by treatment. Germination percentages and seedling development were significantly greater on caged units than on uncaged units by midseason. No significant differences occurred in germination or initial seedling establishment between burned and unburned treatments.

Germination and seedling development depend on the interaction of a seed and seedling with its physical and biological environment. Some of the microsite and seedbed factors affecting germination and seedling establishment are shading, litter and duff cover, soil moisture, competing vegetation, insolation, predation, and the interactions among these variables. Traditional natural regeneration site preparation methods are applied to create the optimal seedbeds for the targeted species.

During the period between seed dispersal and seedling establishment, events occur that frequently determine the fate of individual plants (Fowler 1988). Harper and others (1965) defined a safe site as a zone surrounding a seed or seedling with the stimuli required to break seed dormancy, with the conditions for germination to occur, with sufficient oxygen and water for germination, and with a lack of predators, competitors, and pathogens specific to the seed or seedling.

The microsite size required for germination and establishment varies with the size of the seed and the seedling. The terms "microsite" and "microenvironment" have been used to describe areas ranging from as large as 16.4 ha (Gashwiler 1967) to as small as tree fall mounds and pits (Beatty and Stone 1986). The size of a safe site will vary with the size of the seed or seedling but will encompass the immediate area surrounding the seed or seedling (Harper 1977).

Shearer (1975), Schmidt and others (1976), and Artley and others (1978) evaluated the general ecology and the seedbed and germination requirements of western larch (*Larix occidentalis*). Western larch was found to germinate on a variety of seedbed types, but seedling survival was generally limited to mineral soil seedbeds. Mortality was caused by fungi, predation, insolation, and drought. Geier-Hayes (1987) surveyed the seedling survival of six conifer species, including western larch, on various microsite conditions within 10-m^2 plots in central Idaho but did not evaluate safe site characteristics for germination or initial seedling establishment.

The objectives of this study were to describe and quantify microsite variability of the forest floor in a mixed conifer forest using physical seedbed characteristics important for the regeneration of western larch. Microsite variability was then evaluated as to its impact on the germination and initial seedling establishment of western larch. Safe sites were described and safe site thresholds determined. The physical characteristics having the greatest influence on germination and initial establishment were identified. The influence on the germination and seedling establishment of western larch of shading, burning, and mechanical effects and protecting seeds and seedlings from predation were quantified.

METHODS

Five relatively undisturbed research sites reflecting the natural variation of the forest floor were selected in the fall of 1987 on the University of Idaho Experimental Forest, approximately 48 km northeast of Moscow, ID. The sites were chosen as described by Mueller-Dombois and Ellensberg (1974): "subjectively but without preconceived bias," to represent sites at the ecological edge of western larch. Sites were classified as *Abies grandis/Physocarpus malvaceus* (grand fir/ninebark) habitat type following Cooper and others (1991).

Ten transects, each 15.3 m long, were randomly located across slope contours. At each 0.3 m along these transects, a 5.1-cm diameter circular sample point was established and was quantified with categorical descriptors for the amount of duff, litter, small sticks (<2.5-cm in diameter), vegetation, soil surface roughness (relative soil surface in relation to seed size), and shading (estimate of shading between 12 and 2 p.m.). A combination of these physical characteristics defined a microsite type.

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After the sample points were described, half of each site was randomly selected and the five transects within that half burned with propane torches between October 7 and 11, 1987. The burned sample points were again described with the same categorical descriptors after burning treatment, and all sample points were classified in the fall of 1988, 1 year after treatment.

Two 0.74-m^2 plots were also located on each research site and subdivided into 0.09-m^2 experimental units. The treatments applied randomly to each experimental unit and replicated on each site were: seedbed treatment (burned or mechanical), soil (mineral soil or duff), shading (full or 60 percent sun), and caging (protected or not protected from bird or rodent predation). Hand trowels were used to simulate mechanical site treatments; propane torches were used for burning treatment. Shading racks created the shading factor, and 0.6-cm mesh hardware cloth, sunk 10 cm into the ground and covering the sides and top of the experimental unit, was used to limit bird and rodent predation.

After the second classification in October 1987, seven western larch seeds (four expected to germinate based on germination tests) were distributed on each sample point, and 150 (100 expected to germinate) seeds distributed on each experimental unit.

Beginning in April 1988, the sample points and experimental units were visited every 3 days. The numbers of germinations (radical emerging from seed), germinants (radical entering soil to development of first needles), and initial seedlings (seed cap off and needles visible) were recorded. In this study, seedling establishment referred to seedling survival at the end of the first growing season. The 3-day schedule was maintained for 3 months, then weekly measurements were made for a month, followed by biweekly observations for the remainder of the growing season. A new set of 0.74-m^2 plots was established in the fall of 1988 on the same sites, and this portion of the experiment was repeated during the 1989 growing season.

Statistical tests (ANOVA, Principal Component Analysis, Discriminant Analysis, Regression) were performed on the data to determine sources of forest floor variation, to isolate the variables influencing germination and seedling establishment of western larch, and to determine "safe sites" for western larch germination and seedling establishment.

RESULTS

Microsite Variability

Only 618 of the 135,000 possible different microsite types occurred. Little change occurred on the unburned sample points, while the number of different microsite types (388 to 217) was reduced after burning. The number of burned microsite types that occurred only once was reduced to 49 after burning; the number of these microsite types 1 year later (102) was little different than initial (140) measurements. The microsite type that occurred most often had moderate soil cover, no vegetation or shading, and was the same for pretreatment, posttreatment and 1-year measurements. There was an increase in occurrence of this type after treatment on the burned sample points; after 1 year this microsite type was little different from pretreatment levels. The 10 most common pretreatment types showed little or no change in levels of duff, large vegetation, moss, and soil surface roughness between microsite types, while litter changed the most. There was no difference in the microsite types comprising the 10 most common microsite types posttreatment and 1 year later. Descriptor variables accounted for 96 percent of the variation among forest floor microsites, with shading, litter, and small vegetation associated with approximately 78 percent of the variation.

Germination and Seedlings on Various Microsites

From 17,500 seeds distributed on 618 microsite types, 205 microsite types supported 741 germinations and 200 microsite types supported 656 germinants (fig. 1). By the end of the first growing season, 47 seedlings on 33 microsite types were found. Winter mortality and predation reduced survival to four individuals on three microsite types.

Overall, three variables (duff, sticks, and large vegetation) were never significant descriptors, while site, small vegetation, and soil surface roughness were significant descriptors at all developmental stages. Roughness and litter were significant descriptors until the end of the first growing season, and moss only at the later stages. On burned sample points, litter at the germinant stage and moss at the seedling stage were significant descriptors. On unburned sample points, site, small vegetation, and

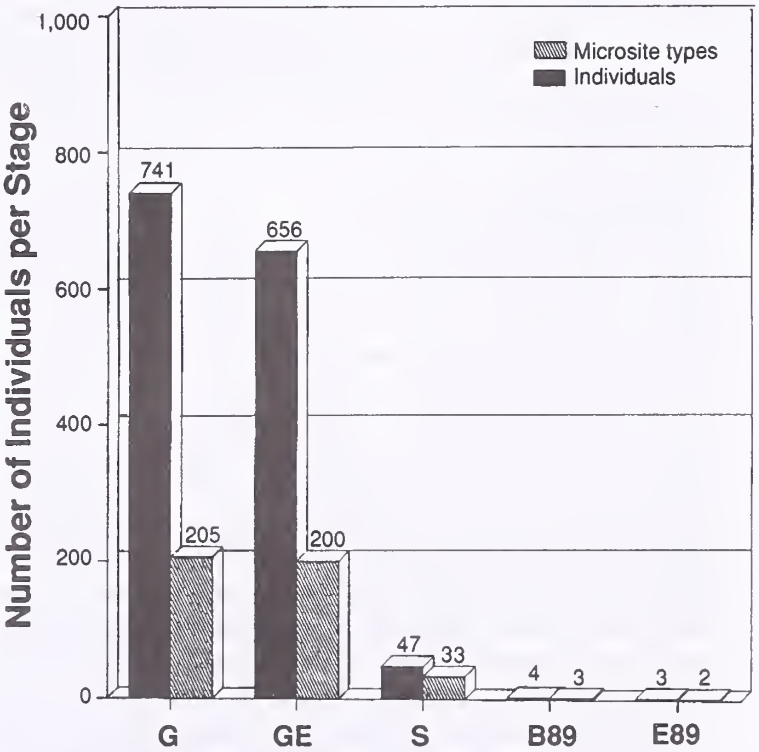

Figure 1—Number of individuals of western larch and microsite types at each developmental stage. G = germination; GE = germinant; S = seedling; B89 = 2d year beginning; E89 = 2d year end.

duff were significant descriptors at early developmental stages, while litter, moss, and shading were significant at later stages.

The number of significant variables and interactions for unburned sample points increased as the seeds germinated and became germinants, with fewer significant interactions at the end of the first growing season. Analysis of burned sample points indicated no significant interactions of variables and only individual variables significant at each seedling stage.

Multiple regression analysis for germination and germinant stages produced R^2's of 0.02 to 0.08 (Oswald 1992). Using only the 37 sample points that supported seedlings at the end of the first growing season, a basic regression model ($Y = A + BX$) explaining 75 percent of the variation for the safe site that supports a western larch seedling at the end of the first growing season on a grand fir/ninebark habitat type was: Seedling survival at the end of first growing season = 1.65 + 2.81 (site) – 0.15 (seedbed treatment x shading) – 0.84 (site x moss).

Seedling Development on Various Seedbeds

No significant ($p < 0.05$) differences in mean number of germinations or germinants were found from shading. Significant differences in number of germinations from caging effects ended May 14 in 1988 and April 22 in 1989, and by June 14 in 1988 and May 28 in 1989 for germinants. The significant variation caused by seedbed treatment in 1988 was found only on May 1 for germination and throughout the study for germinants.

Shading was not a significant factor affecting seedling numbers either growing season. Soil was a significant factor throughout the 1988 growing season but only during the second half of the growing season in 1989. Caging and seedbed treatment were significant factors in both years. In 1988 and 1989, significant differences in seedling numbers were found at each date between caged and uncaged units.

Units protected from predation produced significantly more ($p < 0.02$) seedlings by midseason (June 2 to July 22 in 1988, June 20 to July 20 in 1989), with four to 10 times the mean seedling numbers found on uncaged units, depending on other seedbed treatments. On mechanically treated plots in 1988, shaded units supported more seedlings than unshaded units, as did shaded caged units on mineral soil over the other caged units in 1989. Seedling numbers per plot peaked by early June on burned units both years; the number of seedlings on unburned plots peaked in late May in 1988 and late June in 1989. Rapid reduction in seedling numbers occurred in July both years regardless of treatment, with nonsignificant differences in mean seedling numbers between treatments by August 15 in 1988 and August 7 in 1989.

For seedling numbers during the second half of the growing season, least square regression using the linear model of the form $N = B_0(T) + B_1$, where N = number of seedlings, B_0 and B_1 = slope and intercept, and T = Julian dates between June 20 and October 19, produced the following examples of best fits for uncaged units both years:

Uncaged 1988 burned: $N = -0.24(T) + 1.50 \quad R^2 = 0.91$
Uncaged 1989 mechanical: $N = -0.36(T) + 4.45 \quad R^2 = 0.94$

The caged units were fit best by the logistic model:

$$N = A + C - (A/\,(1 + (A - C/C)e^{\,(-B_0)(B_1)(T)}))^{B_1}$$

where

A and C = upper and lower asymptotes, and B_0 and B_1 = parameters, producing the following example equations:

Caged 1988 burned: $N = 29.52 - (35/(1 + 5.39e^{-0.90T}))^{1.05}$ $R^2 = 0.87$
Caged 1989 mechanical: $N = 92.58 - (100/(1 + 12.48e^{-0.74T}))^{0.99}$ $R^2 = 0.88$

DISCUSSION

Burning reduced microsite variability, as there were fewer total microsite types on burned points. The impact of burning on microsite type variability on these sites using these descriptor variables was short lived; probably, the low intensity and low severity of fire resulted in the rapid recovery.

Moss and large vegetation levels were the same in the most common types after burning and 1 year later, reflecting the absence of these variables on these points and, therefore, were not expected to change within 1 year. The reduction of duff and litter after burning increased the number of microsites with a smooth soil surface from 18 to 70. On these sample points, sticks were rare (zero to five sticks per point), reflecting a lack of sources (large vegetation) on these sites. Litter, the most variable descriptor, appears influenced by outside factors, since PCA tests did not show a strong correlation between litter and the other descriptor variables.

Shading was always the primary variable in the first principal component (42.7 percent of variation). On these sites it was caused by ponderosa pine overshadowing the site and the occasional clumps of oceanspray and ninebark on the sites. Litter, almost entirely pine needles and leaves from tall shrubs, dominated the second principal component (23 percent of variation). The remaining dominant variable, small vegetation, was less patchy than the above variables. Due to the southerly exposure of the sites, we did not expect duff to be important in distinguishing microsite types. Although common on all sites, moss was not found on enough sample points to become a major variable.

The number of western larch seeds germinating and becoming germinants on a similar number of microsite types reflects the ability of western larch to germinate under a wide variety of conditions, even at the dry end of its range. The minimal change in the number of microsite types supporting germination and germinants reflects a lack of difference in safe site (seedbeds with proper conditions) requirements for these developmental stages. The decrease in seedling numbers by the end of the first growing season results from safe site requirement changes between stages, reflected in changes of soil temperature, soil moisture, and plant competition that occurred on these sites during this period. The area usually has a dry, hot period June through August, when most vegetation is under moisture stress. Most of the seedling mortality occurred from June through August, largely due to drought, but predation of seedlings by rodents, insects, and birds was also a factor. Winter losses of 33 seedlings were probably the result of both predation and mortality from moisture and temperature stress the previous growing season (1988).

The importance of site on seedling development reflects the differences that exist in forest floor heterogeneity and safe site distribution within a single habitat type. The lack of statistical significance for duff and small vegetation on burned sample points was not surprising, since duff was often less than 2.5 cm deep on these south-facing slopes before burning and small vegetation was consumed in the fire.

On burned sample points, soil surface roughness was significant at early stages of seedling development, but not important for seedling survival at the end of the first growing season. As seedlings grow, they require additional shade and moisture—as provided by vegetation, litter, and sticks—than in earlier stages, as well as continued protection from predation and competing vegetation. On unburned sample points, the existence of small vegetation and duff was more important at the early developmental stages.

The increased specification of safe site requirements as the seedling develops suggests a multiple pathway development for seedling development. Regression analysis shows the increased specification of safe site requirements with advancing seedling development, especially on unburned sample points. The R^2 (0.74) at the end of the first growing season shows that we were successful in identifying some of the physical characteristics influencing seedling survival on unburned sites for western larch at the dry end of its range. The low R^2's (0.04 to 0.06) for earlier developmental stages on these same sites indicate that additional variables impact western larch germination and initial development.

The differences between unburned and burned sample points were in the interactions between site and other variables. On unburned sample points, the interacting variables (moss, shading) can provide protection from seed predators and shade seedlings from high soil surface temperatures and moisture stress. On burned sample points, the only significant variable for germination was soil surface roughness. Microvariation in soil surfaces should provide some protection from predation and increase soil moisture availability.

Traditional site preparation methods, such as burning to improve seedbeds, may actually decrease survival of western larch once germination is completed. The wide range of safe sites for western larch germination coincides with Schmidt and others (1976), who found western larch germination under a wide variety of conditions. The high mortality rate in the first year also supports previous studies.

The reduction of 17,500 seeds to 47 seedlings after one growing season highlights the interactive nature of microsite characteristics for the different stages of development and the tenuous nature of successful natural regeneration of a species at the edge of its ecological range. The number of safe sites should be fewest on the edge of a species range and in abnormally hot and dry years. This reduction also highlights the natural variation in microsites and potential safe sites for western larch on this habitat type.

Predation greatly affected the success of western larch germination and seedling development. Caged units had significantly greater germination and seedling numbers than uncaged units in both 1988 and 1989. Most predation was of seeds during the fall, winter, and early spring before germination; Schmidt and others (1976) reported similar results for western larch. Burned plots had greater seedling numbers in both caged and uncaged units than unburned plots, indicating improved germination conditions on burned seedbeds with reduced duff depth. When seeds germinated on mineral soil, more survived on mechanically treated plots, confirming the results of Boyce (1985). The overall lack of significant differences from seedbed treatment (mechanical versus burned) was surprising. These results perhaps reflect slight site differences of slope and aspect that on the western, low elevation and dry end of the species' ecological amplitude (Cooper and others 1991) influence germination and seedling development conditions to a greater degree than previously thought.

Through the middle of the first growing season, seedling numbers were three to 10 times higher in treatments protected from predation. However, overall seedling numbers were not significantly different after August 15, regardless of seedling treatment. After a month of dry, hot weather, mortality from heat girdling and moisture stress may have reduced any early benefit of protection from predation, overwhelming any beneficial effect of the shading treatment. Even though seed predation was a major factor in the germination of western larch, it was not a factor directly determining the survival of western larch seedlings at the end of the first growing season.

On mineral soil, seedbed treatment and caging had higher number of seedlings at midseason both years. These results coincide with results of previous studies (Shearer 1975; Boyce 1985; Wellner 1990). Unlike these studies, however, we found no significant differences in the number of western larch seedlings at the end of the first growing season. The best-fit regression lines to seedling numbers show that, although the influence of predation produced dramatically different models, other factors greatly influenced first-year seedling survival. The tenuous survival of western larch seedlings on grand fir/ninebark habitat type at the edge of western larch's ecological amplitude is more likely the reason for the lack of significant differences in seedling numbers at the end of the growing season.

Many individual seeds were removed by seed predators before or during germination; little mortality occurred after germination in the first half of the growing season. The lack of significance of the shading and seedbed treatment variables on germination or seedling development and the low mortality after germination both years suggest a low impact of fungi on seedling survival. Heat girdling has been identified as a major factor in seedling survival (Schmidt and others 1976; Shearer and Halvorson 1967) and may have been a cause of seedling mortality in this study. The role of seed predation was much greater than reported in an earlier study of western larch (Shearer and Halvorson 1967). Seed predation on south-facing and west-facing aspects may be greater than on other aspects due to less snow and warmer habitat for rodents and insects in the interim between conifer seed distribution and germination. We did not separate mortality causes except that caused by predation.

CONCLUSIONS

Microsite variability is an important factor in the availability of safe sites for a species' regeneration. The safe site concept is effective for evaluating natural regeneration requirements for the different stages of seedling development. The differences in safe site for germination and initial seedling establishment show the changing seedbed requirements for the different stages. The effect of seed predation on the natural regeneration process may be understated for western larch, and scarification may not provide sufficient increases in seedling development to warrant its cost over that of shallow duff. On this habitat type, it might be more effective to manage for the natural regeneration of other timber species and expect some natural regeneration of western larch.

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Potentials for Establishment and Cultivation of Siberian Larch (*Larix sibirica* Ledeb.) in the Nordic Countries

Markus Lassheikki
Anders Mattsson

Abstract—Interest in larch cultivation is increasing in the Nordic countries for ecological and socio-economical reasons. Siberian larch is one of the most promising exotics for cultivation in northern Europe. A Nordic project has studied the effect of cultural regimes in nurseries on seedling development and early field establishment.

In the Nordic countries—Sweden, Finland, Norway, Denmark, and Iceland—environmental consideration and aspects of landscape management are becoming increasingly important in forestry. Airborne pollutants and forecasted change in global climate will affect the resources that are available for plant growth and plant composition. For example, nitrogen deposition in southern Finland today already amounts to more than 10 kg/ha/year. As wood production will remain important along with environmental awareness, and as physiochemical changes are likely to occur in forest ecosystems, we have to seek alternative tree species for the site-adapted sustainable forestry that is carried out in the Nordic countries. In this connection, larch may be a species of great interest in the future.

Larch is not a native species in the Nordic countries (fig. 1). However, according to discovered wood fragments and pollen studies (Hirvas 1991; Mäkinen 1982), larch grew in northern Europe before the last glacial period. Larch has not returned naturally to Scandinavia probably due to the humid climate. It has also been postulated that larch just hasn't had enough time to return and has been prevented by edaphic factors and topography.

SIBERIAN LARCH

Random dendrological experiments and, later, designed studies over more than 200 years have given valuable information on the adaptation and productivity of exotic species. Siberian larch is one of the most promising exotic species for cultivation in the boreal and hemiarctic zones of northern Europe (Blöndal 1982; Lähde and others 1984; Martinsson and Winsa 1986) (fig. 2).

Growth and yield of Siberian larch exceeds that of domestic Norway spruce and Scots pine on the best sites (Martinsson 1992; Vuokila and others 1983). Larch can withstand strong winds and is fairly tolerant of frost. Larch is also resistant to some extent against butt rot, although this property has partly been exaggerated (Laine 1977; Palmberg 1969). Larch is also rather resistant to pollutants.

One of the best known stands of Siberian larch is the one at Raivola near Saint Petersburg. The stand was originally established in 1738 for ship building. The first part of this forest was seeded with seed from Archangelsk. Later, the stand was supplementary planted with seedlings (Ilvessalo 1916). The seedlings may be of Ufa origin. Therefore, seed from the Raivola seed source is often believed to contain provenance hybrids.

Stands from the Raivola seed source grow excellently throughout the Northern countries in a wide range of site and climate conditions (Edlund 1966; Lähde and others

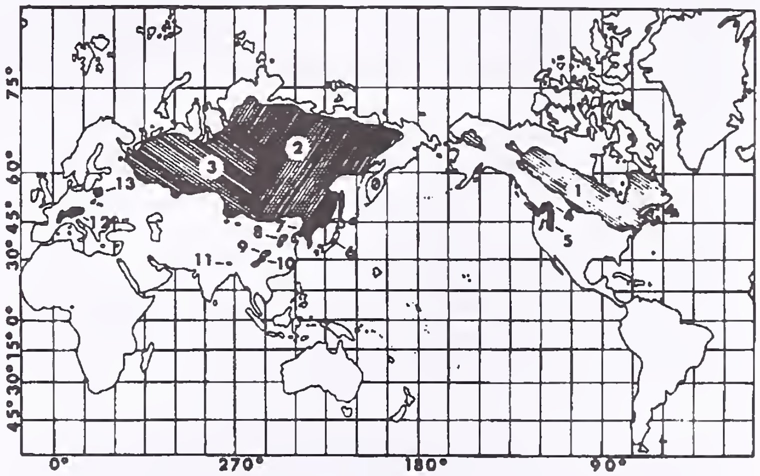

Figure 1—Distribution of larch species over the northern hemisphere (Le Page and Basinger 1991). Legend of scientific names: (1) *Larix laricina* (Du Roi) C. Koch; (2) *L. gmelini* Turcz.; (3) *L. sibirica* Ledeb.; (4) *L. occidentalis* Nutt.; (5) *L. lyallii* Parlatore; (6) *L. kaempferi* (Lamb.) Sargent; (7) *L. gmelini* var. *olgensis* (Mayr) Ostenf. and Syrach Larsen; (8) *L. gmelini* var. *principis-rupprechtii* (Mayr) Ostenf. and Syrach Larsen; (9) *L. potanini* Batalin; (10) *L. griffithiana* (Lindley et Gordon) Carriére; (11) *L. mastersiana* Rehder and Wilson; (12) *L. decidua* Miller; (13) *L. decidua* var. *polonica* (Raciborski) Ostenf. and Syrach Larsen.

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Figure 2—Distribution of Siberian larch (*Larix sibirica* Ledeb.) (Sarvas 1964).

1984; Lines 1990). Several seed orchards of the Raivola seed source have been established since the 1950's. In Finland they amount to about 50 ha (Anon. 1989), producing seed not only for the needs of Finland but also enough for export. There are discussions now on the establishment of seed orchards of this source in Finland solely for the needs of Iceland. As there is practically no background pollination, these seed orchards will give an opportunity to save genetic information.

Siberian larch is a typical pioneer species and needs lots of light for regeneration. Within a closed mature stand, young growth does not occur except in gaps with high solar radiation. Siberian larch regenerates naturally in Scandinavia (Palosuo 1938), which can be seen as the proof of adaptation. Natural regeneration is, however, limited by the number of seed-producing stands. Manual seeding has been used as a successful regeneration method (Ahola 1952). Today it is limited by the price and the small amount of available seed. Therefore, larch is mainly regenerated by planting.

Today, larch forests account for only a few permille of the total forest area in the Nordic countries, and they do not exceed 25,000 ha total. The forests are widely spread and generally rather small.

Estimated yearly seedling production of larch in the Nordic countries is about 5 million, which is much less than 1 percent of the total seedling production. Normally, Siberian larch is planted as pure stands at a density of 1,100 to 2,500 seedlings per ha. Site scarification is common and has a positive influence on early field establishment (Oskarsson and Ottosson 1990). Prescribed burning is also considered beneficial (Edlund 1966), although it is now seldom carried out because of the high cost. On a practical scale, larch has been cultivated fairly well in northern Finland since the 1980's. In a recent study, Valkonen (1992) found that larch had a significantly higher survival than spruce and pine (fig. 3).

Potential uses of larch in the Nordic countries also include afforestation of agricultural fields and sites where competition by weeds and broad-leaved species is strong. Larch is, however, sensitive to competition from weeds, and young plantations must be cared for thoroughly. Larch can also be used as a landscape tree because it is visually pleasing.

In these circumstances there is an obvious need, in the Nordic countries, of more knowledge on cultural regimes in nurseries when producing larch seedlings for successful stand establishment. This is also the subject of a joint Nordic project that has just started.

A NORDIC LARCH PROJECT

The objective of the project, started in 1992 and running to 1994, is to study how different cultural regimes affect larch seedling development in the nursery and affect early field establishment.

The 1992 trials were focused on the hardening processes in the fall. For that reason, Siberian larch seedlings (seed from Neitsytniemi seed orchard in Finland, founded with material of Raivola provenance), all sown in April 1992 at Garpenberg, Sweden (latitude 60°15' N., longitude 16°15' E.), were treated in four ways in growth chambers during 4 weeks in August 1992. The four treatments were:

1. Unaffected daylength—16 hours/night temperature 16 °C (control)
2. Unaffected daylength—16 hours/night temperature 8 °C
3. Short days—8 hours/night temperature 16 °C
4. Short days—8 hours/night temperature 8 °C

To evaluate if these treatments had affected the seedling's hardening process, root samples from each treatment and an unfrozen control were exposed to temperatures of –2 and –7 °C, after which the electrolyte leakage from each sample was measured.

Electrolyte leakage has often been used as a measurement of plant vitality (among many references that could be cited are Colombo and others 1984; Flint and others 1967; McKay and Mason 1991). The theory is that when healthy tissue is immersed in water, free of ions, there is a slight movement of cell contents, including ions, into the surrounding water. The concentration of ions in the solution can then be detected using a conductivity meter. If

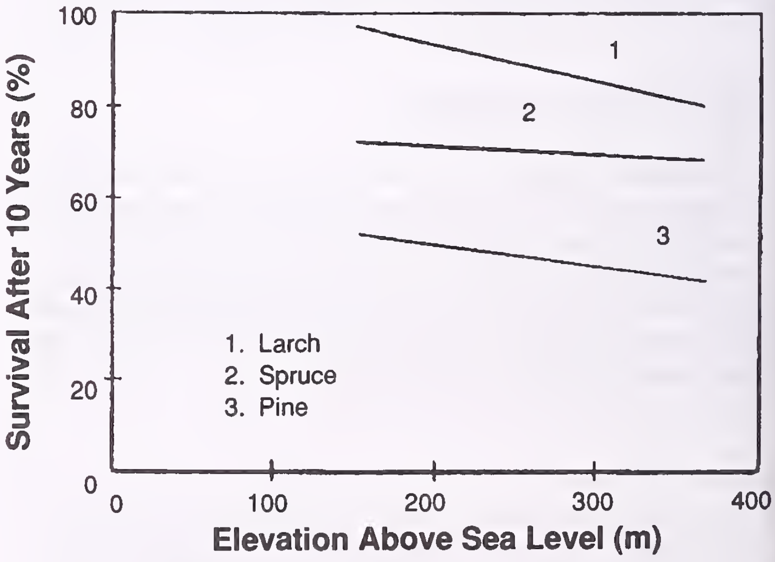

Figure 3—Survival of larch compared to spruce and pine 10 years after planting in northern Finland (Valkonen 1992).

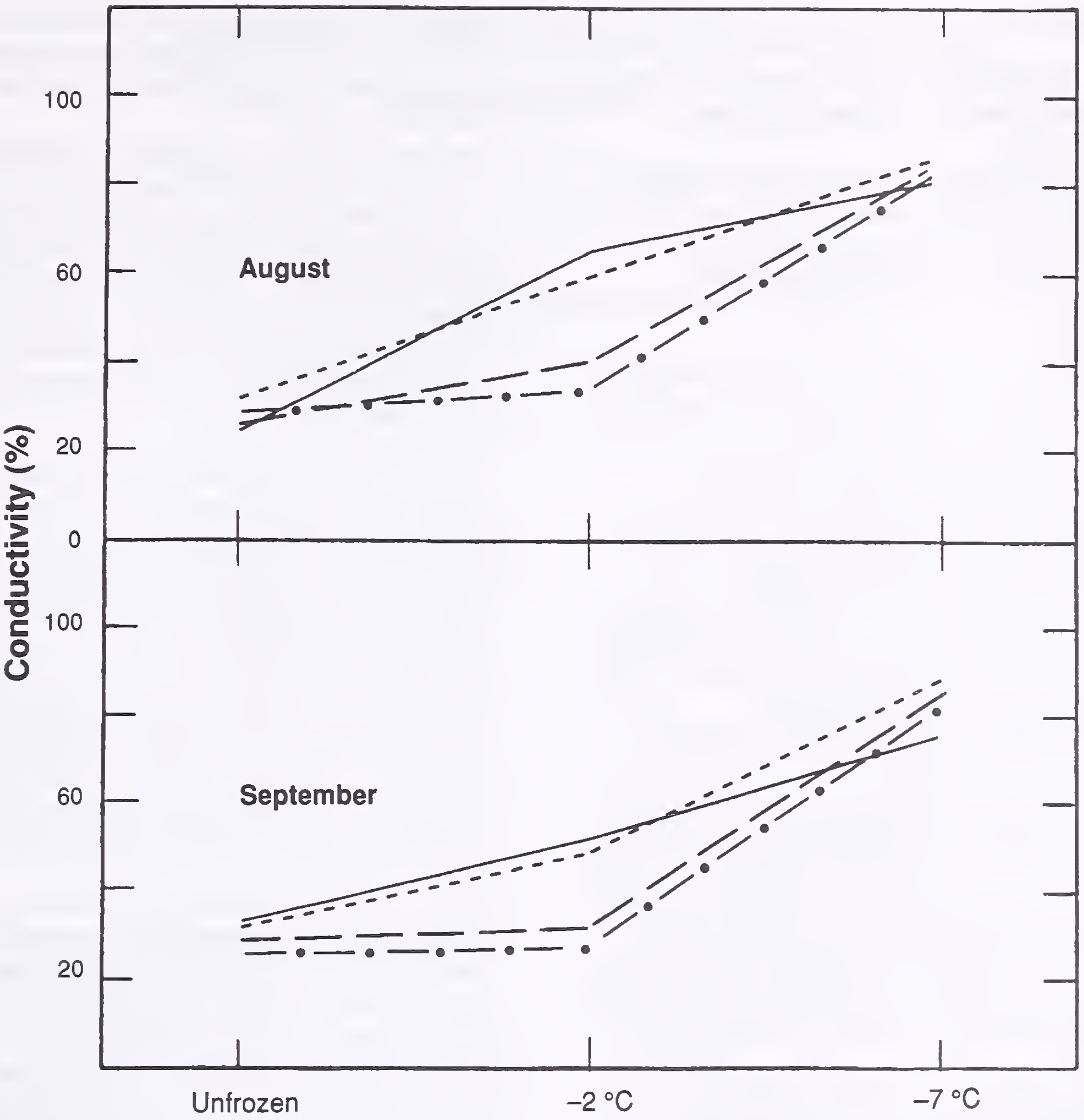

Figure 4—Conductivity (percentage) for unfrozen root samples or samples frozen to –2 or –7 °C. Samples taken from seedlings treated in four ways during 4 weeks in August 1992. —— unaffected daylength/warm nights, - - - - unaffected daylength/cold nights, — — — short days/warm nights, — • — short days/cold nights.

the cell membrane is ruptured in some way, the cell contents will leak at a faster rate, which indicates damage to the cell membrane.

The results from the conductivity measurements of the root samples are presented in figure 4. Two measurements were made, the first at the end of August 1992 (after completion of the short day and night temperature treatment), the upper graph, and the second in the middle of September, the lower graph. The relative conductivity for the given temperatures in the graphs (unfrozen samples, samples frozen to –2 or –7 °C) is calculated as the conductivity expressed as percentage of that in living tissue in relation to that in dead tissue from each treatment. In this case, the root samples were killed at the end of the test in boiling water under pressure for 10 minutes.

Preliminary results in August and September 1992 showed that when frozen to –2 °C, root conductivity from seedlings treated by short days was not affected, indicating better root hardiness for those seedlings. Furthermore, there is a tendency that short days in combination with cold nights, had a positive effect on root hardening. When frozen to –7 °C, all treatments were damaged to the same level.

Other questions focused in the project are the development of dry matter content combined with registrations of the dynamics in root growth capacity during the production phase in the nursery (compare Mattsson 1986). Field performance after outplanting of Siberian larch seedlings, grown under different nursery regimes, will also be studied during coming years.

We hope this project will contribute to better knowledge of suitable nursery regimes, aimed at producing seedlings well adapted to establish future Siberian larch stands in the Nordic countries.

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Response of Western Larch to Site Preparation

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M. F. Jurgensen
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J. R. Tonn
T. B. Jain

Abstract—Western larch (*Larix occidentalis* Nutt.) regenerates and grows adequately on a variety of soils and sites. Mineral soil and burned-over surfaces are excellent for natural regeneration, but organic surfaces also provide adequate seedbeds. Planted western larch are aggressive root producers especially in moist soils. Best development occurs in soils with high organic matter content. Competing vegetation often reduces performance. Site preparation can significantly impact growth and development of this species.

Western larch (*Larix occidentalis* Nutt.) is only one of the many larches found throughout the northern hemisphere. Larch species range from the swamp-dwelling tamarack (*L. laricina* [Du Roi] K. Koch) to the high-elevation alpine larch (*L. lyallii* Parl.). Each can play an important role in its respective forest ecosystem. As our knowledge of forest ecosystem functions and landscape level interactions and connections increases, the maintenance of all ecosystem components, including western larch, becomes increasingly important. In Northwestern United States and Southwestern Canada, western larch is an aggressive seral species that is unique in its ability to rapidly colonize sites, cycle and use nutrients efficiently, and resist attack by insects and diseases. In addition, western larch is an important commercial species. It has a showy fall foliage, and its adaptation to fire makes it an integral part of forest ecosystems in broad landscapes throughout the Inland Northwest.

Western larch grows throughout the Northern Rocky Mountains reaching its best development in southern British Columbia, Canada and in western Montana, northern Idaho, and eastern Washington, U.S.A. Some isolated populations are also found in eastern and central Oregon (Schmidt and Shearer 1990). In the center of its distribution, primarily northern Idaho, western larch is a major component in floristically rich and productive ecosystems. These ecosystems contain some of the most productive sites in the region, in terms of water, scenery, wildlife, and commercial products.

This Inland Empire portion of the western larch range coincides with the center of the western white pine (*Pinus monticola* Dougl. ex D. Don) range (Graham 1990a; Haig and others 1941). The landscape where both species occur is diverse. The topography is steep with elevations ranging from 500 to 1,800 m above sea level (Graham 1990a). It is characterized by large river valleys such as the St. Joe, Clearwater, Priest, and Coeur d'Alene. Western larch grows on all aspects and on soils derived from granite, schists, and basalts (Graham 1990a; Schmidt and Shearer 1990). Often the upper soil layers are loess or ash, important components of the soils in many of these ecosystems (Page-Dumroese and others 1991).

The climate of the Inland Empire is influenced by the Pacific Ocean to the west and by the continental air masses to the east. Summer droughts are common. Precipitation ranges from 710 to 1,520 mm, primarily occurring in the fall and winter. Average snowfall is 2,620 mm.

In the Inland Empire portion of the western larch range, the species grows in association with several other conifers making the resulting ecosystems diverse. Conifer associates range from the seral cohort lodgepole pine (*P. contorta* Dougl. ex Loud.) to high-elevation subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) (table 1). Shrub, grass, and forb competition during early successional stages can be severe. Western larch is an important component of these ecosystems because of its ability to outgrow most of its associates in the early stages of its life (Minore 1979). But if competing shrubs and conifers overtop western larch at an early age, its crown rapidly deteriorates and its vigor declines severely (Schmidt and Shearer 1990).

In the Inland Empire, western larch is a major seral component in over 19 described forest vegetation types (Cooper and others 1991). At the lower elevations these habitat types are typified by climax Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) with the understory indicator ninebark (*Physocarpus malvaceus* [Green] Kuntze). At higher elevations western larch is a major component in subalpine fir habitat types. In the center of the western larch range where the forests are the richest, most diverse, and most productive, it is a component of western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), western red cedar (*Thuja plicata* Donn ex D. Don), and grand fir (*Abies grandis* (Dougl. ex D. Don) habitat series.

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Table 1—Associated vegetation of western larch at the center of its range in the Inland Northwest of the United States (Graham 1990a)

Common name	Scientific name
Conifers	
Western white pine	*Pinus monticola*
Western hemlock	*Tsuga heterophylla*
Western redcedar	*Thuja plicata*
Douglas-fir	*Pseudotsuga menziesii*
Lodgepole pine	*Pinus contorta*
Grand fir	*Abies grandis*
Subalpine fir	*Abies lasiocarpa*
Ponderosa pine	*Pinus ponderosa*
Shrubs	
Huckleberry	*Vaccinium* spp.
Willow	*Salix* spp.
Buck brush	*Ceanothus* spp.
Rocky Mountain maple	*Acer glabrum*
Ninebark	*Physocarpus malvaceus*
Gramoids	
Sedges	*Carex* spp.
Pinegrass	*Calamagrostis rubescens*
Forbs	
False Solomon-seal	*Smilacina* spp.
Brewer's lupine	*Lupinus breweri*
Wild ginger	*Asarum caudatum*

Western larch regenerates naturally in response to forest disturbances. Historically the most common was wildfire. But during the last 100 years, forest management has excluded fire from much of the Northern Rocky Mountains, and reforestation following timber harvest has replaced fire as the primary method of regeneration. Western larch forests timber harvesting and associated slash disposal and site preparation practices can successfully regenerate, but may not benefit long-term forest development because of the destruction of organic materials.

ROLE OF ORGANIC MATERIALS IN FOREST DEVELOPMENT

Organic materials play extremely important roles in the functioning of healthy forest ecosystems. These materials protect surface soils from compaction and erosion and influence soil physical properties such as texture and water-holding capacity (Page-Dumroese and others 1991). Organic materials are important for forest nutrition, especially in the storage and release of nitrogen (Harvey and others 1987; Page-Dumroese and others 1991; Tonn and others these proceedings). In addition, organic materials are a primary site of nitrogen fixation by free living bacteria (Jurgensen and others 1991, 1992). Organic materials on the surface and in the organic rich surface mineral layers of Northern Rocky Mountain soils can provide up to 50 percent of the nitrogen fixation and over 50 percent of the nitrogen storage on some sites (Harvey and others 1987; Jurgensen and others these proceedings). Similarly, organic materials are the primary substrate for ectomycorrhizal activities in many forest ecosystems (Harvey and others 1976, 1991). Organic materials are extremely important for sustaining forests that support western larch.

WESTERN LARCH REGENERATION

Historically western larch has regenerated after wildfires by seed cast from surviving trees. Seedlings germinated and became established on mineral and burned-over seedbeds. These seedbeds were not only important for western larch regeneration but also for most of its major associates (fig. 1).

The seedbeds prepared by wildfires generally reduced the amount of organic matter on the site (Reinhardt and others 1991). Live vegetation was totally or partially destroyed; coarse woody debris on the soil surface was totally or partially destroyed as were the organic materials on and in forest soils. The amount of organic matter consumed depended on the intensity and duration of the fire and moisture content of the material burned. In most cases wildfires left a mosaic of sites containing highly diverse organic materials in a wide array of decay states and amounts.

SITE PREPARATION

The preferred seedbeds for natural western larch regeneration are burned-over surfaces and mineral soil (fig. 1). After germination and establishment western larch is susceptible to overtopping especially in the western hemlock, western redcedar, and grand fir series of habitats (Deitschman and Pfister 1973; Graham 1988). The objectives of site preparation methods developed for regenerating western larch and associates in these habitat types were to create burned-over surfaces, expose mineral soil, remove competing vegetation, and remove habitat for animals that browse seedlings.

Most methods modify the amount, arrangement, and kind of organic materials left on a site. Historically broadcast burning of logging debris was the preferred method of preparing sites for western larch. It removed competing vegetation, exposed mineral soil, and created burned-over surfaces. On many sites conditions for western larch regeneration were created by piling logging debris and scarifying the forest floor using machinery or hand methods (Graham 1990b; Graham and others 1989). If such site preparations are improperly applied they can have detrimental impacts on the organic materials on a site, which in turn can impact forest productivity (Graham and others 1992).

Shelterwoods or seedtrees, in combination with receptive seedbeds prepared through burning or machine scarification, can readily regenerate mixed stands containing western larch (fig. 2). In addition, on the western hemlock, western redcedar, and grand fir forest habitat types, a multitude of other species are also regenerated, often creating forest stands with tens of thousands of trees per hectare.

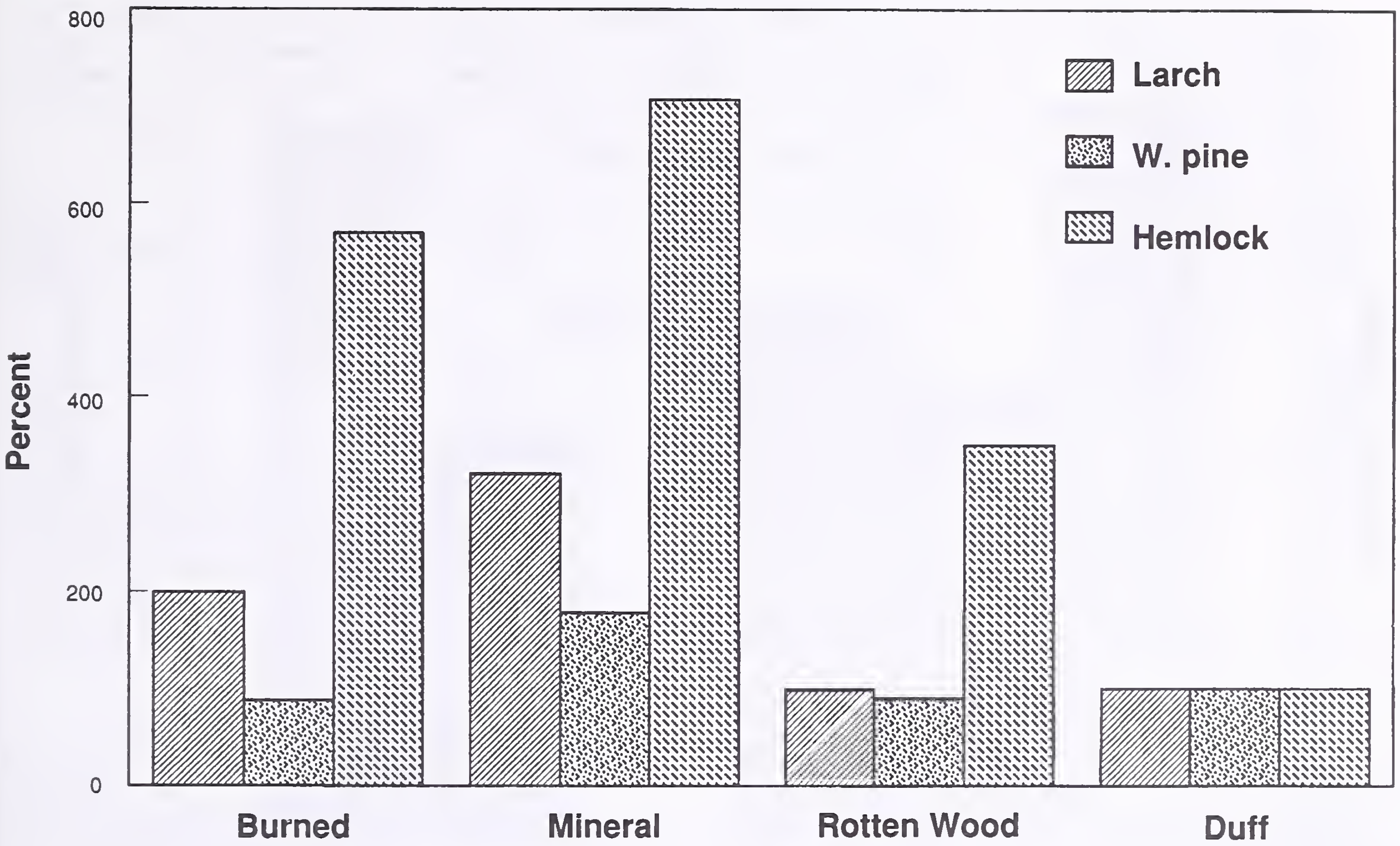

Figure 1—Germination on burned-over, natural mineral soil, and rotten wood, using the germination of typical seed-tree cuttings on duff as the comparison. Thus, germination of the three species on duff is 100 percent, and on other materials is equal, greater, or lesser than the duff germination rate (Haig and others 1941). Larch = western larch, W. pine = western white pine, Hemlock = western hemlock.

In much of the western redcedar, western hemlock, and grand fir ecosystems western larch can regenerate naturally, but because seed production is often sporadic and unpredictable, artificial regeneration is often preferred. Site preparation techniques developed for natural regeneration can be used for artificial regeneration but the need for burned-over surfaces and mineral soil exposure is minimized. For western larch to become successfully established, site preparation must create conditions that allow the species to outgrow associates that usually regenerate profusely (fig. 2) (Deitschman and Pfister 1973; Graham 1988).

ORGANIC MATERIALS AND SITE PREPARATION

Because organic materials are so important to ecosystems where western larch is a component, it is necessary to provide sites for regeneration yet conserve the surface mineral soil and the organic material of the site. If surface organic layers are displace during mechanical site preparation, the remaining soils will have higher bulk densities than minimally disturbed soils (table 2). Displacement of these surface layers also reduces the proportion of the rooting zone that is rich in organic matter. If site preparations concentrate or mound surface layers, bulk densities and organic matter concentrations are not appreciably changed compared to minimally disturbed soils, primarily because soils in the heart of the western larch range often have deep ash-cap soils with exceptional qualities that are difficult to improve (Page-Dumroese and others 1991). Even though the concentration of organic matter is not increased when surface soils are mounded, the amount of organic materials in the rooting zone is increased, making more of the rooting zone rich in organic matter. Similarly, when soil surface layers are displaced, the proportion of the rooting zone with organic materials is significantly reduced (table 2).

Organic matter is important for the maintenance of forest soil nutrition, especially the available forms of nitrogen (table 2). Nitrogen is especially susceptible to loss when the interface between the organic layers and the mineral soils exceeds 400 °C when surface organic layers are burned (Hungerford and others 1991). In the deep, ash-covered soils that often occur in western hemlock habitat types in northern Idaho, the increases in soil nutrition caused by mounding of surface layers is less dramatic than on the shallow ash layers often found on grand fir habitat types. But by displacing the rich ash-covered soils, losses in nutrients, especially available forms of nitrogen, can be significant (table 2). Minimizing losses of soil surface layers is important for maintaining soil nutritional quality.

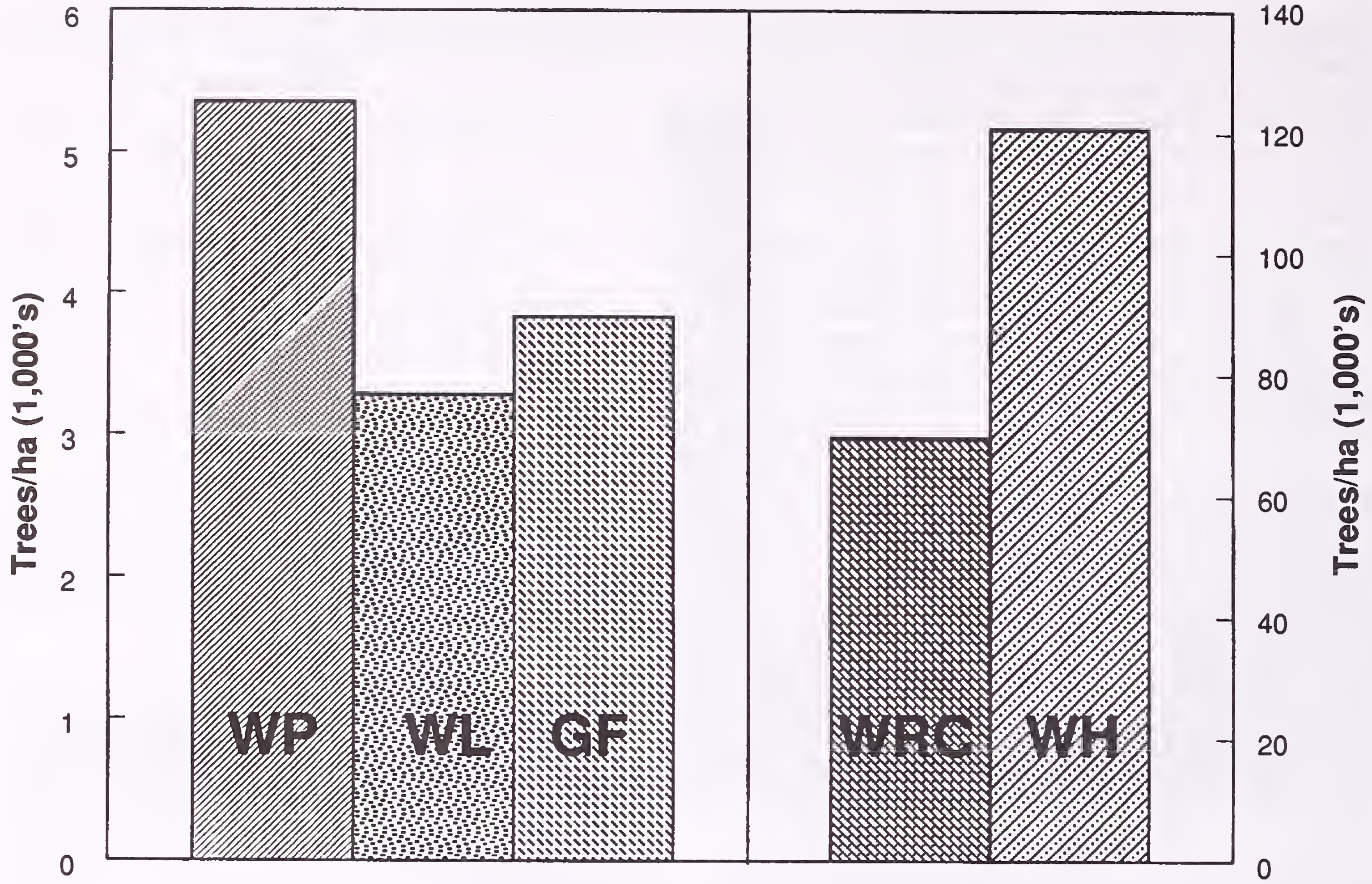

Figure 2—Seedlings germinated 6 to 8 years after timber harvesting using a shelterwood regeneration method (Haig and others 1941). WP = western white pine, WL = western larch, GF = grand fir, WRC = western redcedar, WH = western hemlock.

Western larch is an extremely aggressive seral species and appears able to concentrate nutrients even when a good proportion of site nutrients are removed. For example, when the surface layers (including much of the available nitrogen) were displaced from a site (table 2), western larch seedlings growing in these soils were still able to concentrate nitrogen (table 3). The data in the tables show how aggressive larch can be in capturing nutrients, an important attribute for renewing and sustaining forest ecosystems.

Western larch is capable of capturing nutrients from fertile mineral soil, and regenerates and grows well on

Table 2—Mean soil properties within the seedling rooting zone on a prepared site during the first growing season (Page-Dumroese and others 1986, in press)

Site preparation[1]	Organic components[2]	Organic matter	Total N	NH_4	NO_3^-	Soil bulk density
	Percent			*mg/k*		*g/cm*
			Grand fir habitat type			
Bed	[3]64.1a	17.1a	0.28a	85.5a	21.8a	0.69a
Displaced	14.2b	8.4b	.12a	8.9b	18.1a	.92b
Minimal	38.2c	12.3a	.21a	28.7ab	16.1a	.76a
			Western hemlock habitat type			
Bed	68.3a	22.1a	.46a	121.6a	18.1a	.58a
Displaced	13.4b	10.8a	.36a	75.8b	12.4a	.85b
Minimal	48.4c	27.4a	.21b	112.7a	12.8a	.65a

[1] Site preparation: Bed, bedded top soil and organic matter; Displaced, weeds and surface soil layers removed; Minimal, minimum soil disturbance.
[2] The proportion of the rooting zone containing organic materials.
[3] Different letters indicate significant ($p \leq 0.05$) differences among site preparations.

Table 3—Competing vegetation and tree characteristics for western larch seedlings planted in four site preparations

Site preparation[1]	Competing vegetation[2]	Root weight[3]	Top weight[3]	Height[4]	Root elongation[5]	Total N[6]
	kg/ha	*Grams*		*cm*		*Percent*
			Grand fir habitat type			
Bed	[7]9,192a	0.72a	3.24a	35a	16a	1.26a
Bed-herb	280b	1.39b	5.50b	44b	22b	1.26a
Displaced	684c	.77a	2.16a	29a	13a	1.00b
Minimal	3,760d	.86a	4.05b	45b	13a	1.22a
			Western hemlock habitat type			
Bed	1,711a	2.68a	9.08a	51a	24a	1.45a
Bed-herb	<50b	2.39a	8.89a	43b	25a	1.59a
Displaced	<50b	.90b	2.94b	27c	13b	1.00b
Minimal	<50b	1.05b	3.11b	31c	21a	1.21c

[1] Site preparation: Bed, bedded top soil and organic matter; Bed-herb, bedded soil treated with glyphosate; Displaced, weeds and surface soil layers removed; Minimal, minimum soil disturbance.

[2] Total ovendried root weight 2 years after planting.

[3] Total ovendried top weight 2 years after planting.

[4] Total tree height 2 years after planting.

[5] Total length of tap root plus the longest lateral after one growing season.

[6] Total tree nitrogen after one growing season.

[7] Different letters indicate significant ($p \le 0.05$) differences among the site preparations.

mineral soil substrates (Haig and others 1941; Schmidt and Shearer 1990). However, it will use and attain its best development when located in soils rich in organic matter, preferably with minimal competing vegetation (Cole and Schmidt 1986) (table 3). If the surface organic layers are removed when removing the competing vegetation there is no improvement in seedling performance (table 3). If competing vegetation must be removed during site preparation it should be done with minimal destruction to the forest floor and surface mineral layers. An excellent method of removing competing vegetation, yet retaining organic materials, is through the use of herbicides (table 3). But since herbicides may not be acceptable, other means of removing competing vegetation and retaining organic matter are often used.

Both mechanical methods and fire can be employed to remove competing vegetation and prepare sites for either natural or artificial regeneration. Ideal slash-burning conditions are achieved when the forest floor and upper mineral soils contain enough moisture to prevent destruction of the humus layer and soil wood, not damage the surface mineral layer, and yet remove most of the competing vegetation. These conditions usually exist when lower duff moisture content exceeds 100 percent. At 100 percent moisture content the interface between the organic layers and the mineral soil during burning will usually not exceed the 400 °C threshold. The ability to achieve this objective is also dependent on fuel loadings and moisture contents, forest floor depth, and weather during the burn (Reinhardt and others 1991).

TREE DEVELOPMENT

Root elongation and seedling growth are responsive to soil organic matter, as is height. Western larch tree growth continues to respond to the presence of soil organic matter as trees approach sapling size. By the time western larch reaches 2 m the effects of competing grasses and shrubs are minimal, but differences in tree size caused by early growth soil conditions are still evident (table 4). Impacts of the removal of soil organic matter are likely long lasting and continue to affect tree growth beyond the sapling stage (table 4).

Soil organic materials likely continue to be important to development of western larch as trees mature. Large differences can be projected for the development of western larch based only on the different levels of organic matter available and level of competition. If the impacts of removing surface organic layers rich in organic matter are short lived (gone by the time the trees reach 7.6 cm in diameter), a 4 to 6 percent reduction in total stand yield at age 100 years, will occur. In contrast, removing organic layers can reduce stand yields by 21 to 27 percent if effects of removal last the life (100 years) of the stand (table 4).

Similarly, if organic materials are enriched **and** competing vegetation is controlled, a 5 to 11 percent increase can be projected over the short term. If these benefits are long lived a 63 to 70 percent increased yield can be projected. These projections show the magnitude of increase or decrease that might be achieved with the manipulation of surface organic layers and competing vegetation. Each site and stand may react differently, but the magnitude of the likely changes are significant.

CONCLUSIONS

Because organic materials are important for the development and maintenance of Northern Rocky Mountain western larch forests, all management practices, should be carefully evaluated, in particular site preparations that involve the manipulation of organic materials in forest ecosystems. Western larch is an opportunistic species, regenerating well in a wide variety of forest conditions, including poor ones. However, it reaches best development in soils rich in organic matter with minimal competition.

Table 4—Tree descriptions at 8 years after planting and growth projections to age 100 years using the prognosis model (Wykoff and others 1982)

	Age 9 years	Age 100 years						
		Short-term[1]			Long-term[2]			
Site preparation[3]	Mean height	Mean diameter	Mean height	Total volume	Mean diameter	Mean height	Total volume	Calibration factor[4]
	------- cm	-------	m	m^3/ha	cm	m	m^3/ha	
				Grand fir habitat type				
Bed	161.5	30.7	35.1	203	30.7	37.8	203	1.00
Bed-herb	201.1	33.3	37.2	262	42.2	35.1	525	1.69
Displaced	112.8	31.5	34.8	224	32.0	36.0	235	1.02
Minimal	140.2	32.5	34.4	233	35.8	40.5	323	1.26
				Western hemlock habitat type				
Bed	128.0	36.8	52.4	326	38.4	40.2	384	1.12
Bed-herb	192.0	36.6	41.2	325	40.1	41.5	433	1.23
Displaced	106.7	35.6	37.5	289	31.5	37.5	201	.78
Minimal	128.0	36.6	38.4	309	34.0	38.7	254	.88

[1] The growth rate established by assuming the 5-year height increment of these seedlings slowly attenuates to the average growth rate for the site (calibration of 1.00) by the time the trees reach 7.6 to 12.7 cm in diameter.

[2] The growth rate established by assuming the 5-year height increment is maintained for the 100 years of the projection.

[3] Site preparation: Bed, bedded top soil and organic matter; Bed-herb, bedded soil treated with glyphosate; Displaced, weeds and surface soil layers removed; Minimal, minimum soil disturbance.

[4] Calibration factor from the prognosis model. This is the multiplier used to establish growth rates in the model. A factor of 1.00 indicates that the trees are growing at the rate established for that specific site defined by location, slope, aspect, and habitat type in the model.

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Natural Regeneration and Early Height Development of Western Larch in Subalpine Forests

Carl E. Fiedler

Abstract—Probabilities of western larch stocking following clearcutting were developed for nine habitat type/site preparation combinations in Montana's subalpine zone. The probability that a 1/300-acre plot was stocked with an established (≥3 years old) larch wildling varied from 0.03 to 0.34. Stocking varied inversely with elevation and grass/sedge cover, and was significantly higher on scarified and broadcast burned seedbeds than on untreated ones. Predicted heights varied from 0.3 ft at age 3 to 10.4 ft at age 12.

Western larch (*Larix occidentalis* Nutt.) is a preferred species in the Northern Rockies because of its desirable wood qualities, rapid growth, and pest resistance. Historically, this shade-intolerant species regenerated following stand replacement wildfires. Since the inception of timber harvest in subalpine forests, however, clearcut or seed tree methods have been used almost exclusively to regenerate the mature, mixed conifer forests of which larch is a part.

Because of management interest in maintaining larch as a component in second-growth stands, this study was designed to develop estimates of larch stocking probabilities following clearcutting. Managers need information on which combinations of habitat type and seedbed provide a relatively high (or low) probability of natural regeneration, as well as quantitative estimates of stocking probabilities.

Two factors defined the general focus of this study: (1) National Forest Management Act (NFMA 1976) requirements for adequate stocking of cutovers within 5 years of harvest, and (2) lack of reliable means for estimating the probability of natural regeneration for common habitat type/seedbed combinations. More specifically, the objectives of this study were:

1. To estimate the probability of larch stocking 5 years after clearcutting for nine habitat type/seedbed combinations in the subalpine zone.
2. To develop a height/age curve for young western larch growing in the subalpine zone.

Previous regeneration research in subalpine forests provided valuable information concerning important variables to be included in this regeneration study. Site preparation method, elevation, aspect, slope, grass/sedge cover, forb cover, shrub cover, and time since disturbance have been documented as important variables relative to natural regeneration establishment in studies conducted by Lowdermilk (1925), Barr (1930), Stahelin (1943), Muri (1955), Smith (1955), Day (1963), Roe and Schmidt (1964), Roe and others (1970), Noble and Alexander (1977), and Fiedler and others (1985), among others.

STUDY AREA

The study was conducted within the subalpine zone west of the Continental Divide in Montana. Major tree species in this zone are Engelmann spruce (*Picea engelmannii* Parry), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), lodgepole pine (*Pinus contorta* Dougl.), western larch, and Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco). Study sites were located on the Bitterroot, Flathead, Kootenai, and Lolo National Forests, and the Flathead Indian Reservation. Sampling locations were confined to the lower subalpine forest, and ranged in elevation from 3,700 to 6,800 ft. The lower subalpine habitat types are those generally warm enough to support western larch and Douglas-fir. Sampling was further restricted to the following three habitat types (Pfister and others 1977): *A. lasiocarpa/Clintonia uniflora* (ABLA/CLUN) h.t., *A. lasiocarpa/Menziesia ferruginea* (ABLA/MEFE) h.t., and the *A. lasiocarpa/Xerophyllum tenax* (ABLA/XETE) h.t., *Vaccinium globulare* phase. These three types compose a significant portion of the forest land classified within the lower subalpine forest zone (Fiedler 1990).

METHODS

The approach used in this study was to sample previously treated stands that met certain study criteria. This retrospective approach was an efficient and inexpensive way to study regeneration over a range of conditions, since a 10- to 15-year waiting period was not required before results could be observed.

The pool of potential sampling locations was comprised of stands that met the following criteria: (1) classified within the ABLA/CLUN, ABLA/MEFE, or ABLA/XETE h.t.'s, (2) clearcut between the years 1963 to 1973, and (3) regenerating naturally. Candidate stands were cross-categorized by habitat type (ABLA/CLUN, ABLA/MEFE, ABLA/XETE) and site preparation method (none, scarify, burn) and placed into one of nine categories (for example, ABLA/CLUN-NONE, ABLA/CLUN-SCAR, ABLA/CLUN-BURN, ..., ABLA/XETE-BURN). Sampling sites (stands) were then randomly selected from each of the nine habitat type-seedbed combinations. A 1/300-acre plot, rather than the stand, was the actual sampling unit. However,

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the stand did provide reliable records on several variables of interest (for example, habitat type, site preparation method, year of harvest, year of site preparation), and thereby served as an efficient means of selecting locations to sample.

Field Methods

Sampling was restricted to the ABLA/CLUN, ABLA/MEFE, and ABLA/XETE h.t.'s because these three types account for a large proportion of the timber harvest in the *A. lasiocarpa* series. A 10-year period was selected for the purpose of encompassing a wide range of seed years and weather conditions. The effects of insects, disease, soils, and stand history were assumed to be represented without bias because of the random sampling procedure.

The following information was recorded for each sampling location: (1) identification: national forest, ranger district, compartment, subcompartment, and stand number (or BIA equivalent); (2) site description: habitat type, aspect, slope, and physiography; and (3) date of regeneration cut, date and kind of site preparation, and date of regeneration inventory.

Aerial photographs and contour maps were used to identify areas with similar characteristics of slope, aspect, elevation, topographic position, and site preparation within each stand. Transect lines were then drawn on photographs to encompass as much variation in these variables as possible, since the objective was to sample a range of environmental conditions rather than the stand itself. Circular 1/300-acre (6.8 ft radius) plots, the basic experimental units, were then located at equal intervals along transect lines. Each plot was assigned to one of the nine habitat type/site preparation categories based on its respective attributes.

The following site condition, seed source, seedling, and undergrowth vegetation variables were recorded for each 1/300 acre plot.

Site Conditions—The habitat type for each plot was determined using the Montana habitat type classification system (Pfister and others 1977). Site preparation method was classified as "none", "scarify", or "burn", based on the treatment representing the greatest portion of the plot surface. Plots that showed no evidence of seedbed disturbance were classified as "none". Plots that were mechanically disturbed, whether in the logging process or as a postharvest treatment, were classified as "scarified". Plots that had been burned, whether as a result of broadcast, windrow, pile, or jackpot burning, were classified as "burn". Time since treatment was defined as years since site preparation for plots that were scarified or burned. For undisturbed (none) plots, time since treatment equaled the years since harvest. Aspect was measured to the nearest 10°. Slope was measured in percent. Elevation was recorded to the nearest 100ft.

Seed Source Location—Distance was estimated and vertical angle was measured to the upper crown of the nearest visible seed source in each of four quadrants (uphill, downhill, 90° clockwise from uphill, and 90° clockwise from downhill).

Seedling Characteristics and Stocking Status—Sampling was restricted to subsequent seedlings that were ≥3years old, not counting the current year. Haig and others (1941) reported that trees ≥3 years old have a high probability of survival until competition from the developing stand becomes an active factor. A plot was considered stocked if it had one or more established (≥3 years old) western larch seedlings. Seedling height was measured to the nearest 0.1 ft, not counting the current year's growth. Total age was determined by cutting the tree at groundline and counting annual rings.

Competing Vegetation—The principal shrub, forb, and grass/sedge species were recorded for each plot, along with ocular estimates of the percentage of shrub, forb, grass/sedge, and total cover.

Data Analysis

Different methods of data reduction and analysis were used to achieve the two primary study objectives: (1) to estimate the probability of western larch stocking, and (2) to develop a height/age model for young western larch (ages 3 to 12 years).

Probability of Stocking—The primary emphasis in this analysis was to develop explanatory models that would be useful in interpreting the relative importance of site and treatment variables previously determined to be important in natural regeneration establishment. The specific objective of this analysis was to model the probability of stocking of a 1/300-acre plot for nine habitat type/site preparation combinations. Stocking at the plot level is a dichotomous random variable (1 or 0), since a plot is either stocked (1) with one or more established seedlings, or it is not stocked (0). Probability of stocking was assumed to be related to the independent variables described earlier. Habitat type and site preparation method were categorical variables in the analysis; ABLA/XETE was the reference variable for habitat type, and no treatment (NONE) was the reference variable for site preparation method.

Logistic regression was used to describe the relationship between the probability of stocking, p, and the explanatory variables. Hence the logistic regression model is

$$\text{Equation 1} \qquad \ln \frac{p}{1-p} = \beta_0+\beta_1 X_1+\beta_2 X_2+\ldots+\beta_n X_n$$

where the X_i' s are explanatory variables, and the B_i's are coefficients to be estimated. The probability of stocking for a set of explanatory variables is given by

$$\text{Equation 2} \qquad p = \frac{1}{1 + e^{-(\beta_0+\beta_1 X_1+\beta_2 X_2+\ldots+\beta_n X_n)}}$$

A variable was included in the logistic regression model only if the likelihood ratio statistic associated with that variable was statistically significant (P-value ≤0.05); that is, addition of the variable had to significantly reduce residual variation about the regression.

The fitted model was then used to estimate the probability of larch stocking for a 1/300-acre plot for each of the nine habitat type/site preparation categories. The model was evaluated at the mean time since treatment so that predicted stocking could be compared to observed stocking. For each category, the fitted model was evaluated using means for the continuous variables from that category. For example, the stocking estimate for the ABLA/CLUN-SCAR category was made using the sample means of observations in the ABLA/CLUN h.t. with site preparation "SCAR".

Height/Age Models—Total height and total age data from western larch seedlings were analyzed in two ways. In the first approach, linear regression methods were used to develop a simple height/age model. The square root transformation of the dependent variable, height, was required to stabilize the variance, and to linearize the concave-shaped relationship of height and age.

In the second approach, multiple regression methods were used in an attempt to explain additional variation about the simple (height/age) regression model. The primary objective was to determine if site, treatment, and vegetation variables were significant predictors of tree height. The square root of total height was again the dependent variable and, in addition to age, independent variables were selected from habitat type, site preparation method, elevation, aspect, slope, grass/sedge cover, forb cover, and shrub cover. Categorical variables (that is, habitat type and seedbed) were represented by indicator variables, with XETE as the reference variable for habitat type, and NONE as the reference variable for site preparation method. An F-test (0.05 significance level) was used to determine which explanatory variables were included in the final model.

RESULTS AND DISCUSSION

Probability of Stocking

The probability of stocking for each of the nine habitat type/site preparation combinations was estimated using a single equation.

The first phase of the stocking analysis was aimed at modeling the relationship between site, treatment, and vegetation variables and stocking of western larch.

Elevation, grass/sedge cover, and site preparation method were the only significant explanatory variables in the probability of stocking model (table 1). The functional form of the model is displayed in table 2.

Western larch stocking showed a significant (*P*-value ≤0.001) negative relationship with elevation. The distribution of this species extends down to the lowest elevations found in western Montana, approximately 2,000 ft, well below the lowest elevation (3,700 ft) sampled in this study. However, the upper range of western larch is about 6,500 ft (Habeck 1967), slightly below the highest elevation (6,800 ft) sampled. In this study, no western larch seedlings were found above 6,200 ft. The upper altitudinal limit of trees in the Rocky Mountains has been shown to be related to low temperature (Daubenmire 1943; Pearson 1920). Consequently, a negative relationship between stocking and elevation would be expected with a move from the middle to the upper limit of this species' altitudinal range.

Table 1—Western larch stocking model. Analysis of deviance table. Final model is model D.

Model	Deviance	DF	Li. ratio stat.	DF	*P*-value
A: intercept	875.967	894			
B: A + elev	730.219	893	145.748	1	0.0000
C: B + grass	699.910	892	30.309	1	0.0000
D: C + site prep	685.618	890	14.292	2	0.0008

Table 2—Functional form of the estimated logistic regression model for western larch.

$$\ln [p/1-p] = 7.4724-0.1846\ (ELEV)-0.0286\ (GRASS) + 1.3465\ (SCAR) + 1.0420\ (BURN)$$

where:
ELEV = elevation, in hundreds of feet
GRASS = grass/sedge cover, in percent
SCAR = 1 if site preparation is scarification
SCAR = 0 otherwise
BURN = 1 if site preparation is prescribed burning
BURN = 0 otherwise

Habitat type was evaluated early in the process of developing a probability of stocking model for western larch. Initially, it came in as an extremely important explanatory variable (*P*-value ≤0.0001). However, habitat type did little to reduce the deviance after elevation was introduced into the model, indicating the strength of the relationship between larch stocking and elevation within the altitudinal range (3,700 to 6,800 ft) sampled in this study. When habitat type was included without elevation in the model, stocking of western larch was significantly higher on the ABLA/CLUN h.t. than on the ABLA/XETE h.t. The ABLA/XETE h.t. is colder, drier, and higher in elevation than the ABLA/CLUN h.t., factors which work against establishment of a species best adapted to moderately moist sites at low- to mid-elevations.

The probability of stocking for western larch was also negatively related to grass cover. This relationship is consistent with Schmidt's (1969) observation that treatments that expose mineral soil and reduce grass competition favor natural regeneration of most species, but are particularly favorable for western larch.

Stocking of western larch also showed a strong relationship with site preparation method. Stocking was significantly (*P*-value ≤0.05) higher on both scarified and burned seedbeds than on unprepared ones. Roe (1952) first pointed out the relative advantage of mineral soil seedbeds compared to undisturbed duff for western larch regeneration. Schmidt (1969) reported the significant benefit of both scarification and burning for western larch establishment through reduction of competing vegetation. Ryker (1975) also noted the importance of mineral soil seedbeds for regenerating this species.

Probability of stocking of western larch was not significantly related to time since treatment. Lack of a significant change in stocking over time indicates that the preponderance of regeneration of this shade-intolerant species occurred shortly after treatment, and did not increase measurably thereafter.

Using equation 2 and coefficients from table 2, predicted probabilities of western larch stocking were calculated for each of the nine habitat type/site preparation combinations (table 3). Stocking probability was highest on ABLA/CLUN-SCAR (0.34), and lowest on ABLA/MEFE-NONE (0.03) and ABLA/XETE-NONE (0.03). Observed stocking was also calculated for each habitat type/site preparation combination by dividing the actual number of stocked plots by the total number of plots. For comparative purposes, both predicted and observed stocking are presented in table 3.

Height/Age Relationships

Two types of height models were developed for western larch between 3 and 12 years of age. First, a simple height/age model was developed which can be used to compare predicted heights of naturally-regenerated larch seedlings from this study with estimates for other species or artificially-regenerated larch.

Second, a multiple regression model was developed from the same set of explanatory variables used in the probability of stocking analysis. Habitat type, site preparation method, elevation, aspect, slope, grass/sedge cover, forb cover, and shrub cover were evaluated in addition to age for significant relationships with height.

The functional form of the simple regression of square root height on age for western larch is presented in table 4. The regression was highly significant ($F = 758.4$, P-value ≤ 0.001), with $R^2 = 0.753$, and s.e. = 0.434 ft (table 4). The graph of the estimated height/age relationship is shown in figure 1 (regression of square root height on age transformed to original units). The height/age curve for western larch reflects the rapid early growth previously reported for this species (Schmidt 1969; Shearer 1982). Predicted mean height for western larch at age 3 and age 12 ranged from 0.3 ft to 10.4 ft, respectively.

Only age and elevation were significant explanatory variables in the multiple regression height model for western larch (table 5). The functional form of this model is also shown in table 5. Another height model for young (<20 years old), naturally-regenerated western larch was developed by Ferguson and others (1986). They found no significant relationship between height and elevation for western larch in the grand fir-cedar-hemlock forests of the Northern Rockies. However, larch is well within its range at the low elevations which characterize the grand fir-cedar-hemlock ecosystem, whereas it reaches the upper limits of its range in the ABLA/XETE h.t. (Pfister and others 1977) and in colder portions of the ABLA/MEFE h.t. (Arno and others 1985) in the subalpine zone. Consequently, a negative relationship between height and elevation would be expected for western larch in the subalpine zone.

Table 3—Predicted and observed western larch stocking for nine habitat type/site preparation combinations.

Habitat type/site preparation combination	Probability of 1/300-ac plot stocking	
	Predicted	Observed
ABLA/CLUN—NONE	0.09	0.16
ABLA/CLUN—SCAR	0.34	0.37
ABLA/CLUN—BURN	0.23	0.28
ABLA/MEFE—NONE	0.03	0.00
ABLA/MEFE—SCAR	0.10	0.09
ABLA/MEFE—BURN	0.05	0.04
ABLA/XETE—NONE	0.03	0.00
ABLA/XETE—SCAR	0.10	0.19
ABLA/XETE—BURN	0.04	0.09

Table 4—Simple model for regression of square root height on age for western larch between 3 and 12 years old.

$$\text{Height}^{0.5} = -0.298 + 0.293\ (\text{AGE})$$

Observations	= 249	Degrees of freedom	= 247
Adj. R-squared	= 0.753	Std error of est	= 0.434
Residual SS	= 46.514	F (2,247)	= 758.4
Total SS	= 189.339	P-value	= 0.000

Variable	Coef	Std. Error	t-Stat	P-Value
CONSTANT	−0.298	0.073	−4.087	0.000
AGE	0.293	0.011	27.539	0.000

The relationship of height with elevation was assessed at the mean age of 6 (rounded to the nearest full year) and near the lower (4,000 ft) and upper (6,000 ft) elevational range at which this species was found in the subalpine zone. Predicted mean height ranged from 2.3 ft at 4,000 ft elevation to 1.6 ft at 6,000 ft elevation.

Based on work conducted in western Montana by Schmidt (1969), heights of western larch on scarified and burned seedbeds would be expected to significantly exceed those on untreated seedbeds. However, the relationship of western larch height with site preparation method was not evaluated in this study due to the small sample size on untreated (NONE) seedbeds.

SUMMARY

Traditionally, studies of natural regeneration report regeneration stocking or density (or relative differences in these measures) on a case study basis. In contrast, this study provides quantitative estimates of regeneration probabilities for common habitat type/site preparation combinations over a broad geographic range. It also provides

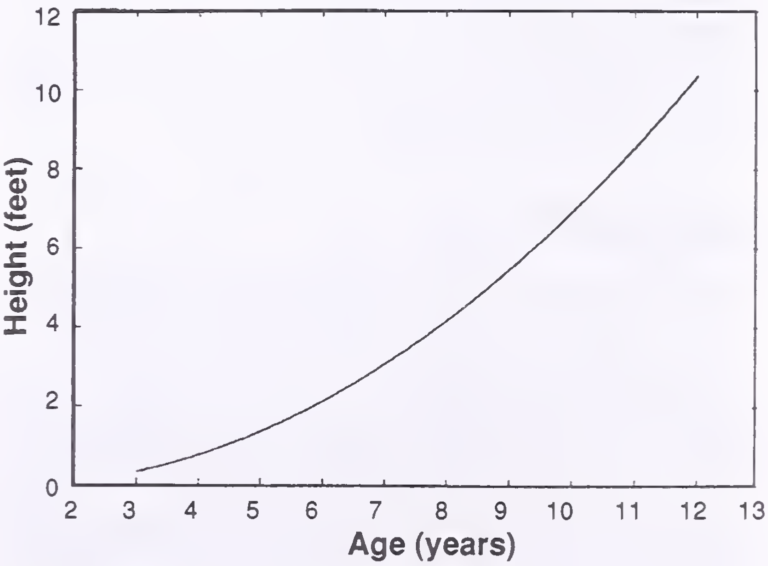

Figure 1—Estimated height/age relationship for western larch between the ages of 3 and 12 years in Montana's subalpine zone.

Table 5—Western larch. Final model for regression of square root height on explanatory variables.

Height$^{0.5}$ = 0.287 + 0.286 (AGE) – 0.012 (ELEV)

Observations = 249 Degrees of freedom = 246
Adj. R-squared = 0.758 Std error of est = 0.429
Residual SS = 45.378 *F* (3,246) = 390.2
Total SS = 189.339 *P*-value = 0.000

Variable	Coef	Std. error	t-stat	P-value
CONSTANT	0.287	0.247	1.164	0.244
AGE	0.286	0.0108	26.510	0.000
ELEV	–0.012	0.005	–2.482	0.013

the means to assess how changes in variables significantly associated with stocking affect stocking probabilities.

Although western larch is a preferred species for post-harvest establishment in subalpine forests, natural regeneration of this species following clearcutting is far from assured. Results from this study indicate that the probability of larch stocking on a 1/300-acre plot is approximately 0.25 or greater for only two habitat type/site preparation combinations (ABLA/CLUN-SCAR; ABLA/CLUN-BURN), and less than 0.10 for five combinations (ABLA/CLUN-NONE, ABLA/MEFE-BURN, ABLA/MEFE-NONE, ABLA/XETE-BURN, ABLA/XETE-NONE).

Probability of larch stocking was also significantly related with elevation and percent grass/sedge cover, and decreased with both. Larch stocking was not significantly related to time since treatment, indicating that few seedlings of this species continue to filter in over time.

A height/age model developed for western larch in the subalpine zone shows that growth is slow for the first several years, but increases rapidly, reaching an average of 10.4 ft by age 12. This species required an average of 8 years to reach breast height (4.5 ft; 1.37 m).

Results of this study indicate that scarification provides the highest probability of obtaining larch regeneration after clearcutting on the ABLA/CLUN, ABLA/MEFE, and ABLA/XETE habitat types. However, probability of stocking is considerably less than 0.50, even on the habitat type/site preparation combination (ABLA/CLUN-SCAR) most favorable for larch establishment. This study also found that even with scarification, planting will commonly be needed if larch is desired as a significant stand component on regenerating cutovers classified within the ABLA/MEFE and ABLA/XETE habitat types.

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Vegetative Propagation of Western Larch

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Abstract—Western larch (*Larix occidentalis* Nutt.) timber has high commercial value, but infrequent cone crops hamper regeneration of the species. Vegetatively propagated larch might furnish planting material. This paper reviews the rooting of stem cuttings, describes a micropropagation method to increase the multiplication yield from axillary buds, and reports some aspects of steckling growth habit relevant to artificial regeneration. Shoot-tip cuttings rooted at high rates, so mass propagation of juvenile western larch from limited seed sources seems feasible. However, steckling quality must be improved.

As vegetative propagation continues to gain importance in the regeneration of certain forest and range plants, the increasing number of vegetatively propagated forest tree species expands the potential of clonal forestry (Ritchie 1991; Zobel 1992). Furthermore, when seed shortages occur, vegetative methods may help to increase the number of species used in native plantings and to conserve threatened populations (Fay 1992; Morgenson 1992; Wagner and others 1992).

One example is the problem of infrequent cone crops that hamper regeneration of western larch (*Larix occidentalis* Nutt.) in northern Idaho (Shearer 1991). Western larch, a timber of high commercial value, grows in the coniferous montane forests of the interior Pacific Northwest of North America (Preston 1976). To meet production goals, northern Idaho nurseries have sown western larch seed from sources several hundred miles away from planting sites. Local gene pools are depleted when natural regeneration fails after harvest and artificial regeneration occurs with off-site seedlings. As a partial remedy, vegetatively propagated larch could furnish an alternative supply of planting material and maintain local genetic diversity.

MAJOR PROPAGATION METHODS

Macropropagation of many conifer species has occurred after harvesting physiologically suitable branch tips from healthy ortets, treating the freshly severed cuttings with fungicide and rooting hormones, placing the cuttings into a well-drained medium, and avoiding water stress while rooting (Wise 1992).

Micropropagation techniques offer alternative opportunities to increase plant numbers, although many gymnosperms multiply less readily than angiosperms (Cheliak and Rogers 1990). The in vitro methods include proliferation of shoots from existing axillary meristems, organogenesis of adventitious buds from juvenile tissue, and induction of somatic embryoids (Schwarz 1992).

Larch Propagation

Propagators have rooted 77 percent of the semihardwood cuttings of tamarack (*Larix laricina*) from 3- to 6-year-old seedlings (Morgenstern 1987), 85 to 95 percent of 0.5-year-old softwood tamarack cuttings (Farmer and others 1986), 73 to 99 percent of softwood cuttings of hybrid larch (*Larix* x *eurolepis*) (John 1986), and up to 100 percent of Japanese larch (*Larix leptolepis*) from 5- to 8-year-old trees (Wunder 1974).

In terms of macropropagation of western larch, Andrews (1980) reported 10 percent overall rooting of the branch cuttings from 50-year-old ortets (with up to 70 percent rooting of the best clone). However, Staubach (1983) and Jaquish (1987) achieved higher overall rooting rates of 40 to 80 percent with 2-year-old and 1.5-year-old ortets, respectively. Eggleston (1991) described difficulties in propagating branch cuttings, and Edson and others (1991) compared the rooting of softwood and semihardwood cuttings after treatment with indolebutyric acid (IBA).

In terms of micropropagation, using embryonic tissue, propagators have regenerated western larch by organogenic and embryogenic pathways. Harry and others (1991) developed a comprehensive protocol to produce plantlets by inducing adventitious shoots on mature embryo tissue. Thompson and von Aderkas (1992) initiated somatic embryoids from immature embryos and established plantlets ex vitro. In contrast, using mature tissue, Chesick and others (1990) induced multiple adventitious buds from 20-year-old buds and stems.

Growth and Form of Rooted Cuttings

Several studies have reported differences of growth rate and habit developed by stecklings (plantable rooted cuttings) and seedlings of some conifer species (Foster and others 1987; Frampton 1992). However, for useful forest regeneration, a vegetatively propagated stock type must survive and grow as efficiently as seedlings.

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This paper reviews our rooting of juvenile western larch cuttings, describes a micropropagation method using axillary buds to increase the multiplication rate, and reports some aspects of steckling growth habit relevant to artificial regeneration.

METHODS AND MATERIALS

Rooting Cuttings

The cuttings were harvested from 1.5-year-old ortets grown from wild seed collected in the Panhandle National Forests of northern Idaho. We conducted six rooting trials in 1988 and 1989 (table 1). Softwood cuttings, consisting of 10- to 15-cm green-stemmed, first-order branch tips, were collected from early to late June 1988. Semihardwood shoots were harvested from mid-July to early September 1988 and in August 1989. The lowermost 3 cm of each stem was defoliated and soaked for 30 seconds in an aqueous suspension of 0.1 percent benomyl. The cuttings were then immediately randomized to two or more IBA treatments (0, 1,000, 3,000, 8,000, 16,000, or 30,000 ppm), inserted in a peat-perlite-vermiculite rooting medium (1:2:3 parts by volume), maintained at 20 to 24 °C, and rooted under intermittent mist in 30 percent shade.

The experiments were randomized block designs. Data were the proportions of rooted and nonrooted cuttings. The analysis used a logistic regression model in a SAS® CATMOD procedure, which estimated parameters by the maximum likelihood method. Likelihood ratios greater than the 0.05 level indicated a satisfactory goodness-of-fit test for the model. Mean separations were obtained by analysis of variance (ANOVA) of the normalized rooting proportions and Fisher's protected LSD at the 0.05 level. We measured caliper (stem diameter) at the base of each cutting and correlated the counts of each size class with rooting success by maximum likelihood log linear analysis. We subjectively assessed root quality by noting position and direction of root emergence.

Table 1—The mean rooting percentage of softwood and semihardwood western larch cuttings after treatment with IBA (Edson and others 1991)

Treatment	Treatment dates					
	Softwood			Semihardwood		
IBA (ppm)	6/6/88	6/30/88	8/3/89	8/28/88	9/6/88	9/20/88
0			44.0a[1]	35.6a		45.9a
1,000	12.0a	17.5a		38.9a	34.1a	
3,000				51.3b		
8,000	7.1b	9.6b	56.0b	51.2b	70.4b	65.7b
16,000			72.0c			
30,000			76.0c			
Mean	9.6	13.6	62.0	44.3	52.3	55.8
P-values	.01	.02	.001	.01	.01	.002
Likelihood	.69	.50	.55	.62	.72	.64
No. cuttings	1,148	560	400	304	332	324
No. ortets	300	150	100	75	75	75
Cuttings/blk	286	140	100	76	83	81

[1] Means with the same letter in a given test are not significantly different as determined by Fisher's LSD at an α level of 0.05.

Micropropagation by Axillary Buds

On July 15, 1988, we severed 40 first-order branch cuttings, 10 to 15 cm long, from the upper crowns of 10, hitherto unpruned, 1.5-year-old ortets. Buds had become macroscopically visible on these sylleptic shoots ("free growth" from current year's buds). All expanded needles were removed from the shoots, and the cuttings were washed under running tap water for 2 hours, surface-sterilized for 15 minutes in an aqueous solution of 20 percent Clorox (5 percent NaOCL) containing 4 drops of Liquinox per liter, and rinsed four times in sterile deionized and distilled water.

A total of 410 excised buds were individually incubated (with bud tips oriented upward) in two blocks of 25- by 150-mm test tubes. Each tube contained 10 mL of Schenk and Hildebrandt (1972) nutrient medium supplemented by 0.7 percent (weight/volume) Difco Bactor agar and 2 percent (weight/volume) sucrose. The tubes were then placed on shelves under cool white fluorescent lights with a photoperiod of 16 hours, light intensity of 3,000 lux, and a diurnal temperature range from 20 to 25 °C. Shoot survival and elongation were tabulated after 1 month in vitro.

Growth and Form of Stecklings

We studied two independent groups of stecklings under greenhouse conditions, group A in 1989 and group B in 1992. Although western larch seedlings normally produce a single upright leader, steckling form may vary. The leader may deviate from the vertical, or the plant may lack a clearly defined leader. Hence, we categorized leading shoots of both groups as orthotropic (upright), plagiotropic (inclined), stunted (no long shoot extension), or multiple stemmed.

Group A Stecklings—After rooting in October 1988, 300 stecklings from the rooting trials were refrigerated for 140 days at 2 °C and transplanted on April 15, 1989, to Spencer-LeMaire Hillson Rootrainers® containing a peat-perlite-vermiculite medium (1:1:1 parts by volume).

On May 1, 1989, the 300 stecklings were placed in a randomized complete block design of 60 stecklings per block at five locations in the greenhouse. Two fertilizer treatments of 50 ppm and 120 ppm nitrogen, applied as 20-20-20 N-P-K, were randomly assigned to 30 stecklings per treatment per block and applied twice weekly for 4 months. Concurrently, 300 1-year-old seedlings were treated similarly to the stecklings. The seedlings had comparable initial shoot heights of 10 to 15 cm. After terminal budset in August 1989, we measured shoot elongation of both stock types and analyzed data by ANOVA. The side-shoots of the stecklings were counted and measured.

In May 1990, we transferred 25 orthotropic stecklings and 25 seedlings to 4-L pots and placed them under greenhouse conditions. To contrast branch development of the two stock types at 4 years of age, we calculated the ratios of long-shoots to short-shoots on their leaders.

Group B Stecklings—The stecklings (originating from 3-year-old ortets) grew for 2 years at the USDA Forest

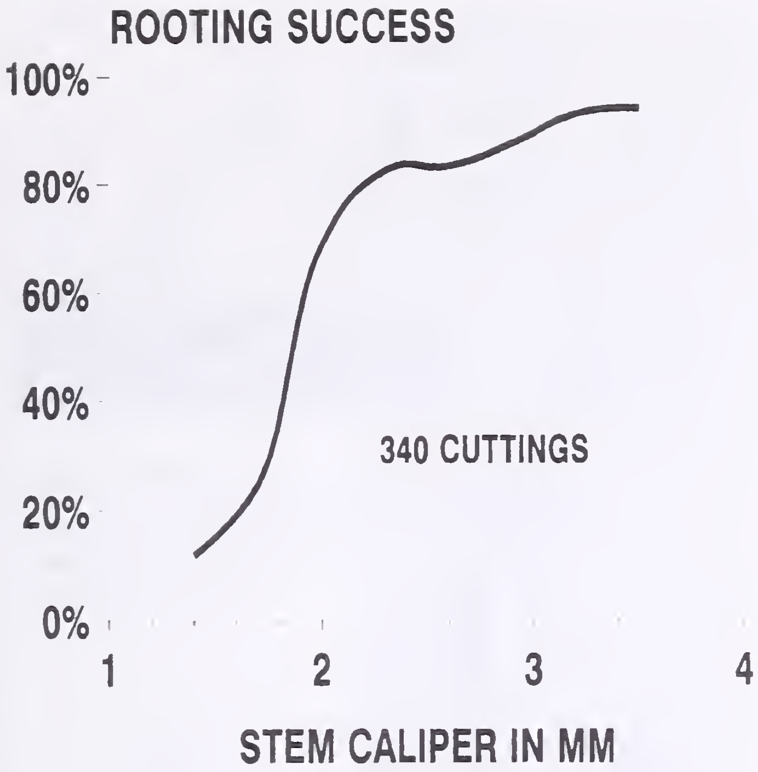

Figure 1—Percent rooting of semihardwood western larch cuttings versus basal stem caliper in millimeters.

Service Nursery near Coeur d'Alene, ID, U.S.A. During the fall of 1990, the cuttings rooted in "supercells" containing a peat-perlite-vermiculite (1:1:1 parts by volume) medium. The stecklings grew in a nursery bed during 1991, were lifted in the fall and placed in cold storage at –2 °C for 120 days. In April 1992, we transplanted 174 of these stecklings to 4-L pots in a University of Idaho Forest Research Nursery greenhouse at Moscow, ID. To maximize long-shoot development and minimize stunting, the stecklings received twice-weekly fertilizations of 20-20-20 N-P-K at 200 ppm nitrogen until September 1, 1992.

We constructed the following classes to reflect growth patterns of the main stem and its subapical shoots: (1) codominant subapical shoots with a totally suppressed main stem; (2) subapical shoots codominant with the main stem; (3) a dominant subapical shoot out-competing the main stem; and (4) a dominant subapical shoot with the main stem totally suppressed.

RESULTS

Rooting Cuttings

The softwood cuttings rooted at a mean rate of 10.9 percent after 60 days in the early summer. In contrast, 54.2 percent of the semihardwood cuttings rooted in the late summer and fall. Increasing the strength of IBA to 8,000 ppm significantly enhanced the rooting success of the semihardwood cuttings to more than 70 percent (table 1).

Root Quality—The pattern of root emergence changed after IBA treatment. Cuttings that received no hormone treatment produced a conspicuously asymmetrical root emergence pattern from the stem base. In contrast, cuttings treated with IBA levels of 8,000 ppm or higher typically developed more fibrous and symmetrical adventitious (and lateral) roots up to several centimeters above the cuttings' base. Root tips curled at 30,000 ppm IBA.

Caliper—Cuttings with caliper greater than 2.0 mm maximum diameter rooted at higher rates than those with less than 2.0 mm maximum diameter (likelihood ratio of 0.98). More than 80 percent of the semihardwood cuttings with caliper greater than 2.0 mm rooted (fig. 1).

Axillary Bud Multiplication

The cuttings taken from the sylleptic shoots of the 1.5-year-old ortets yielded an average of 10 buds per cutting. After 1 month in culture, 96 percent of the incubated buds had survived to develop shoots that averaged a mean length of 8.3 cm. However, despite the day-length extension (16 hours photoperiod) to inhibit onset of dormancy, almost 10 percent of the shoots developed a suppressed terminal bud.

Steckling Growth and Form

Leader Extension and Branch Development—Overall, the leaders of the group A (first-year growth) stecklings extended only about half of the mean length of the seedlings (table 2). The leaders of the orthotropic group B (second-year growth) stecklings developed a mean extension of 37.9 cm after fertilization with 20-20-20 N-P-K at 200 ppm N.

The group A stecklings developed fewer lateral shoots than the seedlings. Of the 150 stecklings that received 120 ppm N fertilizer, only 32 percent developed any side shoots. After 4 years of greenhouse growth, the long-shoot to short-shoot ratio on steckling main stems was 0.45 compared to 6.75 for the seedlings, a major contrast between steckling and seedling stock types (fig. 2). In addition, the lengths of many first-order (lateral) branches of both groups

Table 2—Mean leader extension and mean proportions (percentage) of branching, plagiotropism, and leaders in the 300 stecklings and the 300 seedlings after one growing season at two levels of fertilization with 20-20-20 (N-P-K)

Fertilization ppm nitrogen (20-20-20, N-P-K)	Mean growth response			
	Steckling		Seedling	
	50	120	50	120
Leader extension (cm)	3.0a[1]	11.1b	8.4b	20.6c
Branching (percent incidence of 300)	24a	32a	100b	100b
Plagiotropism (percent incidence of 300)	12a	6a	0a	0a
Suppressed leader (percent incidence of 300)	17a	11a	—	—
Multiple stems (percent incidence of 300)	11a	14a	—	—

[1] Means with the same letter in a given test are not significantly different as determined by Fisher's LSD at an α level of 0.05.

Figure 2—Differences in branch development of steckling and seedling stock types after 4 years of greenhouse culture. Left: A steckling with relatively few long-shoot branches. Right: A seedling with a high proportion of long shoots. Scale bar represents 10 cm.

Figure 3—An orthotropic group B steckling beginning its second year of growth. Scale bar represents 10 cm.

of stecklings approached or exceeded the elongation of their respective leaders.

Leader Form—Fewer than half of the stecklings produced new orthotropic leaders (fig. 3). Slightly more than a third of the stecklings initially developed a single plagiotropic leader. Moreover, we found two types of plagiotropic leaders: either the primary shoot extended in a smooth concave-down curve (fig. 4) or a lateral secondary shoot elongated at a sharp angle to a suppressed terminal shoot (fig. 5). In addition, some leaders failed to elongate (fig. 6).

Slightly lower (but nonsignificant) proportions of plagiotropic and suppressed stems occurred after fertilizing the group A stecklings at 120 ppm N versus 50 ppm N (table 2). By the end of the growing season, however, almost all of the initially plagiotropic leaders of both groups had developed an orthotropic leader (fig. 7), with the exception of a few remaining dormant or aborted plagiotropic leaders. As the number of plagiotropic stecklings declined, the number of orthotropic leaders increased. Likewise, as the number of stunted leaders decreased, the number of multiple-stemmed stecklings increased (table 3).

Almost 30 percent of the group B stecklings produced multiple leaders and shrublike forms (fig. 8). The proportions of the 53 multistemmed stecklings identified within each class of shrublike form were as follows: codominant

Figure 4—A plagiotropic steckling with an inclined leader. Scale bar represents 10 cm.

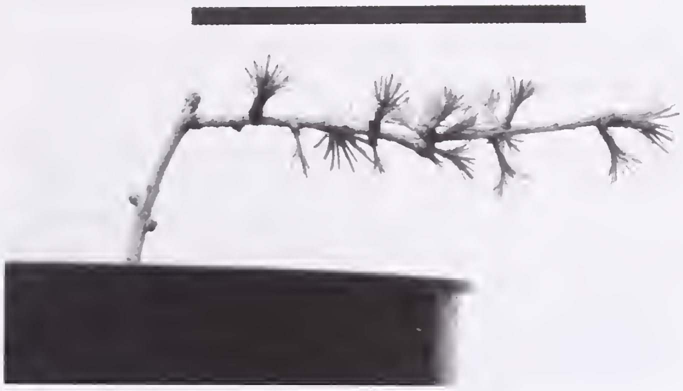

Figure 5—A plagiotropic steckling at the start of year 2 with a first-order branch extending to the right forming a secondary leader immediately below a dormant terminal bud on the primary shoot. Scale bar represents 10 cm.

Figure 6—Stunted stecklings with short terminal shoots. Scale bar represents 10 cm.

subapical shoots with a suppressed main stem (51 percent), subapical shoots codominant with the main stem (22 percent), dominant subapical shoot out-competing the main stem (14 percent), and dominant subapical shoot with the main stem suppressed (13 percent).

DISCUSSION

Rooting Cuttings

The physiological state of the cuttings likely influenced rooting success because the semihardwood cuttings rooted at a consistently higher rate than the softwood cuttings. Morgenstern (1987) reported that tamarack cuttings rooted best at a semihardwood stage of development. If the change from the softwood to the semihardwood state reflects an enhanced rooting competence in the cuttings, then the visible onset of lignification, preceded by a red coloration moving upward from the stem base, defines a useful "window" of rootability.

Because few cuttings with a basal caliper less than 2.0 mm rooted, cultural practices to enhance the diameter of the shoots before harvest would likely increase the rooting success of the cuttings. Some nurseries apply a potassium-rich fertilizer to putatively increase the caliper of containerized western larch seedlings (Wenny and Dumroese 1987). This practice may increase the caliper of ortet shoots.

Figure 7—A formerly plagiotropic steckling with a vigorous orthotropic leader. Scale bar represents 10 cm.

Steckling Production

If branch cuttings root at 80 percent, ortets would yield on average of 16 stecklings per 20 cuttings per ortet. However, many ortets were harvested three times to produce over 50 cuttings in a season. Hence, the steckling yield could potentially exceed 40 ramets per ortet.

Table 3—Changes in the mean proportions (percentage) of orthotropic, plagiotropic, suppressed, and multiple leaders from the start to the end of the growing season. The number of group A stecklings = 300, the number of group B stecklings = 174

Leader type	Group	Percent incidence May	Percent incidence October
Orthotropic (single stem)	A	40.0	64.7
	B	35.3	56.7
Plagiotropic (single stem)	A	34.2	9.0
	B	42.5	13.3
Suppressed (no long shoots)	A	24.4	13.8
	B	19.5	0.6
Multiple stems	A	1.4	12.5
	B	2.7	29.4

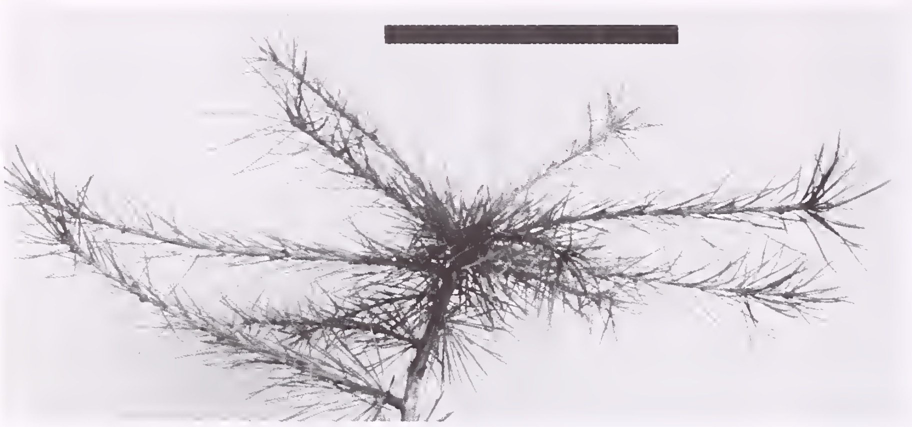

Figure 8—A group B steckling at the end of year 2 with 5 codominant apical shoots and a dormant terminal bud. Scale bar represents 10 cm.

The tenfold shoot multiplication achieved by the in vitro elongation of axillary buds increased the efficiency of the ortet harvest. This simple method allows either rooting the elongated shoot ex vitro as with a normal cutting, or subculturing and rooting in vitro (Harry and others 1991). The second option potentially expands rooting activity from the "window of rootability" in late summer to continuous year-round plantlet production.

Steckling Growth and Form

The typical main stem of a coniferous tree species is apically dominant and subtends lateral branches. A first-order lateral is usually shorter than the leader and exerts less apical dominance over the second-order side shoots that it subsequently develops. Many of the western larch stecklings exhibited similar branchlike characteristics, a phenomenon consistent with their origin as first-order branches. This development of branchlike habit by vegetative propagules, termed "topophysis" (Olesen 1978), has been observed in many species.

Growth—The stecklings produced less shoot growth than the seedlings of comparable size under the same fertilization regime. The optimal level of nitrogen recommended for coniferous seedlings is 100 ppm (Landis and others 1989). Despite fertilization at the higher level of 120 ppm N level, 13.4 percent of the steckling leaders remained as either suppressed short shoots or inhibited long shoots. Adequate steckling growth may require fertilization at a higher rate than normally used for seedlings.

On the other hand, fertilization of the group B stecklings at 200 ppm N resulted in a substantial mean orthotropic shoot elongation of 37.9 cm. Hence, the nitrogen level needed for "normal" steckling growth may be between 120 and 200 ppm N.

Plagiotropism—Forest regeneration requires orthotropic stecklings. Although a third of the western larch stecklings initially developed plagiotropic leaders, only a tenth failed to grow vertically by the end of the first season in greenhouse culture. It is not economical to hold mass-produced stecklings a second year in the nursery, so the approximate 10 percent proportion of the stecklings that persist in growing laterally require some intervention to produce a vertical leader during the first year.

Indirect evidence suggests that upright form may eventually develop even in severely plagiotropic stecklings. First, the small sample of 25 group A stecklings were all strongly orthotropic by their fourth year. Second, forest stands of western larch saplings that have bent laterally from extreme snow loads have recovered their upright form after 4 to 5 years (Schmidt and Schmidt 1979). Third, broken leaders of large western larch trees are often replaced by a first-order branch that upturns over several years.

Shrub Form—The relatively high (29.4 percent) incidence of plants without a dominant leader also poses a problem for forest regeneration from stecklings. Some leaders may have a persistent loss of apical dominance with partially or totally suppressed leaders and branches as long as or longer than the leader.

But as with plagiotropic plants, the shrub form may also be temporary because mature western larch trees with multiple tops resulting from insect damage generally develop a dominant leader within 4 to 5 years (Schmidt and Fellin 1973). Furthermore, the classes of shrublike forms recognized in this study may portray various stages in a transition from shrublike to treelike.

Arranging the shrub classes into a hierarchy of increasing leader dominance could help us predict the potential of shrubs to develop normal tree habit. For instance, the "shrub" forms (27 percent) with a subapical shoot becoming dominant over an elongating leader would likely assume tree form before the other classes.

RECOMMENDATIONS

The economic benefits of using the steckling stock type for containerized artificial regeneration requires development of a dominant orthotropic leader within the first year of culture. Holding recalcitrant plagiotropic or shrub forms for a second year's growth in a nursery would prove too costly for ordinary plantings. Hence, interventions such as pruning, staking, and chemical treatment should be evaluated for their effectiveness in producing a dominant leader within the first year of greenhouse growth.

Because shoot-tip cuttings rooted at high rates, mass propagation of juvenile western larch from limited seed sources seems feasible. However, steckling growth habit must be improved and performance tested in forest conditions before production-scale vegetative propagation can be recommended.

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Cone and Seed Production of Western Larch in Response to Girdling and Nitrogen Fertilization—An Update

Russell T. Graham
Jonalea R. Tonn
Theresa B. Jain

Abstract—Western larch (*Larix occidentalis* Nutt.) is a sporadic cone and seed producer. Because the species is such an important component of the Northern Rocky Mountain forests, methods of increasing seed production are needed. Girdling, fertilizing, and a combination of the two were used on 75-year-old western larch in northern Idaho. Girdling at the base of the live crown was effective in stimulating cone production, while the combination of fertilizing with ammonium nitrate and girdling did not increase seed yield. Fertilizer alone appeared to decrease the number of seeds per cone. Cones from trees fertilized, girdled, and both fertilized and girdled contained heavier seeds than cones produced by untreated trees. Germination of seeds produced on treated trees was greater than on control trees.

Western larch (*Larix occidentalis* Nutt.), an important forest component in much of the Northern Rocky Mountains, is an aggressive pioneer species occurring as a seral component in a variety of forests. Western larch is resistant to most forest diseases and has few serious insect pests. It is highly resistant to damage by fire; mature and older trees can survive repeated surface fires. Because the species grows rapidly and has excellent properties for use in building construction, it is a valuable commercial species throughout the Northern Rocky Mountains.

Cone production by western larch has been sporadic. Cone crops have been infrequent, making seed collection for artificial regeneration difficult and the use of natural regeneration methods doubtful. For example, since 1965 there have been only 2 years (1965 and 1991) that the Coeur d'Alene nursery processed good quantities of larch cones (fig. 1). Because western larch is an important component of Northern Rocky Mountain forests and an unpredictable cone producer, any method or technique that increases seed production would be valuable. This paper reviews an earlier study we conducted on cone stimulation and updates some of our thoughts and conclusions on stimulating western larch seed production (Graham 1986).

CONE STIMULATION

Several cone and seed stimulation trials and experiments have been conducted on different tree species. In northern Idaho female strobilus production was increased in western white pine (*Pinus monticola* Dougl.) by thinning stands; spacings of 9 m (30 ft) proved to be more effective than 6-m (20-ft) spacings (Barnes 1969). Wenger (1954) and Bilan (1960) showed that thinning increased cone production in loblolly pine (*P. taeda* L.).

Fertilization, primarily nitrogen, has been used to stimulate cone production. Western white pine (Barnes 1969), coastal Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco.) (Ebell 1962, 1971), and Rocky Mountain ponderosa pine (*Pinus ponderosa* var. *scopulorum* Engelm.) (Heidmann 1984) increased cone production in response to the application of nitrogen fertilizer. Application of the ammonium forms of nitrogen fertilizer appears to be more effective in stimulating cone production, especially when fertilizer is applied immediately after the initiation of vegetative buds in the spring (Ebell 1972). Fertilization rates have varied from 225 kg/ha (200 lb/acre) to 1,800 kg/ha (1,607 lb/acre) of nitrogen.

Girdling tree stems increased cone production up to 300 percent in loblolly pine (Bilan 1960), Douglas-fir (Ebell 1971), and eastern white pine (*P. strobus* L.) (Stephens 1964). Up to a 20-fold increase in cone production was reported as a result of girdling red pine (*Pinus resinosa* Ait.) (Holst 1959). Girdling at the base of the live crown can be four times as effective as girdling at breast height (Holst 1959). The most effective girdles appear to be overlapping cuts up to an internode apart on the stem or branch that sever the phloem on two sides. Cuts as narrow as a single saw kerf and as wide as 2.5 cm (1 inch) have been used successfully to stimulate cone production.

Because both girdling and fertilization have been used successfully in stimulating cone production in a variety of conifers we elected to test these methods on the sporadic cone producer western larch.

METHODS

Even with infrequent cone production, natural stands of western larch have developed in northern Idaho. Western larch, being an early seral species, regenerated aggressively after wildfires in the St. Joe, Priest, and Coeur d'Alene River drainages. One such area was in the Idaho

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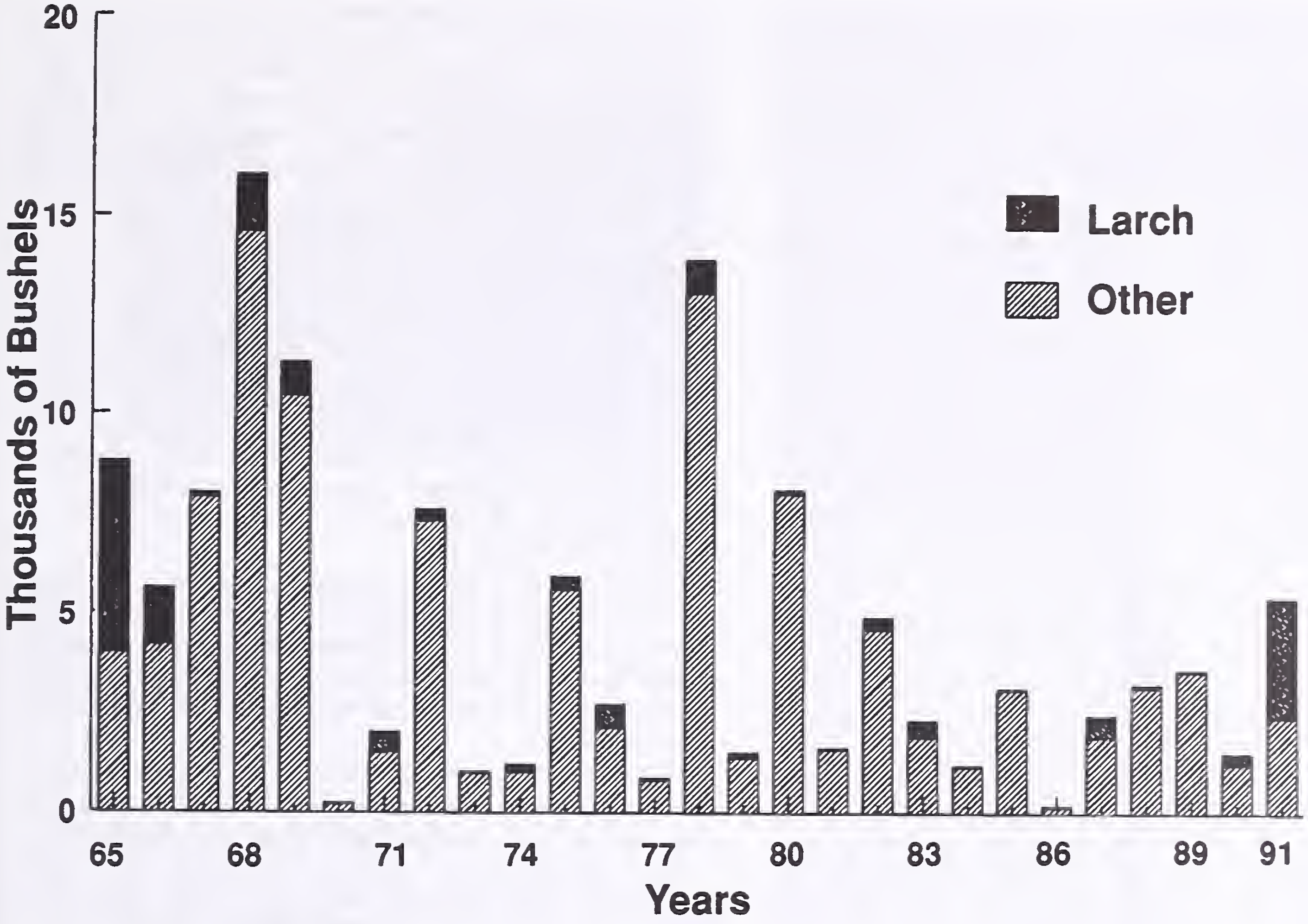

Figure 1—Western larch cones and other species cones processed at the Coeur d'Alene nursery from 1965 through 1991.

Panhandle National Forests near the Idaho-Montana border in the Wallace Ranger District (fig. 2). The 75-year-old stand chosen for use in this study had sporadically produced cones in the past.

The entire stand was thinned to a residual basal area of 9 to 14 m²/ha (40 to 60 ft²/acre). Logging debris was dozer piled. Because western larch initiates growth early, often before snow melt, the treatments were applied late in the fall.

The 72 most vigorous, well-formed western larch trees in the stand were chosen for inclusion in the study. They were divided into 12 six-tree groups with three groups assigned to a replication. Three treatments and a control were applied randomly to the groups within each replication:

- *Fertilize:* 336 kg/ha (300 lb/acre) of nitrogen in the form of ammonium nitrate was applied with a hand spreader under the drip line of the selected trees.
- *Girdle:* The trees were climbed using spurs, and at the base of the live crown one-half the circumference of the phloem was severed using a hand pruning saw. At a bole circumference length below the first, a similar girdle on the opposite side of the tree was cut. This process resulted in two overlapping cuts (fig. 3).
- *Girdle and fertilize:* Six trees were girdled and fertilized in each of the three replications.

Figure 2—Location of the study area.

Eighteen trees were reserved as controls, receiving only the thinning treatment. This treatment strategy resulted in a randomized complete block experiment.

In the fall 2 years after treatment, the trees were climbed using spurs and cones collected from each tree in the study. Seeds were extracted and cleaned at the

Figure 3—Girdling of western larch with a hand pruning saw.

Forest Service, U.S. Department of Agriculture, nursery in Coeur d'Alene, ID. Cones per tree, seeds per cone, and seed weight were recorded. A germination trial was conducted using 0, 14, and 28 days of stratification. An analysis of variance for a randomized complete block design was used to the analyze the data. The means were separated using Duncan's multiple range test.

RESULTS

Girdling alone produced the most cones per tree (fig. 4). No differences were detected in cone production among the control and other treatments. The application of fertilizer appeared to depress the number of seeds per cone; the other treatments all produced about equal numbers of seeds (fig. 5). All of the treatments appeared to increase seed weight compared to seeds produced on the untreated trees (fig. 6).

The stand and tree characteristics in the various treatments were very similar. No tree or stand characteristic appeared to influence cone production (table 1). Based on a significance of 0.163, tree crown ratio was the only characteristic close to explaining a portion of the variance in cone production.

Germination of seeds produced by the treatments was good compared to that of seeds from the control trees. Of the seeds from the treated trees, 12 percent germinated with no stratification, 95 percent after 14 days of stratification, and 96 percent after 28 days of stratification. In contrast, 80 percent of the seeds from the control trees germinated (for 14 days) after 28 days of stratification (fig. 7).

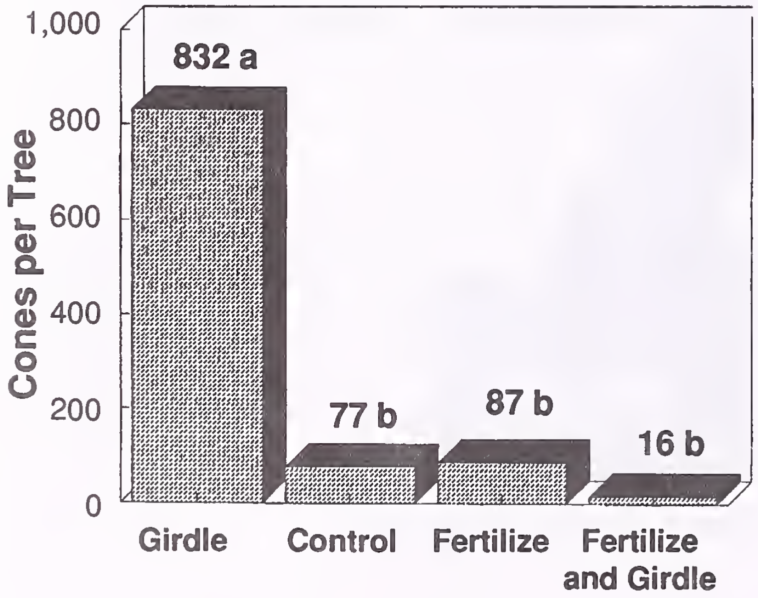

Figure 4—Mean cones per tree produced by western larch after girdling, fertilization, girdling and fertilization, and by control trees. Different letters indicate significant ($P \leq 0.05$) differences among means.

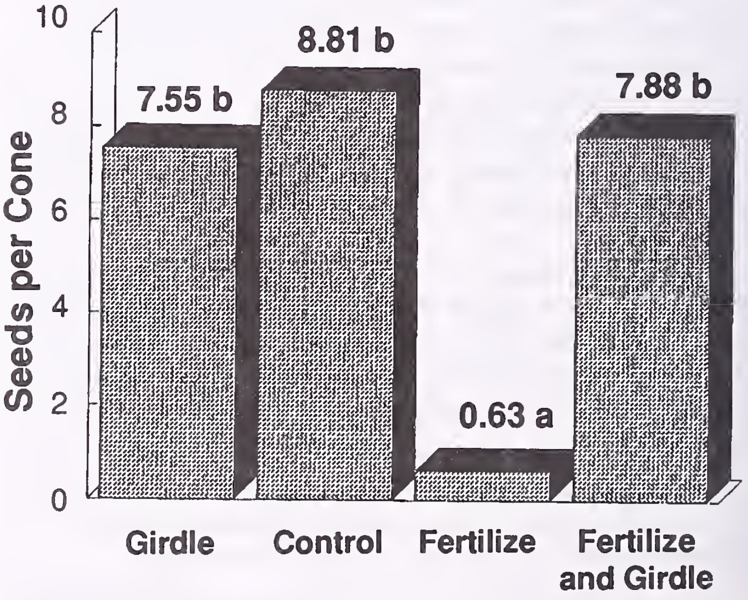

Figure 5—Mean numbers of seeds per cone from western larch after girdling, fertilization, girdling and fertilization, and by control trees. Different letters indicate significant ($P \leq 0.05$) differences among means.

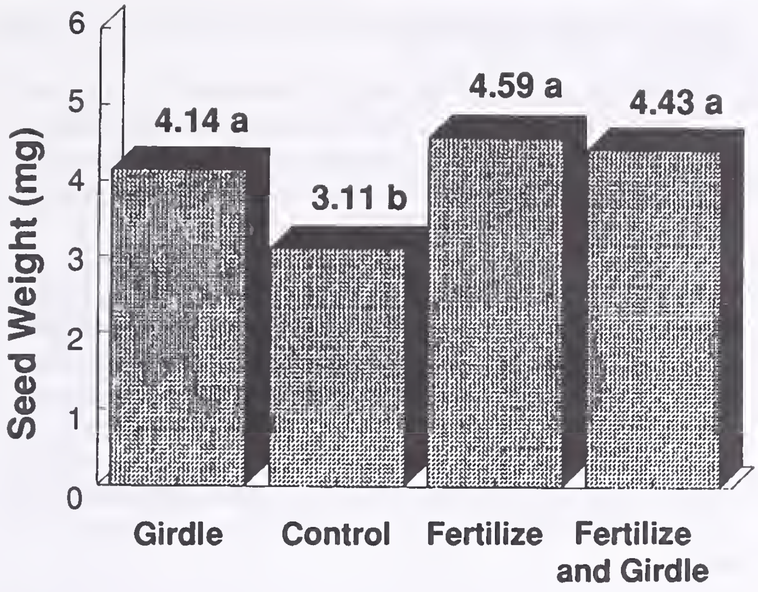

Figure 6—Mean weights of seed produced by western larch after girdling, fertilization, girdling and fertilization, and by control trees. Different letters indicate significant ($P \leq 0.05$) differences among means.

Table 1—Mean tree and stand characteristics for western larch in northern Idaho by treatment and their significance in explaining cone production

Treatment	D.b.h.	Height	Crown ratio	Residual basal area	Crown density
	cm	*m*	*Percent*	*m²/ha*	
Control	34.0a[1]	28.9ab	31.7ab	8.66a	Good
Fertilize	35.3a	29.6a	35.0a	8.43a	Good
Girdle	33.5a	27.5bc	31.7ab	7.90a	Good
Fertilize and girdle	32.8a	27.0c	29.4b	6.89a	Good
Significance	0.752	0.367	0.163	0.752	0.583

[1] Different letters indicate significant ($P \leq 0.05$) differences among treatments.

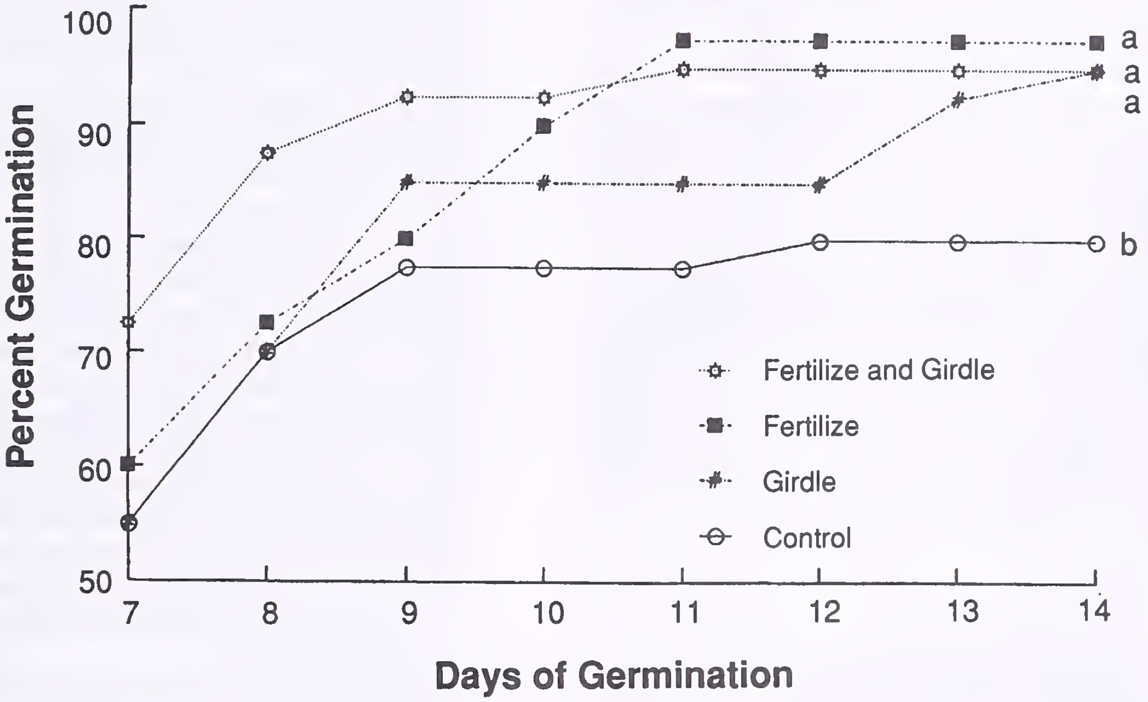

Figure 7—Germination after 28 days of stratification for seeds produced by western larch after girdling, fertilization, girdling and fertilization, and by control trees. Different letters indicate significant ($P \leq 0.05$) differences among means after 14 days of germination.

DISCUSSION

The results from this study were similar to those reported for Douglas-fir (Ebell 1971) that showed girdling was effective in stimulating cone production. Even though the mechanisms initiated by girdling that stimulate cone production are not fully understood, girdling at the base of the live crown could direct solutes back toward the crown. If these solutes contain hormones, nutrients, or a wounding compound that stimulate cone production, they would be at their maximum concentration near the crown. Also, the over-lapping cuts could have increased the moisture stress in the crowns, possibly triggering some type of hormonal or chemical response that stimulated cone production. Some studies used wide cuts (2.5 cm, 1 inch) but the narrow saw kerf widths used in this study healed quickly allowing for retreatment of the trees.

In contrast to studies with other species (Barnes 1969; Heidmann 1984), fertilization alone at 336 kg/ha (300 lb/acre) did not increase cone production. Of the treatments applied in this study, fertilization was the only one that decreased the number of seeds per cone. The effect of fertilization in combination with girdling might have countered the effects of the girdling by increasing the vigor of the trees. Fertilization at higher rates might be more effective in stimulating cone production. Higher fertilization rates may go beyond increasing tree vigor and growth and actually increase stress. This approach may be more effective than the light application of fertilizer used in this study. Fertilizer rates as high as 1,000 to 2,500 kg/ha (893 to 2,232 lb/acre) could be tried.

Tree climbing is dangerous, expensive, and damages trees. Western larch has brittle branches, making working in the crowns of 30-m (98-ft) trees hazardous. The use of climbing spurs damages the tree along the entire stem. Girdling at breast height has been shown to be effective in species such as Douglas-fir (Ebell 1971) and red pine (Holst 1959). Because girdling was so effective in this study it possibly could be effective in stimulating western larch cone production on an operational scale.

APPLICATION

Since we first published the initial results from this study, girdling has been applied throughout the Northern Rocky Mountains. The results of these applications have been highly variable. In eastern Oregon girdling at breast height effectively stimulated cone flower production, but few cones were produced. Likewise, in northern Idaho attempts to girdle western larch to stimulate cones ranged from very effective to very ineffective.

Often the application of girdling is confounded with damage from frost. Frost that occurs when cones are being formed in the early spring often results in empty cones or few cones produced. Therefore, evaluation of the effects of girdling must be balanced with the losses caused by frost.

Where girdling has been applied at breast height, the cuts have often weakened the trees, which made them unsafe to climb and prone to loss from wind. Cuts should be carefully applied so as not to weaken trees if they are going to be climbed or preserved.

With western larch's importance both ecologically and commercially, care needs to be taken to ensure the species is sustained. The use of cultural treatments such as girdling and fertilization to stimulate cone production is viable on some sites and stands. But often more than one contributor exists in the success or failure of a cultural treatment. Therefore, all factors that can affect cone production must be evaluated when considering the use of girdling or fertilization to stimulate cones in western larch.

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Western Larch Stock Types and Season of Planting in Northeastern Washington

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Abstract—Tests of survival and height growth of western larch (*Larix occidentalis* Nutt.) 2+0 bareroot and container seedlings planted in spring and fall show that after two growing seasons, survival was significantly better for 2+0 stock planted in fall. Fall-planted seedlings were significantly taller than spring-planted seedlings.

Western larch (*Larix occidentalis* Nutt.) is an important species on many habitat types in northeastern Washington, U.S.A. The Washington Department of Natural Resources manages over 130,000 acres on which western larch is the primary or a secondary species. Its high value and rapid juvenile growth make it well-suited to shorter rotations and even-aged management.

Prior to this study, Department management recommendations in northeastern and north-central Washington called for planting larch in many cases, but many managers had only limited experience with such planting. Managers need information on survival and early growth of different stock types, especially when planted at different seasons.

Spring planting had been favored for years because survival was thought to be better at that time of year. Problems with spring planting, however, led to an interest in fall planting. For one thing, planting some sites in the fall could relieve pressure on busy spring operations, both in the nursery and in the field. Fall-planted stock would not need extended cold storage. There had also been problems with premature flushing of larch stock stored for spring planting, whereas stock planted in the fall would be ready to grow in the spring as soon as environmental conditions permitted. Access to planting sites was often better in fall than in spring, when roads had to be plowed. Alternatively, waiting for road access in spring often meant that soil moisture at the planting site dropped to unacceptably low levels before stock could be planted.

Disadvantages to fall planting include a possible short time between adequate seedling dormancy at the nursery and the end of the fall planting season, when poor weather conditions preclude planting. This calls for close coordination between the nursery and the planters. Fall-planted seedlings face greater risk of frost heaving, especially on sites subject to alternate freezing and thawing cycles. Fall-planting success can be less predictable than that of spring planting, partly because of weather conditions; a long, dry "Indian summer" can decrease survival.

Planting often favored bareroot stock where competition was intense because it tended to outgrow competing vegetation, being taller to start with. Container stock, however, had several advantages in terms of cost, production time, and ease of handling in the nursery and the field.

This study sought to determine survival and height growth of two western larch stock types, 6-month-old container stock and 2+0 bareroot seedlings, and to determine the better season to plant western larch (spring versus fall) in northeastern Washington.

LITERATURE REVIEW

The physiology, culture, and planting of larch stock has received less attention than is the case with other species commonly planted in northeastern Washington. We know that larch seedlings grow faster than many others; seedlings can rapidly become too large to handle and plant effectively. Larch seedlings tend to develop deep taproots, which are easily broken during lifting, or J-rooted during planting. Schmidt and others (1976) recommended that tops should be 4 to 8 inches tall, with 8-inch roots.

Nursery controls such as density-regulation, restricted watering, and artificial control of day length may be helpful in production of quality stock that will survive and grow well in the field. Vance and Running (1985) studied the effects of light reduction and moisture stress on larch seedlings and concluded that true dormancy might best be induced by control of photoperiod. Barber (unpublished data) found that specially hardened larch container stock survived and grew well after planting in mid-September in north-central Washington.

Several studies on the effect of lifting date on survival of larch stock show that larch is physiologically active longer in the fall than other conifers, so it is important not to lift it too soon. Sinclair and Boyd (1973) recognized this, suggesting that physiological condition of stock was at least as important as the environmental conditions at the planting site. They recommended lifting and planting no earlier than October 15 in northern Idaho. Earlier lifting resulted in poor survival of fall-planted 1-0 seedlings. Morby and Ryker (1979) and McDonald and others (1983) recommended that larch stock be lifted in the fall and stored at 28 or 33 °F in poly-lined bags until spring planting.

Laird and Boyd (1977) compared survival of stock lifted in fall and stored at 28 °F to stock lifted early in spring and stored until planting time, and to "hot-lifted" stock (lifted and planted immediately in spring). The survival of fall-lifted stock was better than that of spring-lifted or hot-lifted stock. Height growth was also better. These

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authors recommended fall-lifting and freezing for 1-0 stock and planting as early in spring as sites were accessible.

Planting date is also important. Larch breaks dormancy earlier than most species, often while still in cold storage, unless frozen. Sinclair and Boyd (1973) reported that foliage became chlorotic and moldy when stored over the winter and that late fall planting (October 15 or later) avoided this problem, resulting in better survival than spring planting.

Schmidt and others (1976) also reported that fall planting, in soil moistened 12 inches deep by fall rains, resulted in better survival than spring planting, unless the site was prone to frost heaving. They concluded that, if larch is to be planted in spring, it should be done as early as possible to avoid premature flushing in storage. Survival declined sharply when nondormant stock was planted.

Information is scarce on the effect of stock type on survival and growth of larch. Sloan and others (1987) summarized the results of 20 studies comparing performance of stock types of different species, none of which dealt with larch. They concluded that, for ponderosa pine, container seedlings survived better than bareroot seedlings on harsh sites; on better sites there was little difference. Owston (1990) concluded that stock type is less important to survival and growth than are initial size and physiological condition at time of planting.

METHODS

Seedlings were grown at the Department's Webster Nursery in Olympia, WA, in 1985. Bareroot stock was 2+0; container seedlings were 6-month-old "Styroblock-4's." Sowing was coordinated with planting dates so that seedlings within a stock type were of comparable age, regardless of whether planted in fall or spring. Dormancy of stock scheduled for fall planting was initiated by withholding water in mid-August for 2+0 stock and early September for container stock. Bareroot stock for spring planting (in 1986) was lifted in November 1985 and stored at 33 °F until planting.

Three study sites in Pend Oreille County, WA, were selected and designated King's Road (3,230 ft, 20 percent slope, southeasterly aspect, ABGR/PHMA/PHMA habitat type), Mount Pisgah (3,000 ft, 15 percent slope, southwesterly aspect, ABGR/PHMA/PHMA h.t.), and Deer Valley (3,050 ft, 25 percent slope, easterly aspect, PSME/PHMA/SMST h.t.). Habitat types are as described by Cooper and others (1991).

Minimal site preparation was done to facilitate planting, but the seedlings did not receive any special consideration not normally afforded operational planting stock. At the time of planting, fall rains had moistened the soil to a depth of 8 to 10 inches at the King's Road site; soil was dry and powdery at the other two. Soil moisture was high at all sites during spring planting.

Trees were planted October 15 and 16, 1985, and April 14 and 15, 1986. Thirty trees per row were planted 1 ft apart, in rows spaced 2 ft apart. Four rows were planted to each stock type. Initial heights were measured at the time of planting.

Survival and height growth were assessed at 6, 12, and 24 months from time of planting. Trees were considered "alive" if they had any green needles left at the time of measurement. No attempt was made to record specific causes of mortality, although major animal damage was noted. Survival data were analyzed by the Kruskal-Wallis test and height growth data by standard analysis of variance (Wilson 1990).

RESULTS AND DISCUSSION

Overall, bareroot stock survived better than container stock after two growing seasons. The difference was statistically significant (0.05 level) but not striking. This agrees with Owston (1990) who reported that survival differences between stock types on the same site are likely to be small.

Figure 1 shows survival of the four treatments for the first and second growing seasons. After one growing season, the only significant difference was between the highest and lowest treatments, fall-planted bareroot and spring-planted container stock (88 and 64 percent, respectively; $P = 0.01$). This was again true after two growing seasons (80 and 58 percent; $P = 0.05$). In addition, the difference between fall-planted bareroot and fall-planted container stock was significant at the 0.01 level (80 and 64 percent).

Thus, from the standpoint of survival, bareroot stock planted in the fall is the best treatment. Spring-planted container stock appears to be the least desirable alternative. These results generally agree with those of Sinclair and Boyd (1973), who reported that, of the four species they tested (larch, Douglas-fir, grand fir, and Engelmann spruce), larch was the most sensitive to lateness of spring planting, especially in drier habitat types. They also reported that fall-planted 1+0 larch had consistently good

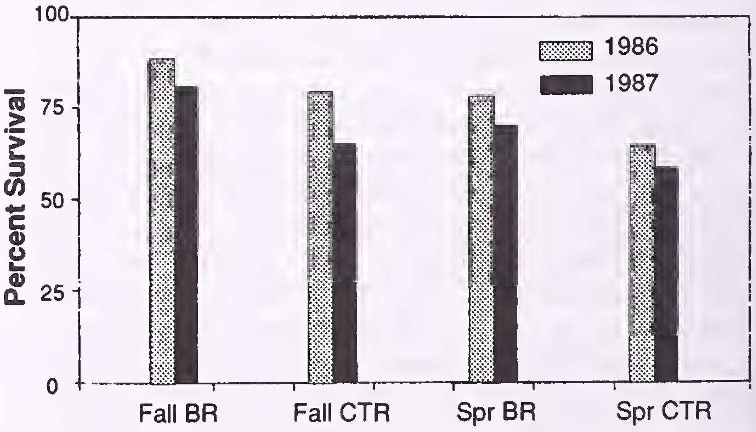

Figure 1—Survival of bareroot (BR) and container (CTR) seedlings outplanted in spring and fall, through first two growing seasons.

survival only when planted in mid-October. They suggested that this was due to physiological condition of the stock at the time of lifting and planting, in response to shorter photoperiods and cooler temperatures.

Mean height increments are shown in figures 2 and 3. Bareroot seedlings grew about the same in the first year, regardless of season of planting. By contrast, container stock grew much better when planted in the fall and actually suffered a height loss from animal damage when planted in spring. First-year height growth of fall-planted container stock was significantly greater than that of bareroot stock (table 1), although this was not enough to overcome the greater initial height of the bareroot stock.

Analysis of first-year height growth also indicated a significant interaction between stock type and season. This is interpreted to mean that it is important to match the stock type to the season of planting; in other words, height growth is dependent on proper selection of stock type for the season in which it is planted.

Analysis of variance indicated that there was no difference in second-year height growth of bareroot stock and container stock, but there was a difference due to season of planting (table 2). Fall-planted seedlings grew significantly more in their second season than spring-planted seedlings.

Figure 4 summarizes total heights 2 years after planting. Heights at the Mount Pisgah site were especially good; several trees (fall-planted bareroot stock) were almost 4 ft tall at 4 years, and were easily outgrowing competing vegetation, primarily grasses and low shrubs.

Analysis indicated a significant difference in total height due to planting season for container stock (table 3). This implies that fall planting is preferable for container stock. Bareroot seedlings were equally tall after 2 years, whether planted in spring or fall.

Table 1—First-year height growth, ANOVA

Source	Sum of squares	Degrees of freedom	Mean squares	F-ratio	Probability level
Season	498.80	1	498.80	72.56	0.00**
Stock type	41.39	1	41.39	6.02	0.01**
Season x stock	338.21	1	338.21	49.20	0.00**
Error	1,656.80	241	6.87		

**Significant at 0.01 level.

Table 2—Second-year height growth, ANOVA

Source	Sum of squares	Degrees of freedom	Mean squares	F-ratio	Probability level
Season	797.52	1	797.52	11.95	0.00**
Stock type	1.04	1	1.04	0.02	0.90
Season x stock	35.91	1	35.91	0.54	0.46
Error	13,877.77	208	66.72		

**Significant at 0.01 level.

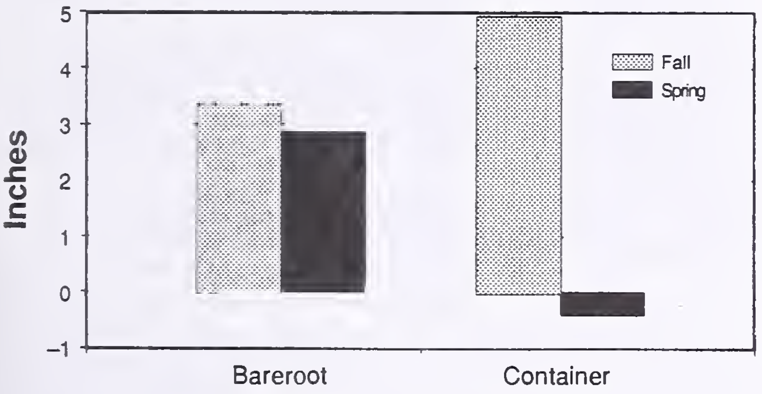

Figure 2—First-year height growth of bareroot and container seedlings outplanted in spring and fall. Spring container stock suffered animal damage, hence the net loss.

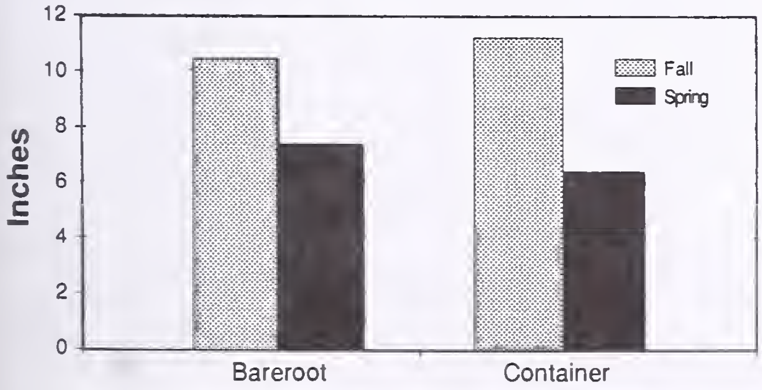

Figure 3—Second-year height growth of bareroot and container seedlings outplanted in spring and fall.

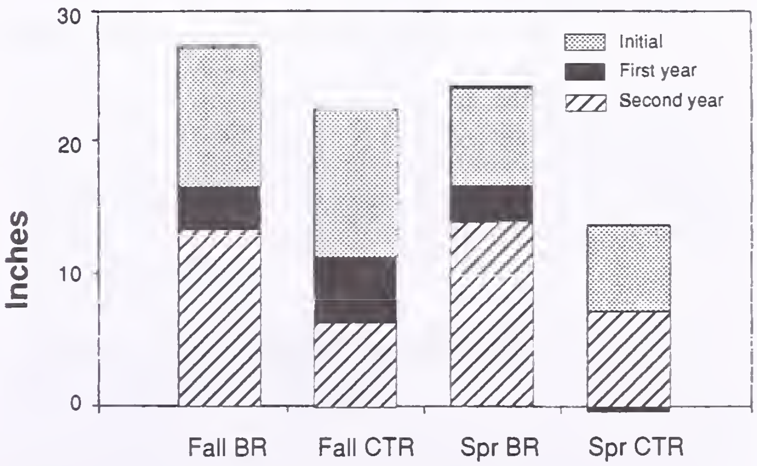

Figure 4—Cumulative height growth of bareroot (BR) and container (CTR) seedlings outplanted in spring and fall. Spring container seedlings suffered animal damage, hence the net height loss in first year.

Table 3—Second-year total heights, ANOVA

Source	Sum of squares	Degrees of freedom	Mean squares	F-ratio	Probability level
Season	1,775.19	1	1,775.19	18.66	0.00**
Stock type	2,898.58	1	2,898.58	30.47	0.00**
Season x stock	456.85	1	453.85	4.77	0.03**
Error	19,785.27	208	95.12		

**Significant at 0.01 level.

CONCLUSIONS

Initial survival, height growth, and total height all indicate that fall planting of western larch is preferable to spring planting in northeastern Washington, and that 2+0 bareroot stock is preferable to 6-month container stock. If planting operations must be conducted in the spring, it is still preferable to plant bareroot stock.

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Growing Western Larch in a Container Nursery

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Abstract—Western larch (*Larix occidentalis* Nutt.) in containers in greenhouses grew to a variety of sizes after control of fertilizers and photoperiod lengths. A basic growing regime for a nursery in northern Idaho, U.S.A., is provided as a guide. Using an integrated pest management plan greatly reduces the need for pesticides.

Western larch (*Larix occidentalis* Nutt.), an important timber species in the Inland Northwest of North America, occurs from western Montana to eastern Oregon and Washington and northward into southern British Columbia (Rudolf 1974). In northern Idaho this species occurs in nearly pure stands or in mixtures with Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco) and western white pine (*Pinus monticola* Dougl. ex D. Don). Western larch grows best on deep, moist, porous soils in high valleys and on mountain slopes of northern and western exposure (Harlow and others 1979). Mature tree heights average 35 to 55 m, and stems are about 1 m in diameter at breast height. Generally, the species begins to bear cones around 30 years of age (Rudolf 1974) and may produce cones every year (Shearer 1986). Larger diameter, full-crown dominant and codominant western larch produce more cones more frequently (Shearer 1986). However, viable seed crops can be much more infrequent, with up to 10 years between seed crops (Rudolf 1974). Seed may be transferred ±245 m in elevation and about 0.75° latitude (Rehfeldt 1983).

In northern Idaho, western Montana, and eastern Washington, nursery managers grow western larch for artificial regeneration as 1+0 bareroot, 2+0 bareroot, or 1+0 container stock. In table 1 we provide an estimate of western larch grown by stock type in the Northern Rocky Mountains. In this area, about 60 percent of the nurseries are strictly container operations, and about 9 percent of their annual production is western larch. Although western larch is a small component of most seedling crops, it is especially challenging because of its rapid growth.

We feel most container nurseries in this region, including our own, grow western larch much the same way. Therefore, we provide as a guide our basic regime for growing larch in containers for reforestation and conservation in northern Idaho (46.5° N. latitude and 117° W. longitude).

SEED QUALITY

The first step in successfully growing western larch in containers is to evaluate the seed. Seed quality is actually described by a number of attributes: seeds per kilogram, seed purity, soundness, and viability.

Seeds Per Kilogram

For northern Idaho, larch seeds generally average around 350,000 per kg. Actual seeds per kilogram can vary substantially, and an accurate determination is necessary to prepare the appropriate amount of seed for planting. We calculate seeds per kilogram by weighing five replications of 100 seeds to the nearest 0.01 g. We then place mean weight into this equation:

$$\text{Seeds per kilogram} = \frac{\text{100 seeds}}{\text{mean weight of 100 seeds in grams}} \times \frac{\text{1,000 g}}{\text{kg}}$$

Seed Purity

We determine purity by removing the "debris" from an 8-g sample (approximately 2,500 seeds). Seed cleaning machinery operated by skilled technicians should achieve more than 95 percent purity.

$$\text{Purity \%} = \frac{\text{clean seed weight}}{\text{clean seed wt. + debris}} \times 100$$

Soundness Percentage

We determine percentage of hollow seeds by x-raying a 100- to 200-seed sample, although this could also be achieved by cutting the same number of seed. If more than 5 percent of the seeds are hollow, the seedlot should be reprocessed by pneumatic or gravity means to eliminate empty seeds.

Viability—Stratification and Germination Tests

The most important aspect of seed quality is how well the seed will germinate. We determine germination capacity and energy so an appropriate amount of seed can be prepared for planting. Western larch germinates best if given a 28-day cold/moist stratification period. We

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Table 1—Estimated quantities of total reforestation seedlings and total western larch grown in various stock types in eastern Washington, northern Idaho, and western Montana

	1+0 bareroot		2+0 bareroot		1+0 container	
	Total	Larch	Total	Larch	Total	Larch
Federal	2,200,000	1,500,000	14,500,000	2,400,000	4,200,000	220,000
State	0	0	100,000	20,000	1,340,000	120,000
Private	0	0	1,000,000	6,000	4,200,000	514,000
Industry	0	0	0	0	6,600,000	765,000
Total	2,200,000	1,500,000	15,600,000	2,426,000	16,340,000	1,619,000

prepare seed for stratification by first placing seed into a fine mesh bag and soaking it 48 hours in running tap water to help remove inoculum of potential pathogens and to imbibe the seed. We then suspend the mesh bag in a plastic bag so seeds are not soaking in water, and hang the bags in refrigerated storage at 2-3 °C for 28 days. After 28 days, we again rinse the seed 24 hours in running tap water and place them into plastic germination trays. We replicate tests four times with 100 seeds per replication and germinate seed under 8 hours of light at 18 °C. Cumulative counts are made at 7, 14, 21, and 28 days.

The same stratification procedure is followed for preparing seed for planting. We limit the amount of seed in mesh bags to 1 kg. After the final rinse, we quickly surface-dry the seeds and store them at 2-3 °C until planting.

PLANTING

Once seed quality is assessed we can calculate the amount of seed necessary for our crop. Using probability tables (see Tinus and McDonald 1979), we determine the number of seed needed per cell to achieve around 98.5 percent cell occupancy. Most nurseries generally oversow the contracted quantity to ensure enough seedlings are produced to satisfy the agreement. Oversow factors vary from nursery to nursery, but the Forest Research Nursery uses a 10 percent factor. After learning seed germination, desired seedling quantity, seed purity, sound seed percentage, and seeds per kilogram, we calculate seed requirements for the crop as follows:

$$\frac{(\text{Desired seedlings}) \times (\text{Oversow factor}) \times (\text{Seeds per cell})}{(\text{Seeds per kilogram}) \times (\text{Purity percent}) \times (\text{Soundness percent})}$$

We are currently growing larch in two containers: Ray Leach Pine Cells® and the Copperblock® 45/340 (styro 20's). Pine cells have a volume of 66 mL, while the styro 20's have a cell volume of 340 mL. Generally, most nursery managers in northern Idaho and western Montana use 60- to 80-mL containers for reforestation seedlings, while we use the larger 340-mL containers for conservation seedlings used by the public. Copperblocks are so named because their cell walls are coated with copper to encourage chemical root pruning. In copper-treated containers we grow seedlings with shorter first order roots, more third and fourth order roots, and few if any roots growing down the outside of the rootplug. We find chemically root-pruned seedlings are also easier to remove from their containers.

We use a 50:50 peat:vermiculite soilless growing medium without supplemental dolomite. Usually, growing medium pH is between 4.2 and 4.6. A Gleason flat filler automatically fills containers with growing medium. Our crews moisten the bottom 1 to 2 cm of the containers before running them through to prevent medium from falling through the drainage holes. This machine fills about 100 containers per hour. Once filled, we send containers through an Old Mill Seeder. This precision sowing machine uses a photocell to electronically regulate the amount of seed delivered to each cell of the container. We found it works extremely well for small-seeded species, including western larch (Wenny and Edson 1991). Once sown, we top-dress containers with about 6 to 8 mm of white silica grit using a hand-held dispenser (Dumroese and others 1990). We then place containers on greenhouse benches.

RECORD KEEPING

The most important aspect of growing western larch, or any species, in containers is keeping detailed records of all cultural manipulations to the crop. This aids the decision-making process for altering the regime to improve stock viability, provides a permanent record of pesticide applications in the event of litigation, and in a multiple-worker environment, communicates current crop status to all workers.

We measure seedlings every 2 weeks for height and root collar diameter (r.c.d.) growth. Our technicians chart averages for the seedlot or species on a personal computer and compare growth rates to target growth curves. The target growth curve is based on past experience and contract specifications (fig. 1). Actual growth, as compared to target growth, is what drives modifications to the growing regime—increasing fertilizer rates if growth is lagging or decreasing rates if growth is exceeding targeted rates. Therefore, we apply fertilizers according to seedling phenology, not by calendar days. Computer programs using commercially available software make these modifications easy (Wenny 1989).

ENVIRONMENTAL MONITORING

We monitor maximum and minimum air temperature (on thermometers and a hygrothermograph), growing medium temperature, humidity, and pH and electrical conductivity of irrigation, fertigation water (irrigation water

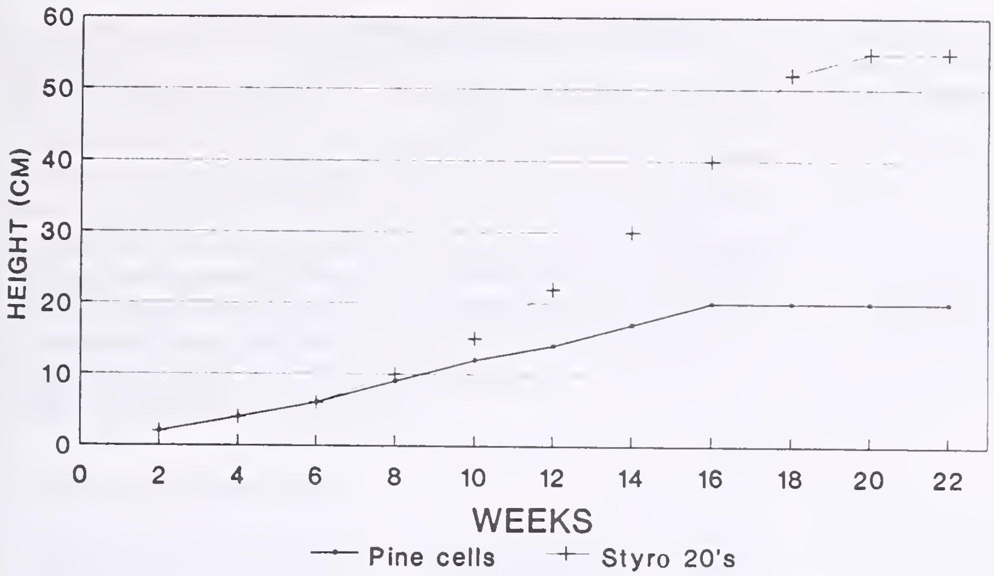

Figure 1—Target height curves for container-grown western larch in styro 20's and pine cells.

with injected liquid fertilizer in solution), and leachate from the growing medium.

FERTILIZERS, PHOTOPERIOD, AND TARGET HEIGHT

We grow one crop of western larch each year. Our crews sow seeds during the first week of April. For seedlings in pine cells, our target height is 16 to 20 cm, while 50 to 60 cm is the target for styro 20's (fig. 1). We know from experience our larch crops generally set bud and stop height growth during the first 2 weeks of August (about week 16), regardless of fertilizer regime.

GROWING REGIME

Our nursery uses rolling benches, and 86 percent of the area is in production. Once planted, technicians irrigate containers with an overhead, traveling-boom irrigation system until the medium is thoroughly moist. Phosphoric acid is injected into the irrigation water to adjust pH to around 5.5. We apply light mists of acidified irrigation water only on warm, sunny days to keep the zone around germinating seeds slightly moist.

Initial Growth

Crews thin seedlings to one seedling per cell by removing extra germinants with tweezers or fingers as soon as the majority of seedlings have shed their seedcoats. Thinning is more efficient if done before lateral root development. Seedlots with high germination energy tend to shed their seedcoats rapidly. Once seed coats are shed, we apply nutrients during each twice-weekly irrigation. During initial growth phase, week 3 through week 6, we inject a liquid fertilizer solution of Peters Conifer Starter® (7-40-17) at a rate of 42 ppm nitrogen (N) supplemented with micronutrients. Micronutrients include magnesium sulfate, manganous sulfate, solubor (boron), and Sequestrene 330 (chelated iron) (see Wenny and Dumroese 1987 and table 2). We continue to add phosphoric acid to lower fertigation water pH to around 5.5.

During this period, we maintain day temperatures of 24-27 °C and night temperatures around 18 °C. Medium temperature (recorded at 8 a.m. daily) averages 18 °C. We extend photoperiod to 24 hours by using intermittent, all-night lighting (see Landis and others 1992) and 300-watt incandescent bulbs.

Accelerated Growing Phase

For seedlings in pine cells, this phase lasts from week 7 through week 10 (table 2). We continue twice-weekly fertilizer applications, and seedlings are given 120 ppm N of Peters Conifer Grower® (20-7-19) alternated with 81 ppm N liquid calcium ammonium nitrate (CAN 17®) (17-0-0-8.8). At week 10, if growth is on target (seedlings are about 50 percent of desired, final height), we leach the medium with copious amounts of water to remove excess fertilizer and salts.

Like the pine cells, we give seedlings grown in styro 20's twice-weekly fertilizer applications from week 7 but continue them through week 14. We alternate Peters Conifer Grower at 192 ppm N with 257 ppm N CAN 17.

Coasting Phase and Bud Initiation

Beginning with week 10 for pine cells and week 14 for styro 20's, we irrigate seedlings only when medium has become barely moist (table 2). Our greenhouse technicians daily select seedlings at random, remove the seedling from the cell, and visually examine and feel medium for dryness. Although quite subjective, we feel this method has some advantages: disease and insects can be surveyed at the same time; by random selection, seedlings seldom examined because of inaccessibility are checked; and by inspecting the rootplug, we gain insight as to how the root system is developing.

Extended photoperiod is discontinued. We set day temperatures for 16 to 21 °C and night temperatures of 10 to 16 °C. We maintain medium temperatures between 14 and 16 °C with these air temperature ranges.

Table 2—Growing regime for western larch grown in Ray Leach Pine Cells and the Copperblock 45/340 (styro 20)[1]

Germination and initial growth	Accelerated growing phase	Coasting phase and bud initiation	Root collar diameter growth
		Pine cells	
Weeks 3-6	Weeks 7-10	Weeks 10-16	Weeks 16-storage
Peters Conifer Starter at 42 ppm N with micronutrients[2] applied twice weekly.	Peters Conifer Grower at 120 ppm and micronutrients alternated with 81 ppm N from CAN 17. Seedlings fertilized twice each week.	Alternate micronutrients with 81 ppm CAN 17. Fertilized only when rootplug is barely moist.	Peters Conifer Finisher at 24 ppm N alternated with 161 ppm N from CAN 17. Peters Foliar Feed at 648 ppm N once every 2 weeks. Fertilized only when rootplug is barely moist.
		Styro 20's	
Weeks 3-6	Weeks 7-14	Weeks 14-16	Weeks 16-storage
Peters Conifer Starter at 42 ppm N with micronutrients applied twice weekly.	Peters Conifer Grower at 192 ppm N and micronutrients alternated with 257 ppm N from CAN 17. Seedlings fertilized twice each week.	Alternate micronutrients with 81 ppm CAN 17. Fertilized only when rootplug is barely moist.	Peters Conifer Finisher at 24 ppm N alternated with 161 ppm N from CAN 17. Peters Foliar Feed at 648 ppm N once every 2 weeks. Fertilized only when rootplug is barely moist.

[1] From Wenny and Dumroese 1987.

[2] Micronutrients consist of magnesium sulfate at 24 ppm S, manganous sulfate at 11 ppm S, solubor at 0.46 ppm B, and Sequestrene 330 at 4 ppm Fe.

Western larch in pine cells will "coast" from week 10 through budset, about week 16, during which time seedlings continue to grow, regardless of nutrient applications or moisture conditions. Total height at terminal bud set is about twice that at the end of the accelerated growing phase. Our larch generally give us a 100 percent increase in height as they "coast" to budset. During this coasting period, we alternate micronutrients with 81 ppm N CAN 17 whenever the medium is barely moist.

This "coasting" effect is important. Our research indicates no cultural practice short of inducing mortality will stop height growth, although photoperiod control by shading may be a method. Nursery managers can prepare for these "coast" height increases by switching to the bud initiation phase before the seedlings are at desired heights.

For a crop of about 90,000 seedlings, we use about 33,800 L of water during the first 15 weeks of production, and 64 percent of that is drained from the nursery (Dumroese and others 1991). Fortunately, larch uses nitrogen fairly efficiently during this period, when compared to western white pine or Douglas-fir, and only about 35 percent of the total N applied is wasted and leaves the nursery. We monitor and treat our waste water in a constructed wetland (Dumroese and Wenny 1992b; Dumroese and others 1991).

Root Collar Diameter Growth

At about week 16, terminal buds are becoming visible, and height growth has coasted to a stop. From now until lifting, we give seedlings in both container types 24 ppm N in the form of Peters Conifer Finisher® (4- 25-35) alternated with 161 ppm N CAN 17 each time irrigation is necessary (table 2). Also, seedlings receive 648 ppm N Peters Foliar Feed® (27-15-12) every 2 weeks from budset to about the end of October. This treatment, especially for larch in pine cells, quickly boosts foliar N levels depleted during the "coasting" phase and increases r.c.d. and bud length (Montville and Wenny 1990). The r.c.d. delivery specifications are 2.3 mm, but we set our target at 3 mm.

Cold Hardiness, Extraction, and Cold Storage

As early as the first of October, seedlings may become purplish in their needles, which indicates carbohydrate accumulation and the beginning of physiological changes caused by cooler temperatures and reduced photoperiod. Beginning around mid-October we allow air temperatures within the greenhouses to go ambient, but maximum temperatures are kept below 16 °C. Temperatures remain about ambient until seedlings are packed for cold storage in early January. However, minimum temperature allowed in greenhouses is –2 °C, and the rootplug is prevented from remaining frozen. By this time, the LD_{50} for cold hardiness is more than –20 °C. From late October until trees are put into cold storage, irrigation is necessary only about once every 3 to 4 weeks.

We thoroughly water seedlings before removing them from their containers. For large reforestation orders, we place 20 seedlings into nonsealed plastic bags, and 25 bags are placed upright into a reusable, poly-lined and sealed wax box. For small public sales, we place seedlings into sealed plastic bags in groups of 20 or 5, depending on container type. Our seedlings are stored at 0 to 2 °C. We have successfully stored seedlings in this manner for up to 9 months.

INTEGRATED PEST MANAGEMENT PLAN

At the Forest Research Nursery, three main pests threaten larch crops: *Fusarium* diseases, *Botrytis cinerea* (gray mold), and Lepidoptera larvae. Our pesticide philosophy is based on monitoring and sanitation. Stressing a clean growing environment has allowed us to drastically reduce our pesticide usage (Dumroese and others 1990). For one crop, for example, we applied pesticides only four times, twice for damping-off and twice for larvae. We apply pesticides only as a last resort.

Fusarium Diseases

Fusarium can be a major problem with growing container seedlings. It can elicit disease as damping-off, cotyledon blight, hypocotyl rot, or root disease. *Fusarium* inoculum is everywhere, and prudent managers will develop an integrated pest management plan to manage this pathogen (James and others 1990). A major inoculum source is previously used containers (James and others 1988). We immerse used containers in hot water (77 °C) for 15 seconds for hard plastic containers or 1 minute for styroblock containers to remove inoculum.

After planting, we rely on proper cultural practices to reduce damping-off: maintaining low medium pH with acidified irrigation water, using white silica grit to allow air circulation around the root collar zone, keeping relative humidity low, and delaying nitrogen fertilization until germination is complete. During daily inspections, we remove germinants showing symptoms of damping-off and tally losses by seedlot. Also during this period, seedlings with retained seed coats may show signs of cotyledon blight, needles necrosis originating at the seed coat. We also remove these seedlings. If our threshold damage levels are exceeded, we may apply fungicides for control (Dumroese and Wenny 1992b).

Once stems lignify, seedlings may begin to show symptoms of *Fusarium* root rot: chlorotic needles that turn necrotic, resulting in the seedling turning brown to red-brown and dying. The seedling tip may also wilt into a shepherd's crook. Again, we remove infected seedlings and cells as soon as evident.

Botrytis cinerea

From mid-September until the seedlings are shipped for planting, infection by *Botrytis* is inevitable. The symptoms are webs of gray to gray-brown mycelium growing on and around dead and dying needles that have either fallen from seedlings or are still attached. Tan or brown-watery stem lesions may also be present. Levels of *Botrytis* will increase as needles begin to drop.

Sanitation and cultural control is the best way to manage this disease. Keeping relative humidity low and increasing aeration help reduce spore germination and further growth of the fungus (Sutherland and others 1989). We accomplish this by watering less frequently and early in the morning, improving ventilation by spreading containers apart, regulating temperature, or some combination of these. We use an under-bench, forced-air ventilation system, shown to improve aeration and reduce disease incidence (Peterson and Sutherland 1990). We also add a spreader (R-11®) to irrigation water to foster evaporation from needles and brush foliage with a piece of plastic pipe to gently remove water droplets from needles. Having shorter target heights and growing seedlings at a slower rate also decreases disease incidence (Dumroese and others 1990).

Removing dead material from the growing area also reduces disease incidence (Sutherland and others 1989; Wenny and Dumroese 1987). We routinely inspect larch and remove any dead seedlings, especially after budset initiation treatments. As the season progresses and needles begin to drop, an appreciable accumulation of needles can develop on top of containers. This mat of needles is slow to dry after irrigation and can be an excellent location for *Botrytis* development. We use a shop vacuum to remove this layer of dead needles and find it helps reduce *Botrytis* incidence (Dumroese and Wenny 1992a).

We routinely inspect seedlings in cold storage for *Botrytis*. Preventative methods are the best way to control this problem and include the following: (1) pull, wrap, and store only vigorous, disease-free seedlings; (2) store seedlings for the shortest duration possible; (3) routinely inspect a sample of each lot, especially lots containing significant quantities of dead needles as these can be an initial food base for the pathogen; (4) if possible, immediately ship seedlings showing mold problems (Sutherland and Van Eerden 1980). Mold growth can also be reduced by dropping the storage temperature for fully hardened seedlings to below freezing.

Lepidoptera Larvae

This pest is more of a nuisance than a cause of damage, although affected areas can be severely ravaged. Pest incidence is also higher in the spring. We refrain, if possible, from using photoperiod lights until the spring solstice, thereby reducing attraction of adults to nursery lights until later in the season. When daily checks show damage, we determine if it is isolated or widespread. If isolated, larvae are hand picked, and the isolated area is sprayed with *Bacillus thuringiensis* (Dipel 2X®). If widespread, we treat the entire crop with *Bacillus thuringiensis* twice, 2 weeks apart.

RESULTS AT OUR NURSERY

Using this regime and pine cells, we are able to consistently grow western larch seedlings 20 cm tall with r.c.d. between 2.5 and 3 mm (fig. 2). About 99 percent of total seedlings requested are delivered with a nominal 10 percent oversow. We avoid pesticide control of *Botrytis* by sanitation and cultural manipulation of the crop.

Decreasing seedling density and increasing available rooting volume by using styro 20's allows us to increase fertilizer application rates and to grow seedlings averaging 50 cm tall and 6 to 9 mm r.c.d. (fig. 2). These larger seedlings work well on sites with brush competition or browsing. Chemical root pruning allows easier lifting from containers, less worker fatigue, and improved root egress.

Figure 2—Seven-month-old western larch seedlings grown in styro 20's (left) and pine cells (right).

We feel the most important aspect of any growing regime is continually monitoring seedling growth as the regime progresses. Height and r.c.d. measurements can then be used to modify or change the regime as seedling growth dictates during one growing season and between growing seasons. We have developed this regime from 10 years of records on fertilizer application rates and resultant seedling growth, and we plan to modify it in the future in pursuit of high-quality western larch seedlings.

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The Role of *Larix* in Icelandic Forestry

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Abstract—During the last decade considerable changes have occurred in Icelandic forest policy and larch planting. Forests for land reclamation and recreation are now priorities. Larch is eminently suited for both priorities. Today foresters are looking at several larch species for planting and for trials, and accelerated breeding programs have begun. The inland areas of East and North Iceland have proven to be the most suitable for larch cultivation.

CLIMATE

Iceland lies on the northern reaches of the cold-temperate, climatic zone, between latitudes 63° and 66° north. The climate is maritime, with short, cool summers and long, but relatively mild winters. The weather is unstable, which is due to the country being situated on the boundary zone of two, very different air currents, one of tropical origin and the other polar. Consequently a constant stream of low pressure cells pass over the country, especially during winter. Although Iceland is not very large there are considerable variations in climate between the different regions. This is most noticeable with respect to windiness and precipitation. Furthermore the length of the growing season varies considerably between regions. Climatological data from five weather stations is presented in table 1 and their geographical positions are shown on figure 1.

Ragnarsson (1990) divides Iceland into several climatic regions, maintaining that production forestry is a feasible proposition in three of these regions. Icelandic forestry is predominantly based on introduced species of which the genus *Larix* is the most important. The climatic regions are shown on figure 2, from which it can be seen that 11 percent of the land area is suitable for forestry (Ragnarsson 1990).

SOILS

Iceland is built up by basaltic eruptions, which occurred during the Tertiary and Quaternary periods along the Mid Atlantic Ridge. The older Tertiary formations, known as the Plateau Basalts, are found in the eastern and western parts of the country. Whilst the younger, the Palogonite Formations, occur along the central part, where volcanic activity still occurs (Kjartansson 1956).

The inorganic fraction of Icelandic soils is basaltic in origin and, on freely drained sites, soils have an acidity of around pH 6,5. For the most part the soils are built up of loess, within which a variable number of volcanic tephra layers occur. Commonly they are from 0,50-1,00 m thick, but can be 5-6 m in thickness near to the active volcanoes. One characteristic of such soils is that they are prone to frost heaving (Jóhannesson 1960).

NATIVE WOODLANDS

Birch (*Betula pubescens* Ehrh.) is the only native species in Iceland that forms woodland. Other woody species associated with the birch are: the willows (*Salix lanata* L. and *S. phylicifolia* L.), which are common and abundant all over Iceland; rowan (*Sorbus aucuparia* L.), which is found in most districts as a scattered component of the woodlands and the very rare aspen (*Populus tremula* L.), which has only been found on six sites in the North and the East (Davidsson 1980).

Today the area of natural woodland covers 1 to 2 percent of the land, but originally covered at least 30 percent prior to settlement, some 1,100 years ago (Sigurdsson 1977; Thorsteinsson 1972).

CULTIVATION OF *LARIX* IN ICELAND

The earliest larch trials were established just after the turn of the century. European larch (*Larix decidua* Miller) and Siberian larch (*L. sibirica* Ledeb.) were planted as specimen trees or in small groups. At this time the Russian (or Sukachev) variety (*Larix sukaczewii* Dylis) had not been separated from Siberian larch (Dylis 1947). Hence all early imports are designated under Siberian larch.

The first larch stand of any extent was established with the planting of 1 hectare, of Archangel provenance, at Hallormsstadur in East Iceland, in 1938 (Bjarnason 1957). It was inspired by the promising growth of some of the earlier plantings, especially in the inland areas of the North and East of the country. Planting of larch on a nationwide scale began in 1951 when a Siberian provenance, from the Khakass Autonomous Oblast, was introduced. Since then Siberian and Russian larches have been planted annually, with the greater area in the northern and eastern districts. Today Russian larch is the most commonly planted exotic in Iceland (Blöndal and Benedikz 1990). Up to and including 1992 some 7 million larch seedlings have been planted, of which 97 percent are of the Siberian and Russian species.

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Table 1—Climatic data from five weather stations,1971-1980

Station	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**
	(m)	------*° C*------		----*-Days*-----		*° C*	*d.d*	------*mm*------		*Percent*
Reykjavík	52	9.2	11.9	12	162	0.8	560	799	315	53
Lambavatn	5	8.6	11.0	8	148	0.1	463	993	387	79
Akureyri	23	9.0	13.0	49	142	0.8	524	470	144	68
Hallormsstaour	60	9.2	12.7	43	143	0.2	498	757	183	77
Sámsstaoir	90	9.6	12.8	26	168	1.2	651	1,273	530	58

Explanations: 1. Elevation (m); 2. Mean summer tetratherm (June-Sept.) in ° C; 3. Mean max. summer tetratherm (° C); 4. No. days with max. temp. >15 ° C; 5. Growing season (No. days = 5 ° C); 6. Mean temp. Feb.-March ° C; 7. Temperature sum above 5 ° C in day-degrees; 8. Mean annual precipitation (mm); 9. Mean precipitation May-Sept. (mm); 10. Calmness - percent days where wind speed is 0-3 on Beaufort scale.

Refs.: Columns 1-4, 6, 8, and 9 from Ragnarsson, H. (1990); columns 5, 9, and 10 from Gíslason, H. (1989). Both sets of data taken from records of the Icelandic Meterological Office.

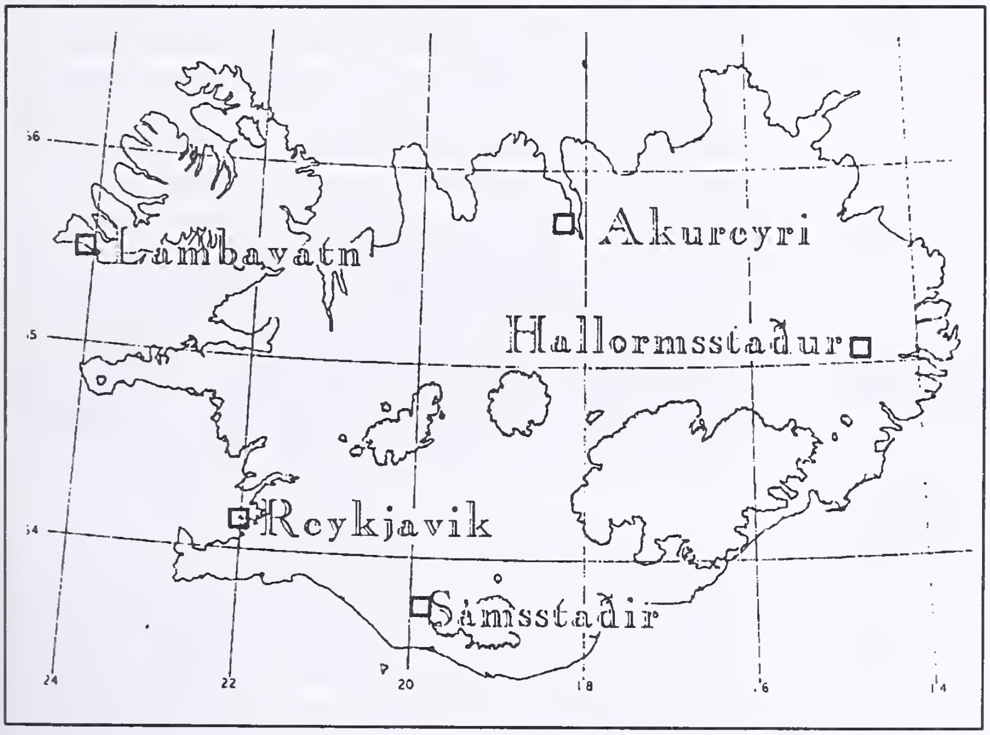

Figure 1—Map of Iceland showing the location of the weather stations in table1.

Figure 2—Map of Iceland showing the division of the country into forestry areas (from Ragnarsson 1990). Darkened areas are suitable for reforestation with exotics.

NATIONAL SURVEY OF LARCH PLANTATIONS

In 1985 the Iceland Forest Service made a countrywide survey of the growth of larch stands (Snorrason 1987). The survey covered 144 stands planted in 1965 and earlier (fig. 3). The conclusions from the survey were:

- Inland sites in the North and East are, climatically, the most suitable for cultivating larch as a timber crop.
- *L. sukaczewii* and *L. sibirica* are the most promising larch species.
- *L. sukaczewii* generally shows better stemform than other species and the northernmost provenances were, generally, the best.
- There was greater variation in growth and form within populations than between them.
- Site fertility has a greater influence on form and volume production than origin does. This was the only factor to be proven statistically in the survey.
- Larch has little future as a timber tree in South Iceland except, possibly, on inland sites.
- Increased and better designed silvicultural research is essential if larch cultivation is to be improved.

SEED PROCUREMENT

In view of the above conclusions the difficulty of obtaining seed from Archangel district, where the most suitable provenances originate, is a serious problem.

From 1949 to 1968 some 110 kg of seed from seven provenances from Archangel district was obtained. However, between 1969 and 1989 only a single 10 kg lot (in 1984) was acquired and even that seed (from Plesetsk) was purchased from Sweden (Blöndal and Benedikz 1990). In 1990 50 kg of larch seed from the Pinega River area in Archangel district was obtained (Snorrason and Blöndal 1990).

Between 1951 and 1977 some 15 kg of seed was procured from larch plantations in Finland and Norway (Blöndal and Benedikz 1990). All the Finnish stands could be traced back to the renowned larch plantation at Raivola in Russian Karelia, which had been established in 1738, using seed from the Archangel district (Heikinheimo 1927; Hagman 1990).

Larch seed orchards were first established in Finland and Sweden in the mid-1950's. Other orchards were established there and in Norway between 1961 and 1974. The largest are in Finland and were established between 1971 and 1974. All the clonal material in these orchards originates from Archangel district with the exception of a small orchard built up of Siberian material (Blöndal and Benedikz 1990). Scandinavian seed orchards are the main source of larch seed for Icelandic forestry today. The first batch of improved seed was acquired in 1969 from the Mo och Domsjö orchard in Sweden and this was the only source of Russian larch sown in Iceland until 1981. After which seed was obtained from Norwegian and other Swedish orchards. Since 1986 nearly all larch seed has been obtained from Enso-Gutzeit's orchard at Imatra

Figure 3—Regional Division of Iceland, 1-10, and the locations of the sample plots, black dots, surveyed 1985.

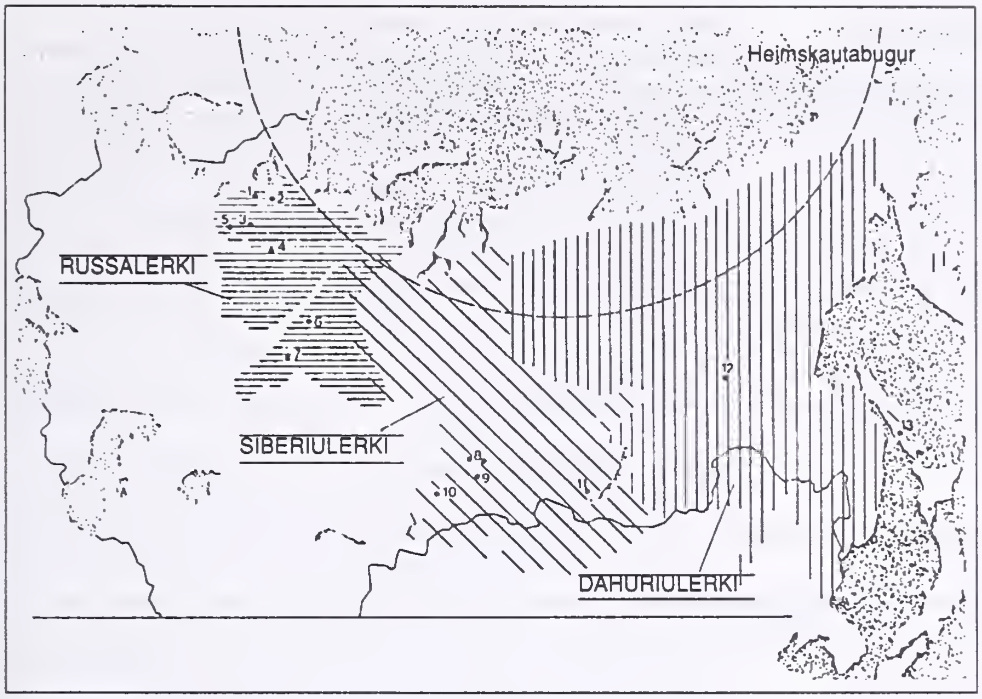

Figure 4—The map shows the distribution of the three contiguous larch species growing in the Soviet Union and the origin of the provenances in the Iceland Forest Service survey of 1985 (from Snorrason 1987).

in Finland. Up to and including 1991 some 216 kg of seed have been procured from Nordic seed orchards.

During this period it was much easier to get seed of Siberian larch from natural stands. The first introduction of certified origin came from the Sayan Mountains in Khakass A.O. in 1947. Up to 1986 some 166 kg of Siberian larch seed has been sown in Icelandic nurseries, most of which has come from the Altai region (fig. 4) and nearly all collected in natural forests.

During the last decade considerable changes have occurred in Icelandic forest policy and with it a change in the objects of larch planting. Forests for land reclamation and for recreation are now priorities. Larch is eminently suited for planting on eroded land and is much sought after for planting for recreation purposes. In both cases lower demands are made as regards to form and growth rate and there has been a considerable increase in larch planting outside of its optimum area.

Today foresters are looking at other larch species for these purposes and for trials in the areas not considered suitable for the Russian and Siberian varieties. Namely: European larch; tamarack (*Larix laricina* [Du Roi] K. Koch) and hybrid larch (*L.* x *henryana* Rehder.). Up to now plant production of these species has been very small, for instance only 13 kg of European larch seed were imported from 1900 to 1990, and virtually no provenance research has been made on these species.

TREE IMPROVEMENT WORK

Research work into accelerated breeding of larch has been started in Iceland. This is based on greenhouse production seed from superior clones of Russian and Siberian larch. Further work on hybridization of various larch species is proposed at a later stage (Eysteinsson 1992). In addition a project has been initiated to establish a seed orchard of Russian larch abroad. Larch produces seed in Iceland but due to the unstable winter climate seed viability is very low (Anon. 1993).

SPECIES OF *LARIX* PLANTED IN ICELAND

Table 2 lists all species of larch which have been tested in Iceland. For some species only a few specimen trees occur, namely *Larix kaemferi* Sarg. and *L. occidentalis* Nutt. and experience is extremely limited, as it is with some of the species described below.

ECOLOGICAL STATUS

As mentioned earlier by far the greater proportion of larch in Iceland is of the Russian or Siberian species. Hence the following remarks pertain more or less to our experience of their cultivation. More experience is needed on the cultivation of the three other species of interest, *L. decidua*, *L. laricina* and *L.* x *henryana*, before any definite conclusions can be made on their general suitability.

Optimum Regions

The inland areas of East and North Iceland have proven to be those most suitable for larch cultivation. Of the sites shown in table 1, Akureyri and Hallormsstadur fall within this zone. The climate there is less maritime than at the other stations and it is of interest that the only climatic parameters which differ to any degree are:

- Number of days with maximum temperature = 15 °C.
- Mean temperature for February-March.
- Frequency of calmness.
- Precipitation during the growing season.

Therefore one can assume that it is these parameters which are of importance for the success of the larches.

Table 2—Icelandic experience with various species of *Larix*

Species	Year	Introduced No. of provenances			Conclusions				
		Nat.	Plt.	S.O	Exp.	Stem	Yield	Fr.	Dis.
L. sukaczewii	1913	13	7	11	++	++	++	—	—
L. sibirica	1951	13	—	1	++	+/+	++	+	+
L. decidua	1905	16	2	—	+	+	++	++	—
L. gmelini v. *japonica*	1950	—	2	—	++	+	+	+	—
L. laricina	1951	6	—	—	+	+	+	—	—
L. gmelini	1956	5	—	—	(+)	+	+	—	—
L. x *henryana*	1957	—	3	3	+	++	++	++	—
L. lyallii	1970	3	—	—	++	+	+	—	—

Explanations:
Nat. = natural stands.
Plt. = plantations.
S.O = seed orchards.
Exp. = experience: ++ considerable, + limited, ++ very limited (+) virtually failed.
Stem = stem form: ++ very good, + good, +/+ variable, + poor.
Yield = ++ vigorous, + reasonable growth, + slow.
Fr. = frost susceptibility: ++ very susceptible, + susceptible, — fairly good resistance.
Dis. = susceptibility to die-back disease: + susceptible, — occasionally infected or no records.

Optimum Sites

Snorrason (1987) showed that the most vigorous larch stands were found on moist, freshly-drained soils. They were characterized by a mixed forb-grass vegetation (Ragnarsson and Steindórsson 1963), in which *Geranium sylvaticum* L. and *Equisetum arvense* L. occur with various grasses such as *Hierochloë odorata* (L.) PB., *Agrostis tenuis* Sibth. and *Deschampsia flexuosa* (L.) Trin.

Pioneer Qualities

Larches have shown themselves to be able to colonize various sites, such as eroded land, gravel, and on sparsely vegetated soils characterized by *Kobresia myosuroides* (Vill.) F. & Paol., *Empetrum nigrum* L., and, *Dryas octopetala* L. Once the canopy closes, which is after about 15 years, the vegetation completely changes. First to gramineous species (Óskarsson 1984) and with increasing canopy height various forbs such as *Geranium sylvaticum*, which characterizes the vegetation mature woodlands, together with various grass species.

Mycorrhiza

Association with mycorrhizal fungi is one of the reasons for explaining the larches' ability to succeed on the poor sites described earlier. At first only the bolete (*Suillus grevillei* [Klotzch.] Sing.), was known to form mycorrhiza with larch and it is found wherever larch is cultivated. Two other species, known to form mycorrhiza with larch in its native habitat, *Tricholoma psammopus* (Kalchbr.) Quel. and *Gomphidius maculatus* (Scop.) Fr., have recently been found on larch in East Iceland (Hallgrímsson 1987).

Colonization

In 1966 naturally regenerated seedlings of Russian larch were found for the first time in the 1938 plantation at Hallormsstaour. Today hundreds of self-sown larch trees can be found adjacent to this stand. Natural regeneration of both the Russian and Siberian species occurs at several other woodlands.

Mixtures

Larch has generally been planted as a monoculture in Iceland. However, a few small areas, which were planted up as mixtures with Norway spruce (*Picea abies* [L.] Karst.) 30 to 40 years ago can be found. Norway spruce thrives in mixture with the larch, as do other spruce species, such as sitka spruce (*Picea sitchensis* [Bong.] Carr.) and the hybrid *P.* x *lutzii* Little. In these mixtures the spruce seems to be the main benefactor as it is usually more vigorous and of a more healthy color than in pure stands. While the spruce grows more slowly initially it seems likely that it will catch-up with the larch eventually.

A similar, nursing effect can be seen on lodgepole pine (*Pinus contorta* Dougl. ex Loud.) in mixtures with larch, although not to the same extent. The benefits of planting hemlocks (*Tsuga heterophylla* [Raf.] Sarg. and *T. mertensiana* [Bong.] Carr.) under larch canopy has also been observed. The hemlocks being, apparently, healthier and more vigorous under larch than under birch.

Mixtures of spruce and pine with larch are now more frequently used on open (deforested) areas by the Iceland Forest Service. This is not only to nurse the evergreen species, which benefit most from mixtures, but also as an insurance against total failure of one of the crops.

Disease

Around 1970 a die-back disease became apparent on larch and was observed in most parts of the country. The disease was diagnosed as being caused by *Phacidium coniferarum* (Hahn) DiCosmo, Nag Raj & Kendrick (Roll-Hansen & Roll-Hansen 1971). The symptoms appeared following several cold summers at the end of the 1960's and in the wake of two climatic blows during 1964 and 1966. There was a slight amelioration in the climate during the next decade and the disease incidence fell, leaving behind stands of deformed larch in the areas where its cultivation was borderline. It was observed that the effects of the disease depended on (1) species, (2) provenance, and (3) climatic factors. The greatest danger occurs during late winter when a warm spell breaks dormancy and the trees are damaged by a following cold spell, which all too frequently occurs.

Pests

So far no serious insect pests have been found on larch in Iceland. The only species that causes significant damage is the weevil (*Othiorrhyncus nodosus* Müller) whose larva feed on the roots of seedlings, often killing young plants (Hallgrímsson 1992). The seriousness of the damage has only recently been realized, and its extent has yet to be established.In view of the importance of larch, investigations into weevil damage have been initiated (Anon. 1992). It is very likely that this insect has been responsible for much of the mortality recorded in other young conifer plantations as it is not species specific.

In East Iceland feral reindeer occur and they have caused considerable damage to young larch plantations during snow-heavy winters. Reindeer are confined to the East and are not a problem in other regions.

SILVICULTURE OF LARCH IN ICELAND

Planting Stock

Until the early 1980's planting stock was raised as 4-year-old transplants (2/2). They were planted with a Norwegian-type mattock until 1960, after which a semi-circular spade was used. Since the 1980's the bulk of larch planting-stock has been in container trays, usually as 1/0 seedlings in 50 ml plugs. If more vigorous stock is needed then 2/0 seedlings in 100 ml or 150 ml plugs are planted. Where possible the soil is worked prior to planting, either disced or plowed, and drained if necessary.

Russian larch seed, which generally shows a lower germination than that from Siberia and is heavier, yields on average from 25,000 to 40,000 plants/kg.

Planting Density

Today larch is planted at a density of 2,500 to 4,000 seedlings per hectare. The various provenances are variable as to their form and the planting density varies according to the provenance chosen. Initial density is more important when the aim of the plantation is timber production and greater demands are made on stem quality. Relatively dense plantations are made in order to have a choice of stems and to ensure clear and knot-free (small knotty core) stemwood during the first 20 years of the rotation. For recreation and land reclamation forests fewer trees are planted, 2,500/ha.

Thinning

Using the above-mentioned densities it is expected that the stands will need thinning after 20 to 30 years and that it is possible to fell 30 to 40 percent of the trees at the first thinning. Present practice assumes that the stands will be thinned 2 to 4 times over the rotation, depending on the fertility of the site and the objects of the planting. Hence recreation areas will be more open than production forest and normally as mixtures of species. The trees in recreation woodland are expected to have larger and deeper crowns than in production stands.

Larch stands are expected to have a rotation of 80 to 120 years and the final crop to be 400 to 600 stems/ha.

YIELD

Permanent yield plots have been established in several larch stands at Hallormsstadur in East Iceland, which is considered the optimum region for larch. The 1938 stand, which originates from Archangel, has a mean annual increment (mai) of 7 m^3/ha at 50 years of age. In younger stands in that area, planted between 1951 and 1965, yields of 3-5 m^3/ha are recorded (Benedikz 1986). These are lower yields than from the older stand and it is probable that the decrease in growth reflects the climatic deterioration which occurred after 1960, especially between 1965-68 when sea-ice lay on the northern and eastern coast-lines until mid-June.

Table 3 gives some idea on the growth of the various larch species cultivated in Iceland.

PRACTICAL USE OF *LARIX* IN ICELAND

Basically 3 uses are envisaged for *Larix* species in Icelandic forestry, as explained here and in table 4.

Wood Production

It is feasible to grow larch for timber production in the eastern and northern inland areas below 200 m elevation. Larch can be either planted pure or in mixtures with other timber species such as pine and spruce.

Shelterwood

Larch seems to be an ideal tree for nursing less hardy and more demanding species, such as sitka spruce in the

Table 3—Maximum height at diameter at breast height recorded on Icelandic specimens of various *Larix* species

Species	Age	Max. ht.	D.b.h.	Provenance
		m	*cm*	
L. sukaczewii	54	18.5	40	Archangel
L. decidua	84	17.0	56	Unknown
L. sibirica	41	16.0	—	Sayan Mtns.
L. laricina	36	7.6	—	Fairbanks, Alaska
L. x henryana	30	11.0	—	Scotland

Table 4—The practical use of *Larix* species in the various categories of forestry and horticulture in Iceland

Species	Soil prot.n /reclam.n.	Timber prod.n.	Recr.n.	Ornamental	Shelterbelts
L. sukaczewii	X	X*	X	X	X
L. sibirica	X	(X)*	X	X	X
L. decidua	(X)		X	X	X
L. laricina	(X)		X	X	
L. x henryana			X	X	X
L. lyallii				X	
L. occidentalis				X	
L. kaempferi				X	

(X) On a small scale. * Pioneer species.

South and West and for sitka hybrid and Norway spruce in the North and East. It can be planted without the expectation of getting utilizable timber, either as a pioneer for underplanting with less hardy but more valuable species or in a mixture at establishment.

Other Purposes

Larch has proved itself to be a valuable species for land reclamation, for planting in recreation areas, and for horticultural purposes.

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Silvics of *Larix principis-rupprechtii* Mayr.

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Huacheng Xu

Abstract—Prince rupprecht's larch (*Larix principis-rupprechtii* Mayr.) occupies the high-elevation mountains of northern China. Its values are not only for the high-quality wood it produces but also for protection of soil and water. Compared to other sympatric conifers, prince rupprecht's larch is shade intolerant, cold resistant, water sensitive, and widely adapted to different soil types. Its growth rate is higher than other sympatric evergreen trees, at least in the juvenile stage. Local seed source exhibits well in artificial regeneration.

Prince rupprecht's larch (*Larix principis-rupprechtii* Mayr.), a deciduous conifer, is an important forest species in the middle- to high-elevation mountains of northern China. It is valuable not only for high-quality wood but also for its multiple functions: protection for soil and water, habitat for wildlife, and esthetic beauty.

Prince rupprecht's larch belongs to the Pinaceae family. Within the *Larix* genus, it used to be recognized as a variety of other *Larix* species (Chinese Flora Editorial Committee 1978). Today, most taxonomists and botanists agree that *Larix principis-rupprechtii* Mayr. is a unique species although it is close to *L. gmelinii*.

NATURAL DISTRIBUTION

Prince rupprecht's larch (fig. 1) grows in a small range of northern China, ranging from 36°31' to 43°30' north latitude, and from 111° to 118° east longitude. It ranges north to Huangang ridge, Inner Mongolia Autonomous region, next to *Larix gmelinii;* south to Taiyue Mountains, Shanxi province, near to *L. chinensis.* It is believed that prince rupprecht's larch once occupied a much broader range in the temperate zone (Ma 1990). Increases in human population and clearcutting for crops have reduced the original habitat of larch to the high-elevation mountains. As a result, its distribution becomes discontinuous and islandlike today.

Elevational distribution of prince rupprecht's larch is from 1,500 to 2,800 m. In Hebei province, it grows naturally above 1,500 m in Weichang and Longhua; 1,800 m in Xinglong; 2,000 m in Tuoliang Mountains; and between 2,000 and 2,600 m in Xiaowutai Mountains. Of all stands, the biggest growing area is in Xiaowutai Mountains, about 6,267 ha. However, in northern Hebei, such as Weichang, which was a royal hunting field in the Qing Dynasty, the natural range of larch was much broader than it is today.

In Shanxi province, prince rupprecht's larch grows in the Heng Mountains (1,500 to 2,180 m), Wutai Mountains (1,600 to 2,800 m), Guanqin Mountains (1,750 to 2,600 m), and Guandi Mountains (1,850 to 2,600 m). The broadest range is in the Guanqin Mountains, about 12,360 ha.

HABITAT

Prince rupprecht's larch is shade intolerant, cold resistant, and widely adapted to a variety of soils. Mean annual temperature within the larch habitat is about –2 to –4 °C, mean temperatures are 15 °C in July and –20 °C in January. Annual absolute minimum temperature is –44.8 °C. The frost-free season varies from about 80 to 90 days. In Guandi Mountain, Shanxi, trees break buds when air temperature is 0 °C; needles begin to elongate at 2.7 °C; and pollen shed at 5 °C (Ma 1990), indicating strong cold resistance. There was no frost damage when 1-year-old seedlings were planted in Linkou, Helongjiang (latitude 45°17' north, longitude 130°14' east).

Prince rupprecht's larch is relatively sensitive to precipitation and soil moisture. Annual precipitation in larch habitat averages about 400 to 700 mm. Lower than 400 mm, such as in the mountains of steppe zone, no larch grow although temperature is suitable for it. Thus, drought sensitivity is another genetic characteristic of this species. Consequently, water deficiency becomes a limited factor to introduce larch to arid areas.

Compared with other evergreen conifers, prince rupprecht's larch exhibits lower drought tolerance and possibly lower water-use efficiency than its sympatric species: *Pinus tabulaeformis, Pinus sylvestris* var. *mongolica, Picea wilsonii,* and *Picea meyeri.* In contrast to *Larix gmelinii,* flood-tolerance of prince rupprecht's larch is lower.

Prince rupprecht's larch can grow in a variety of soils, such as drab soil and other soils developed from loess, but it grows the best in the mountain brown loam soil or brown-grey loam soils developed from granite, gneisis, and shale (Chinese Tree Species Editorial Committee 1978).

Natural stands of prince rupprecht's larch appear either to be pure or to grow with other tree species (Chinese Academy of Forestry 1953; Yu 1955). Above 1,800 m of altitude, it grows with *Picea wilsonii, Picea meyeri, Betula platyphylla* Suk., and *Betula albo-sinensis* Burkill; in the south of the range (low elevation), it grows with *Pinus tabulaeformis* and *Quercus* L. When growing with *Picea,* larch is always succeeded by *Picea.* Yu (1955) found that the ratio of the

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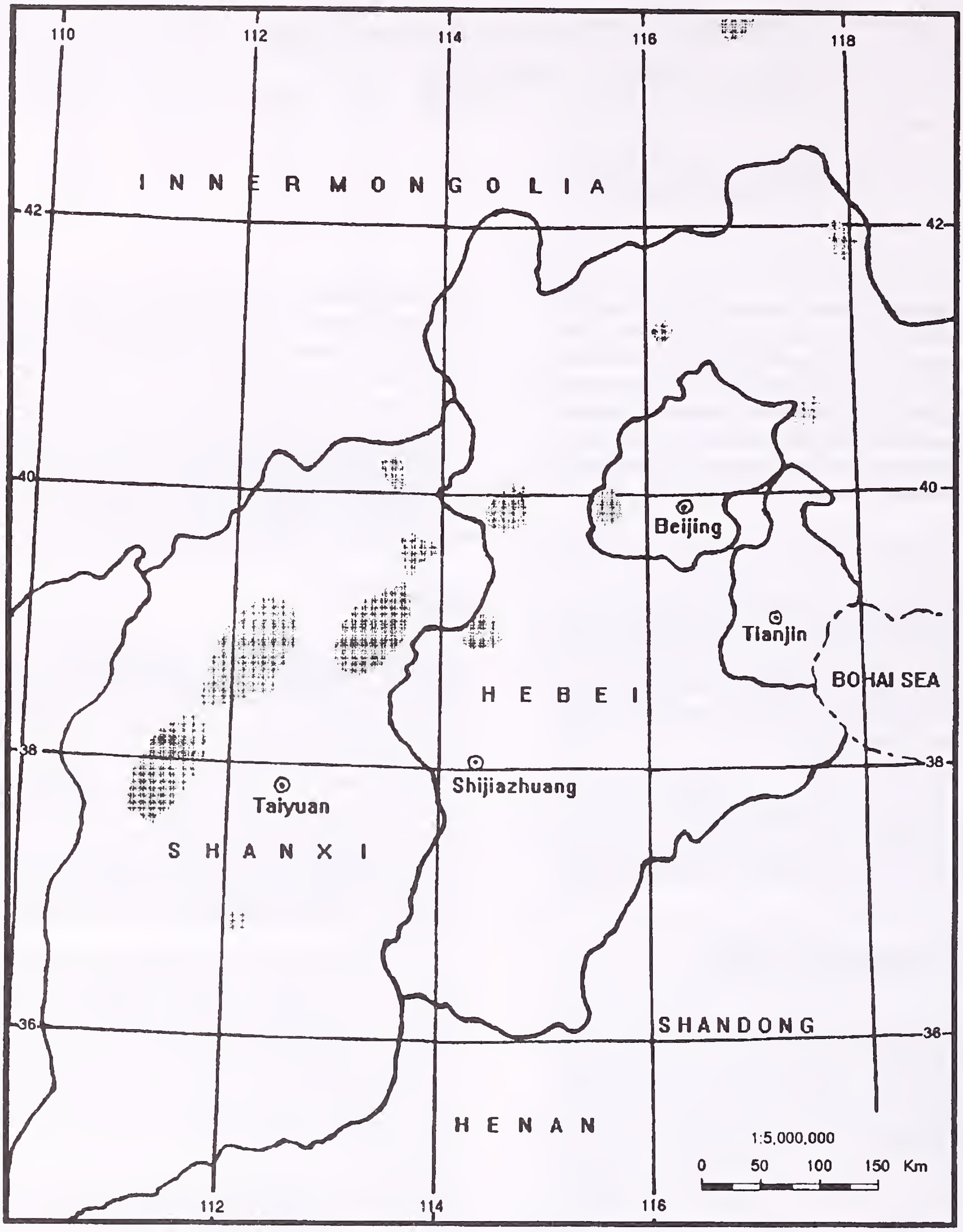

Figure 1—The natural distribution of *Larix principis-rupprechtii* Mayr.

number of larch and *Picea* was always smaller in mature stands than in younger stands, indicating the trend of succession.

GENETICS AND BREEDING

The basic karyotype of prince rupprecht's larch observed from root tip materials (Zhang and others 1985) has shown clearly that the diploid chromosomes are 24, the same as other *Larix* spp. However, *Larix principis-rupprechtii* and *L. sibirica* have 12 chromosomes with median centromere and 12 with submedian centromere, whereas *L. gmelinii, L. leptolepis,* and *L. olgensis* have 12 with median centromere, 10 with submedian centromere, and two with subterminal centromere. According to karyotype classification, Zhang and others (1985) suggested that the evolutionary trend of *Larix* species was from *L. sibirica* to *Larix principis-rupprechtii* to the other three species. *Larix* (with an asymmetrical 2A or 2B type) should be a more evolved genus than *Pinus* (with a symmetrical 1A type).

Tree improvement of prince rupprecht's larch started in 1965. In the early stage, seed stands were selected, rogued, thinned, and managed to produce seeds for reforestation. As a result, the proportion of sound seeds to seed weight was superior to seeds from nondisturbed stands (Chinese Tree Species Editorial Committee 1978). Since the 1960's, several hundred plus trees have been identified. These phenotypically superior trees have been grafted into clonal seed orchards (Fu and others 1989).

Provenance testing of prince rupprecht's larch started in 1980. Preliminary results have been reported (Ma 1990): (1) for seedlings from lower latitude, such as the Guandi Mountains, height growth is slightly superior to seedlings from the north but statistically not significant; (2) the ratio of roots to shoot length was higher in northern provenances than in southern ones, indicating different drought tolerance; and (3) there were no differences in frost resistance, needle morphology, and phenology among provenances. It has been suggested, in this regard, that regeneration should use local seed sources.

Although only one paper of progeny test results has been published, several progeny trials have been established. According to Zhang (1980), significant 4-year height differences were detected among families. Individual heritability for height averaged 0.22 but varied with age.

In conclusion, variation among families within population is more pronounced than variation among populations in prince rupprecht's larch. Because the natural distribution of this species is limited to a narrow area within one climatic zone and high elevations near timber line, population variation should not be great. On the other hand, the microclimate along the mountains of northern China varies tremendously, indicating high pressure of natural selection. Not surprisingly, natural selection causes family differentiation.

Interspecific hybrids of prince rupprecht's larch and *Larix leptolepis* have exhibited substantial heterosis. Height and diameter were about 30 and 15 percent greater from hybrids than from open-pollinated seeds (Wang and Ding 1987). Heterosis for cold tolerance, resistance to *Guignarclia laricina* and mice were higher in Bengxi, Liaoning (Wang and Ding 1989). However, according to Kurahashi's (1988) investigation for 30 years, the hybrid of prince rupprecht's larch and Japanese larch has lower resistance to vole and hare damage than other combinations such as *Larix gmelinii* x *L. leptolepis.* Because most foresters think that prince rupprecht's larch is close to *L. gmelinii,* we believe that both species can be easily crossed.

GROWTH

Prince rupprecht's larch is one of the fastest growing species. Height and diameter growth rate of larch is two to three times faster than *Picea* in 50-year-old stands in Guanqin Mountains of Shanxi and substantially faster than *Pinus tabulaeformis* at age 30 in Xiaowutai, Hebei province (Hebei Forest Editorial Committee 1988).

Maximum height growth of larch takes place about age 20, whereas maximum diameter growth at breast height (d.b.h.) occurs at about age 30. In Guanqin Mountains, average timber production was 187.5 m^3/ha in a 25-year-old stand, and 309 m^3/ha in a 40-year-old stand (Hebei Forest Editorial Committee 1988).

Larch has two maximum annual growth periods in diameter and one in height (Zhang and others 1987). Height growth is in late June and early July. The first diameter growth period is in late May and early June; the second one is during August. Clearly, as soon as the early needles completely elongate (middle May), they begin to fix carbon through photosynthesis. In this time the cambium becomes a carbon sink. Later, photosynthesis supports the height growth as the meristem is a sink prior to the second diameter growth.

Although prince rupprecht's larch grows in high-elevation mountains, its growth rate is higher in low elevation within its range. Average height and d.b.h. were 10.89 m and 10.40 cm, respectively, for 30-year-old larch at 2,000 to 2,200 m altitude in Guanqin Mountains. As altitude increases to 2,600 to 2,800 m, height and d.b.h. were 6.09 m and 7.05 cm, respectively. Similarly, latitude influences growth. Within Shanxi, the growth rate of stands in the south is higher than in the north. One explanation for these trends is the length of growing season. At low elevation and low latitude, the growing season is longer.

The critical problems of reforestation in this species are the low germination capacity and the low survival in the seedling stage. To promote germination capacity and seed germination energy, Chang and Liu (1989) stored seeds in snow during winter with dehydration-rehydration twice. Seed germination capacity increased from 55.3 percent in control to 65.7 percent after treatment. Seed germination energy enhanced from 20.8 to 51.3 percent. Another method to increase survival of seedlings is to cut off part of the roots before transplanting them, which promotes more roots, increasing the area for more water and nutrients uptake (Lei 1985).

Competition for resources of larch with grasses and shrubs is weak in the juvenile stage. In the north of Shanxi, average height and diameter near ground were, respectively, 90 and 2.5 cm growing in open ground and 50 and 0.8 cm growing with shrubs in 7-year-old trees. However, when larch was intercropped with *Astragalus adsurgens*, an N-fixation grass, the survival of larch seedlings was 94 percent and height was 10 percent greater than that in a pure plantation in Xiji, Hebei (Wang and Sun 1987). We believe that nitrogen is a critical nutrient for larch growth, especially during the juvenile stage.

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Variability of Growth and Survival Among Families of a Widely Adapted Seed Source of *Larix Sibirica* in Finland

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Abstract—The Raivola seed source of Larix sibirica can be used over a wide geographic and climatic range in Finland. Phenotypic plustree selection has resulted into genetic gain in growth rate, compared to respective unselected stands. Further selection of clones is recommended as there exists genotype x environment interaction in the height growth. In the most northern localities, provenances from northwest Russia might survive better.

Siberian Larch (*Larix sibirica* Ledeb.) is an introduced tree species in Finland, but the nearest natural stands are growing only 200 km from the eastern border of Finland. Most Siberian larches planted in Finland originate from a single seed source, the so-called Raivola forest near St. Petersburg in Russia (fig. 1). Starting in 1738, this forest was established for ship-building purposes in several steps. First part of the trees originate from Archangelian area 600 km northeast and the second part comes from the Ufa region in southern Ural mountains about 1,500 km east of the forest (Metzger 1935). The proportions of these two origins are somewhat uncertain (Ilvessalo 1923). The planted forest proved to be very successful, stem volumes exceeding 1,000 cubic meters per hectare have been measured at the age of 183 years (Ilvessalo 1923). Consequently, seedlings of the Raivola origin were planted in Finland in 1865. Those trees are often considered as first generation provenance hybrids.

As a second step, offspring of these trees was used to distribute the species over Finland. Other seed sources were utilized in a few cases. Since the 1940's, about 100 trees of these second generation offspring have been selected as parent trees for breeding and grafted to the seed orchards. Most of the selected trees represent 2nd generation in Finland, and it is thought that natural selection during this period has created some level of adaptation on the local scale. In our study we test this hypothesis and investigate the potentials of further selection.

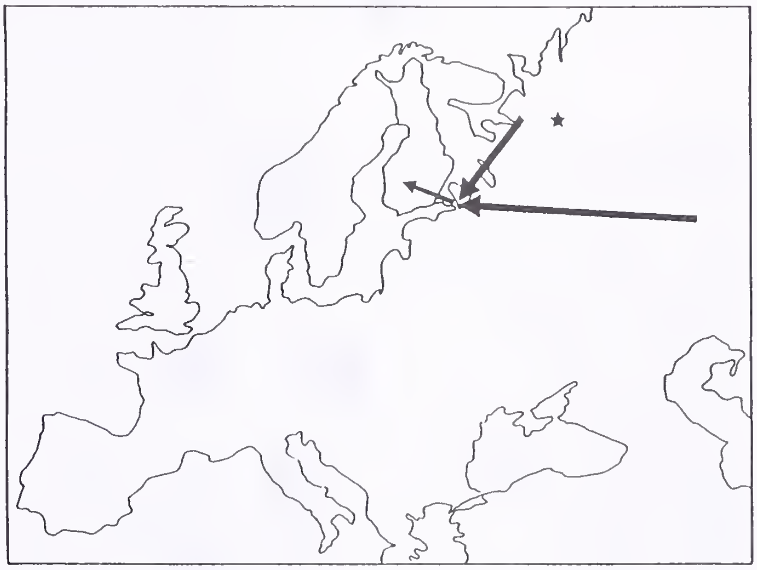

Figure 1—Thick arrows indicate the origins of the main provenances of Raivola forest, one from Archangelian area in the north and the other from Ufa in the east. Star indicates the Pinega area.

MATERIAL

The present material consists of 35 open-pollinated plustree families planted in two sets of trials, referred as A and B. Originally, 25 plustrees of Raivola origin were selected from three localities (A-C in fig. 2) in southern Finland. Remaining 10 trees belong to the Pinega provenance, originating 200 km east of Archangel (fig. 1). They were selected from a stand growing in northern Finland (area D in fig. 2). Northern and southern clones were grafted in separate seed orchards.

Trial A is planted on seven localities ranging from latitude 61°N in the south to the latitude 67°N in the north and trial B on two localities around latitude 67°N (fig. 2). Trial A comprises four families from area A, nine from area B, and 12 from area C. Trial B consists of the 10 northern progenies, two families from area C and two from area B. Unselected Raivola material from southern Finland and a Siberian provenance east of the Ufa region (about 62° E, 58° N) were planted as a control.

Randomized blocks design was used in all trials with a plot size of 25 trees and six to eight replications on each test site. Height and survival were measured at the age of 10 years. Plot means of height and percentage survival were used in the analysis of variance. Pairwise comparisons were based on Student's t-test.

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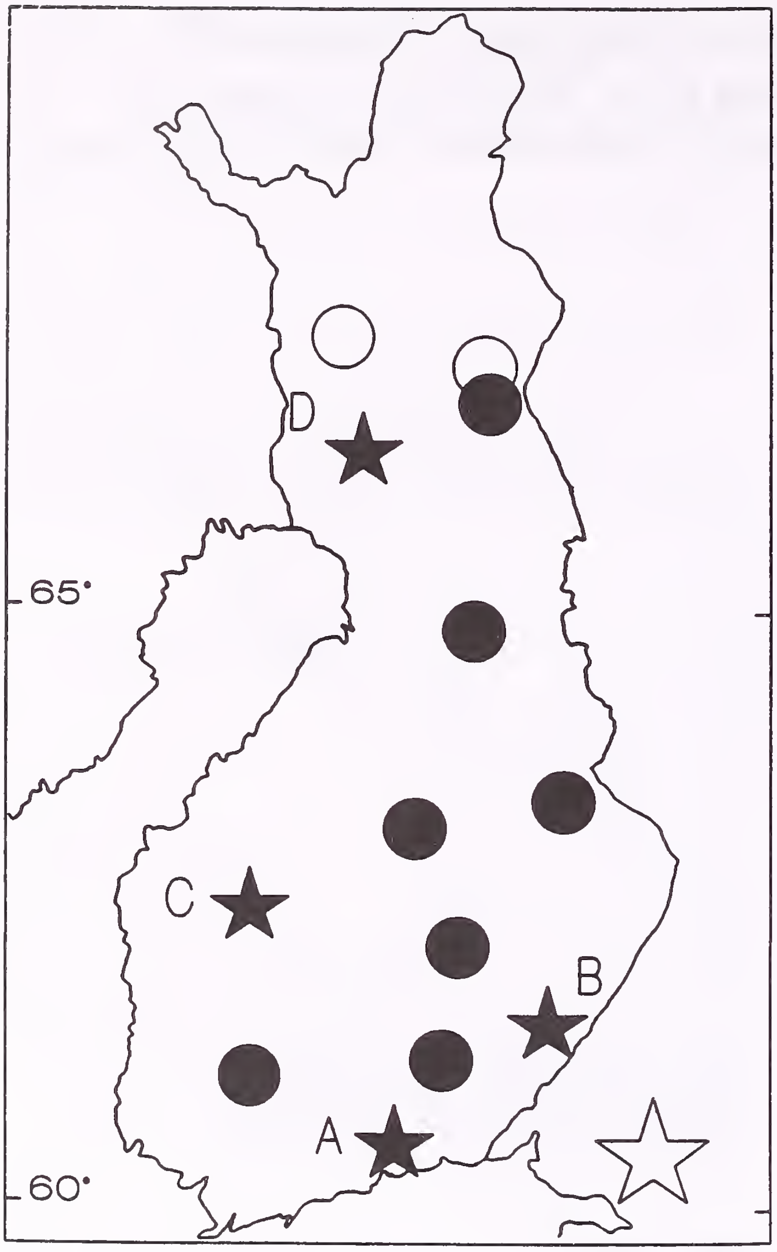

Figure 2—Test sites and plustree selection areas in Finland. Solid circles = trial A, open circles = trial B, solid stars = plustree selection areas A-D. Open star indicates the Raivola forest.

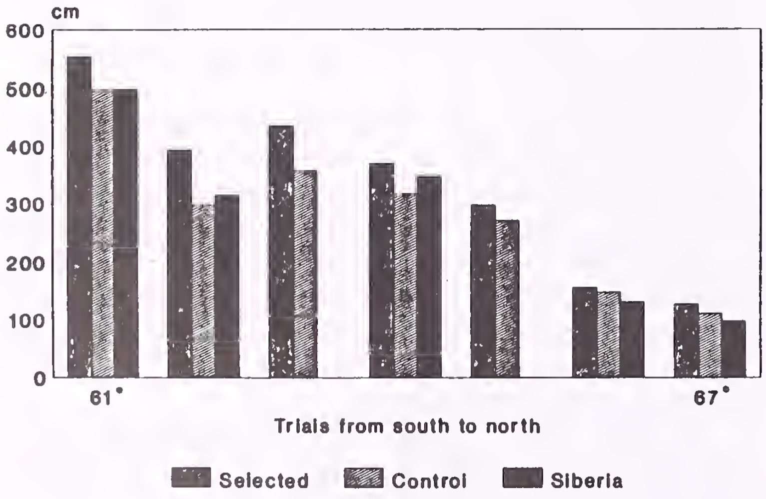

Figure 3—Mean height at the age of 10 years in test series A. Unselected Raivola material is used as the control.

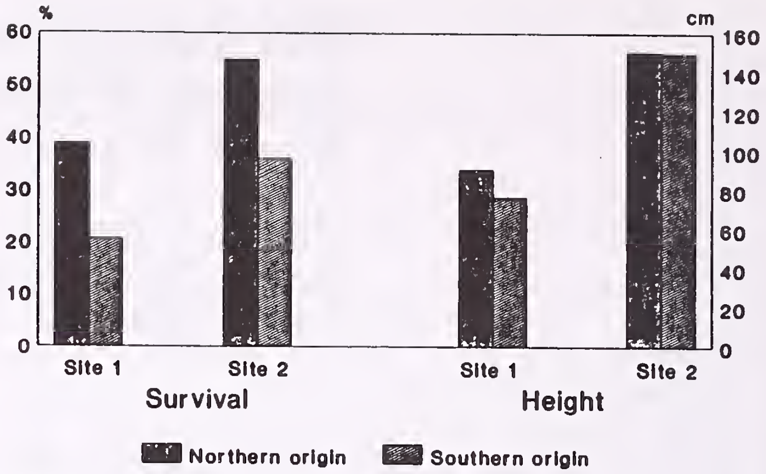

Figure 4—Mean survival and height at age 10 of the Pinega provenance ('Northern origin') and Raivola origin selected from Southern Finland ('Southern origin').

RESULTS AND DISCUSSION

10-Year Height

In general, the progenies of the selected trees grow significantly better (F=9.54, P<0.01) than the unselected Raivola material and better than the Siberian provenance (fig. 3). However, the measurements were taken at the age of 10 years and maternal effects due to seed size may still have some influence on the results.

The difference in height between Pinega plustree progenies and Raivola origin is not significant in trial B (see fig. 4). The result is slightly surprising because earlier results (Tigerstedt and others 1983) have shown that the growth of Raivola origin is better than that of Archangelian provenance. The expression of the possible hybrid vigor in the Raivola trees may be restricted to the southern areas. No difference could be detected between the groups A, B, and C in the southern plustrees.

The between-family component in height growth is significant (F=2.08, P<0.01) in the larger test series (A) indicating that there is potential for further selection among the southern clones. Also, interaction between family and test site is highly significant (F=5.10, P<0.001). The correlation coefficients between interaction effects (from analysis of variance) and estimated average annual temperature sum (with a threshold value of 5 °C, Kolkki 1966) of test site are statistically significant in the case of four families. More detailed, two progenies show a clear decreasing and also two progenies a clearly increasing trend along the south-north-gradient (fig. 5).

Survival of the Seedlings

Trial B shows that the seedlings of the Pinega provenance survive significantly better (F=26.1, P<0.001) than Raivola material in the northern areas. The effect is more pronounced in harsh conditions, when overall survival is low (fig. 4).

In trial A, mean survival of seedlings is reasonable high (40-50 percent) even in the northernmost localities, although the climatic gradient is very wide—annual heat sum ranges

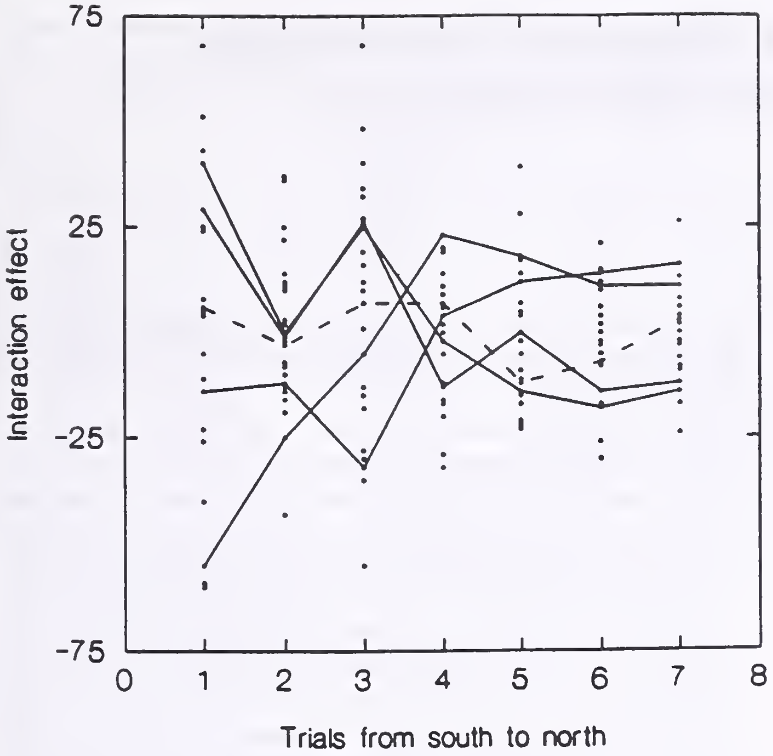

Figure 5—Family x test site interaction effects in the height of the southern progenies in test series A. Solid lines indicate the families with statistically significant increasing or decreasing trend, dashed line indicates the most stable family.

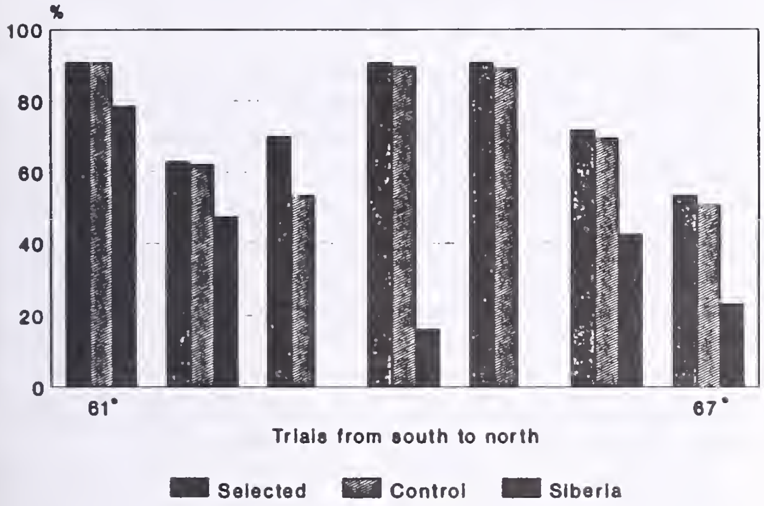

Figure 6—Survival at age 10 years of the seedlings in test series A. Unselected Raivola material is used as the control.

from 790dd in the north to 1270dd in the south. The Raivola origin survives far better than the continental Siberian one, especially in the north (fig. 6). The slight differences between the families were not significant, also the interaction between family and test site was not detectable. No significant differences in the survival between the three southern plustree localities (A-C) could be detected in this trial. It is possible that natural selection in the south has not been intensive enough to cause any measurable local adaptation. If this is true, we can treat all families originating from southern Finland as one group. However, all southern clones in this material are kept in the same seed orchard and free pollination may override the differences between the plustree origins.

CONCLUSIONS

The fairly good survival of the seedlings throughout trial A is consistent with the idea that the feasible utilization area of the Raivola origin is astonishingly wide when compared to the respective area of the native coniferous tree species in Finland (see Tigerstedt 1990). It is a very valuable source for forest regeneration. The northern Pinega provenance survives better in the most extreme localities and consequently, it might be reasonable to consider the usage of this provenance in the most northern localities. However, results on the yield of older trees are required.

Also, more precise selection of the clones is necessary, if further tests will confirm the genotype x environment interaction. Specifically, there is a good reason to restrict the utilization area of families showing correlation between annual heat sum and height growth.

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Stockability of Western Larch and Implications for Management

Frederick C. Hall

Abstract—Stockability of western larch (*Larix occidentalis*) is evaluated by use of growth basal area (GBA): the basal area at which dominant trees grow at 1.0 inch per decade in diameter (25 mm/dec). Data from 54 plant associations in eastern Oregon and Washington showed that western larch ranged from 45 to 210 percent of grand fir (*Abies grandis*) GBA. A range of 50 to 140 percent of normal basal area per acre (BA/A) was found, a threefold difference that suggests several productivity levels within a site index (SI) class. Site index class 100 varied from 40 to 135 cubic feet per acre per year for a 3.4-fold difference. In the grand fir/big huckleberry (*Vaccinium membranaceum*) association of the Wallowa Mountains, western larch GBA is 65 percent of normal BA/A, 100 percent of lodgepole pine (*Pinus contorta*) GBA, 80 percent of Douglas-fir (*Pseudosuga menziesii*) GBA, and 60 percent of grand fir and Englemann spruce (*Picea engelmannii*) GBA's.

Wide variation in stand densities for western larch (*Larix occidentalis*) have been found in Oregon and Washington. Its dominance and growth performance in various plant communities was sampled during ecological investigations by the USDA Forest Service ecological program. This paper discusses some aspects of western larch stockability.

Stockability is the capacity of a forest site to grow trees. It refers to the ecological ability of a site to support a certain maximum number of trees of a given size. For example, a poor site at maximum stocking may be capable of supporting 200 western larch trees per acre averaging 10 inches diameter at breast height (d.b.h.) for a stand density of 110 square feet basal area per acre (ft^2 BA/A) or a stand density index (SDI) of 200. A good site at maximum stocking may be able to support 500 trees per acre, averaging 10 inches d.b.h., for a stand density of 270 ft^2 BA/A or an SDI of 500. The stand densities, when mean diameters are 10 inches, of 110 and 270 ft^2 BA/A (or SDI's of 200 and 500) represent both maximum stocking and maximum intertree competition for the two sites due to differences in environmental limits imposed on productivity (Gholtz 1982).

This paper uses an index for stockability called growth basal area: the basal area per acre at which dominant trees grow at the rate of 1.0 inch per decade (in/dec) in diameter. Tree diameter growth is used as a measure of competition and BA/A as a measure of stand density (Hall 1987).

Growth basal area is not a relative measure of stockability such as SDI, relative density, tree area ratio, or crown competition factor. Rather, it is a site specific index utilizing measurements of tree diameter growth and stand basal area (Hall 1987).

The underlying assumption used with GBA is that tree diameter growth reflects competition. Slow diameter growth, such as 1.0 in/dec., indicates significantly greater competition than does 3.0 in/dec. The assumption is that a decreasing rate of diameter growth is directly related to increasing competition. Most thinning studies have validated this assumption by showing a direct inverse relationship between stand density and diameter growth wherein residual tree diameter growth increased with a decrease in BA/A for western larch (Cole 1984; Roe and Schmidt 1965; Seidel 1980, 1984, 1987), ponderosa pine (*Pinus ponderosa*) (Barrett 1972, 1981, 1982; Lynch 1958; Oliver 1972; Ronco and others 1985; Seidel 1989; Stage 1958), lodgepole pine (*Pinus contorta*) (Dahms 1971, 1973), and Douglas-fir (*Pseudotsuga menziesii*) (Harrington and Reukema 1983; Reukema 1979; Reukema and Pienaar 1973; Tappeiner and others 1982; Williamson 1982).

Diameter growth is used as a point of reference for indexing stockability of forest sites in the same way that age is used in site index (SI). The diameter growth rate of 1.0 in/dec. was selected as a reference point for indexing stockability. It is not a maximum or minimum diameter growth guide for thinning or other treatment any more than SI age is a management guide. Basal area per acre is then used as a measure of stockability just as height is used with SI as a measure of site quality.

Growth basal area is determined by measuring stand BA/A and diameter growth of dominant trees, relating these to a curve or equation, and determining or calculating GBA (Hall 1987). In this way, tree diameter growth performance is used to evaluate potential of the site for stockability just as height growth is used with SI.

Growth basal area can be used for more than indexing stockability. It can be used on a stand specific basis to estimate precommercial thinning, predict diameter growth rate from thinning, or prescribe thinning to establish a desired diameter growth rate (Hall 1987). Growth basal area can also be used to refine productivity estimates of western larch when it is combined with site index (SI-GBA), and it can be used to compare stockability of western larch with its competitors.

STOCKABILITY OF WESTERN LARCH AND ASSOCIATED SPECIES

Table 1 illustrates GBA of western larch compared to normal BA/A at age 100 according to Schmidt and others (1976) for various site index classes in ten plant associations of eastern Oregon and Washington and to the GBA for Douglas-fir, grand fir, ponderosa pine, lodgepole pine,

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Table 1—Western larch (WL) growth basal area (GBA) compared to GBA's for Douglas-fir (DF), grand fir (GF), ponderosa pine (PP), lodgepole pine (LP), subalpine fir (AF), and Englemann spruce (ES) for 10 plant associations in eastern Oregon and Washington. Site index (SI) class and normal basal area per acre (BA/A) at age 100 are from Schmidt and others 1976.

Association	Age 100 SI/normal BA/A	GBA						
		WL	DF	GF	PP	LP	AF	ES
GF/VASC (1)[1]	75/220	110	130	150	80	130		
DF/ARUV (4)	75/220	120	120		150	150		
GF/VAME-BLUE (1)	75/220	160	180	180	120	100	200	180
GF/VASC/LIBO2 (1)	90/240	170	170	210		140	100	180
AF2/TRCA3 (3)	90/240	270	280	130		250		
GF/VAME-WALLO (2)	100/250	160	200	270		160		270
GF/TABR/LIBO2 (1)	100/250	130	240	280				170
GF/CLUN (2)	120/270	205	250	285	240	170		260
GF/POMU/ASCA3 (1)	120/270	200		245				425
RC/ARNU3 (3)	120/270	375	370		315	140		255

[1] See appendix for species codes.
(1) Johnson and Clausnitzer 1992
(2) Johnson and Simon 1987
(3) Williams and others 1990
(4) Williams and Lillybridge 1983.

subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*). Western larch GBA varied from 55 to 100 percent of that for Douglas-fir, 45 to 210 percent of grand fir, 60 to 145 percent of Englemann spruce, 80 to 170 percent of subalpine fir, 80 to 140 percent of ponderosa pine, and 80 to 160 percent of lodgepole pine GBA. Seidel (1989) found similar differences in diameter growth between ponderosa pine and lodgepole pine when growing together.

Because GBA represents 1.0 in/dec. diameter growth, 45 percent of grand fir GBA means that western larch will grow half as fast in diameter as grand fir in the GF/TABR/LIBO2 (see appendix for codes) association. At 210 percent of grand fir GBA in the AF/TRCA3 association, it means western larch grows twice as fast in diameter as grand fir. These differences in species performance can be used in developing stand treatments designed to attain various management objectives.

WESTERN LARCH STOCKABILITY COMPARED TO NORMAL

Western larch GBA is often different from the normal BA/A shown for a given SI class. Table 1 lists normal BA/A at age 100 in each of four SI classes for western larch (Schmidt and others 1976). Normal BA/A at older ages are higher; for example, SI 100 at age 100 is 250 BA/A while at age 200 it is 280 BA/A. In the GF/VASC association, western larch is about 50 percent of normal, approximately equal to normal in the AF/TRCA3 association and 140 percent of normal in the RC/ARNU3 association.

Figure 1 illustrates SI and GBA combinations for western larch in Oregon and Washington. Each point represents one of 54 plant associations. Each association is an average of five to 20 sample plots. At each plot, between two and five trees of each important species are measured for their height, age, rate of radial growth, and stand basal area in the vicinity of each tree. On multiple species plots, up to 15 trees may be measured. Therefore, each point is an average of GBA's for 10 to 25 western larch trees.

Growth basal area for western larch in figure 1 ranges from 90 to 420 ft^2 BA/A. The variability of GBA within SI classes ranges from 170 to 345 percent. For SI 80, GBA varies from 110 to 190 ft^2 BA/A for 170 percent variability, SI 100 varies from 90 to 310 ft^2 BA/A for 345 percent, and in SI 120, it varies from 170 to 420 ft^2 BA/A for 245 percent variability.

This variation in western larch GBA within an SI class suggests that prescribing stand treatment based on normal

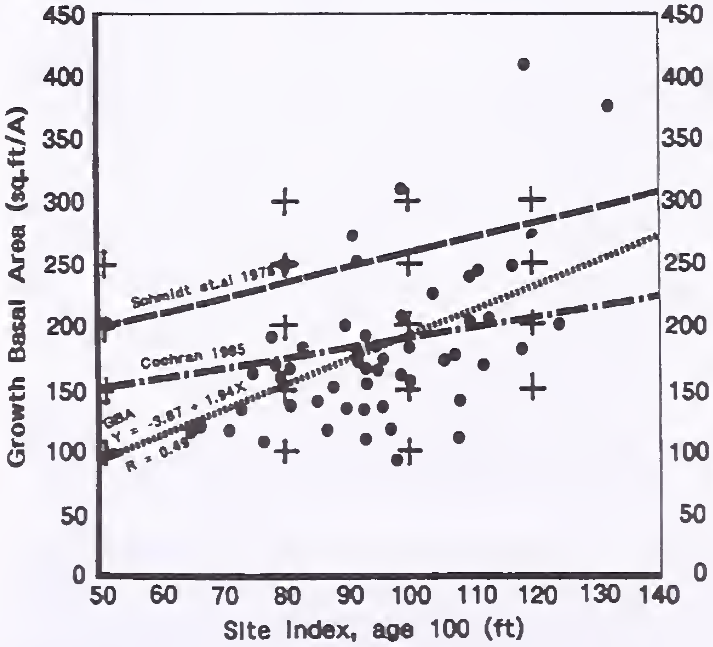

Figure 1—Normal basal area per acre (BA/A) at age 100 years and GBA (plotted points) (Y axis) as functions of average western larch site index (X axis) for 54 plant associations in Oregon and Washington. The "+" points identify productivity levels shown in table 2.

stocking could lead to disappointing results. It also suggests that combining GBA with SI (SI-GBA) is a way of showing different stockabilities within an SI class and thus a means for refining productivity estimates of western larch.

WESTERN LARCH PRODUCTIVITY

Figure 1 shows normal BA/A at age 100 by SI from two sources: Schmidt and others (1976) for western larch in the northern Rocky Mountains and Cochran (1985) for larch in Oregon and Washington. Cochran's normal BA/A are about 75 percent of Schmidt's, possibly a reflection of western larch geographic range. Cochran's data came from the southwestern edge of larch distribution while Schmidt's were closer to the center of its range. A comparison of their data and distribution of GBA relationships clearly suggest different stockabilities within an SI class.

Tree physiology supports the concept of a range in stockability within an SI class, according to Kozlowski (1971) and Zimmermann and Brown (1971). They discussed how terminal and cambial growth (height and diameter growth) differ. If they are different, there should be physiological reasons why an SI (height growth) class could have more than one stockability level (diameter growth class). Thus, GBA may be combined with SI, shown as SI-GBA, to not only identify variation in stockability but also to index differences in productivity within an SI class.

Growth basal area when combined with SI includes three elements of stand growth: height growth expressed by SI, diameter growth indexed by "G" of GBA, and BA/A measured by "BA" of GBA. The missing element is tree size.

Using the combination of SI-GBA as an index of productivity is of interest only if an SI class has a range of stockabilities within it, and therefore a range of productivity. This range may be evaluated by comparing data from Schmidt and others (1976), Cochran (1985), and the distribution of GBA in figure 1. Research in Europe has clearly documented a range of productivity so broad that three levels have been established within a site index (height/site) class (Assmann 1970; Bradley and others 1966).

The concept of a range in productivity within an SI class is receiving increased attention in the United States (MacLean and Bolsinger 1973). Hagglund (1981) discussed site evaluation by SI, mean annual increment, and soil/topographic characteristics, as did Carmean (1975). Curtis (1981) discussed yield tables past, present, and future and predicted multiple productivity levels per SI class. Recently, Monserud (1984) dealt directly with the problems of SI as a site indicator and discussed reasons for multiple yield classes.

Dahms (1966) showed productivities for lodgepole pine SI 78 (index age 100) of 87 and 137 cubic feet per acre per year (cf/A/YR). Later, he compared Rocky Mountain and central Oregon lodgepole pine, finding 104 versus 64 cf/A/YR for SI 80 (Dahms 1973). Most recently, Cole and Edminster (1985) showed significantly different productivity for SI 80 lodgepole pine. Their northern model estimated 71 and their central model 105 cf/A/YR. These three references imply a range from 64 to 137 cf/A/YR for SI 80 lodgepole pine, a variation of 215 percent.

Both SI and GBA are determined in the field according to stand growth performance—SI according to tree age and height, GBA according to tree diameter growth and stand BA/A. Thus, the concept of SI-GBA is a site specific system. The number of GBA classes (stockability classes) within an SI class is influenced by a species' range of stockability which often is reflected in the geographical distribution and environmental amplitude of that species.

The combination of GBA with SI does several things. First, it provides a convenient method for identifying different productivity levels. Second, it offers a means by which stand treatment can be prescribed. And third, it is a system by which the productivity classes can be identified in the field.

An SI class can have multiple GBA classes depending on how class intervals are defined and therefore multiple productivity levels (table 2). Productivity by SI-GBA class in table 2 was calculated by the equation:

$$PI = SI*GBA*K$$

where PI is the productivity index in cubic feet per acre per year, SI is site index measured in feet for age 100, GBA is ft^2 BA/A at age 100, and K is the constant 0.0044 ($n = 92$, $SE = 0.00015$, $CI(p@.05) = 0.00030$ at 7 percent of the mean) (Hall 1987).

Using this formula, the productivity index for SI 100 from figure 1 (GBA's of 90 to 310) ranges from 40 to 135 cf/A/YR for 340 percent variation. Table 2 lists the productivity indexes of western larch in four SI classes by five GBA classes and compares them to normal (Schmidt and others 1976). Plus (+) marks in figure 1 represent the productivity classes of table 2. Most fall well within the data base.

Clearly, a western larch SI class has different productivities. These differences should be recognized if SI is used as a primary factor in estimating stand productivity (Schmidt 1978).

PLANT ASSOCIATIONS

Plant associations (habitat types, potential natural communities) often characterize western larch growth

Table 2—Western larch productivity index expressed as cubic feet per acre per year (cf/A/YR) for four site index (SI) classes and four growth basal area (GBA) classes compared to normal BA/A and mean annual increment (MAI in cf/A/YR) at age 100 according to Schmidt and others (1976).

	SI age 100			
	50	80	100	120
Age 100				
Normal MAI	30	65	85	110
Normal BA/A	190	225	250	270
	cf/A/YR			
GBA class				
100	25	35	45	
150	35	50	65	80
200	45	70	90	105
250	55	90	110	130
300		105	130	160

Table 3—Comparison of two similar plant associations relating western larch (WL) GBA to normal BA/A at age 100 and to four associated species: Douglas-fir (DF), grand fir (GF), Engelmann spruce (ES), and lodgepole pine (LP). Site index (SI) classes and normal (BA/A) at age 100 are from Schmidt and others (1976).

Association	Age 100 SI/normal BA/A	GBA WL	DF	GF	LP	ES
GF/VAME-BLUE (1)	75/220	160	180	180	100	180
GF/VAME-WALLO (2)	100/250	160	200	270	160	270

(1) Johnson and Clausnitzer 1992
(2) Johnson and Simon 1987.

characteristics. Two have been chosen from table 1 that have similar floristic characteristics but differ in western larch SI and GBA: GF/VAME from the Blue Mountains (Johnson and Clausnitzer 1992) and from the Wallowa Mountains (Johnson and Simon 1987), shown in table 3.

Western larch GBA is similar between the associations, but the SI is highly significantly different at only 75 ft in the Blue Mountains compared to 100 ft in the Wallowa Mountains. Western larch is 25 percent less productive in GF/VAME-BLUE. Larch GBA is also different from normal: 75 percent in the Blue Mountains vs. 65 percent in the Wallowa Mountains.

These plant associations clearly show major differences between western larch GBA and four closely associated species. In GF/VAME-BLUE, larch is about equal to GBA for grand fir (GF) and Engelmann spruce (ES) but in GF/VAME/WALLO it is only 60 percent of these species GBA. For lodgepole pine (LP) GBA, western larch is 160 percent in GF/VAME-BLUE compared to equal in GF/VAME-WALLO. Plant associations suggest different tree growing environments, thus they may be used to refine management.

DISCUSSION

Western larch stockability (GBA) varies from 90 to 420 ft^2 BA/A, a 4.7-fold difference in Oregon and Washington. Within an SI class it can vary 3.4-fold. This suggests that productivity within an SI class can also vary by 3.4-fold. The relationship of western larch GBA to associated species is also quite variable; for example ranging from 45 to 210 percent of grand fir GBA. Much variation is characterized by plant associations. Land managers can refine prescriptions when western larch stockability characteristics are understood.

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APPENDIX

Species Codes

AF	Subalpine fir	*Abies lasiocarpa*
DF	Douglas-fir	*Pseudotsuga menziesii*
ES	Engelmann spruce	*Picea engelmannii*
GF	Grand fir	*Abies grandis*
LP	Lodgepole pine	*Pinus contorta*
PP	Ponderosa pine	*Pinus ponderosa*
RC	Western red cedar	*Thuja plicata*
WL	Western larch	*Larix occidentalis*

ASCA3	Wild ginger	*Asarum caudatum*
ARNU3	Aralia	*Aralia nudicaulis*
ARUV	Bearberry	*Arctostaphylos uva-ursi*
BLUE	Blue Mountains	(Geographic locator)
CLUN	Clintonia	*Clintonia uniflora*
LIBO2	Twinflower	*Linnaea borealis*
POMU	Swordfern	*Polystichum munitum*
TABR	Western yew	*Taxus brevifolia*
TRCA3	Falsebugbain	*Trautvetteria caroliniensis*
VAME	Big huckleberry	*Vaccinium membranaceum*
VASC	Grouse huckleberry	*Vaccinium scoparium*
WALLO	Wallowa Mountains	(Geographic locator)

Biomass and Production of Three Types of Dahurian Larch Virgin Forest in the Great Xinganlin Mountains, China

Feng Lin
Yang Yugong

Abstract—Biomass and production of three larch types—*Rhododendron-Larix, Ledum-Larix,* and *Sphagnum-Ledum-Larix*—were measured on stands of average age 175 years in the Great Xinganlin Mountains in northeast China. *Rhododendron-Larix* had the highest biomass at 285.27 tons per hectare. *Ledum-Larix* had the highest annual net production at 9.86 tons per hectare.

The study of biomass and production is the core of researching forest ecological systems. Since the 1960's, the scientists in many countries, such as America, Japan, the Soviet Union, and European countries, have studied it actively. The forest scientists of China have been studying in this field since the end of the 1970's, but it is only limited to such tree species as *Cunninghamia lanceolata*, *Pinus taiwanensis*, *Pinus tabulaeformis*, *Pinus sylvestris* var. *mongolica*, *Pinus koraiensis,* and others in their immature human-made forests. We have less research in the biomass and production of mature natural forests. Studies on mixed forests of *Pinus koraiensis* and broadleaf trees in Changbaishan Mountains, *Picea meyeri* forest, *Picea crassifolia* forest, and *Pinus tabulaeformis* forest were started only several years ago.

In 1982, we studied the biomass and production of three natural forest types, in Dahurian larch (*Larix gmelini*) virgin forest of the Forestry Bureau of Genher in the Great Xinganlin Mountains, in northeast China. The three types with the widest distribution in this region are and *Sphagnum-Ledum-Larix* forests.

METHODS OF STUDY

Dahurian larch (*Larix gmelini*) is the main forest species in this region, which adapts itself to almost every site type. According to the differences in habitat conditions, it is divided into eight forest types. It should be pointed out that the types of *Larix gmelini* forests have been changed because of the change of its habitat conditions due to the exploration and utilization of the forest resources in this region since the 1950's. For instance, *Herbs-Larix* type, which was the principal type at the beginning of the 1950's, was replaced by *Ledum-Larix* type. The area of *Rhododendron-Larix* type was also becoming smaller and smaller, whereas, the area of *Sphagnum-Ledum-Larix* type seems to be expanding. In order to show the present situation of *Larix gmelini* forest in this region, we selected three—*Rhododendron-Larix*, *Ledum-Larix*, and *Sphagnum-Ledum-Larix* types to study their biomass and net production.

In order to compare biomass and production of the three types, we allocated one sample plot for each in their central distribution area, which belongs to the Forestry Bureau of Genher. We measured the diameter and height of every tree on these plots and calculated species composition, growing stock, and other stumpage factors. We set up five quadrants on each sample plot to study the undergrowth. At a typical position in each sample plot, a soil profile was made for observation.

Afterwards 26 trees were selected to be cut down from different diameter classes, 13 from *Rhododendron-Larix* type, 6 from *Ledum-Larix* type, and 7 from *Sphagnum-Ledum-Larix* type.

After measuring the total weight of all fresh branches and leaves, 10 percent was oven-dried for calculation of total dry weight. For sampling the root, one-fourth of the root from one side of each sample tree was dug out, oven-dried, and divided into three classes: thick roots (diameter over 5.0 cm), medium-sized roots (0.2 to 5.0 cm), and thin roots (under 0.2 cm).

Stem weight was determined by diameter classes. Three sample trees were chosen from each sample plot and stem analysis was used to calculate their production. As for shrubs, 5 to 10 stems were used for weighing.

The net production of stem, bark, branches, roots, and needles was calculated by commonly used methods. The net production of brushes and herbs was determined by dividing biomass by age.

BIOMASS AND PRODUCTION OF *RHODODENDRON-LARIX* FOREST

This type of forest usually grows on north slopes with a gradient of about 20°. It is almost a pure stand in species composition, but sometimes it is mixed with small amounts of *Betula platyphylla* and *Pinus sylvestris* var. *mongolica*. The community is a one-storied forest with a stocking of 0.4 to 0.9 and site class of 2-3. It has well developed shrub layers composed mainly of *Rhododendron davurica* and other species such as *Ledum palustre* var. *angustum* and *Vaccinium vitis-idaea*. But its herb layer does not develop well because of tall and thick shrubs. The regeneration of *Larix gmelini* in this forest type depends on a few good regenerations and the density of undergrowth.

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Table 1A—Biomass of *Rhododendron-Larix* type (ton/ha)

Parts	Tree layer	Underwood	Ground cover	Total
Stem	143.95		143.95	
Bark	33.39		33.39	
Branch	10.87		10.87	
Needles	1.96		1.96	
Cones	0.08		0.08	
Total	190.25	10.86	0.02	201.13
Collar	18.90		18.90	
Thick root	27.70		27.70	
Medium root	11.29		11.29	
Thin root	1.07		1.07	
Total	58.96	25.08	0.10	84.14
Total	249.21	35.94	0.12	285.27

Table 1B—Net Production of *Rhododendron-Larix* type (ton/ha/yr)

Parts	Tree layer	Underwood	Ground cover	Total
Stem	2.02		2.04	
Bark	0.47		0.47	
Branch	0.15		0.15	
Needles	1.96		1.96	
Total	4.62	0.56	0.01	5.19
Underground	0.84	1.29	0.02	2.15
Total	5.46	1.85	0.03	7.34

The age of trees on the investigated sample plot was 186 years old, species composition 100 percent *Larix gmelini*, average d.b.h. 24.6 cm, average height of trees 24.3 m, 792 stems per hectare, growing stock 450 m^3 in total, and average annual growth 2.4 m^3. Total plant biomass and net production of the type are shown in tables t1A and B.

By statistical analysis, it is found that the biomass of a single tree in this type is closely related to the product of its squared d.b.h. and height.

BIOMASS AND PRODUCTION OF *LEDUM-LARIX* FOREST

This type of forest usually grows on north-hillsides with gradients below 5° or on half north-hillsides or flat hillock and little waterlogged places near streams. There is high moisture content in the soil with stagnant water, there usually are permafrost horizons, and the soil has little gleization.

The site class is 3-4, and the forest is almost pure. Crowding level is 0.4 to 0.8. The principal species in the shrub layer are *Ledum palustre* var. *angustum* associated with *Vaccinium vitis-idaea* in some of the places with stagnant water. There are some water tolerant species such as *Betula fruticosa* associated with *Spiraea salicifolia* and *Lonicera eacurulea*. Its coverage is about 80 to 90 percent. There are a few herb species, but moss layers are thick and dense with a lot of species, composed mainly of *Sphagnum squarrosum* and *Aulacomnium palustre*. The regeneration of *Larix gmelini* in this type is poor and saplings can only be found on some local upheavings.

The age of the sample stand investigated was 175 years old with an average height and d.b.h. of 17.4 m and 17.3 cm respectively. There are 811 stems per hectare and growing stock is 163 m^3, annual average growth is 0.9 m^3, and total biomass is 196.08 ton per hectare (table 2A). For net production of this type see table 2B.

From tables 2A and 2B, we find that the net production of the tree layer and that of the shrub layer are almost equal, but the ground layer production is very low.

BIOMASS AND PRODUCTION OF *SPHAGNUM-LEDUM-LARIX* FOREST

Compared with the *Ledum-Larix* forest, this forest type occurs on more marshy areas and grows on low-lying land, but sometimes this forest type can be seen on north hill sides. Where it grows, the soil is in serious gleization because of stagnant water accumulation and presence of a glacial soil layer. In places that are extremely waterlogged with low-temperatures and lack of nutrients, only *Larix gmelini* can grow and regenerate. But the net production of the forest type is the lowest among all types in this region. The site class of this type is 5, generally with trees distributed sparsely and unevenly, with many small, diseased, and decayed trees. There are shrub species such as *Ledum palustre* var. *angustum* and *Vaccinium vitis-idaea* that are very dense, and small amounts of *Ribes pauciflorum*, *Betula fruticosa*. The principal species of moss is *Sphagnum actifolium*. There are very few regenerated trees in this type.

The age of investigated sample stand was 107 years old, with an average d.b.h. and height of 8.0 cm and 8.1 m,

Table 2A—Biomass of *Ledum-Larix* Type (ton/ha)

Parts	Tree layer	Underwood	Ground cover	Total
Stem	57.26		57.26	
Bark	19.02		19.02	
Branch	6.96		6.96	
Needles	1.46		1.46	
Cones	0.08		0.08	
Total	84.73	29.94	0.04	114.71
Collar	9.10		9.10	
Thick root	16.95		16.95	
Medium root	6.05		6.05	
Thin root	0.51		0.51	
Total	32.61	48.60	0.16	81.37
Total	117.34	78.54	0.20	196.08

Table 2B—Net Production of *Ledum-Larix* Type (ton/ha/yr)

Parts	Tree layer	Underwood	Ground cover	Total
Stem	1.71		1.71	
Bark	0.56		0.56	
Branch	0.21		0.21	
Needles	1.46		1.46	
Total	3.94	1.87	0.01	5.82
Underground	0.97	3.04	0.03	4.04
Total	4.91	4.91	0.04	9.86

Table 3A—Biomass of *Sphagnum-Ledum-Larix* type (ton/ha)

Parts	Tree layer	Underwood	Ground cover	Total
Stem	32.76		32.76	
Bark	6.59		6.59	
Branch	3.02		3.02	
Needles	0.53		0.53	
Cones	0.03		0.03	
Total	42.93	17.43	31.68	92.03
Collar	3.50		3.50	
Thick root	11.71		11.71	
Medium root	1.94		1.94	
Thin root	0.35		0.35	
Total	17.50	3.08	2.53	23.11
Total	60.43	20.50	34.21	115.14

Table 3B—Net production of *Sphagnum-Ledum-Larix* type (ton/ha/yr)

Parts	Tree layer	Underwood	Ground cover	Total
Stem	0.57		0.57	
Bark	0.11		0.11	
Branch	0.05		0.05	
Needles	0.53		0.53	
Total	1.26	1.24	5.28	7.78
Underground	0.30	0.22	0.02	0.54
Total	1.56	1.46	5.30	8.32

respectively. There 2,934 stems per hectare with growing stock of 75 m³, and average annual growth 0.7 m³. The total plant biomass and net production of this type are shown in tables 3A and B.

By statistical analysis, it is also found that the biomass of a single tree in this type is closely related to the product of its squared d.b.h. and height as found in the two preceeding types.

COMPARISONS OF BIOMASSES AND NET PRODUCTIONS

Biomass

The differences of the three types in biomass are very obvious. The *Rhododendron-Larix* type is the highest among them at 285.27 ton per hectare; that of the *Ledum-Larix* type 196.08 ton and the *Sphagnum-Ledum-Larix* type, only 115.14 ton.

Though the biomass of the tree layer is the highest among the total plant biomass of each forest type, the biomass of tree layer of *Sphagnum-Ledum-Larix* type is just a little higher than that of the underwood and field layer, which have 60.43 and 54.71 tons per hectare, respectively. This is because the site of *Sphagnum-Ledum-Larix* type is waterlogged and has low-temperature and poor soil, which restrains tree growth. On the contrary, *Ledum palustre* var. *angustrum* and mosses can grow and regenerate well under such conditions. In comparison, the site of *Ledum-Larix* type is a little better, and the biomass of its tree layer is a little higher than the total biomass of underwood and field layers. The water and nutrient condition in *Rhododendron-Larix* type is beneficial to the growth of trees. Though shrub growth in it is luxuriant, the biomass of trees is not affected—it is six times that of the other plant layers.

The differences of root biomass in these three types are also obvious. The biomass of root in *Rhododendron-Larix* type is 58.96 ton per hectare, the *Ledum-Larix* and *Sphagnum-Ledum-Larix* types are 32.61 and 17.50 ton, respectively. It is very interesting to note that the thin roots of each type are distributed in different depths in the soil. The thin roots of the first type are mainly distributed in the 30 to 60 cm layer below the soil surface, that of the second type is in the 20 to 50 cm layer, but those in the third type are in the 0 to 20 cm layer. The shallow distribution of thin roots in the third type is because of the gathering of peat moss and lack of oxygen and nutrients, but the adventitious roots growing from the lower part of the stem help the tree absorb the limited nutrients in the surface soil. This biological feature of *Larix gmelini* illustrates its adaptation to a soil with waterlogging and lack of oxygen.

Annual Net Production

The annual net production of the three forest types are: 7.34 ton (*Rhododendron-Larix* type), 9.86 ton (*Ledum-Larix* type), and 8.32 ton (*Sphagnum-Ledum-Larix* type) per hectare. These results show that tree growth has not been stopped even though all trees were overmature, as mentioned earlier. Though the differences between net production of the three types are small, differences in distribution of the net production of different portions of the community are quite obvious. For example, net production of the tree layer of *Rhododendron-Larix* type is 5.46 tons per hectare, which is 74.5 percent of total net production of this type. Production of the tree layer in the *Ledum-Larix* type is 4.91 tons, about 50 percent of the total, while that in the *Sphagnum-Ledum-Larix* type is 1.56 tons, only 18.4 percent of the total. This is explained by the differences in the site.

But the proportion of stem and root net production of the three types is about the same. For example, in the *Rhododendron-Larix* type, net production of the stems and roots is 37.4 and 15.4 percent of the total tree layer, respectively. In the *Ledum-Larix* type they are 34.8 and 19.8 percent, respectively, and in the *Sphagnum-Ledum-Larix* type are 36.5 and 19.2 percent, respectively.

If the total net production of the tree layer in the *Sphagnum-Ledum-Larix* type was taken as 100, the *Ledum-Larix* type would be 312 and that of the *Rhododendron-Larix* type would be 376. So the net production of the tree layer in the *Sphagnum-Ledum-Larix* type is very low compared with the other two types. But the net production of its underwood and field layers is 3.3 times that of its tree layer in this type. Therefore, we should improve the stand conditions of *Sphagnum-Ledum-Larix* type to raise net production of its tree layer.

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Yield and Productivity of Siberian Larch (*Larix sukaczewii* Dyl.) in Northern Sweden

Owe Martinsson

Abstract—Twenty small stands of larch, mainly *Larix sukaczewii* Dyl. (Siberian larch), were investigated in northern Sweden. The age of the stands varied between 34 and 89 years. The increment of tree height was still considerable at 90 years. The productivity was highly variable depending on site quality. On the most productive sites the Siberian larch was overgrowing the native conifers. On poor, dry, or flat sites, or sites with a too high water table, the productivity of Siberian larch was inferior to that of native conifers. High productivity was found on high-altitude sites.

Larch has been grown in Sweden for more than 200 years. Still, there are many opinions and great hesitation among Swedish foresters as to the use of larch in forestry. The concerns are:

- Lack of maintenance of older larch stands and existing trial plots
- Lack of knowledge in choice of site and provenance
- Lack of suitable seed sources
- Hesitation about the wood properties and the use of larch wood

The earliest plantations of larch in Sweden were done in the 1760's in the southern part of the country. Seedlings of European larch (*Larix decidua* Mill.) had been imported from Scotland, where it was introduced from Tirolia about 100 years before (Schotte 1916). The Siberian larch was introduced into northern Sweden later. In 1754, Carl Linneus wrote a proposal to the Swedish parliament that the Siberian larch and the Siberian stone pine (*Pinus sibirica*) should be used for afforestation of the bare Scandinavian mountains. Not until the 1890's was any significant import of larch seed from Russia undertaken. In 1892, for instance, 80 kg of larch seed was imported by the Swedish state forest agency. Some of the nicest older larch stands still existing in northern Sweden originate from this seed import.

Seen in a prehistoric perspective, there are strong indications that larch as well as several other "exotic" tree species were present in Scandinavia as late as the last interglacial (Frenzel 1968; Hirvas 1983; Robertsson and Ambrosiani 1988). The present poverty of species that can be recognized in Scandinavia is explained by repeated glaciations during Pleistocene time and the geographic barriers that have prevented the original flora from returning. Several species existing today as important tree species east or southeast of Scandinavia probably had a natural distribution in Scandinavia during early Pleistocene. Among these are European silver fir (*Abies alba*), Siberian fir (*Abies sibirica*), Siberian stone pine (*Pinus sibirica*), Serbian spruce (*Picea omorica*), Macedonian pine (*Pinus peuce*), and larches (*Larix decidua* and *L. sukaczewii*). Only 4,000 years have passed since Norway spruce (*Picea abies*) and beech (*Fagus silvatica*) returned to the Scandinavian peninsula. Scots pine (*Pinus sylvestris*) and birch (*Betula pendula*) have existed in Scandinavia more than twice as long. Larch (*Larix* Mill.) is representing the most common on genus among trees in the boreal forests of Siberia including several species. The most widely distributed species of larch in Siberia are *Larix sukaczewii* Dyl., *Larix sibirica* Ledeb. and *Larix gmelini* Rupr. In this article Siberian larch is reserved for *Larix sukaczewii* Dyl. only.

In northern Sweden several small stands of Siberian larch (*Larix sukaczewii*) were established between 1900 and 1940. Many of these stands have been used as trial plots and investigated two or three times (Edlund 1966; Remröd and Strömberg 1977; Wiksten 1962). The objective of this report is to revise the increment of tree height and stem volume of these stands. However, several of these stands suffer from bad maintenance. In most cases no thinning has been done during the last 20 years.

MATERIALS AND METHODS

Materials from 20 larch stands are included in this presentation (fig. 1). Usually only one trial plot exists in each stand. In four of the stands, two plots have been established. Records of tree height, diameter at breast height, dominant height, damage of trees, bark thickness, and site index were collected. Where it was possible information of site index and dominant height of adjacent stands of native conifers (Norway spruce or Scots pine) also was collected. Basic information about the stands, the trial plots, and the site properties is given in tables 1 and 2.

Processing of Data

Dominant Height—On processing of data for dominant height, earlier collected information was also used (Edlund 1962; Remröd and Strömberg 1977; Wiksten 1962). When I included data from the last revision, the development of dominant height did not follow the courses developed by these authors. However, the dominant height did follow the courses developed by Voukila and others (1983). The site index was therefore determined

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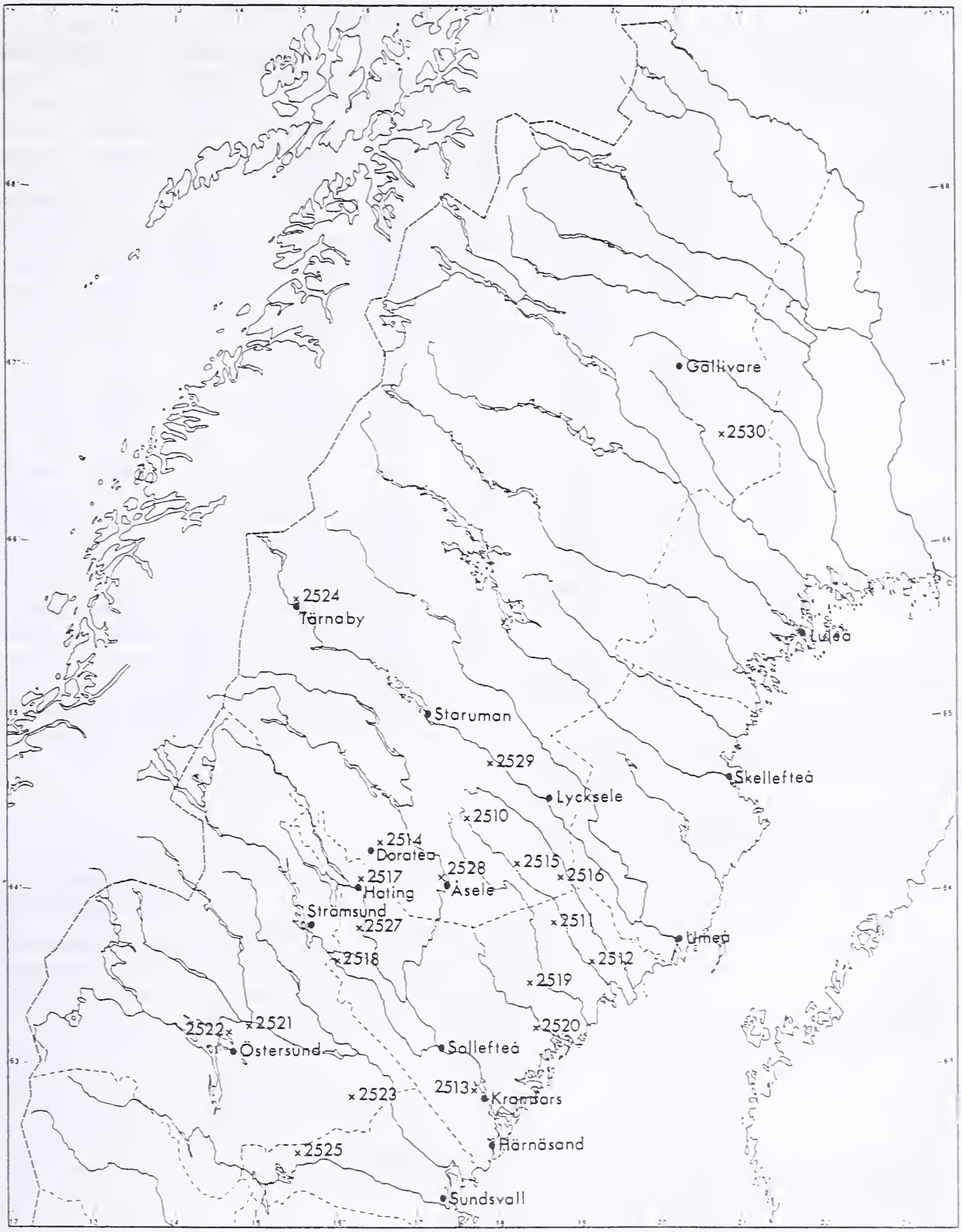

Figure 1— Localities of the investigated larch stands.

Table 1—Names, geographic positions, and time for establishment and revisions of the experimental plots

Plot number	Site	Earlier number	Lat., °N.	Long., °E.	Alt.	Plot area	Establishment		Date of measurement		
							Year*	Way**	II	II	III
					m	*m²*					
2510	Sandsjö	P6	64°29'	17°41'	535	590	1938 v	p	6212—	771018	870521
2511	Bredträsk	P10	63°53'	18°33'	290	750	1940 v	p	610714	761006	870514
2511	Bredträsk (tall)		63°53'	18°33'	290	750	1940 v	p	610714	761006	871008
2512	Toböle	P11	63°37'	19°15'	75	383	1931 v	p	—	761005	870504
2513	Öd	P19	62°57'	17°46'	40	288	1928 v	p	611129	760921	870506
2514	Måntorp	P50	64°22'	16°25'	445	516	1937 v	p	—	761118	870523
2515-1	Norrby	P51	64°16'	18°18'	460	1,000	1940	p	610711	761112	870519
2515-2	Norrby	P52	64°16'	18°18'	460	1,000	1940	p	610712	761112	870519
2516	Vargålandet	P53	64°12'	18°48'	300	1,190	1936	p	611116	761103	870519
2517-1	Valåberget	P54	64°08'	16°11'	300	927	1932 h	p	591010	761116	870524
2517-2	Valåberget	P55	64°08'	16°11'	300	1,050	1932 h	p	591011	761117	870525
2518	Täxan	P56	63°41'	15°57'	350	450***	1934 v	p	611206	761122	870510
2519	Nybyn	P57	63°37'	18°23'	370	632	1930 v	s	581013	761110	870513
2520-1	Moliden	P58	63°24'	18°25'	70	745***	1930 v	s	581016	761111	870512
2520-2	Moliden	P58	63°24'	18°25'	70	745***	1930 v	s	581016	761111	870512
2521	Lit	P59	63°17'	14°50'	370	390	1935 v	p	6212—	761123	870509
2522	Ås	P60	63°15'	14°33'	390	600	1915 v	p	6212—	761123	870509
2523	Kälarne	P61	62°54'	16°06'	360	635	1918 v	p	611208	761124	870508
2524-1	Tärnaby	P62	65°43'	15°22'	540	253***	1898 v	s	611212	761107	870526
2524-2	Tärnaby	—	65°43'	15°22'	540	485	1953?v	s	—	—	870526
2525	Alby	P65	62°29'	15°29'	220	375***	1935?v	p	6212—	761126	870507
2527	Smedsböle	SFI 326	63°53'	16°15'	214	465***	1904	p	4410—	5509—	870525
2528	Åsele	SFI 327	64°12'	17°17'	320	893	1900	p	6609—	7108—	870522
2529	Åskilje	SFI 631	64°56'	17°48'	280	755	1898	p	6308—	7008—	870302
2530	Sarvisvaara	—	66°44'	21°17'	400	450	1952	p	—	—	870818

*v = spring, h = autumn.
**p = planting, s = seeding.
***The plot area is changed from earlier revisions.

Table 2—Site conditions of the experimental plots

Plot number	Site	Soil texture	Type of vegetation	Exposition	Movability of ground water*	Site class, H100, (m)	
2510	Sandsjö	Fine morain	Grass	SW	L	L30	T20
2511	Bredträsk	Fine morain	*Vaccinium myrtillus*	Even	S	L33	T26
2511	Bredträsk (Scots pine)	Fine morain	*Vaccinium*	Even	S		T26
2512	Toböle	Fine sand	Grass	Even	S	L33	T26
2513	Öd	Silt	Low herbs	NE	L	L36	T30
2514	Måntorp	Fine morain	Grass	Even	K	L30	T24
2515-1	Noorby	Medium morain	Grass	Even	S	L27	T22
2515-2	Norrby	Medium morain	Grass	NW	K	L30	T22
2516	Vargålandet	Medium morain	*Vaccinium myrtillus*	E	L	L33	G22
2517-1	Valåberget	Medium morain	Low herbs	SE	L	L33	G26
2517-2	Valåberget	Medium morain	Grass	SE	L	L30	G26
2518	Täxan	Medium morain	Low herbs	SW	L	L36	G30
2519	Nybyn	Medium morain	Grass	SW	L	L27	G24
2520-1	Moliden	Medium morain	*Vaccinium myrtillus*	E	L	L27	G26
2520-2	Moliden	Medium moiran	*Vaccinium myrtillus*	E	L	L27	G26
2521	Lit	Fine morain	Low herbs	Even	S	L33	T22
2522	Ås	Fine morain	Low herbs	Even	K	L30	T22
2523	Kälarne	Medium morain	*Vaccinium myrtillus*	Even	S	L27	G26
2524-1	Tärnaby	Fine morain	Low herbs	SW	L	L24	G22
2524-2	Tärnaby	Fine morain	Low herbs	SW	L	(L36)	
2525	Alby	Coarse morain	Low herbs	W	K	L30	T23
2527	Smedsböle	Fine morain	*Vaccinium myrtillus*	Even	K	L30	G18
2528	Åsele	Fine morain	*Vaccinium vitis ideus*	Even	S	L24	T20
2529	Åskilje	Medium morain	Grass	Even	S	L27	T20
2530	Sarvisvaara	Fine morain	*Vaccinium vitis ideus*	Even	S	L27	T20

* L = longer periods; K = shorter periods; S = nonexisting.

according to the development of the dominant height illustrated by Vuokila, and all trial plots were classified according to H100: L27, L30, L33, or L36.

Based upon the collected material, functions for dominant height over time were developed. Functions based on two different methods were created. One of these methods follows Vuokila's function for dominant height with the addition of a correction term. The second method was developed by Tveite (1968).

Dominant Height According to Vuokila—According to Vuokila and others (1983), the increment of the dominant height of larch in Finland follows the function:

$$I_h5 = e^{(1.874-1.0035*\ln(T)+1.10264*\ln(H)-0.0411495*H)} \qquad \text{(F1)}$$

where:

I_h5 = Increment of dominant height during the future 5 years, m
T = Age of the stand, years
H = The present dominant height, m.

From already existing graphs the dominant heights of site index L27, L30, L33, and L36 were determined at stand age 40 years. Using function 1 and the collected data, the course of dominant height up to age 100 years was calculated. The calculated course for dominant height deviated more or less from the dominant height recorded in the field. The deviations usually increased with increasing age. Based on the differences between the calculated and the recorded dominant heights, a correction (C) was calculated according to the following model:

$$C = a+b(A)$$

where:

A = age of the larch stand, years.

Using this correction term, new corrected courses based on Vuokila's functions were made.

Dominant Height According to Tveite—This method is also called "the deviation method" and was described by Tveite (1968). Starting from a fixed level for dominant height at a certain age, such as 40 years, the course is determined by the mean value of the future (and the previous) 5 years. The form of the course to a great extent depends on the level of the starting point. I decided to start the calculation of the courses so that they coincided with dominant height 12.95, 15.40, 18.00, and 20.90 m at age 40 years. At this age these dominant heights are identical to H100 of site index L27, L30, L33, and L36, according to Vuokila and others (1983).

Stem Volume—The stem volume of the stands was calculated according to functions by Carbonnier (1954) for individual trees:

$$vpb = 10^{-4}\,(0.4801(d^2h) + 8.860(d^2) - 0.1012(d^3) - 8.406(dh) + 197.2(h)) \qquad \text{(F2)}$$

$$vub = 10^{-4}\,(0.4716(d^2h) + 4.572(d^2) - 0.09787(d^3) - 3.111(dh) + 82.28(h)) \qquad \text{(F3)}$$

where:

h = Total tree height above ground, dm
d = Breast height stem diameter, mm
vpb = Stem volume above stump including bark, dm^3
vub = Stem volume above stump excluding bark, dm^3.

According to Eichhorn (1904), a general relationship exists between the stem volume of the stand and the dominant height. The stand volume is approximately proportional to the square of the mean height of the stand. The dominant height exceeds the mean height with 1.0 to 1.5 m. Therefore the same relationship should exist for stand volume over dominant height reduced by 1.0 to 1.5 m.

Using regression analysis, the relation was calculated between the stand volume, with and without bark, and the dominant height reduced by 0.0, 1.0, and 2.0 m. Of the three relations the one using dominant height reduced by 1.0 m gave the best correlation. Using this relation, the stand volume production prognosis was calculated for each site index. For this prognosis the calculated dominant height according to Tveite's method was used.

Comparing the Production of Other Tree Species—The production of larch was compared to other native conifers in two ways:

1. Recorded production of larch was compared to expected production of Scots pine (or Norway spruce) in adjacent stands, where the site index had been determined according to the dominant height and the production according to yield tables by Ekö (1985).
2. Expected production of larch for site class index L27, L30, L33, and L36 was compared to expected production of Scots pine according to Ekö (1985).

In addition to this, the production of larch was compared to the production of lodgepole pine on four sites and on one site with Douglas-fir.

RESULTS

In addition to calculating dominant height and stem volume, I also assessed damage, bark volume, and production in comparison to other tree species.

Dominant Height

Figure 2A-E shows the recorded development of the dominant height for 19 larch stands and the courses for dominant heights calculated according to Vuokila and others (1983). Two plots were not included in these figures due to lack of earlier data. The 19 stands were classified according to site index in the figures.

Dominant Height According to Vuokila—The deviation in meters between recorded and expected dominant height according to Voukila and others (1983) is shown in figure 3. Based on these deviations, corrected

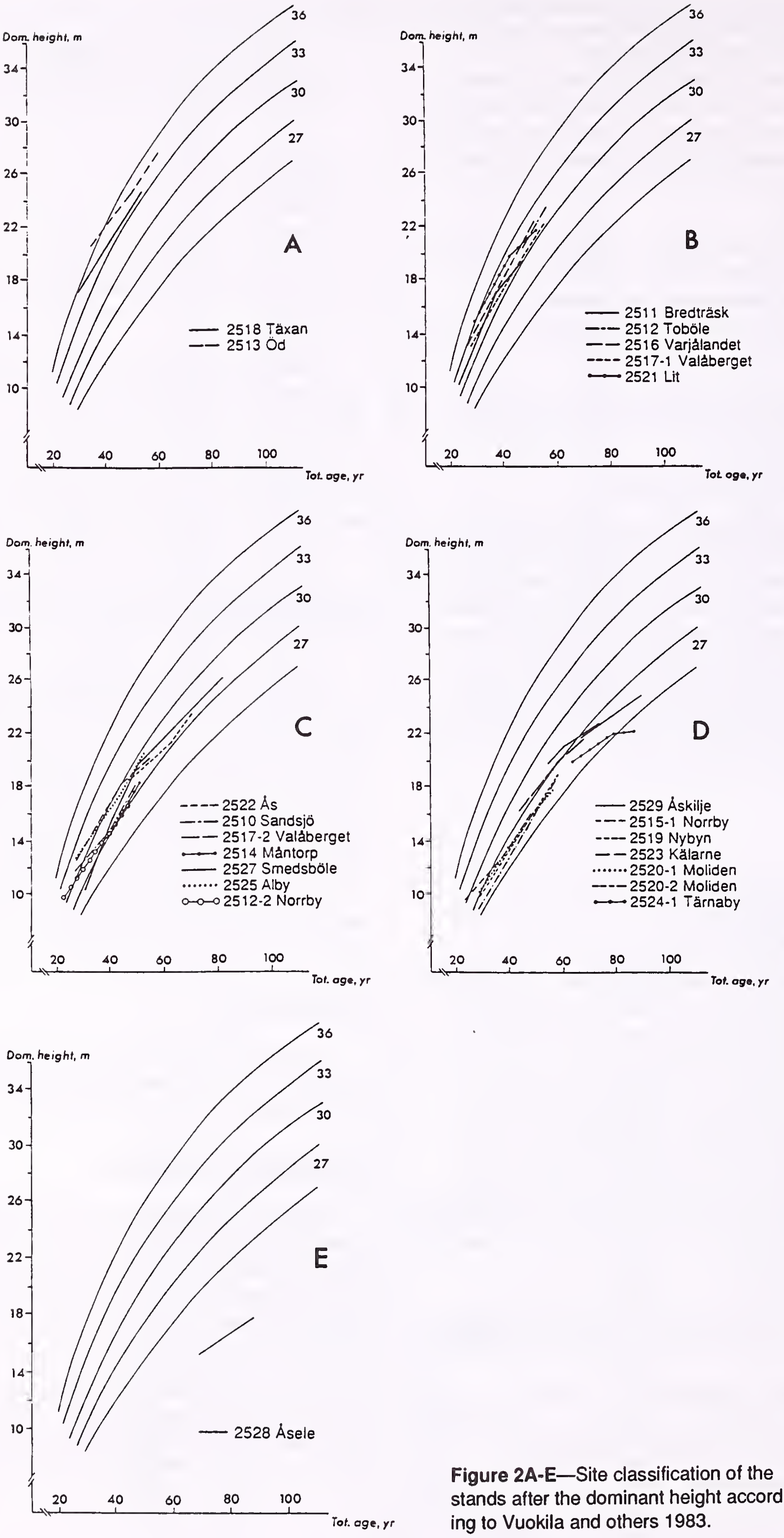

Figure 2A-E—Site classification of the stands after the dominant height according to Vuokila and others 1983.

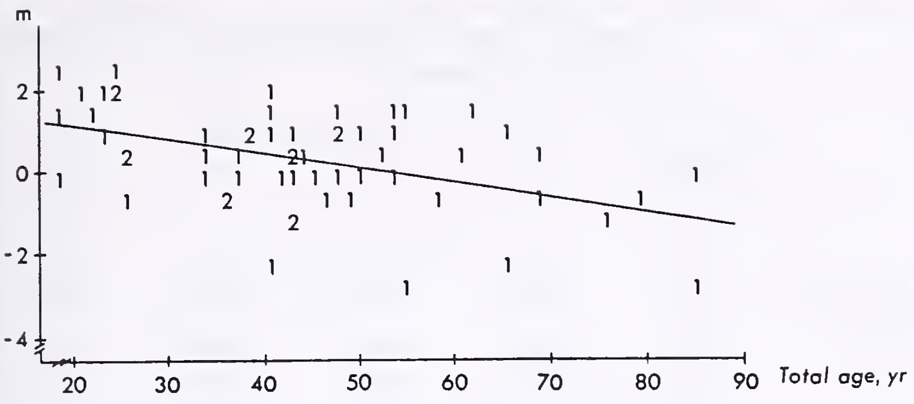

Figure 3—The deviations between observed dominant height and the dominant height according to Vuokila and others 1983 in figure 2.

graphs for dominant height were calculated according to the model:

$Hdom = V + Corr$

where:

$Hdom$ = Dominant height of the stands
V = Dominant height according to Vuokila and others (1983)
$Corr$ = 1.7937 – 0.03465* (age of stand, years).

Corrected courses for dominant height, based on Vuokila's functions, are shown in figure 4.

Dominant Height According to Tveite—The courses of dominant height based on Tveite's method are shown in figure 5. The same courses are also mathematically

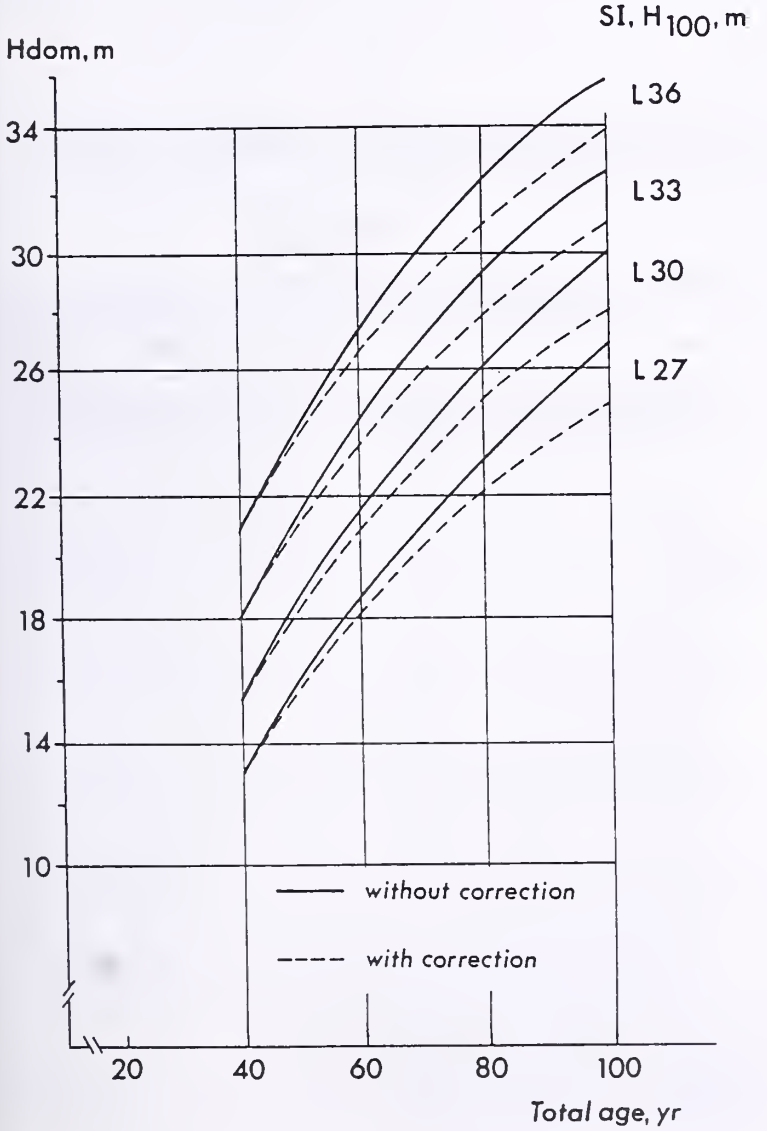

Figure 4—The dominant height according to Vuokila and others 1983 after correction to fit to the investigated larch stands.

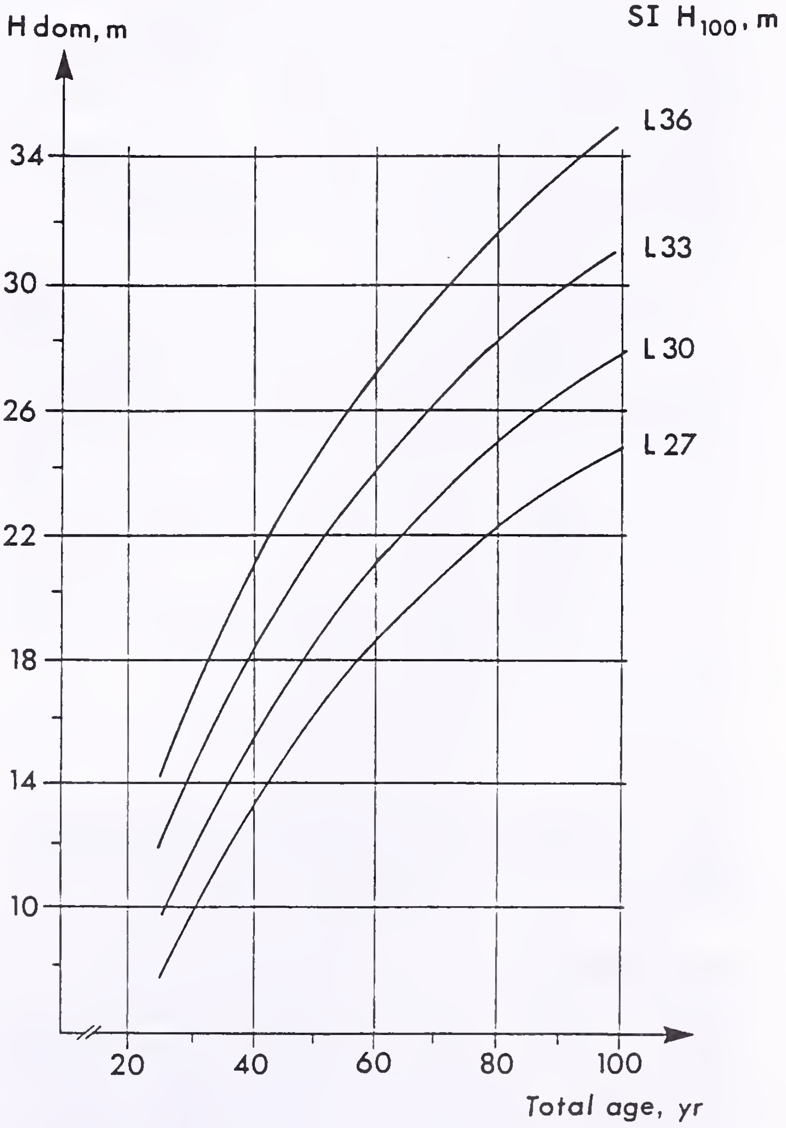

Figure 5—The dominant height of the investigated larch stands according to "the deviation method" (Tveite 1968).

Table 3—Functions for the development of dominant height at four site indexes

Dominant height of site index		Function[1]	Mean error in regression coefficient	r^2	
m					
L27	=	12.48029*ln(t) − 32.54287	0.24441	0.99542	(F5)
L30	=	13.10348*ln(t) − 32.39733	0.25004	0.99565	(F6)
L33	=	13.95411*ln(t) − 32.91034	0.31419	0.99395	(F7)
L36	=	14.89322*ln(t) − 33.46500	0.41662	0.99070	(F8)

[1] t = age of stand, years.

described in table 3 in four functions. In table 4 the dominant height is calculated according to these functions. The courses of dominant height expressed in figure 5 and tables 3 and 4 were used for the prognoses of production.

Stem Volume

The relation between dominant height and the total stem volume production is shown in table 5 (function 9) and figure 6. For calculation of function 9 three stands were excluded: 1513 Öd, 2524 Tärnaby, and 2527 Smedsböle. These stands have large stem volumes calculated on a per-hectare basis and cover small areas. Significant margin effects can be expected.

If the function for total production is calculated on dominant height reduced by 2 or 0 meters instead of 1 as in function 9, slightly different functions are achieved:

$$Vpb = e^{(2.0187*\ln(Hdom-2)-0.1320)} \quad r^2 = 0.9876 \qquad \text{(F10)}$$

$$Vpb = e^{(2.3525*\ln(Hdom)-1.3616)} \quad r^2 = 0.9875 \qquad \text{(F11)}$$

At a dominant height of 35 meters, these functions express a total production which is 5 percent lower or 5 percent higher, respectively, than the production achieved by function 9.

Figure 7 shows the total stem volumes recorded in the field plots together with the calculated values according to function 9. The calculated courses for stem volume increment including and excluding bark volume are also shown in table 6. The mean annual increment including and excluding bark is shown in figure 8.

Damage

The three most frequent types of damage recorded were snow break, forked stem, and crooked stem. The frequencies of these damages are shown in table 8.

Bark Volume

On an average the bark volume represents 26 percent of the gross stem volume of larch trees, which is approximately twice as much as the bark share of volume in Scots pine. However, the share of bark volume in the investigated larch stands varies between 12 and 35 percent (table 7). The reason for this big variation has not been explained.

Table 4—The dominant height in meters of *Larix sukaczewii* in northern Sweden. The designation of site index according to Vuokila and others 1983

Total age	Site index, H100 L27	L30	L33	L36
Years		- - - - - *m* - - - - -		
25	7.63	9.78	12.01	14.47
30	9.91	12.17	14.55	17.19
35	11.83	14.19	16.70	19.49
40	13.50	15.94	18.56	21.47
45	14.97	17.48	20.21	23.23
50	16.28	18.86	21.68	24.80
55	17.47	20.11	23.01	26.21
60	18.56	21.25	24.22	27.51
65	19.55	22.30	25.34	28.71
70	20.48	23.27	26.37	29.81
75	21.34	24.17	27.34	30.84
80	22.15	25.02	28.24	31.80
85	22.90	25.82	29.08	32.70
90	23.62	26.57	29.88	33.55
95	24.29	27.27	30.63	34.36
100	4.93	27.95	31.35	35.12

Table 5—The functional relation between the total stem volume in cubic meters per hectare and the dominant height

Volume	Function	Mean error in regression coefficient	r^2	
Vpb^1 =	$e^{(2.1868*\ln(Hdom-1)-0.7360)}$	0.0526	0.9877	(F9)

[1] Vpb = stem volume in cubic meters per hectare including bark and top; $Hdom$ = dominant height in meters.

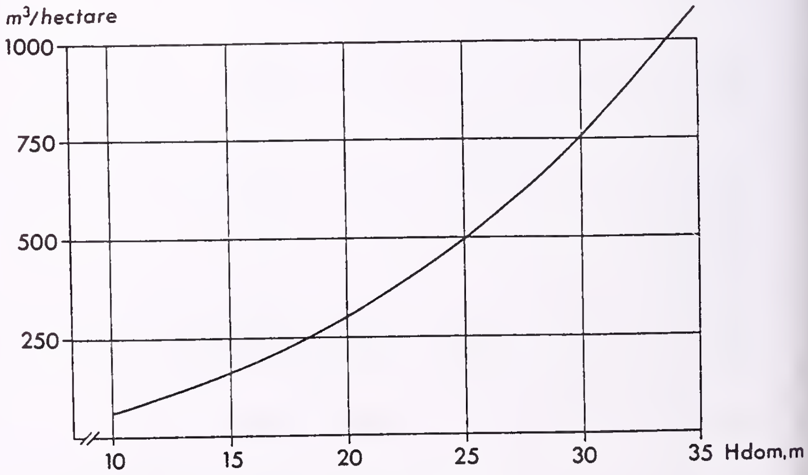

Figure 6—The relations between the total production of stem volume and the dominant height of the investigated stands.

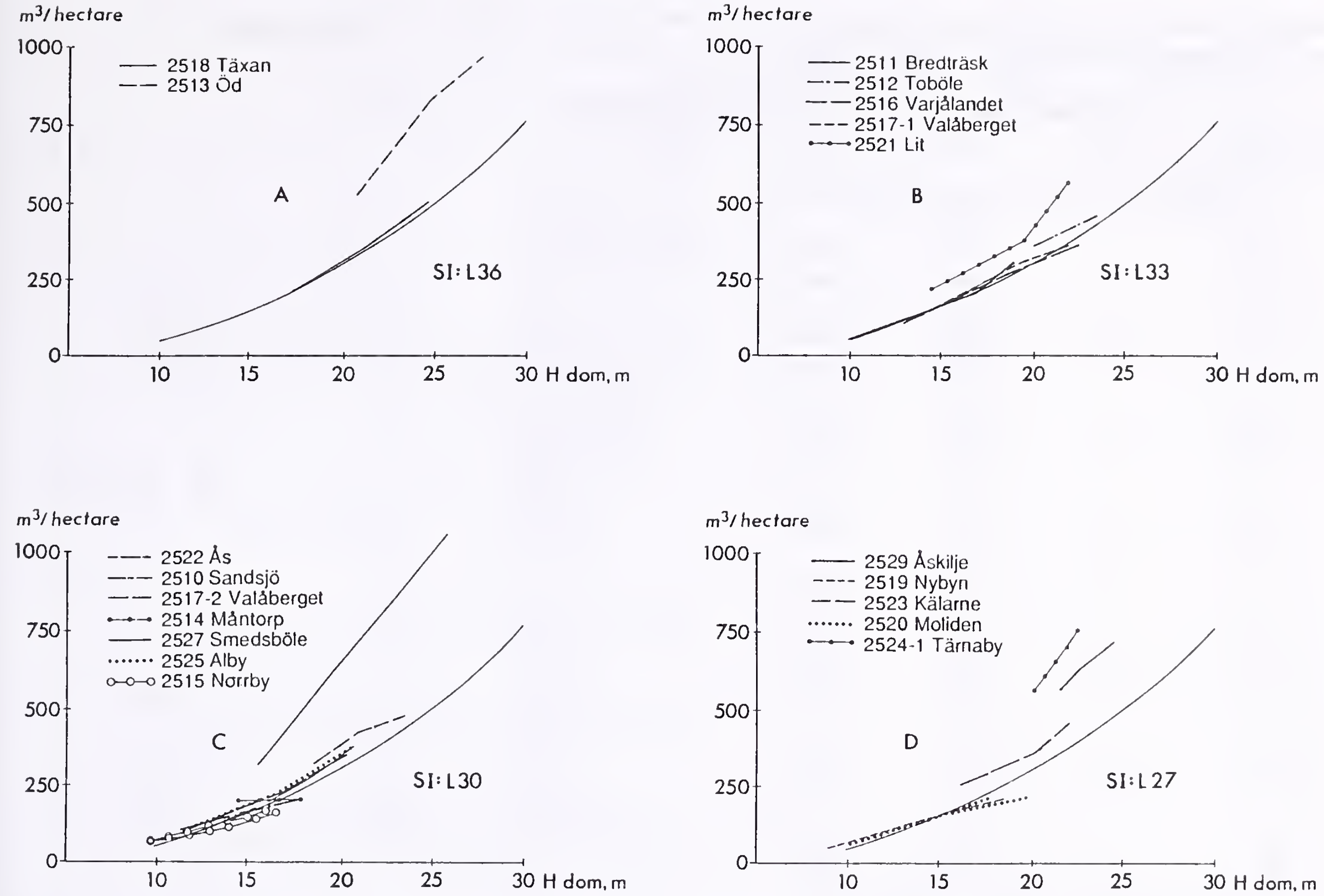

Figure 7A-D—The development of stem volumes of the stands and grouped according to site class.

Production of Larch Compared to Other Tree Species

Table 9 shows the recorded total production per hectare and year of larch together with expected production of Scots pine (P) or Norway spruce (S) in adjacent stands. The production of pine or spruce is based upon yield tables by Ekö (1985), corresponding to the production in closed stands with one or two thinnings during a rotation period.

This comparison indicates a big variation in the productivity of larch. In some of the sites larch has produced much more than the native tree species, in other sites less. On an average this table shows that the production of larch is 25 to 40 percent superior to the native conifers depending on site index. These figures include the volume of bark. Corresponding figures calculated under bark are 10 to 25 percent less.

The difference between the production of larch and that of pine or spruce varies a lot between sites, probably depending on local site conditions and the tending of the stand; for example, genetic origin of seed, spacing, and thinnings. In general the difference increases with increasing site index. In 13 cases larch was compared to pine and in nine cases to spruce. Compared to pine, larch usually is superior in stem volume production, and this superiority increases with site index. Comparisons to spruce are more difficult because of the problems in finding properly managed spruce stands.

A direct relation between the estimated site index of Scots pine and that of larch is shown in figure 9. This relation is also expressed in function 12:

$$SI(P) = 0.822{*}SI(L) - 1.531 \qquad r^2 = 0.74699 \qquad \text{(F12)}$$

where:

$SI(P)$ = site index for Scots pine, H100, m
$SI(L)$ = site index for larch, H100, m.

Site index L27 is equal to P20.8; L30 is equal to P23.2; L33 is equal to P25.7; and L36 is equal to P28. Table 10 shows the average annual production of Scots pine and Siberian larch between age 30 and 100 growing on equal sites. In this case the expected production of larch is compared to the expected production of Scots pine. For both species bark is included. At age 100 the production of larch exceeds that of larch with 2 percent at site index L27/P20.8 and with 64 percent at site index L36/P28. The corresponding figures for comparing stem volume excluding bark are 12 and +38 percent, respectively. The difference in productivity of Scots pine growing on a rich versus a poor site is relatively small, while the productivity of larch is more than twice as much in L36 compared to L27.

Table 6—Prognosis of stem volume production per hectare based upon 16 stands of *Larix sukaczewii* in northern Sweden

	Site index, H100, m			
Total age	**L27**	**L30**	**L33**	**L36**
Years	- - m^3 *stem volume per hectare, excluding bark* - -			
25	22	41	67	104
30	42	70	106	156
35	65	100	146	209
40	89	131	186	261
45	113	163	227	313
50	138	194	267	363
55	162	225	306	411
60	186	255	344	459
65	210	285	381	506
70	234	314	417	551
75	258	343	453	595
80	280	370	488	638
85	301	398	521	679
90	325	425	554	720
95	346	451	586	759
100	367	476	618	798
	- - m^3 *stem volume per hectare, including bark* - -			
25	30	55	91	141
30	57	94	143	211
35	88	135	197	282
40	120	177	252	353
45	153	220	307	423
50	186	262	361	491
55	219	304	413	556
60	252	345	465	621
65	284	385	515	684
70	316	424	564	745
75	348	463	612	804
80	379	500	659	862
85	409	538	704	918
90	439	574	749	973
95	467	609	792	1,026
100	496	643	835	1,078

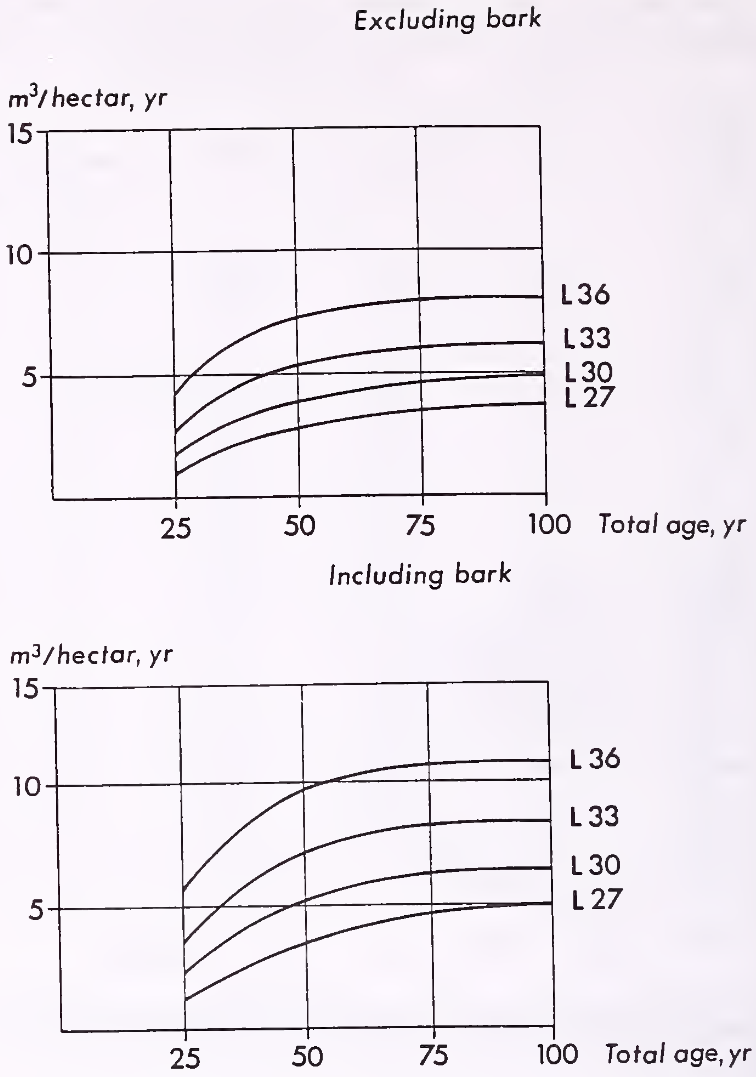

Figure 8—Mean annual increment of four site qualities including or excluding bark volume.

Site index of spruce and larch was compared in a similar way. However, no significant correlation could be found. A high site index of larch sometimes corresponds to a high, sometimes to a low site index of spruce.

Four of the larch stands are close to contemporarily established stands of lodgepole pine (*Pinus contorta*). These stands are 2510 Sandsjö, 2512 Toböle, 2511 Bredträsk and 2513 Öd. In Öd a small stand of Douglas-fir (*Pseudotsuga menziesii*) was established the same year as the larch and the lodgepole pine. Table 11 shows the total production of all tree species present on the four sites.

More detailed information about these 20 larch stands and the processing of collected data is given by Martinsson (1990).

DISCUSSION

Increment of Dominant Height

The most remarkable difference between this investigation and earlier investigations of the same larch stands made by Wiksten (1962); Edlund (1962); and Remröd and Strömberg (1977) is the course of dominant height increment over time. The courses of dominant height described by Remröd and Strömberg are considerably more curved,

Table 7—The bark volume in percentage of the total larch stem volume

Plot No.	Site	D.b.h. of mean tree basal area	Percent bark of stem volume
		mm	
2510	Sandsjö	207	27
2511	Bredträsk	204	12
2512	Toböle	191	27
2513	Öd	351	21
2414	Måntorp	201	26
2515-1	Norrby	181	27
2515-2	Norrby	184	27
2516	Vargålandet	185	24
2517-1	Valåberget	218	28
2517-2	Valåberget	172	28
2518	Täxan	276	27
2519	Nybyn	161	20
2520-1	Moliden	178	31
2520-2	Moliden	192	31
2521	Lit	216	27
2522	Ås	279	28
2523	Kälarne	232	29
2524-1	Tärnaby	289	16
2525	Alby	187	27
2527	Smedsböle	351	35
2528	Åsele	163	28
2529	Åskilje	328	26
2530	Sarvisvaara	188	28

Table 8—Frequency of damage in the larch stands. The figures indicate number of larch trees

				Of the living trees		
Plot No.	Site	Dead	Living	Top broken	Crooked	Double top
2510	Sandsjö	18	39	12	9	—
2511	Bredträsk	1	72	3	4	—
2512	Toböle	1	51	—	—	—
2513	Öd	—	20	1	—	—
2514	Måntorp	3	34	—	4	2
2515-1	Norrby	13	57	4	6	3
2515-2	Norrby	23	68	13	15	3
2516	Vargålandet	13	151	—	2	3
2517-1	Valåberget	13	75	—	11	1
2517-2	Valåberget	70	132	—	12	6
2518	Täxan	—	30	1	1	2
2519	Nybyn	3	70	10	—	6
2520-1	Moliden	16	43	10	—	1
2520-2	Moliden	6	44	4	—	—
2521	Lit	—	49	—	1	—
2522	Ås	4	27	—	—	—
2523	Kälarne	—	46	—	3	—
2524-1	Tärnaby	—	21	1	2	5
2524-2	Tärnaby	—	29	3	—	6
2525	Alby	—	51	1	5	—
2527	Smedsböle	—	36	—	11	—
2528	Åsele	1	52	—	—	—
2529	Åskilje	—	33	—	—	—
2530	Sarvisvaara	—	45	—	2	1

Table 9—Mean annual increment of larch per hectare and year at latest revision or at growth culmination and expected mean annual increment per hectare and year of Scots pine or Norway spruce on the same site at total age 80 years

Plot		M.A.I. larch		M.A.I. pine/spruce		
		On bark	Under bark	On bark	Under bark	Tree species*
		- - - - - - - - - - - -	- - - - - - - - - - - - m³/(ha*year)	- - - - - - - - - - - -	- - - - - - - - - - - -	
			Site index L24			
2528	Åsele	1.9	1.4	3.4	3.0	(T)
			Site index L27			
2524	Tärnaby	8.7	7.3	4.5	3.8	(G)
2515-1	Norrby	3.2	2.7	5.1	4.4	(T)
2523	Kälarne	6.3	4.5	5.0	4.3	(G)
2520	Moliden	3.9	2.7	4.8	4.1	(G)
2519	Nybyn	3.2	2.6	5.0	4.4	(G)
2529	Åskilje	8.5	6.3	3.8	3.3	(T)
2530	Sarvisvaara	4.7	3.4	3.5	3.1	(T)
			Site index L30			
2515-2	Norrby	3.7	2.5	5.1	4.5	(T)
2514	Måntorp	5.1	3.8	6.1	5.3	(T)
2510	Sandsjö	4.5	3.3	2.7	2.4	(T)
2517-2	Valåberget	6.3	4.6	5.4	4.7	(G)
2522	Ås	6.7	4.9	5.2	4.5	(T)
2527	Smedsböle	(12.4)	(8.0)	2.3	2.1	(G)
2525	Alby	6.5	4.7	5.3	4.6	(T)
			Site index L33			
2511	Bredträsk	6.2	5.5	5.8	5.1	(T)
2521	Lit	10.1	7.4	5.2	4.5	(T)
2517-1	Valåberget	6.6	4.7	5.4	4.7	(G)
2512	Toböle	7.8	5.7	6.9	6.0	(T)
2616	Vargålandet	7.2	5.5	3.7	3.3	(G)
			Site index L36			
2513	Öd	(16.0)	(12.6)	8.4	7.2	(T)
2518	Täxan	9.42	6.9	7.3	6.4	(G)

*Native alternative tree species for site classification. T = Scots pine, G = Norway spruce.

which gives lower values of dominant height at the end of the rotation period. Remröd and Strömberg have no detailed description of their mathematical methods more than "Hdom is set to predetermined levels at age 50 years at breast height."

Wiksten has explained the mathematical function he used for the calculation of the dominant height:

$$Hdom = (x/a+bx)^3$$

where:

$Hdom$ = The dominant height of the stand
x = Total age of the stand
a,b = Constants determined for the dominant height at stand age 50 years.

Thus, the only point where the calculated course of dominant height definitely corresponds to the values recorded in the field is at stand age 50 years. Wiksten is referring to Pettersson (1955) who used this and similar functions to describe the course of dominant height of naturally regenerated coniferous stand, mainly Scots pine.

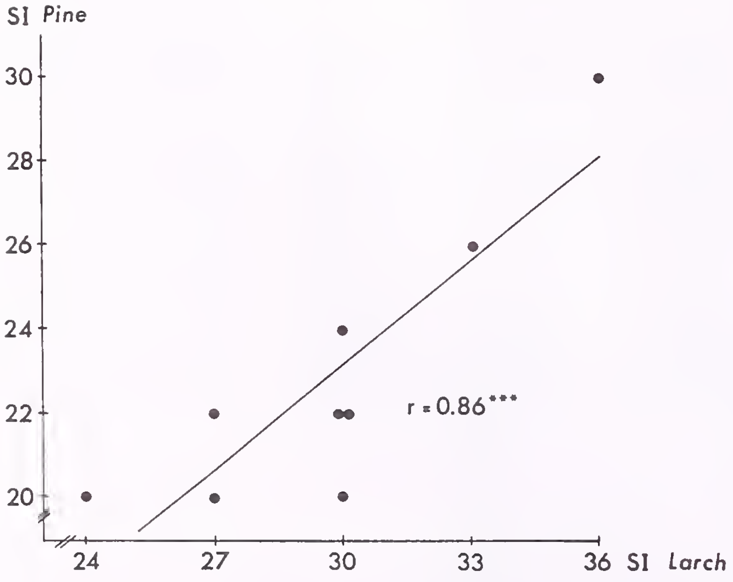

Figure 9—The relation between site index of larch and Scots pine on the same site.

Table 10—Mean annual production of stem wood, meters cubed per hectare, year of *Larix sukaczewii* and Scots pine growing under similar site conditions and the production of larch in percentage of Scots pine

	Site index											
	L27/T20.8			L30/T23.2			L33/T25.7			L36/T28.0		
Age, year	Larch	Pine	Percent	Larch	Pine	Percent	Larch	Pine	Percent	Larch	Pine	Percent
					Including bark							
30	1.9	2.5	76	3.1	2.8	111	4.8	3.6	133	7.0	4.4	159
40	3.0	3.5	86	4.4	3.9	113	6.3	4.8	131	8.8	5.7	154
50	3.7	4.1	90	5.2	4.5	116	7.2	5.7	126	9.8	6.4	153
60	4.2	4.6	91	5.8	5.0	116	7.8	6.0	130	10.4	6.7	155
70	4.5	4.7	96	6.1	5.1	120	8.1	6.2	131	10.6	6.7	158
80	4.7	4.8	98	6.3	5.2	121	8.2	6.2	132	10.8	6.7	161
90	4.9	4.9	100	6.4	5.2	123	8.3	6.2	134	10.8	6.7	161
100	5.0	4.9	102	6.4	5.2	123	8.4	6.1	138	10.8	6.6	164
					Excluding bark							
30	1.4	2.2	64	2.3	2.5	92	3.5	3.2	109	5.2	3.9	133
40	2.2	3.1	71	3.3	3.4	80	4.7	4.2	112	6.5	5.0	130
50	2.8	3.6	78	3.9	4.0	98	5.3	5.0	106	7.3	5.6	130
60	3.1	4.0	78	4.3	4.4	98	5.7	5.3	108	7.8	5.9	130
70	3.3	4.1	80	4.5	4.5	100	6.0	5.5	109	7.9	5.9	133
80	3.5	4.2	83	4.6	4.6	100	6.1	5.4	113	8.0	5.9	135
90	3.6	4.3	84	4.7	4.6	102	6.2	5.4	115	8.0	5.9	136
100	3.8	4.3	88	4.8	4.6	104	6.2	5.4	115	8.0	5.8	138

Table 11—Stem volume production in neighboring stands of lodgepole pine, Scots pine, and Douglas-fir

Plot No.	Site	Tree species	Stand age	Total production	Plot area
				m³/ha	*m²*
2510	Sandsjö	Scots pine	49	64	*
	Sandsjö	Lodgepole pine	53	211	1,500
	Sandsjö	Larch	49	220	590
2511	Bredträsk	Scots pine	47	237	750
	Bredträsk	Lodgepole pine	53	370	1,000
	Bredträsk	Larch	47	292	750
2512	Toböle	Scots pine	56	374	*
	Toböle	Lodgepole pine	56	496	900
	Toböle	Larch	56	434	383
2513	Öd	Scots pine	58	601	560
	Öd	Lodgepole pine	58	578	740
	Öd	Larch	58	944	288
	Öd	Fir	58	900	230

* From Ekö 1985.

Edlund (1962) is referring to Wiksten's method of calculation of the dominant height and has used the same method.

Tveite's method for describing the dominant height is similar to those used by Wiksten (1962), Edlund (1962), and Remröd and Strömberg (1977) in one aspect: the starting point of the course is set to a predetermined level. The main difference between Tveite's method and the one used by the other three authors is that Tveite is using data collected in larch stands to describe the whole course of dominant height. Of particular importance for the reliability is the age of the larch stand on which the courses of dominant height is based. The researched stands used by Wiksten, Edlund, and Remröd and Strömberg are mainly the same stands as the ones I have used but at a younger stage. In my material no larch stand is older than 89 years. Between age 80 and 90 there are four stands, but the basis for the courses between 90 and 100 does not exist in my field data.

Vuokila's function for dominant height is based on 26 permanent plots of which some have reached the age of 100 years. Most of these stands are in the age interval of 60 to 80 years. The courses of dominant height developed by Vuokila coincide well with those described by Tovstoljes (1916) based on the old, famous larch stands in Raivola. Figure 10 shows the dominant height of Siberian larch calculated by Wiksten (1962), Remröd and Strömberg (1977), Vuokila and others (1983), and me. The dominant height according to Wiksten does correspond fairly well to the one I have described for the highest site index. On more poor sites the course of dominant height is more curved according to Wiksten. However, it should be stressed that I have excluded material from site index below H100 = L27. The dominant height according to Remröd and Strömberg corresponds fairly well with those I have investigated up to age 30. After that the differences are big, since the dominant heights according to Remröd and Strömberg more or less even out at age 70.

The weak points in my material are the sizes of the plots, the bad management of the stands (no or few thinnings), and too little data from the upper ages. Therefore, the courses for dominant height at the upper ages may be adjusted when more information is collected from these and other stands in the future. However, for the present the most reliable courses for describing the dominant height of Siberian larch in northern Sweden is the one illustrated in figure 10D.

Increment of Stem Volume

The prognosis for the stem volume increment is based on two important relations: (1) the relation between stand age and dominant height and (2) the relation between the stem volume of the stand and its dominant height. The second relation is independent of site index, according to Eichhorn (1904). In the investigated material a strong correlation was found between the stem volume and the dominant height. This relation is probably more clear cut than the relation between stand age and dominant height.

The stem volume production of the investigated stands should be considered as a result of production under the given conditions. The total material is small as well as the individual plot areas. Margin effects because of too small plot areas may occur in some cases. Factors that could have increased the total volume production are, for instance: genetic origin of seed, choice of site, method for stand establishment, and regular thinnings. It is well known that Siberian larch is influenced by site conditions. The soil water, site exposure, and soil texture have probably greater influence on larch than on many other tree species. The Siberian larch as well as the Japanese and the European larches (*Larix kaempferii* and *L. decidua*) need rich sites and slopes with mobile soil water for high production.

Comparing Production of Larch to Other Tree Species

The stem volume production of larch was compared to other tree species in adjacent stands. This comparison was based on site classification determined by assessment of dominant height. Two stands 2511 Bredträsk and 2523 Öd larch stands could also be compared to contemporarily planted stands of Scots pine adjacent to the larch stand.

In 47 years the Scots pine stand at Bredträsk produced 237 m^3 per hectare, while the larch on the same site and at the same time produced 292 m^3 per hectare, or 23 percent more. In Öd the Scots pine stand produced 601 m^3 per hectare, while the larch produced 944 m^3 per hectare. For both species bark volume is included. In 2511 Bredträsk the share of bark is 12 percent of the total stem volume of larch. This is less than the average and approximately the same as for Scots pine. In 2523 Öd the share of bark is 21 percent of larch stem volume.

In four sites larch was also compared to lodgepole pine and in one site to Douglas-fir. This comparison indicates that the volume production of larch is superior to lodgepole pine at high elevations and in hilly sites with mobile soil water.

Published data by Gadestedt and Wikman (1988) from plots of Siberian larch not included in this material prove the high productivity of this species in northern Sweden. In some of these plots more than 300 m^3 per hectare was produced in 30 years.

Examples of poor production of larch also exist. Many such larch stands have been classified as failures and abandoned. One possible exception is 2528 Åsele, where larch, depending on site quality, evidently is not the optimal choice of species. On this site Scots pine produced 79 percent more stem volume than larch, calculated excluding bark and 114 percent more including bark.

The Influence of Provenance

The genetic origin of the investigated material is unknown in most cases. Except for plot 2520 Moliden, the origin of the seed source probably is the northern part of European Russia or allochtone stands in Finland.

The trials for provenance research on *Larix sukaczewii* and other Asiatic larch species is incomplete in Sweden. However, one 30-year-old trial including 30 provenances of larch mainly from Siberia indicates that the second generation of Swedish-grown Siberian larch, provenance Visingsö, is competitive to directly introduced material (Martinsson 1990). Most of the successful plantations of Siberian larch in northern Sweden originate from Archangel oblast in northern Russia or the allochton stands in Raivola in Karelia. Other seed sources that have proved good growth is for instance Sverdlovsk (latitude north 57°00', longitude east 60°00'), Sonskij (latitude north 54°00', longitude east 90°00') ,and Askitzky (latitude north 53°00', longitude east 90°00') (Jonsson 1978).

CONCLUSIONS

Regarding increment of height growth and stem volume of Siberian larch in northern Sweden, the following conclusions can be drawn:

- The increment of dominant height is continuing still at an age of 90 years.
- On rich sites in northern Sweden the production of stem volume of larch excluding bark exceeds the one of Scots pine with 10 to 25 percent .
- Siberian larch is more sensitive to ground conditions than Scots pine.

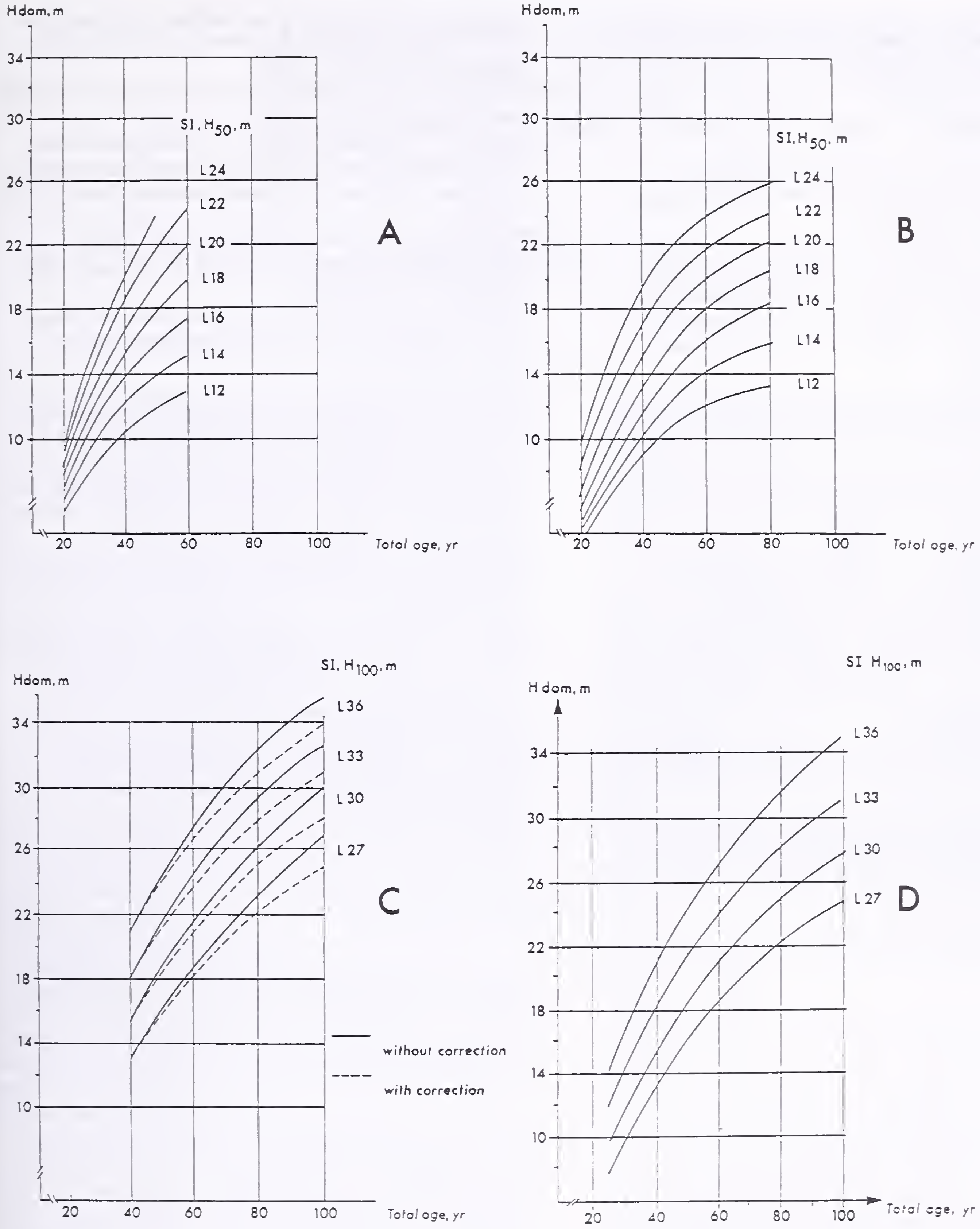

Figure 10—The development of the dominant height of Siberian larch according to four investigations: A = Wiksten 1962, B = Remröd and Strömberg 1976, C = Vuokila and others 1983, D = material in this investigation processed according to Tveite (1968).

- This investigation gives clear examples of Siberian larch being superior in productivity to native conifers in some sites in northern Sweden.

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Development of Western Larch in Mixed Stands in Washington's Cascade Range: Implications for Prioritizing Thinning Treatments

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David F. Cobb

Abstract—The development of mixed-species, even-age stands follows relatively predictable patterns. Stand development was used to estimate differentiation potential in mixed-species stands, which included western larch (*Larix occidentalis*), in the Wenatchee National Forest, Washington State, U.S.A. Stands that can differentiate are a management priority because of their lower susceptibility to insects and diseases, greater wind firmness, and faster stand growth rates. A stand prioritization system that ranks the potential of stands to differentiate gives higher priority for using relatively scarce thinning resources.

When financial resources are insufficient to meet precommercial thinning needs, land managers face difficult decisions regarding where to expend these resources to achieve the greatest benefits. These decisions are more difficult when stands occur across wide environmental gradients and encompass stands with different species compositions and growth habits. This is the case in the Wenatchee National Forest in eastern Washington, U.S.A., where stands range across steep gradients related to elevation and distance from the Cascade Crest.

Prioritizing stands of such diverse characteristics for precommercial thinning requires information on stand development patterns and, particularly, potential for stand differentiation in both single and mixed-species stands. Stand differentiation is defined as the divergence of individual tree growth rates in a stand after the onset of competition (Oliver and Larson 1990).

Differentiation is usually first apparent as differences in diameter growth rates, but height growth rates are also affected and are of great importance because relative height growth rates describe a tree's ability to maintain crown position. This divergence allows trees with faster growth rates to suppress and sometimes kill slower growing trees as a stand develops. The dominating tree may have a competitive advantage such as being older, or on a favorable microsite, or it may be a faster growing individual or species. A well-differentiating stand is one where some trees are easily outcompeting others, and dominant tree size may approach that of similar open-grown trees. Trees suppressed and killed in a differentiating stand represent some loss in recoverable volume that might have been "placed" on surviving trees if thinning had occurred earlier. However, a well-differentiating stand is a relatively healthy alternative to the slowly differentiating stand where thinnings are not planned (Oliver and Larson 1990).

The opposite of a well-differentiating stand is a stand approaching stagnation or experiencing height repression. Height repression refers to the stand condition where overcrowding reduces tree height and diameter growth and slows the process of stand differentiation. Height repression occurs over a range of degrees of stand differentiation from the nearly stagnated stand where height repression is severe, to the differentiating stand where height growth is reduced only slightly. With an increasing degree of height repression, a stand will experience reduced vigor and a greater susceptibility to insect and disease problems, develop at a slower rate, and produce less wood increment (Oliver and Larson 1990).

This paper discusses mixed-species, even-age stand development patterns for stands in the Wenatchee National Forest, paying particular attention to stands where western larch (*Larix occidentalis*) is a component. It also examines what factors are important in affecting differentiation of these stands and the implications of these factors in prioritizing stands for precommercial thinning.

Current guidelines for management on the Wenatchee National Forest require maintenance of stand vigor and promotion of stand structures and species compositions that avoid serious risk of damage from mammals, insects, diseases, wind, snow, and fire. Because of the overriding goal of maintaining stand vigor and the uncertainty of future use, stands are prioritized for precommercial thinning with regard to their potential for differentiation without treatment. Stands that differentiate will maintain a higher level of growth, vigor, and a greater resistance to damaging agents when left untreated than stands that differentiate poorly. A rapidly growing, differentiating stand also offers the most options for future treatment and the most

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flexibility for meeting diverse management objectives without being thinned. Stand differentiation is a function of the variability in growth of component trees. Because this variation in growth rates can be due to species differences, understanding mixed-species stand development was necessary for development of a prioritization system. Other factors were also examined including crown sizes as represented by live crown ratios, and number of trees and crop trees per unit area.

MIXED-SPECIES STAND DEVELOPMENT

Two recent studies in the Wenatchee National Forest provided descriptions of mixed-species stand development over a range of site quality.

Cobb and others (1993) reconstructed even-age stand development patterns in grand fir plant associations: a mid-elevation climax series on the east-slope of the Washington Cascade Range. In stands consisting of western larch, and various combinations of lodgepole pine (*Pinus contorta*), Douglas-fir (*Pseudotsuga menziesii* var. *glauca*), and grand fir (*Abies grandis*), western larch dominated in all stands (fig. 1). In stands where lodgepole pine was present, the height growth rates of western larch and lodgepole pine were similar with western larch achieving a greater height in all stands. Similar development patterns have been reported by others across the range of western larch (Boyd 1959; Cole and Schmidt 1986; Mosher 1965; Schmidt and others 1976; Seidel 1987). Lodgepole pine was experiencing a relatively recent slowdown in height growth that has been observed in other studies (Schmidt and others 1976). The slowdown in lodgepole pine growth is more evident in average diameter growth patterns over time for the same stand (fig. 2).

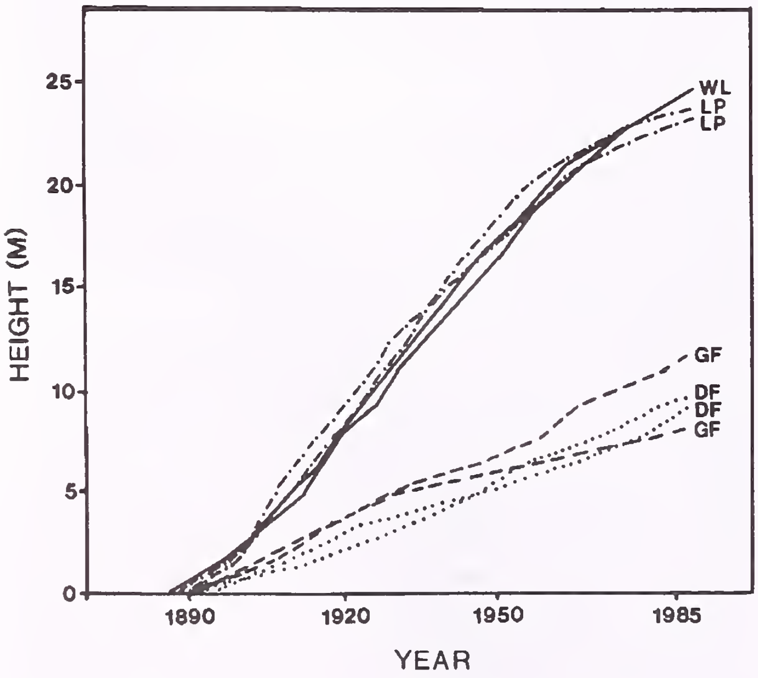

Figure 1—Height growth development for a mixed-species, even-age stand in grand fir climax series. WL = western larch, LP = lodgepole pine, DF = Douglas-fir, GF = grand fir.

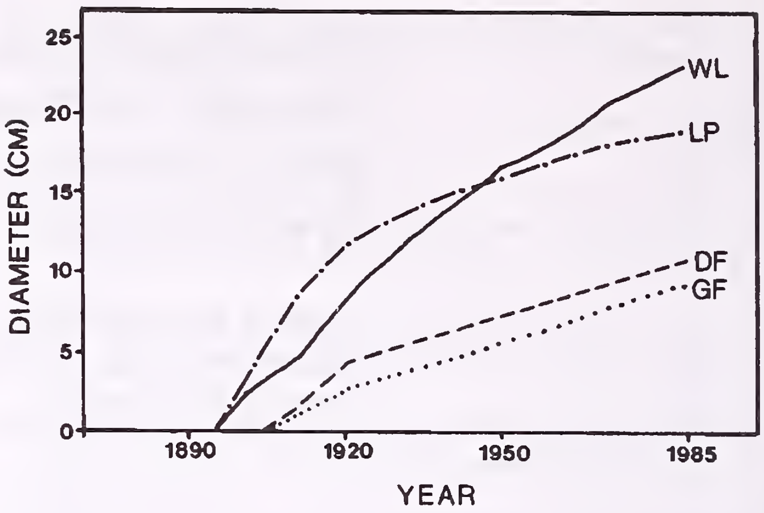

Figure 2—Average breast height diameter development for each species for an even-age, mixed-species stand in grand fir climax series. WL = western larch, LP = lodgepole pine, DF = Douglas-fir, GF = grand fir. This stand is the same shown in figure 1.

Changes in the species stratification patterns occurred when species composition varied slightly from that displayed in figure 1 in the stands sampled by Cobb and others (1993). For example, when lodgepole pine was absent, Douglas-fir assumed an intermediate crown position between western larch and grand fir. When Douglas-fir was absent, grand fir formed a higher stratum than when Douglas-fir was present.

The second mixed-species stand reconstruction study in the Wenatchee National Forest examined young stand development across a gradient of climax series from high-elevation stands near Cascade Crest to low-elevation stands. Five “working groups” were previously designated (table 1) and generally follow the climax series classification for the Wenatchee National Forest (Williams and Smith 1991). Each climax series consists of a set of plant associations with variable productivities, but all plant associations within a climax series have similar climax vegetation potential. Western larch is found in each of these working groups, although it is not found in every plant association.

A total of 20 reconstruction plots were scattered across the five working groups in the two southernmost districts of the Wenatchee National Forest: the Naches and Cle Elum Ranger Districts. Plots were located in young postprecommercial thinning-age stands whenever possible. In some cases, young even-age stands were not available because even-age management is a relatively recent (post-1960) phenomenon in the Wenatchee National Forest. In other cases, even-age stands resulting from stand replacement disturbances are too old or have had their age structure altered by past cutting practices.

Height and diameter growth patterns of individual trees were reconstructed using either reconstructive stem analysis techniques or measuring heights of annual branch whorls and tree ages at breast height and tree base with an increment borer.

Western larch was observed in nine of the 20 reconstruction plots. In the mountain hemlock (*Tsuga mertensiana*)

Table 1—Strata, climate type, and climax series for the five climax series included in prioritization system

Strata	Climate type	Climax Series or Working Group
I	Warm dry	Douglas-fir
II	Warm moist	Grand fir
III	Cool moist	Pacific silver fir or western hemlock
IV	Cold dry	Subalpine fir
V	Cold moist	Mountain hemlock

climax series, western larch was found in one of two reconstruction plots. In this less than 30-year-old stand, western larch occupied an upper canopy position along with subalpine fir and lodgepole pine (fig. 3).

In the subalpine fir (*Abies lasiocarpa*) climax series, western larch occurred in four of five plots and was a dominant in all four of these plots. Figure 4 presents the development of one plot that included several planted ponderosa pine (*Pinus ponderosa*) of probable offsite origin. Western larch and white pine (*Pinus monticola*) had similar height growth rates over the most recent 5 years, while the ponderosa pine was having trouble competing.

Western larch was found in three of four reconstruction plots in the grand fir climax series. The development of western larch in these plots was similar to that shown in figure 1: western larch grew at a similar rate as lodgepole pine but tended to dominate Douglas-fir (fig. 5).

One plot in the Douglas-fir climax series included western larch. In this Douglas-fir/bearberry-bitterbrush (*Pseudotsuga menziesii/Arctostaphylos uva-ursi - Purshia tridentata*) plant association, western larch was unable to compete with ponderosa pine and Douglas-fir (fig. 6).

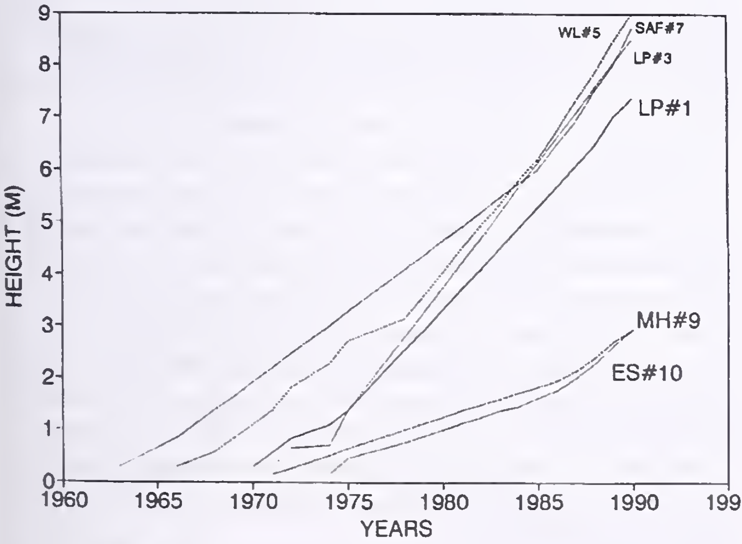

Figure 3—Early stand development in a mixed-species stand in mountain hemlock climax series. Western larch occupied dominant canopy position but subalpine fir and lodgepole pine were also growing well. WL = western larch, SAF = subalpine fir, LP = lodgepole pine, MH = mountain hemlock, ES = Engelmann spruce (*Picea engelmannii*).

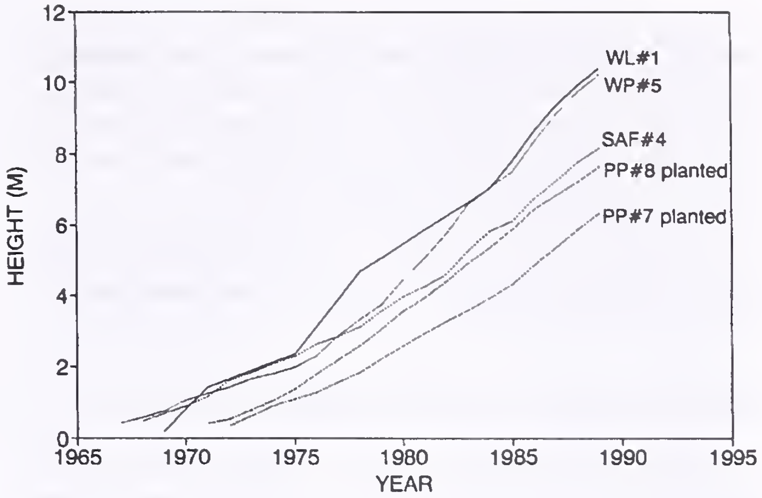

Figure 4—Early stand development in a mixed-species stand in subalpine fir climax series. The ponderosa pine on this plot were most likely planted from an offsite seed source. WL = western larch, WP = western white pine, SAF = subalpine fir, PP = ponderosa pine.

PREDICTING STAND DIFFERENTIATION

Data Source

Data from the Managed Stand Survey system provided initial measurements from permanent plots in the Wenatchee National Forest for development of this prioritization system. The Managed Stand Survey, a USDA Forest Service, Pacific Northwest Region forest inventory, sampled plantations over 10 to 20 years old, and natural stands that met

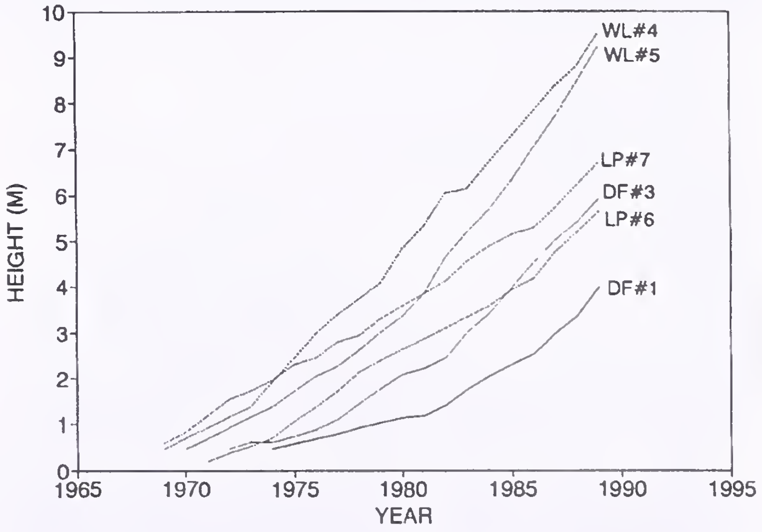

Figure 5—Early stand development in a mixed-species stand in grand fir climax series. The young stands sampled followed patterns similar to those shown in figure 1. WL = western larch, LP = lodgepole pine, DF = Douglas-fir.

current standards for stand management (USDA Forest Service, Region 6, 1990). Some young multiple-storied stands with vigorous understories were also included in the Managed Stand Survey. Variables used in the construction of the prioritization system included live crown ratio, trees per acre, height, and basal area growth.

Only data from the Naches and Cle Elum Ranger Districts were used in this analysis. The prioritization system is therefore only directly applicable to these two districts, although it may have some application in other areas.

Stand Origin and Stand Structure

The prioritization system separates stands with different stand origins or structures. Three different stand origins/structures were included: (1) planted stands; (2) stands originating from natural regeneration; and (3) stands with older residual trees. This classification corresponds to the classification used in the Managed Stand Survey.

Planted stands were assumed to have less variability and to differentiate more slowly than comparable stands. Planted stands generally have less species diversity, more uniform spacing, less age variability, less genetic variability, and less microsite variation because of site preparation and selection of planting site locations (Oliver and Larson 1990).

Natural regeneration stands were defined as even-age stands originating from natural reproduction. Stands could include a component of planted trees, but most crop trees were of natural origin.

Stands with older residual trees included stands receiving overstory removal, or similar treatments, and generally consisted of two canopy strata. The upper stratum may have included scattered older, residual trees, whereas the understory may have been a more fully stocked stratum of advance regeneration or natural regeneration. Both strata may have been less than commercial size, but some trees may be larger than minimum commercial sizes. Size was a particularly poor measure of age in these stands, as some trees may have a history of suppression and may be old. The prioritization system was not designed for uneven-age management applications.

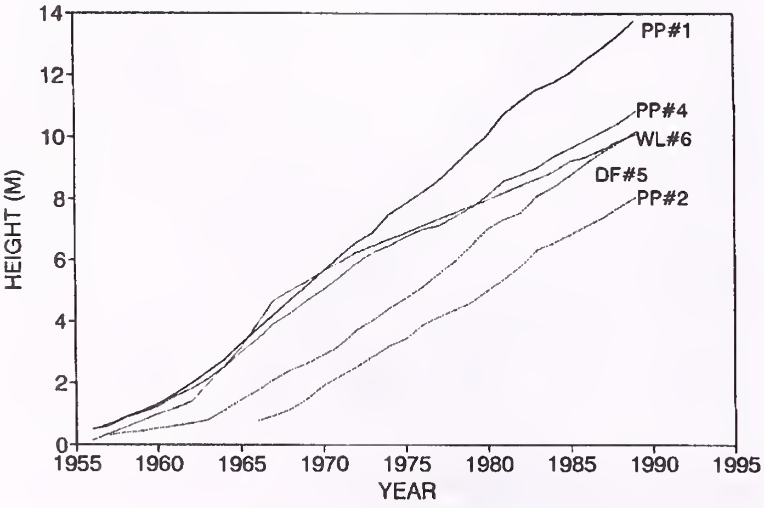

Figure 6—Early stand development in a mixed-species stand in Douglas-fir climax series. Western larch was unable to compete on this dry site. WL = western larch, PP = ponderosa pine, DF = Douglas-fir.

Species Composition

Within climax series and stand origin/stand structure classes, stands were further subdivided by species composition. Species composition or species diversity among crop trees may have a large effect on stand development and differentiation. For example, mixed-species stands are likely to differentiate faster than single-species stands because of differential height growth rates of species (Oliver and Larson 1990).

For this prioritization system, stands were considered single-species stands if 80 percent or more of dominant and codominant (crop) trees were of one species. This is less conservative than the 90 percent of trees of the same species that compose pure stands as defined in some silvicultural textbooks (Daniel and others 1979). Stands in eastern Washington and elsewhere in the Inland Northwest usually include many species, and few include one species in concentrations greater than 80 percent (plantations and post-fire stands of lodgepole pine may be a notable exception).

In stands with an upper canopy consisting of 80 percent or more of one species, an average crop tree of the predominant species is likely to be competing with trees of the same species on three sides. This stand is therefore likely to develop more like a single-species stand than a mixed stand. For this prioritization system, stands with 80 percent or more of one species were assumed to be more density sensitive than mixed-species stands (less than 80 percent of one species) and, when all other factors were equal, were given higher priorities for precommercial thinning.

Factors Affecting Differentiation

Stands experiencing height repression or that are differentiating slowly can be characterized as having high stocking levels, short crowns, or low levels of variation in tree heights. All three of these characteristics were found to be important variables for predicting differentiation.

Live crown ratio (using functional live crown: small or isolated lower branches below main crown were disregarded when estimating live crown ratio) was an effective measure of differentiation and tree vigor in most cases. Trees with live crown ratios of 70 percent and higher generally showed superior percentage increases in basal area during the previous 5 years in most climax series (fig. 7). Percentage basal area provided the best measure of relative growth in the Managed Stand Survey data. Stands in which live crown ratios of crop trees average 70 percent or greater are generally differentiating well or are not experiencing severe intertree competition, or both.

A case where live crown ratio is a less sensitive measure of differentiation may be in some higher elevation stands where few intolerant species are found and where all or most trees have relatively long crowns. For example, young, mixed-species stands of Pacific silver fir (*Abies amabilis*), western hemlock (*Tsuga heterophylla*), noble fir (*Abies procera*), and Douglas-fir within the Pacific silver fir climax series showed no consistent stratification patterns during

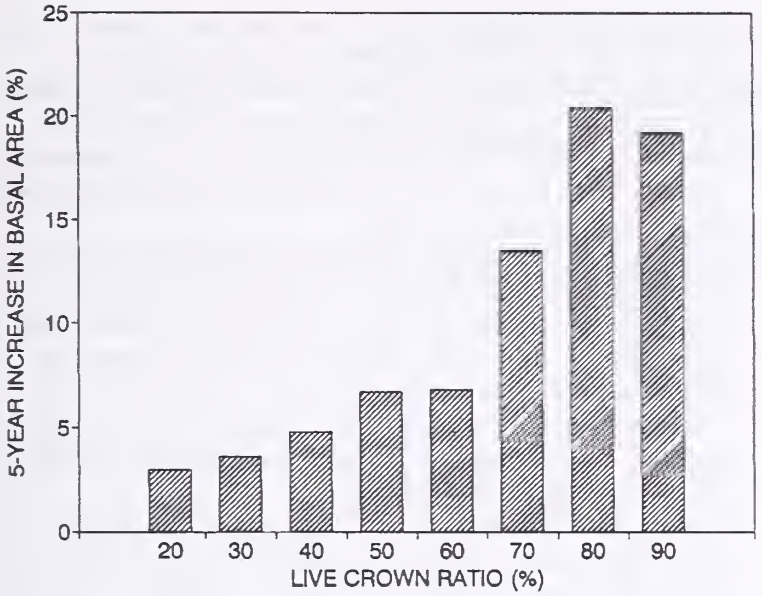

Figure 7—Average percentage 5-year increase in basal area for all species in mixed-species natural stands in Douglas-fir climax series.

the reconstruction analyses. In these stands, live crown ratio may still be a good indicator of individual tree vigor, but more restrictive standards for average live crown ratio may be necessary to predict differentiation.

PRIORITIZING STANDS FOR PRECOMMERCIAL THINNING

This prioritization system was constructed for stands with average tree heights larger than some minimum (usually 3 to 5.5 m or 10 to 18 feet depending on species composition) and that have not reached commercial size. Within this range of average tree sizes, it was assumed that most stands could be thinned to achieve some form of growth response or meet some management objective. However, for the objectives of maintaining or promoting stand differentiation, growth, and vigor, some stands represent higher priorities for expending limited resources for thinning. Stands at low densities (less than 150 trees per acre) or with crop trees having long live crown ratios (greater than or equal to about 70 percent) may not require a precommercial thinning to maintain stand differentiation. These stands may still be considered to be a low priority for thinning because thinning may be warranted to meet some management objectives.

Five priorities were assigned to each stand within the precommercial thinning size range. All climax series, stand types (species compositions), and stand structures are ranked on the same scale with the same five priorities (table 2). Two stands with completely different species compositions and structures that have the same priority were assumed to have equal need for precommercial thinning to maintain stand differentiation, growth, and vigor. Other concerns, such as wildlife habitat, esthetics, or accessibility, may alter the ranking of priorities and are important considerations. However, all concerns other than maintaining stand differentiation, growth, and vigor are beyond the scope of this prioritization system.

Table 2—Definitions of priorities for precommercial thinning

Very High Priority—Stands in need of an immediate reduction in density. These stands are experiencing height repression and prone to insect and disease problems.

High Priority—Stands that will soon need a reduction in density. Stands have limited potential to differentiate without precommercial thinning.

Medium Priority—Stands that are experiencing a moderate degree of height repression but may differentiate without precommercial thinning.

Low Priority—Stands that will probably differentiate without precommercial thinning but might benefit from a treatment that favors certain species.

Very Low Priority—Stands with no apparent need for a precommercial thinning treatment but may need treatment in the future with ingrowth, or to favor certain species, or to meet other management objectives.

Recommended Crop Tree Densities

Current stand management trends throughout the Pacific Northwest and elsewhere are toward lower stocking levels. The number of crop trees per acre used in this prioritization system reflect this trend because these stocking levels fluctuate from 150 to 200 trees per acre. In general, after precommercial thinning, stocking levels for stands should consist of mostly ponderosa pine, lodgepole pine, or western larch at 150 trees per acre. Stands consisting of Douglas-fir, grand fir, or mixed stands of predominantly these species have recommended stocking levels of 200 trees per acre. These differences by species correspond to those of the April 1987 USDA Forest Service Timber Stand Improvement Handbook guidelines for the Pacific Northwest Region where recommended stocking levels for young ponderosa pine stands are roughly 80 to 100 trees per acre lower than for Douglas-fir stands (USDA Forest Service 1987). Cochran's (1985) stocking guide for western larch provides another alternative for identifying appropriate stocking levels for stands in eastern Oregon and Washington.

Management objectives should be used to determine the appropriate postthinning stocking level. A high stocking level will result in higher total wood volume production and lower average tree sizes than a low stocking level, which will result in less volume production but larger average tree sizes. At the stand development stage requiring a precommercial thinning, average tree size is probably a greater concern than total volume production: hence lower stocking levels are recommended in this prioritization system. Lower stocking levels are also more likely to produce trees of higher vigor and with greater insect and disease resistance than stands with higher stocking levels.

Thinning Recommendations

Thinning from below (such as a low thinning) is recommended for all precommercial thinning treatments. Previous research in the eastern Cascades (Seidel 1986, 1987) indicates low thinning achieves superior results by reducing mortality and leaving trees that are more resistant to wind, snow, and ice damage. Thinning from below also offers the best opportunity to select genetically superior individuals.

Stand establishment and thinning practices in the Wenatchee National Forest that favor mixed-species stands are encouraged. Mixed-species stands offer the most future alternatives for management, the most resistance and flexibility for avoiding disease and insect problems, and more capability to differentiate. Usually, mixed-species stands can be thinned from below while still maintaining a mixed-species composition. However, in stands that are differentiating into stratified mixtures (fig. 1), thinning from below may reduce species diversity by favoring a dominating species. Thinning decisions in these stands should consider management objectives and the implications of reducing species diversity or, alternatively, removing some dominant trees to favor a slower growing species.

Existing disease or insect problems or potential problems should also be considered when selecting species to remove or remain in a precommercial thinning operation. For example, species susceptible to laminated root rot should not be left near, or in, root rot centers, or spruce budworm susceptible species should not be left in areas susceptible to budworm infestation.

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Growth and Development of Native and Exotic Larches in Newfoundland and Labrador, Canada

Charles M. Harrison
J. Peter Hall

Abstract—Newfoundland and Labrador, Canada, are larch country, although to now the species has played a minor role in forest economy. Several species of commercial forest trees and several exotic species plantations have met with varying success. While spruce and fir have some advantages over larch, various larch species will likely find more favor with industry in the next century because of shortages of other species.

To date, larch has played a minor role in the forest economy of Newfoundland and Labrador, Canada. The lone native species, eastern larch or tamarack (*Larix laricina* [Du Roi] K. Koch), occurs singly or in small groups throughout the Province. The annual cut is negligible compared to that of black spruce (*Picea mariana* [Mill] B.S.P.) or balsam fir (*Abies balsamea* [L.] Mill), the two main commercial species in the Province. This does not mean it does not have commercial potential. White spruce (*Picea glauca* [Moench] Voss), which also occurs singly or in small groups, is considered one of our most valuable pulpwood and sawtimber species and is used almost as much as black spruce for reforestation.

Several species of exotic larches have also been planted here, with varying degrees of success. The most widely planted has been Japanese larch (*L. leptolepis* [Sieb. and Zucc.] Gord.). It has also been the most successful, especially on the West Coast. In some parts of the Province, it is subject to winter burn, although it has done well at Pynn's Brook, about 40 km east of Corner Brook, on a site on which Sitka spruce is killed back above snow level every winter. The second most widely planted species has been European larch (*L. decidua* Mill), and it has also done well in some locations. Other species that have been tried include Siberian larch (*L. sibirica*), Dahurian larch (*L. gmelinii*), and Dunkeld larch (*L. xeurolepis* Henry). Their performance has not been overly impressive, but it may be that they haven't really received a fair trial as only a few sources have been tried in a few locations.

A modest larch planting program is under way in Newfoundland. On the average, of a total of about 8 million seedings a year planted in this Province, about 250,000 are larch, mostly Japanese. The paper companies can include about 5 percent larch in their newsprint under the current pulping process. They are not particularly anxious to increase this percentage and would just as soon use only spruce and fir. Formerly, industry frowned upon tamarack because it is denser than the spruces and tends to sink. Thus, it could not be floated down river to the mills. Even though this practice has all but ended, old biases remain. Besides, larch offers no particular advantage over spruce and fir; and because the pulping process would have to be altered to accommodate higher percentages of it, its favor with the companies has not significantly increased.

The companies' attitude toward larch could quickly change in the early 21st century, though, when an anticipated shortage of spruce and fir timber occurs. Because of its fast growth rate, larch could help alleviate that shortage if planted in quantity now. One advantage to growing larch here is that there are no porcupines in the island portion of the Province. Another advantage is that fire, to which larch is quite susceptible, is not as much a threat here because of the wet soils and wet climate. Again, this advantage applies more to the island than to Labrador.

LARIX LARICINA

Eastern larch is native throughout the Province except for extreme northern Labrador, which is arctic tundra. It makes its best growth on better drained uplands but will often produce merchantable stems on bogs and other sites where black spruce will only produce small, scrubby trees of no commercial value. Considerable variability exists between and within stands for both growth rate and form characteristics such as stem straightness, branch size, branch angle, and crown diameter. This variability ranges from 9 to 24 percent, and selecting for form characteristics results in no sacrifice of growth rate (Hall and Harrison 1983).

Eastern larch, black spruce, and white spruce have been selected for a breeding program in Newfoundland. Balsam fir was not included because too much effort would have to be put into selecting for insect resistance and because it is such a prolific natural regenerator that it would be difficult to replace natural stands with improved strains even if they were developed. Plus-tree

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selection in larch is expected to be completed in 1992, and a seed orchard established by 1993.

LARIX LEPTOLEPIS

Japanese larch has been one of the most impressive exotics throughout Atlantic Canada. In Newfoundland, it has generally outperformed native spruces, eastern larch, and other exotic larches. There have been exceptions to that rule. A large plantation near Roddickton, on the Northern Peninsula, died out completely. Other plantings in the colder parts of the Province have also received considerable winter damage. Much of this is windburn, occurring January through March, but there is also sometimes freeze damage after spring flush.

Newfoundland is notorious for retarded springs, with frosts and even snowfalls sometimes occurring well into June. Native species have adapted to this, although even they are not entirely immune to late frost damage. But it is a major problem with exotics. Many of the exotic species that have been tried and have failed here have done so because they flush too early and are hit by late frosts nearly every year. The surprise is that the Japanese larch plantation at Pynn's Brook has fared so well. That inland site is subject to temperatures as low as the –30's °C in midwinter, with high winds. And it is certainly no less susceptible to late frosts than the average Newfoundland site. This may indicate that if the right provenances are chosen, the species could thrive in colder areas of the Province, possibly including parts of Labrador.

The persistence of winter temperatures well into spring can also interfere with seed production. Below-freezing temperatures during the period of active pollen development can result in sterile pollen (Eriksson 1968). Only during unusually late cold spells, even for Newfoundland, does this significantly affect native tamarack, but the risk is greater with exotic larches because they produce flowers earlier in the season (Hall and Harrison 1983). This would present an obstacle to any breeding program in an exotic larch in that either the orchards and breeding gardens would have to be located out of the Province, or we would have to be prepared to tolerate seed crop failures a large percentage of years.

Another problem with Japanese larch is that it does not do well in very wet soil. At Pynn's Brook, there are some very wet areas interspersed amongst the areas planted to Japanese larch and the other exotics. Where the Japanese larch is planted into the wet areas, it has much poorer survival and growth rates. Because much of Newfoundland is wet soil, this does place another restriction on the use of Japanese larch in this Province.

At Bottom Brook arboretum, in one of the mildest, most well-drained, and most fertile areas of the Province, Japanese larch outperformed all other species, native and exotic, at least with respect to height growth. Survival was generally less than the native species and some exotics. The Japanese larch had straighter boles than the native tamarack, as it does nearly everywhere in the Province that it survives.

LARIX DECIDUA

Although European larch has not been planted here as much as Japanese larch, where it has been planted, it has generally not put on quite the growth of Japanese larch. On good sites, it has been comparable to native eastern larch. On poor sites it has lagged behind both. It still has straighter boles than eastern larch. Its survival rate was better than that of Japanese larch, which may at least partially account for its lower mean height growth. If the weaker Japanese larches died off, the mean height of that species would be figured from only the more vigorous. The weaker European larches, by surviving, would have dragged down the species average. Thus, it is much too early to conclude that European larch has no place in Newfoundland forestry. Much more experimentation is needed before we will know whether it can make a contribution to the Province's economy.

LARIX XEUROLEPIS

Dunkeld larch has been planted less in Newfoundland than either Japanese or European larch. Its main trial was near Stephenville, in the same general area as Bottom Brook. It was planted alongside eastern, Japanese, and Siberian larch. It outgrew all other species, and survived better than either of the other exotic species but not better than eastern larch. These results generally showed that Dunkeld larch, as well as other exotic larches, had good potential as reforestation species (Hall 1983). As with European larch, much more experimentation is needed before we will know what role Dunkeld larch can play in the future of forestry in this Province.

LARIX SIBERICA

This is another species that had been tried only at a few locations with mixed results. In the Stephenville trial, it was the slowest grower and poorest survivor. At Pouch Cove, north of St. John's, it was damaged by a late June frost shortly after planting. This was possibly not a fair trial, though, because the seedlings had been raised in a greenhouse that spring and had not been subjected to cold temperature prior to planting. A trial has been planted near Goose Bay, Labrador. Many of the seedlings in that trial were chewed off by mice. The same thing happened to adjacent trials of jack pine and Scots pine, so we shouldn't jump to any conclusions that Siberian larch seedlings are any more susceptible to rodent damage than other species. More experimentation with Siberian larch is planned for Labrador.

LARIX GMELINII

Dahurian larch has had only a token trial here. It was not particularly impressive, but no valid conclusions can be drawn from such a limited test. Considering its native range, eastern Siberia, it does not seem unlikely that it would do well in Labrador and perhaps the island as well. Further testing of this species is planned, especially for Labrador.

OTHER LARCHES

In 1988 all-spruce trials were established in two Newfoundland locations. Various species of the genus *Picea* were planted in a replicated design to obtain a comparison between species as well as between geographical sources within species. Early results indicate that these tests may yield valuable information and that the concept could be profitably applied to other genera. The genus *Larix* would be well suited to such tests, as it consists of only 10 species, a manageable number. The number of geographical sources per species would range from one or two for the Asian species of limited range to two dozen or so for *L. laricina*. We are currently seeking different sources of the various larches for these trials. Theoretically, golden larch (*Pseudolarix amabilis* Rehd.) might also be included. But several seedlings at Wooddale Provincial Tree Nursery in 1986 did not survive the winter in an unheated greenhouse, so it is unlikely this species would thrive anywhere in the Province.

CONCLUSIONS

Newfoundland and Labrador are definitely larch country. Although only one species is native to the Province, and it forms only a small component of the merchantable forest, the potential of the genus is great. Greater genetic gain through selective breeding can probably be realized for native eastern larch than for any other commercial forest tree species in the Province. At least two or three exotic species appear to be capable of making a contribution to our forest economy. With a pulpwood shortage predicted for the early to mid-21st century, it seems imperative that we begin immediately to place greater emphasis on fast-growing genera such as *Larix*.

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Climatic Influences on Radial Growth of Subalpine Larch in the North Cascade Mountains

David W. Peterson
David L. Peterson

Abstract—Dendroecological techniques were used to investigate relationships between climate and radial growth of subalpine larch. June temperature is the most important variable for predicting ring width. Spring snowpack depth and previous-year spring and summer temperatures are also important. Differences in growth response to climate among sites appear to be related primarily to site moisture conditions, as evidenced by differences in correlations of growth with spring snowpack depth and previous summer temperatures.

The possibility of rapid climate change over the next century, in response to increasing atmospheric concentrations of carbon dioxide and other greenhouse gases, has stimulated interest in relationships between trees and their environment. General circulation models (GCM's) predict increases of 1 to 6 °C in mean summer and winter temperatures in the Pacific Northwest, but the models are unable to confidently predict changes in precipitation (Mitchell and others 1990). We need to understand the way climate influences tree establishment, growth, and mortality to make meaningful predictions of forest response to climate change.

Dendroecological techniques can be used to study the response of trees to past climate change (Peterson and Peterson 1991). Mature conifers contain, within their annual growth rings, a biological time series of growth responses to annual variation in climate. By comparing the annual variations in ring width to variations in monthly and seasonal climatic data, we can develop descriptive models of tree growth response to climate. These models can then be used to predict likely growth responses to different climate change scenarios.

We use dendroecological techniques in this study to examine the effects of climate on radial growth of subalpine larch (*Larix lyallii*). Subalpine larch is a common timberline tree species in the eastern portion of the North Cascade Mountains in Washington, U.S.A., and southern British Columbia, Canada (Arno and Habeck 1972). As a shade-intolerant species, subalpine larch is found primarily on north-facing slopes and ridges, above the continuous forest line in the subalpine zone. It is also successful as an early invader of open scree slopes and other rocky areas below the forest line.

STUDY AREA

The study area is located at Harts Pass (48°43' N., 120°39' W.) on the Okanogan National Forest in the North Cascade Mountains of Washington State. Harts Pass is at 1,850 m elevation, with nearby peaks rising to 2,400 m. The area was last glaciated in the late Pleistocene (Crandell 1965), and the landscape is characterized by broad, steep-sided, U-shaped valleys. Soils are generally entisols and shallow inceptisols.

The vegetation at Harts Pass is typical for the subalpine zone of the eastern North Cascades. Subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) form continuous closed forest on valley floors and slopes up to 1,900 m. A subalpine parkland with subalpine fir, Engelmann spruce, subalpine larch, and whitebark pine (*Pinus albicaulis*) extends from the forest line up to treeline at about 2,200 m. Subalpine larch and whitebark pine dominate the upper parts of this zone, maintaining an upright growth form in areas where fir and spruce occur primarily as krummholz. Subalpine larch inhabits primarily north-facing and east-facing slopes, while whitebark pine is found mostly on south-facing slopes. Understory vegetation in the larch stands includes *Vaccinium scoparium, V. deliciosum, Phyllodoce empetriformis, Cassiope mertensiana, Antennaria alpina, Pachystima myrsinites*, and *Phlox diffusa.*

CLIMATE DATA

Mean monthly temperature and total monthly precipitation values were used from divisional climatic data from 1895 to present (WeatherDisc Associates, Inc. 1990). Divisional data combine temperature and precipitation records from several recording stations within a climatically similar region. We use data from division 6 (east slope Cascades) rather than division 5 (west slope Cascades) because large peaks to the south and west of Harts Pass create a rain-shadow effect characteristic of the eastern Cascades. Spring (April 1) snowpack data are from snow course and SNOTEL records for Harts Pass (1941 to present). Four missing snow depth values were estimated from the snow course records for Park Creek Ridge, 35 km southwest of Harts Pass.

The climate in the eastern Cascades (fig. 1) is typified by warm, dry summers and cool, wet winters, which allow deep snowpacks to accumulate at higher elevations. Normal precipitation at Harts Pass is about 160 cm per year, with

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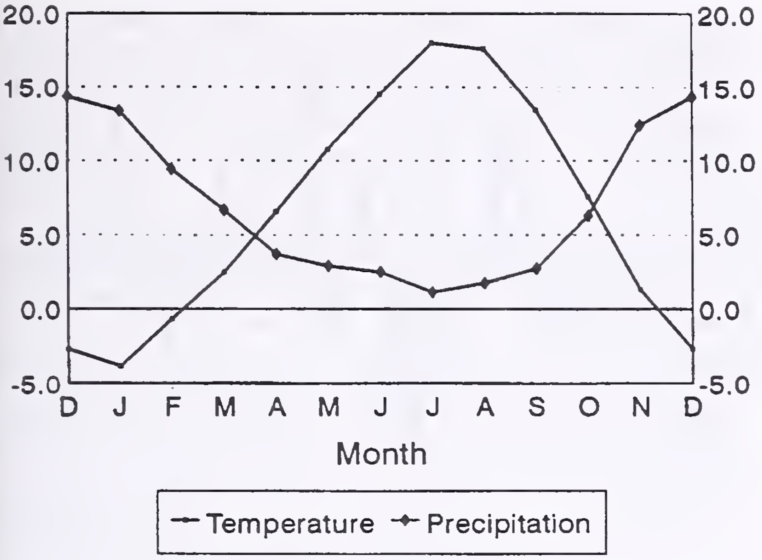

Figure 1—Average mean monthly temperature (in Celsius) and total precipitation (centimeters) for Washington climate division 6 (east slope Cascades).

about 90 percent of this total falling in the months October through May.

METHODS

Four sites were selected for study in summer 1991. All sites are within 3 km of Harts Pass, and the greatest distance between sites is 5 km. Two of the sites (F1 and F2) are near the forest line on slopes facing north and northeast. The other two sites (R1 and R2) are on low ridges, in open larch stands. At each site, we sampled at least 20 larches, removing two cores from cross-slope sides of each tree at a height of 110 cm using an increment borer. The cores were stored in paper straws for transport and storage. Species, location, and diameter (at 110 cm height) were recorded for each tree sampled.

Cores were mounted in wooden blocks and polished with progressively finer grades of sandpaper until ring boundaries were clearly visible. The cores were crossdated (Fritts 1976) to ensure accurate dating of each ring. Crossdating was performed initially by visually identifying common marker years and ring-width patterns (Stokes and Smiley 1968; Swetnam and others 1985) and later verified using the computer program COFECHA (Holmes 1983). Individual rings were measured to the nearest 0.01 mm with an incremental measuring system that uses a microscope connected to a television camera and monitor (Robinson and Evans 1980). Randomly selected 20-year segments (one per core) were remeasured by a second lab worker to ensure measurement accuracy.

Growth trends (longer than 10 years) were removed from the crossdated ring width series by fitting a flexible cubic spline curve (Cook and Peters 1981) to each series and dividing the observed value by the value predicted by the spline curve (fig. 2). The resulting time series of index values had stationary means and constant variance. A standard arithmetic mean function was used to combine the individual tree core series into a mean growth index series for each sample group and an overall mean series. These mean series (or chronologies) retain the common growth patterns among the individual cores, while removing the responses of individual trees to small-scale disturbance or release events.

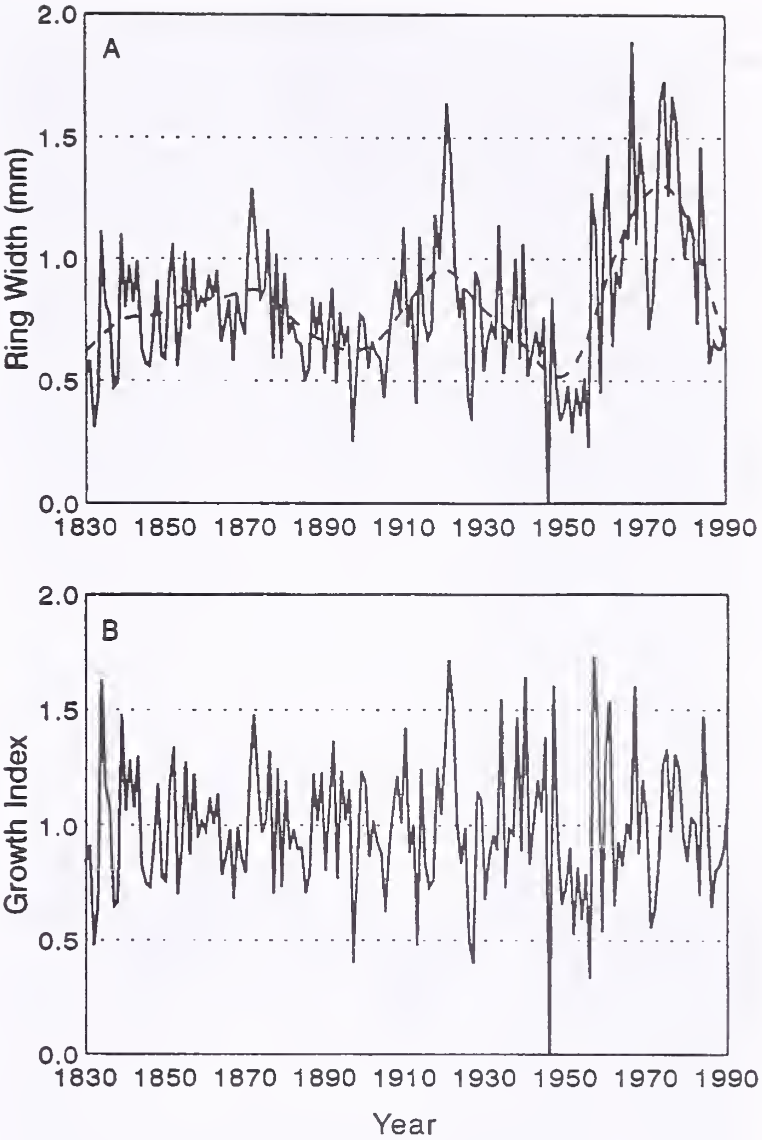

Figure 2—Standardization of individual tree cores ring width series. (A) Ring width series (solid line) is fit with a flexible cubic spline curve (dashed line). (B) Growth index series produced by dividing ring width by spline curve value for each year.

Correlation analysis was used to identify possible relationships between growth index and monthly temperature and precipitation records for 1941 through 1990. Climate records for 24 months prior to the end of the growing season were used in the correlations, because growth in one year may be affected by climatic conditions the year before (Mikola 1962). We also examined correlations between the chronologies and spring (April 1) snowpack depth to see if spring snow depth, which influences the snow meltout date and summer soil moisture, had any influence on growth.

RESULTS AND DISCUSSION

The climate variable with the strongest influence on larch ring width is mean June temperature in the year of ring formation (fig. 3a). June temperature is positively correlated with growth index at each site ($r = 0.33$-0.49) and is the best single month predictor of growth. Mean June and July temperature is also a good predictor of growth at some sites. Similar relationships between ring width and June temperature have been reported for subalpine larch elsewhere in the North Cascades (Heyerdahl 1991) and in the Northern Rocky Mountains (Colenutt and Luckman 1991).

June temperature could be important for a variety of reasons. Budburst generally occurs during May (Worrall 1993), so June is a time of leaf expansion and is probably also the time when earlywood growth begins. Warm temperatures might benefit both of these processes. June temperature is probably also a measure of light availability. Warm, sunny days could allow high levels of photosynthetic production during maximum daylength, when melting snow provides an abundant supply of water, and may increase light intensities through reflectance.

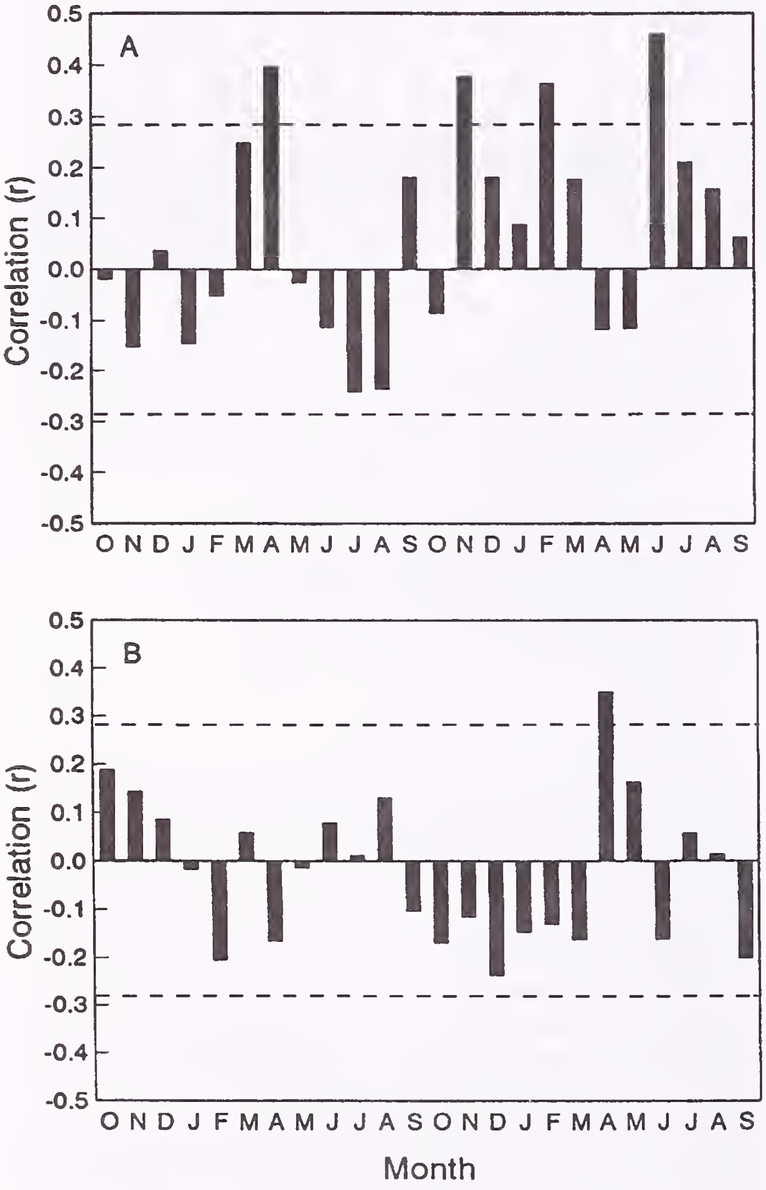

Figure 3—Correlations between mean larch growth index series (all sites, all cores) and monthly climate variables for 24 months prior to the end of the growing season in which the ring is formed. Dashed line indicates significant correlations ($p = 0.05$). (A) Monthly mean temperature. (B) Total monthly precipitation.

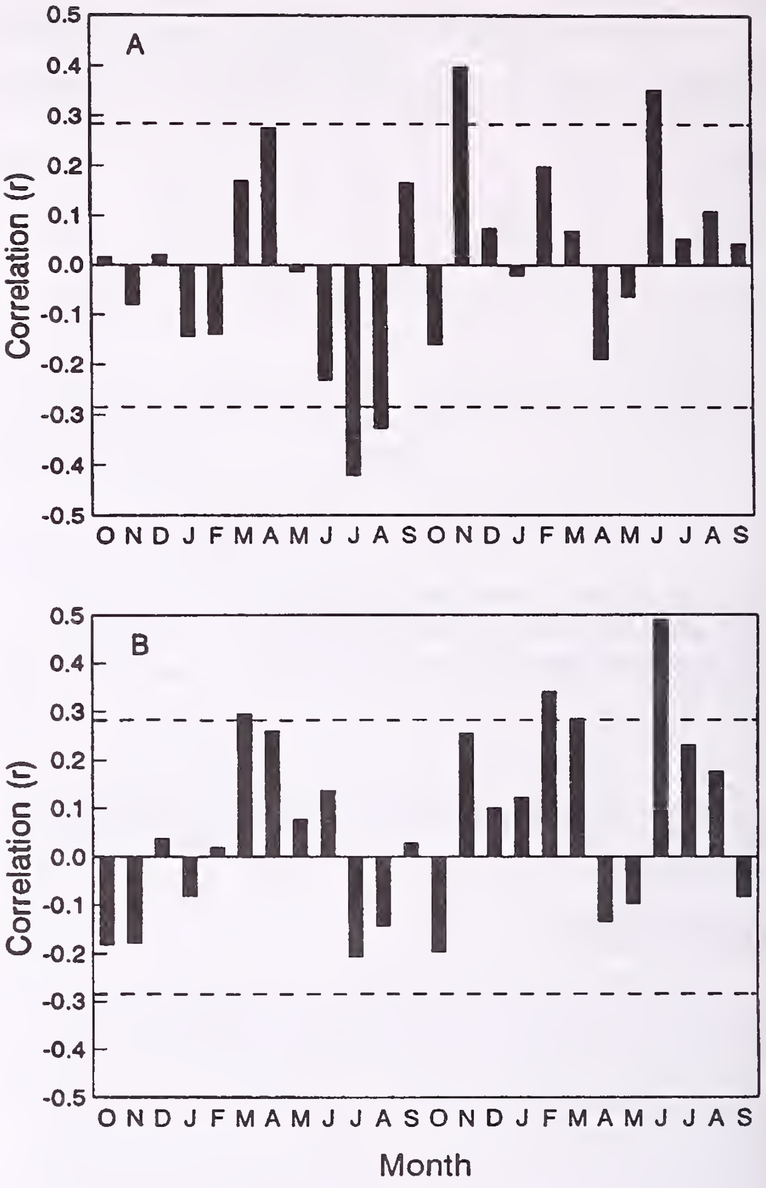

Figure 4—Correlations between mean growth index series for two sites and monthly mean temperature variables. Dashed line indicates significant correlations ($p = 0.05$). (A) Chronology R1-LA, from a relatively dry ridgetop site. (B) Chronology F2-LA, from a cool, wet, north-facing forest line site.

The next most important factors influencing ring width are spring and summer temperatures of the previous year. Previous April temperature is significantly correlated ($p < 0.05$) with growth index at all sites except for one forest line site, where the correlation with March temperature is stronger (fig. 4b). Negative correlations between previous July and August temperature and growth index are found at all sites but are significant only at a relatively dry ridgetop site (fig. 4a).

These previous-year variables probably affect ring width through their influence on carbohydrate reserves, which are important for early summer tree growth (Kozlowski and Keller 1966) and vegetative bud development. Worrall (1993) found a close correlation between April and May temperature and date of budburst for subalpine larch in southern British Columbia, so the positive correlations with previous April temperature might reflect the positive effects of an early budburst the previous year. It is not clear, though, why an early budburst would benefit growth the following year and not current-year growth. One possibility is that an early budburst lengthens the growing season and allows trees to build up carbohydrate reserves. Another is that it gives the following year's buds more time to develop, possibly increasing leaf area the following year.

The negative correlations between growth and previous summer temperature can be explained by summer drought effects on photosynthetic production. Stomatal conductance in subalpine larch is sensitive to both low humidity and low soil moisture (Richards 1981), so warm, dry conditions could lead to reduced photosynthesis. Warm temperatures can also lead to higher respiration rates.

The remaining significant climatic variables are related to winter temperature and spring snowpack. Growth is negatively correlated with spring snowpack depth (fig. 5) and positively correlated with November and February temperatures (figs. 3a, 4a,b). The snowpack correlations are significant only for the north slope sites, probably reflecting differences in snowpack accumulations among sites. In general, snowpack appears to have a strong effect only in years with deep spring snowpack and below-average June temperatures.

The generally positive correlations between growth and monthly temperature variables (figs. 3a, 4b) suggest that the warmer temperatures predicted under most global climate change scenarios could lead to improved growth of subalpine larch in the North Cascades. The exception would be on some sites such as R1 (fig. 4a) where warm and dry summer conditions may already limit growth. There is also, undoubtedly, some upper temperature limit above which increased temperatures are no longer favorable. Our data do not indicate what this limit might be.

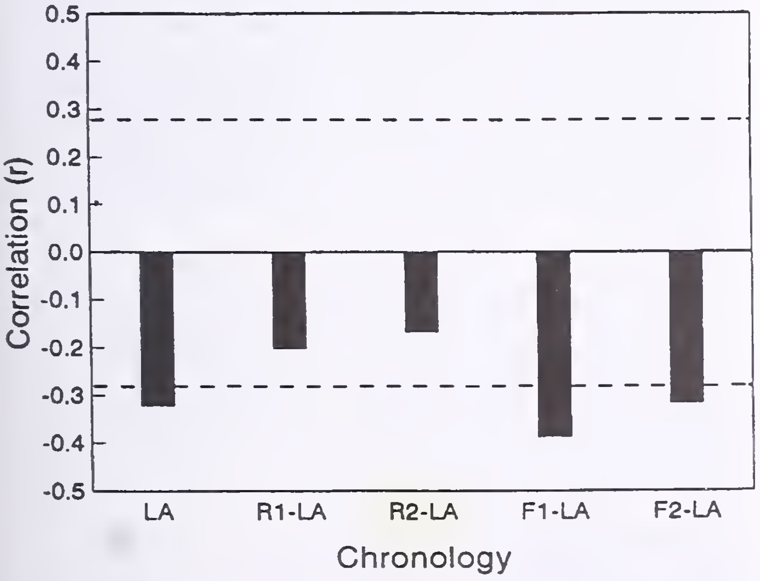

Figure 5—Correlations between mean growth index series and April 1 snowpack depth for 1941 through 1990. Chronology codes: LA—mean larch chronology for all sites; R1-LA—Ridgetop #1; R2-LA—Ridgetop #2; F1-LA—Forest Line #1; F2-LA—Forest Line #2.

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Precommercial Thinning Response in 7-Year-Old and 50-Year-Old Western Larch: Past Growth and Future Prognosis

Fred C. Martin
Hollis W. Barber, Jr.

Abstract—Two precommercial western larch thinning trials—one thinned at age 7 and the other thinned at age 50— were examined for density, diameter, basal area, height, and volume trends. Future volumes were projected with the Stand Prognosis Model. Early thinning appears preferable to late thinning or natural stand management, resulting in increased diameter growth and eventually in greater volume on fewer but larger trees. Thinning may also increase species and size distribution diversity in future stands.

In two, continuing precommercial thinning experiments in western larch (*Larix occidentalis* Nutt.)—one in a 7-year-old stand and the other in a 50 year-old stand—we are comparing the effects of different thinning intensities and different thinning ages on tree and stand growth over time. Additional details concerning experimental design, plot installation, and previous measurement can be found in Barber (1989, 1992). The physical characteristics of the two trials were as follows:

	Blue Goat trial	**Rattlesnake trial**
Latitude/longitude	48°40'/119°45'	46°45'/120°55'
Slope/aspect	5 percent/NE	5 percent/NW
Elevation	4,300 feet	4,500 feet
Precipitation	30 inches	30 inches
Habitat type	*Abies lasiocarpa* / *Linnea borealis* (Williams and Lillybridge 1983)	*Abies grandis* / *Calamagrostis rubescens* (Williams and Smith 1992)
Soil type	Stony sandy loam from granite	Stony loam from basalt
Site index	45 feet (Summerfield 1980)	67 feet (Cochran 1985)
Thinning age	7 years	50 years
Prethinning trees per acre	20,000	2,000

STUDY AREA AND EXPERIMENTAL DESIGN

The young stand thinning experiment, called the Blue Goat trial, was started in 1979 in naturally regenerated larch. The study area is about 20 miles northwest of Omak, WA, U.S.A., in the Sinlahekin drainage. The parent stand was clearcut in 1971. At the time of plot installation the site was heavily overstocked with up to 20,000 trees per acre (TPA), 90 to 95 percent larch, and a few Douglas-fir (*Pseudotsuga menziessii* var. *glauca* Franco) and Englemann spruce (*Picea engelmannii* Parry). Trees were 3 to 7 feet tall at time of thinning.

The 50-year-old stand, called the Rattlesnake trial, approximately 15 miles northwest of Yakima, WA, U.S.A., in the Little Rattlesnake Creek drainage, was thinned in 1981. The experiment is in a stand that originated from fire. The overstory was mostly larch with a dense understory of Douglas-fir, grand fir (*Abies grandis* Lindl.), and suppressed larch, ponderosa pine (*Pinus ponderosa* Laws.), and willow (*Salix* sp.). Stand density prior to thinning varied from 1,900 to 3,100 TPA. There was virtually no shrub-herb layer in the understory.

Although the experimental design was similar in both studies, there were differences. The Blue Goat trial consisted of 10 randomized plots—two controls and two plots for each of the following spacings, in feet: 3 by 3 (4,840 TPA) , 6 by 6 (1,210 TPA), 12 by 12 (303 TPA), and 15 by 15 (194 TPA). All treatment plots were square and had 36 trees plus buffer trees at the treatment spacing, resulting in variable plot sizes between treatments. The control plots were square 0.01 acres each. Treatment plots were thinned in July 1979. The leave-trees were the dominant larch to simulate a low thinning.

The Rattlesnake trial consisted of two replicates of controls and three spacings, 12 by 12, 15 by 15 and 18 by 18 feet (134 TPA). Each plot was a randomly located square 0.1 acre with a one-tree buffer. Trees were thinned in 1982. Larch was favored when possible, although a few Douglas-fir, ponderosa pine, and grand fir were left on the treated plots.

METHODS

At the Blue Goat trial, diameters of all trees were measured yearly between 1980 and 1984. Heights of all trees on treatment plots and a subsample of 36 trees on control plots were measured in 1978, 1980, and 1982. Prior to the 1984 remeasurement, new height sample trees were selected. On each plot, 15 trees were randomly selected,

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apportioned to 0.5-inch diameter classes such that the entire range of diameters was sampled, with two-thirds of the height-sample in trees exceeding plot mean diameter. The number of height trees allotted to a diameter class was proportional to the total number of trees in a class. Beginning in 1984 the remeasurement was extended to 2 years for all tree characteristics. Base to live crown measurements were added in 1988.

At the Rattlesnake trial, diameters were measured in 1981, 1984, 1988, and 1991. Heights were measured in 1981 but were later found unreliable due to undetermined measurement errors. Subsamples of 12 to 15 new height trees per plot were selected at random in 1985; two-thirds exceeded the arithmetic plot mean diameter breast height. Initial heights for the 1981 measurement years were backdated using these later measurements and proc edures described by Barber (1992). Heights were remeasured in 1991, and base of live crown measurements were added at that time.

We analyzed past growth trends primarily by graphical examination. We computed average density, diameter, basal area, height, and volume characteristics for each treatment and plotted over measurement year. Density included trees per acre and a relative density (RD) measure defined as the ratio of basal area to the square root of quadratic mean diameter (Curtis 1982). Diameter and diameter increment were based on arithmetic means, not quadratic means. Increments were computed as periodic annual increment by dividing actual increment by the period length. Cubic-foot volume was computed for both trials, and Scribner board-foot volume was computed for the Rattlesnake trial. Cubic-foot volume was for total stem, and board-foot volume was for trees 7 inches and larger to a 6-inch top. We calculated volumes using the Stand Prognosis Model (Wykoff and others 1982).

To evaluate the significance of treatment differences, we used a one-way analysis of variance for diameter, basal area, height, and volume increment. Differences between individual treatments were evaluated using Tukey's HSD. The increment examined was the average periodic annual increment over the entire trial length, 14 years at Blue Goat and 10 years at Rattlesnake. Because the Blue Goat trees were quite small (about 0.1-inch diameter at breast height and 4.5 feet) at the beginning of the study, analysis of increment is comparable to analysis of the 1992 absolute dimensions.

We examined expected future yield trends for the Blue Goat trial using the northern Idaho variant of the Stand Prognosis Model. Although this model was fit to data from outside the region of this trial, it was deemed more realistic than growth models currently available for this locale. Yield projection for the Rattlesnake trial used the Eastern Cascade variant of the Prognosis Model. Cubic and board-foot volume projections between the two trials (or variants) should not be compared with respect to absolute values because the variants incorporate potential site productivity differently. The value of the growth projections lies in the relative comparison of the treatments and not in the estimation of absolute future values.

Input to the Stand Prognosis Model consisted of the full tree lists from each plot. We calibrated the model for mortality, diameter growth, and height growth based on the beginning and ending measurements for each trial, 1978 through 1992 for Blue Goat and 1981 through 1991 for Rattlesnake. The model was run with provision for automatic establishment of regeneration during the projection period. We projected each treatment to age 100 years for Blue Goat and age 130 for Rattlesnake. Cubic and board-foot volume yields were output for each 10-year period. We evaluated the ending tree lists of the Blue Goat simulation with regard to expected diameter distribution and species composition.

BLUE GOAT TRIAL PAST GROWTH

Mortality measured as trees per acre was relatively light on the control plots and nonexistent on the thinned plots (fig. 1). Nearly 300 TPA per year had died on the controls from 1979 through 1993. If this trend continues the Blue Goat control plots will have stocking levels comparable to the Rattlesnake controls at similar ages—that is, 50 years. Mortality on the control plots began as the RD approached a value of 60, considered a threshold value for competition-induced mortality (Davis and Johnson 1987). The RD for the control plots is approaching a believed upper biological limit (fig. 2). The Rattlesnake control plots have remained at a similar RD level since the plots were installed. The 3- by 3-foot treatment plots have exceeded an RD of 60 since 1988 but have not yet experienced mortality. The uniformity of spacing and lack of dominance differentiation may have contributed to this high survival rate.

Diameter and diameter increment trends were proportional to spacing—that is, greater spacing between trees implied greater diameter (figs. 3 and 4). Growth response was immediate in all treatments, and in 1992 it was 4.5 times greater at the widest spacings than the controls. The decline in increment between 1984 and 1986 was attributed to drought. Analysis of variance showed significant treatment effects over the last 14 years for diameter increment ($F = 37.63$, $p = 0.001$). Pairwise comparisons

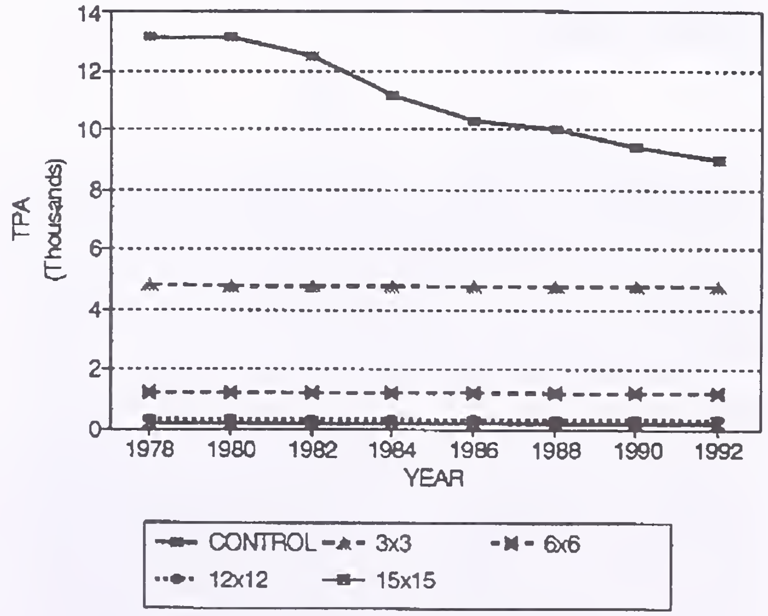

Figure 1—Trees per acre (TPA) by year for the Blue Goat thinning trial.

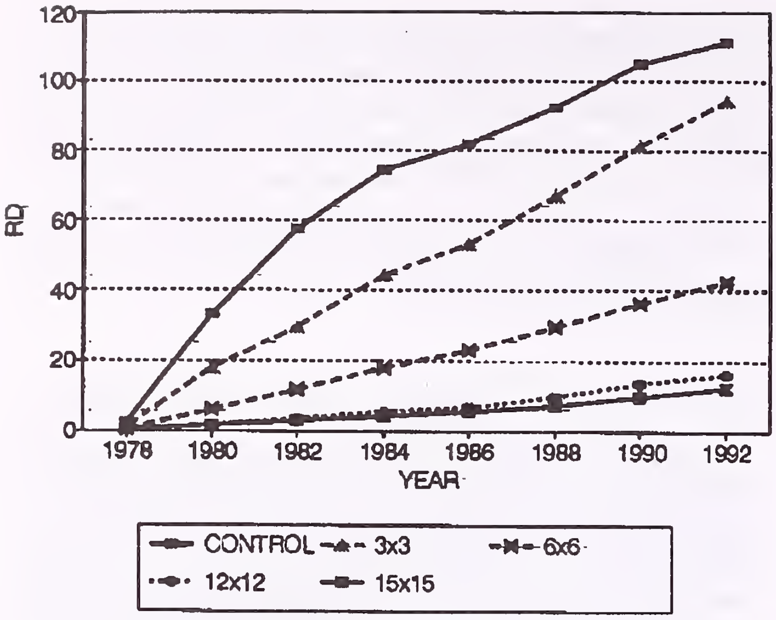

Figure 2—Relative density (RD) by year for the Blue Goat thinning trial.

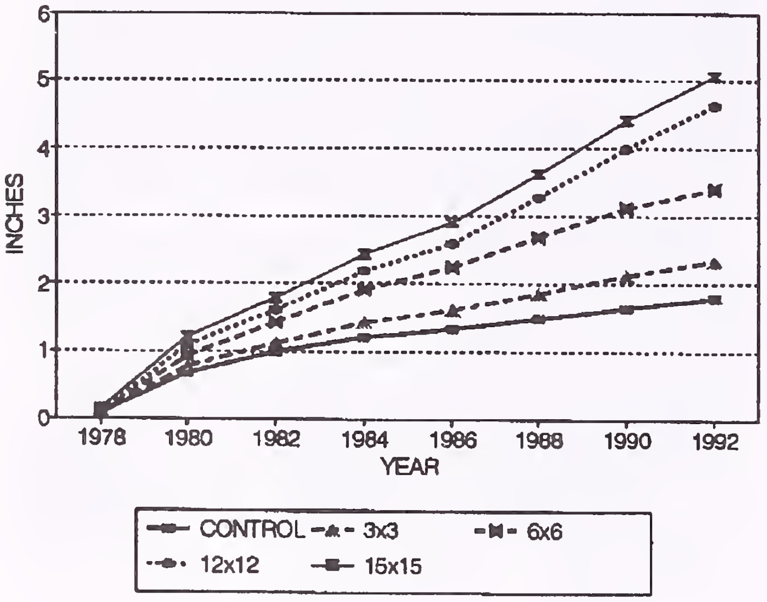

Figure 3—Diameter growth by year for the Blue Goat thinning trial.

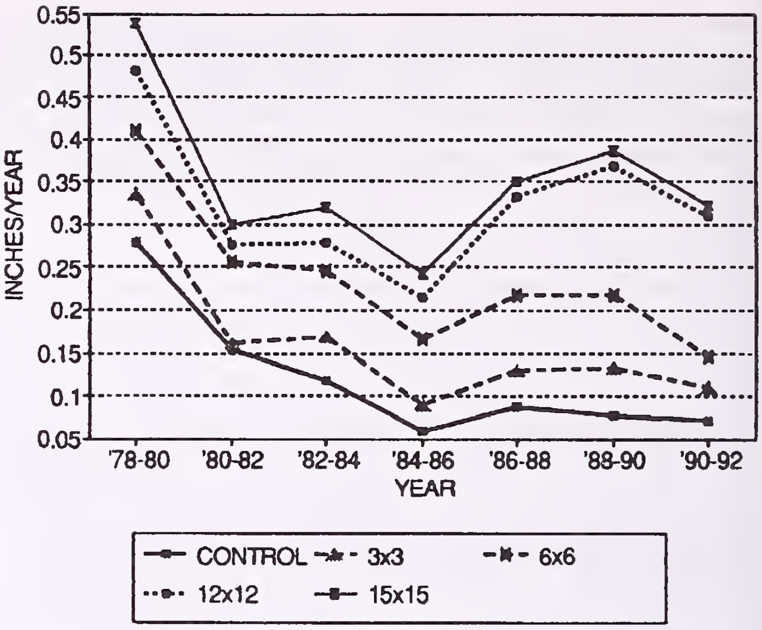

Figure 4—Periodic annual diameter increment for the Blue Goat thinning trial.

confirm the increasing trend of increment with increasing spacing (table 1). Pairwise comparisons based on only the 36 largest trees for each plot show the same separation of treatments. Average diameter for the two widest spacings at age 19 were equal to the average diameter for the Rattlesnake control plots at 60 years of age.

Basal area in 1992 was nearly identical for the control and 3- by 3-foot spacing, even though the 3 by 3 had 47 percent fewer TPA (fig. 5). Current basal area increment on the 3 by 3 spacing is nearly 50 percent greater than the control, whereas the 6- by 6-foot spacing and controls have nearly equivalent increment (fig. 6). Total basal a rea and increment on the wider spacings (12 by 12 and 15 by 15) continue to lag behind the denser treatments. This suggests that they have yet to fully occupy the site (consistent with their RD values, fig. 2). Significant differences existed for basal area increment between treatments ($F = 15.5$, $p = 0.005$) and pairwise comparisons (table 1) support the obvious separation between basal area yields shown in figure 5.

Height appeared proportional to spacing (fig. 7), but this general trend was not apparent for periodic annual increment (fig. 8). Significant differences in height increment over the 14 years of measurement between treatments were not detected ($F = 2.62$, $p = 0.159$). Analysis of variance based on only the five tallest trees per plot also showed no significant differences. The general trends do, however, suggest that differences in height between treatments may eventually become important. The decline in increment for the1990 through 1992 period was attributed to terminal damage from western spruce budworm (*Choristoneura occidentalis* Freeman) and not to a culmination of height increment.

Total cubic-foot volume was inversely proportional to spacing with the control consistently having the highest volume (fig. 9). In recent years increment in the 3 by 3 spacing has surpassed the control, and current increment in the 6 by 6 treatment nearly equals the control (fig. 10).

Table 1—Tukey's HSD pairwise comparison for different increment measures between treatments for the Blue Goat trial. Underlined treatments are not significantly different at the 0.05 level

Increment	Control	3 by 3	6 by 6	12 by 12	15 by 15
D.b.h. (inches)	0.161	0.150	0.232	0.317	0.348
Height (feet)	1.245	1.243	1.491	1.703	1.683
Basal area (ft^2)	10.519	10.339	5.736	2.490	1.9557
Volume (ft^3)	91.607	82.464	54.429	25.286	20.571

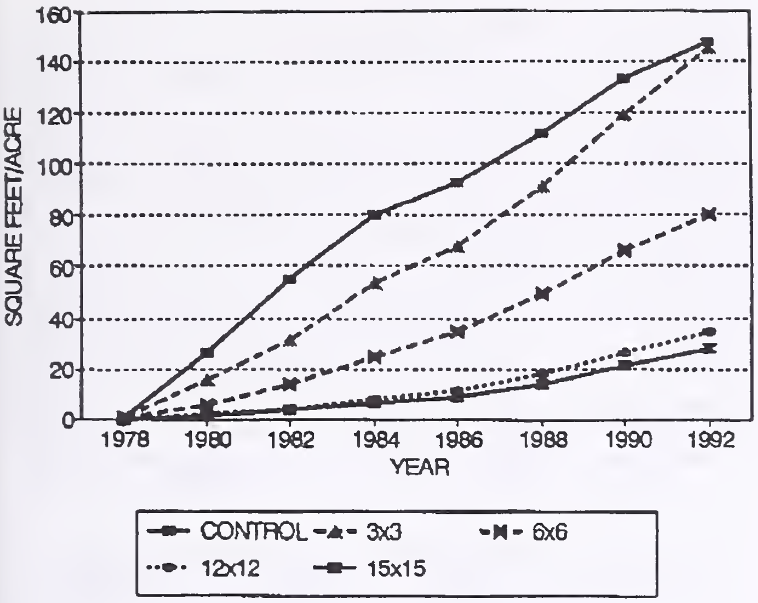

Figure 5—Basal area growth by year for the Blue Goat thinning trial.

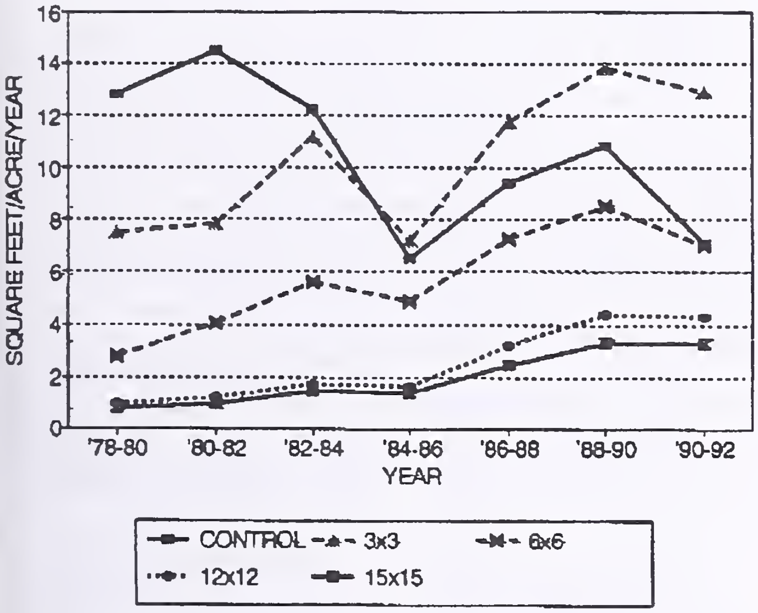

Figure 6—Periodic annual basal area increment for the Blue Goat thinning trial.

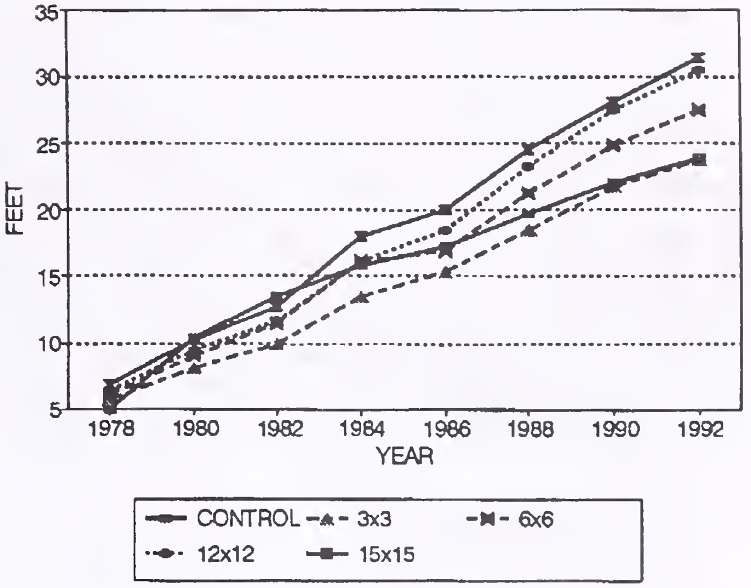

Figure 7—Height growth by year for the Blue Goat thinning trial.

Treatment effects on volume increment were significant ($F = 8.1$, $p = 0.021$), and pairwise comparisons support the pattern of figure 9 with the control and 3 by 3 significantly different from the 12 by 12 and 15 by 15 treatments.

RATTLESNAKE TRIAL PAST GROWTH

Mortality in the Rattlesnake trial was largely confined to the control plots where an average of 20 TPA per year died between 1981 and 1991 (fig. 11). Most mortality was due to suppression. Average diameter breast height (d.b.h.) was 3.2 inches for trees that died compared to the overall mean of 5.5 inches. During the same period only two trees died on thinned plots. The RD on the control treatment has averaged 105 over the entire study period, whereas RD for all thinned treatments remained below 35, nearly an open grown condition.

Mean d.b.h. was larger on thinned plots principally because of thinning from below (fig. 12). Analysis of variance showed significant differences between treatments for d.b.h. increment ($F = 30.08$, $p = 0.003$). Pairwise comparisons showed that the thinnings were significantly different from the control but not from each other (table 2). Diameter increment generally increased over time for the widest spacing (18 by 18), was erratic on the other thinnings, and generally decreased on the control (fig. 13). Response to thinning in this older stand has been slow as evidenced by the increment graphs. In addition, increment cores taken in 1990 indicated a lag of about 7 years before radial growth response was plainly visible. This delay may be due to low crown ratios, which averaged

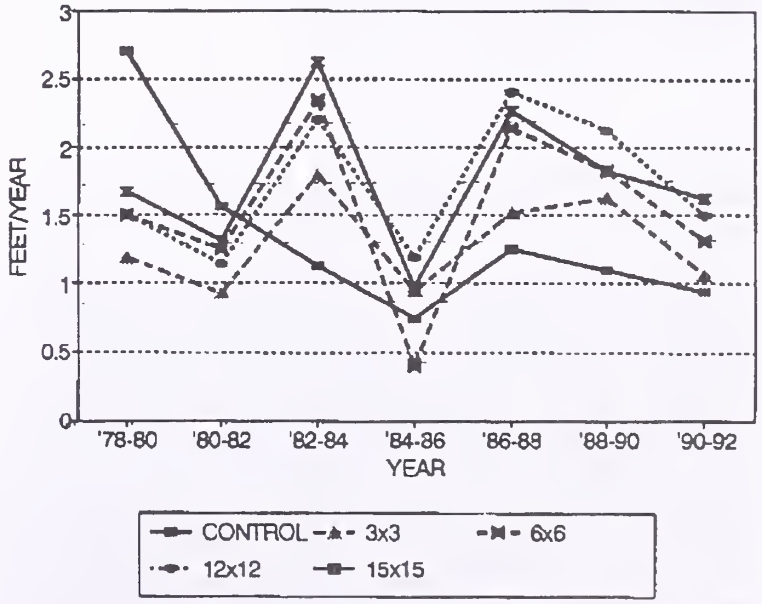

Figure 8—Periodic annual height increment for the Blue Goat thinning trial.

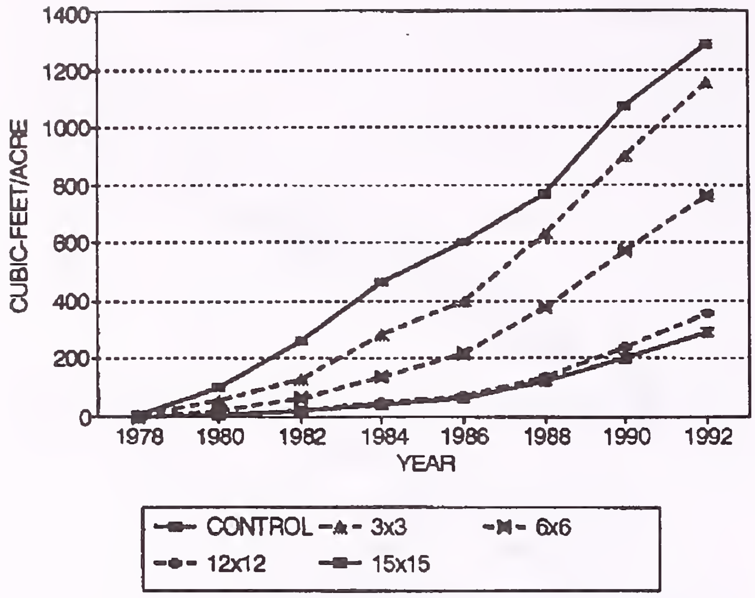

Figure 9—Cubic-foot volume growth by year for the Blue Goat thinning trial.

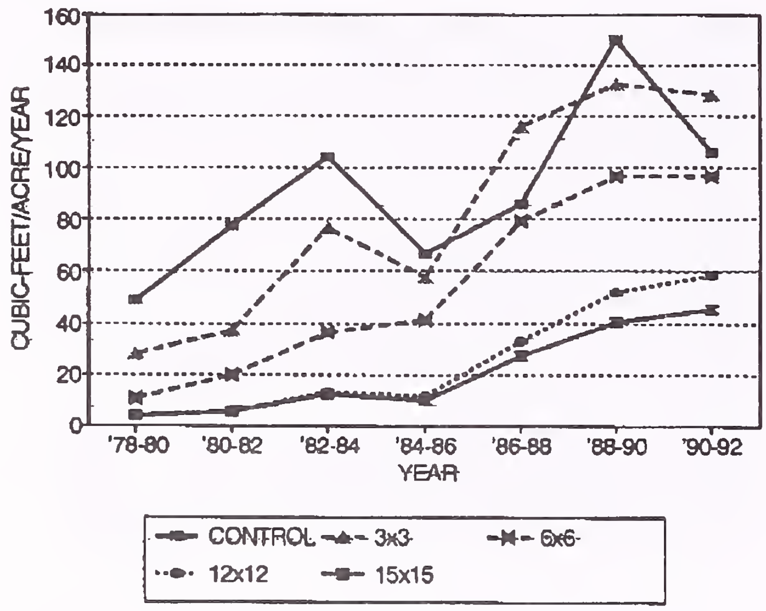

Figure 10—Periodic annual cubic-foot volume increment for the Blue Goat thinning trial.

only 38 percent at time of thinning. Live crown ratios averaged 44 percent in 1991, and diameter growth may improve further as crowns continue to build.

The most distinctive feature of basal area in the Rattlesnake trial is an apparent maximum reached on the control (fig. 14). Barber (1992) reported this maximum as higher than generally reported in the literature and may be partly due to the presence of more tolerant grand fir and Douglas-fir in the understory of the control. Basal area increment has declined to nearly zero in the control treatment, although increment was quite large in the initial measurement period (fig. 15). This decline in basal area is due to a combination of mortality and reduced diameter increment, probably caused by high competitive stress. Significant differences were identified between the

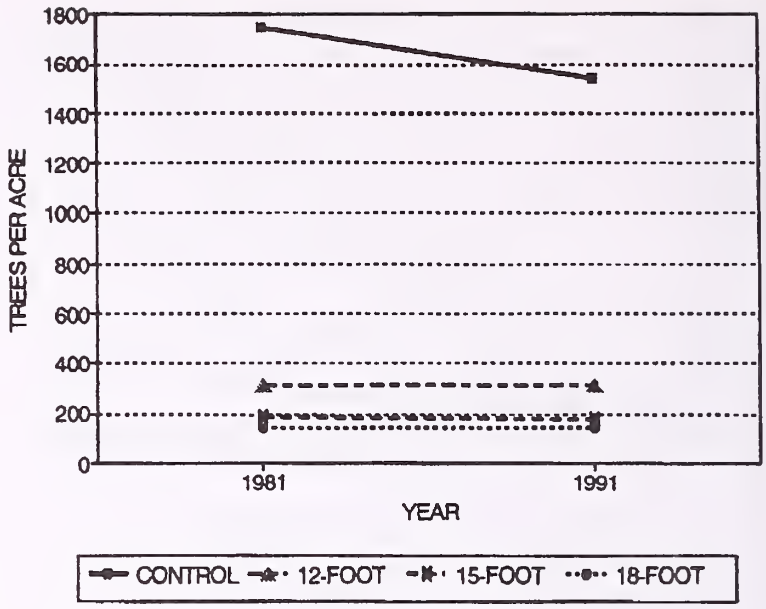

Figure 11—Trees per acre (TPA) by year for the Rattlesnake thinning trial.

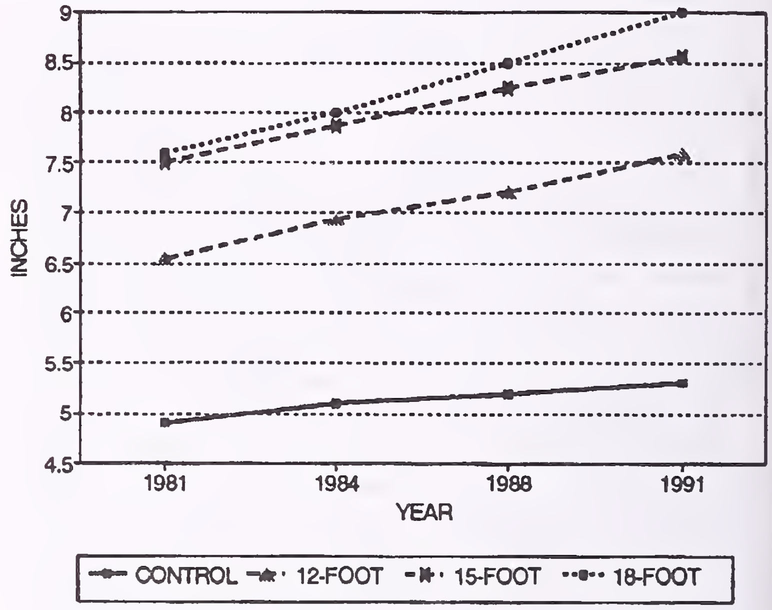

Figure 12—Diameter growth by year for the Rattlesnake thinning trial.

Table 2—Tukey's HSD pairwise comparison for different increment measures between treatments for the Rattlesnake trial. Underlined treatments are not significantly different at the 0.05 level

Increment	Control	12 by 12	15 by 15	18 by 18
D.b.h. (inches)	0.034	0.099	0.100	0.140
Height (feet)	0.12	0.10	0.44	0.52
Basal area (ft^2)	3.204	2.429	1.761	1.630
Volume (ft^3)	51.90	50.85	45.80	43.90
Volume (bfS)[1]	225.5	193.5	190.5	188.0

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[1] bfS is board feet Scribner.

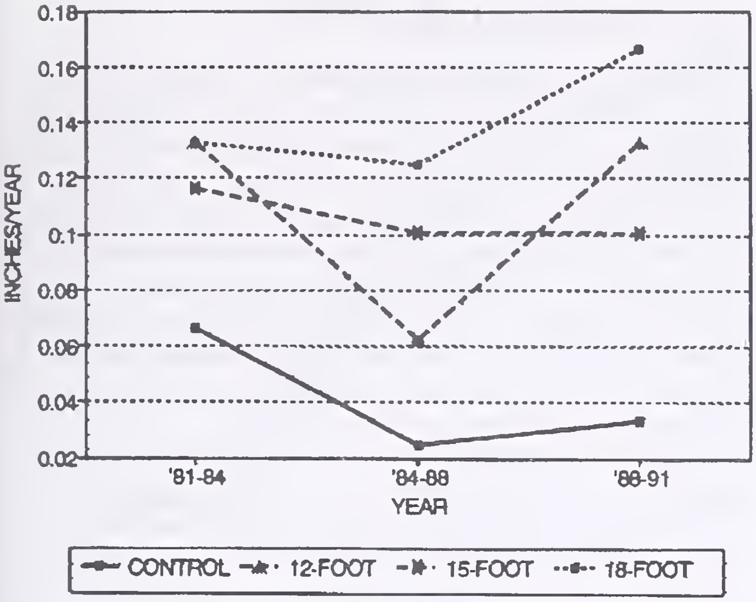

Figure 13—Periodic annual diameter increment for the Rattlesnake thinning trial.

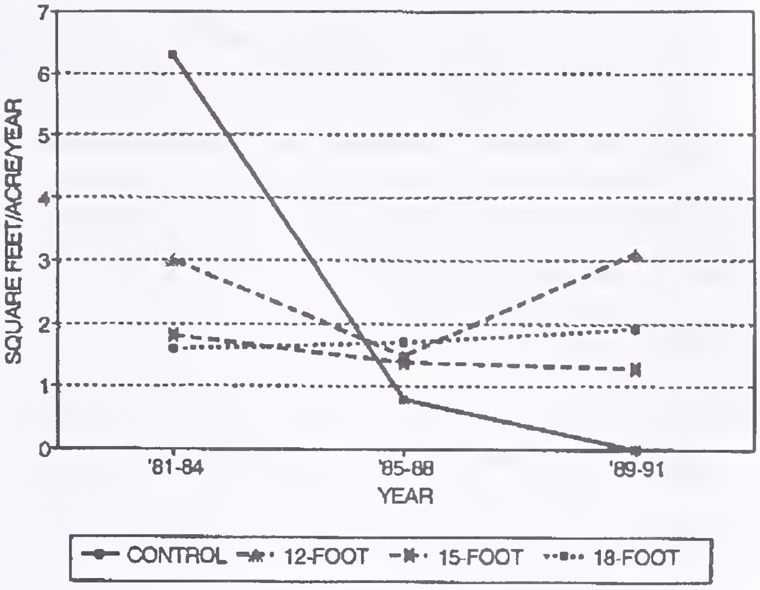

Figure 15—Periodic annual basal area increment for the Rattlesnake thinning trial.

treatments (*F* = 21.91, *p* = 0.006), and pairwise comparisons indicated that these differences were due to differences between the widest spacings and the control and 12 by 12 treatments (table 2).

Height and height increment were proportional to spacing (fig. 16). Pairwise comparison of increment confirmed the significance of the height trends shown in figure 16—that is, the two widest spacings had greater increment than the control and 12 by 12 treatment (table 2). Annual increment even at the widest spacings, however, was quite low, about 0.5 feet per year. Barber (1992) compared height increment at Rattlesnake to other larch growth and yield studies and noted that increment at Rattlesnake was lower than expected. He attributed this to early overstocking, suggesting that precommercial thinning should be conducted at ages younger than at Rattlesnake.

Total volume is greatest in the control and proportional to spacing for both cubic and board-foot measures in the thinnings (figs. 17 and 18). The large differences in total board-foot volume between the control and thinned treatments implies that considerable merchantable volume was removed by thinning at this advanced age, although nearly all of the material was less than 8 inches d.b.h. Cubic or board-foot volume increment was not significantly different between any of the treatments (*F* = 0.52, *p* = 0.688, and *F* = 0.32, *p* = 0.812, respectively). Because of the larger diameter and height increment on thinned plots, board-foot volume increment on thinned treatments is expected to surpass the control in the near future.

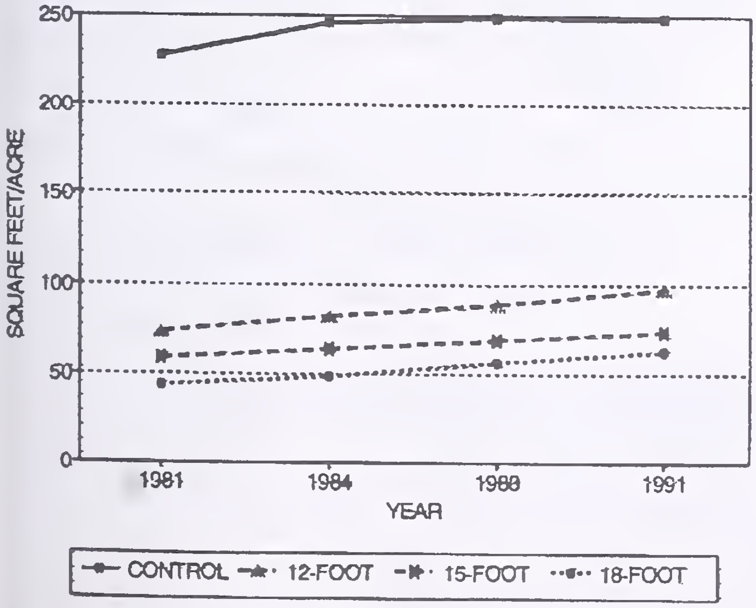

Figure 14—Basal area growth by year for the Rattlesnake thinning trial.

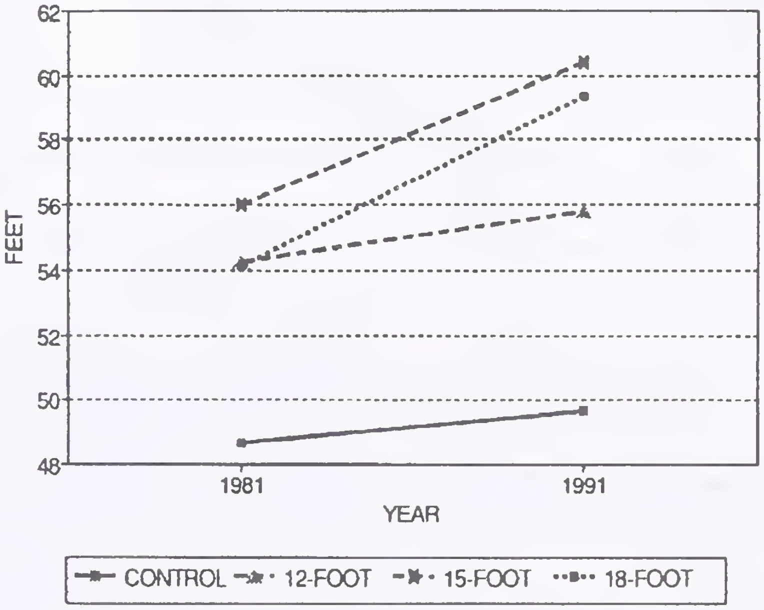

Figure 16—Height growth by year for the Rattlesnake thinning trial.

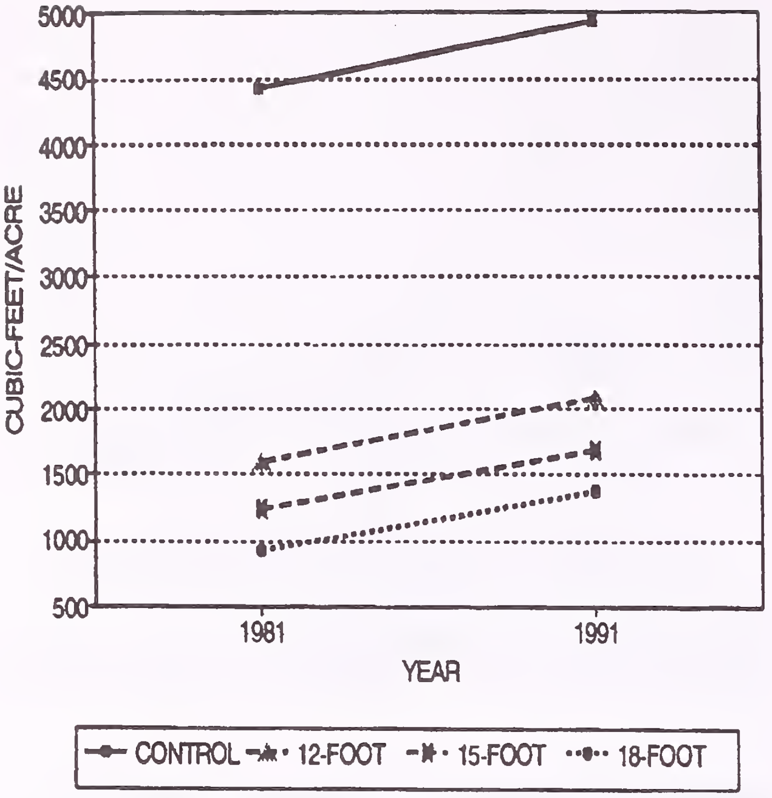

Figure 17—Cubic-foot volume growth by year for the Rattlesnake thinning trial.

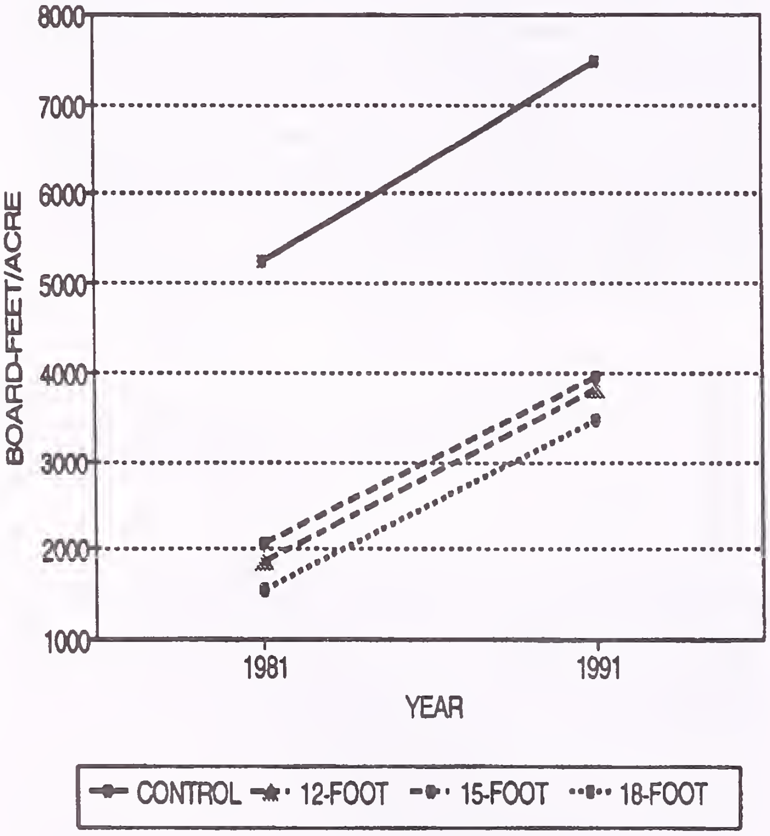

Figure 18—Board-foot volume growth by year for the Rattlesnake thinning trial.

ANTICIPATED GROWTH

Results from the Prognosis Model show that both cubic and board-foot volumes on the wider spacings will surpass volume on the control and narrowest spacing at Blue Goat (figs. 19 and 20). An interesting feature of these projections is the crossing of the yield curves for the control and 3 by 3 thinning, resulting in larger yields for the control. This behavior is consistent with the actual growth trend of the 3 by 3 thinning in that a lack of dominance differentiation has increased density without increasing mortality, possibly leading to delayed mortality of larger trees compared to the natural stand condition.

Eventually the projected yield curves of all treatments appear to cross for both cubic and board-foot volume. This suggests that depending on the time frame, each spacing attains a maximum yield relative to each other. The crossing of yield curves is attributed to increasing mortality and eventually lower growth rates as competition increases with stand density. The yield curves for merchantable volume exhibit less crossing and less variation, particularly for the three wider spacings. This results because the smaller trees, which are more likely to die, are not included in the board-foot volume calculations. Although board-foot volumes may be similar, this volume is distributed on fewer larger trees as spacing increases (table 3).

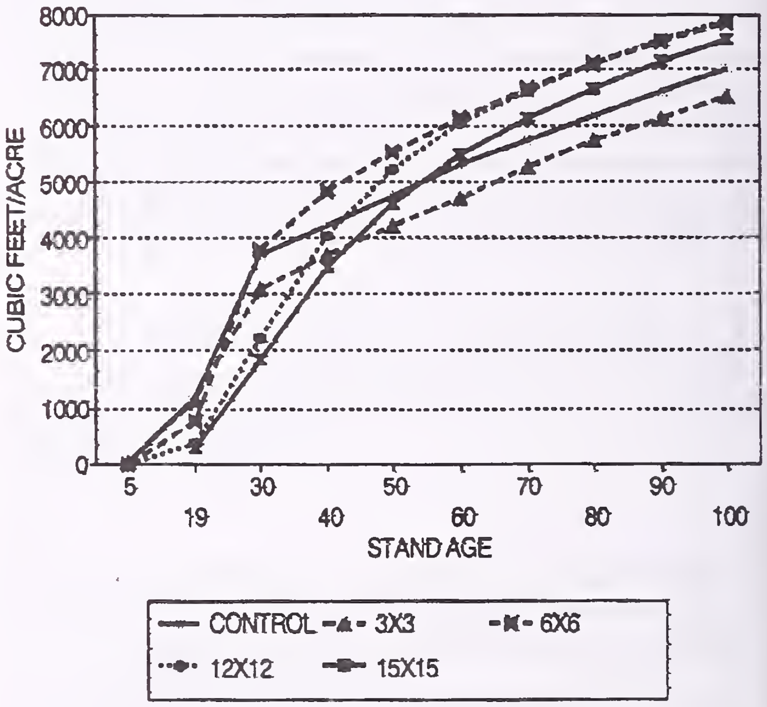

Figure 19—Projected board-foot yield for the Blue Goat thinning trial. The projection begins at age 20; earlier values are actual yields.

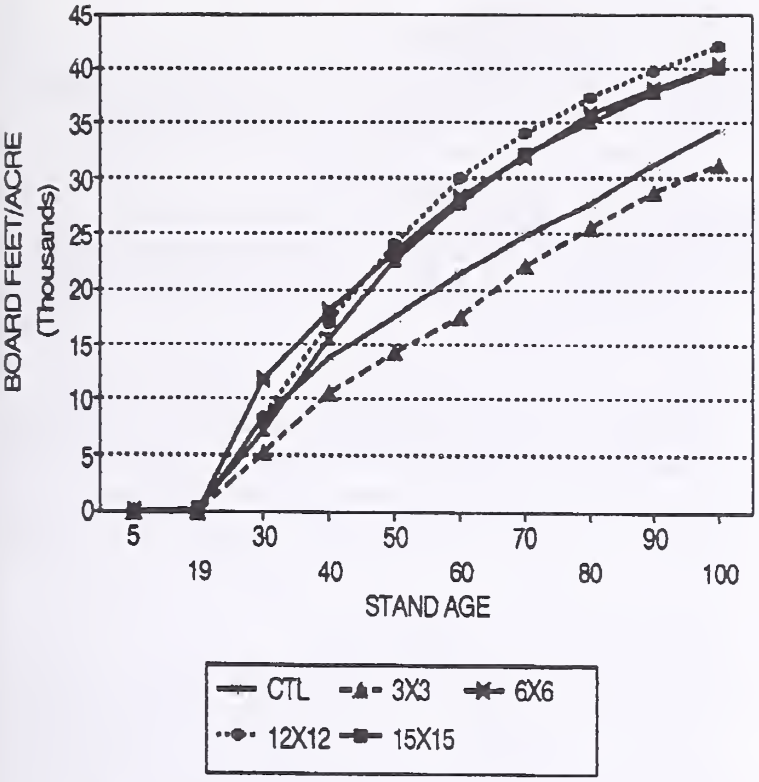

Figure 20—Projected board-foot yield for the Blue Goat thinning trial. The projection begins at age 20; earlier values are actual yields.

Yield projections for the Rattlesnake trial show a similar although less extreme pattern (figs. 21 and 22). Yield of the control is eventually overtaken by the 12 by 12 treatment for cubic volume and by both the 12 by 12 and 15 by 15 treatments for board-foot volume. Barber (1992) showed that 20 years after thinning, the present net worth (based on standard price and interest assumptions) for the 12 by 12 treatment exceeded all other treatments including the control. This resulted from a combination of equal or greater volume and larger diameters for the 12 by 12 treatment compared to the control. Yields from the 15 by 15 and 18 by 18 treatments remained below the 12 by 12 treatment over the entire projection period.

Examination of tree lists at the end of the projection period for the Blue Goat trial revealed similar total trees per acre for all treatments (including the control), from 703 TPA to 811 TPA. During the simulation, numerous trees were added by the regeneration establishment submodel, ranging from 549 TPA on the control to 1,630 TPA for the 12 by 12 treatment. Most of the regeneration occurred as subalpine fir (*Abies lasiocarpa* Nutt.) and other tolerant species. Ending species composition was similar among all treatments with a slight trend toward greater numbers of tolerant species with decreasing initial spacing.

None of the regenerated trees exceeded 6 inches at the end of the projection period. Ending sizes for the original larch were quite different between treatments (table 3). Both the percentage and absolute number of trees in the larger d.b.h. classes increased as initial spacing increased. The shape of the diameter distribution for all treatments was bimodal but was wider for initial wider spacings.

CONCLUSIONS

1. Early thinning in western larch significantly increases diameter growth, reduces mortality, and if given sufficient time produces maximum volumes on larger trees. Height growth may be improved by early spacing, but the evidence from this study is not yet conclusive.
2. Early thinning that does not adequately reduce intertree competition may decrease dominance differentiation and result in early stagnation as suggested by the projection of the 3 by 3 treatment.
3. If thinning is initiated after crown ratios have receded below 40 percent, growth response will be delayed (a 7-year delay was noted in this study). Projections indicate that volume losses to thinning will require at least 20 years to recover.
4. Projections indicate that early thinning may increase the species and size diversity of the stand over time by permitting greater regeneration and ingrowth of tolerant species and producing a greater number of larger trees and a wider distribution of tree diameters.

Table 3—Projected number of western larch trees per acre and percentages within treatments by 6-inch diameter class for the Blue Goat trial at age 100

Treatment	Control	3 by 3	6 by 6	12 by 12	15 by 15
Inches					
0- 6	229 (54%)	149 (39%)	120 (41%)	104 (46%)	112 (52%)
6-12	42 (10%)	96 (25%)	47 (16%)	10 (4%)	2 (1%)
12-18	98 (23%)	95 (25%)	56 (19%)	40 (18%)	32 (15%)
18-24	50 (12%)	31 (8%)	53 (18%)	40 (18%)	34 (16%)
24-30	3 (1%)	8 (2%)	14 (5%)	31 (14%)	31 (15%)
30-36	0 (0%)	0 (0%)	2 (1%)	2 (1%)	3 (1%)
Total	422	380	292	227	214

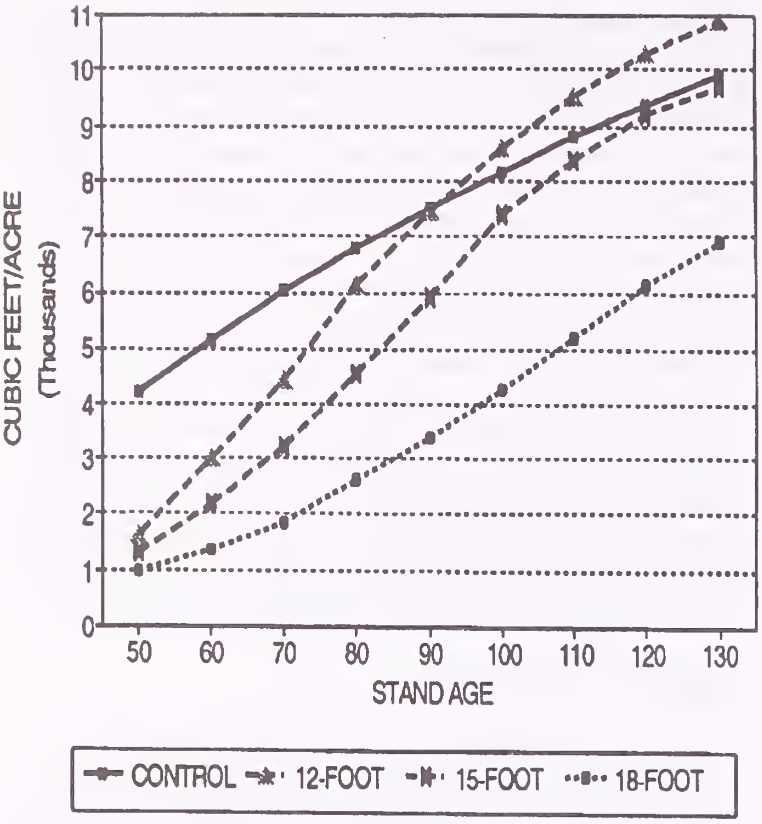

Figure 21—Projected cubic-foot yield for the Rattlesnake thinning trial. The projection begins at age 60; earlier values are actual yields.

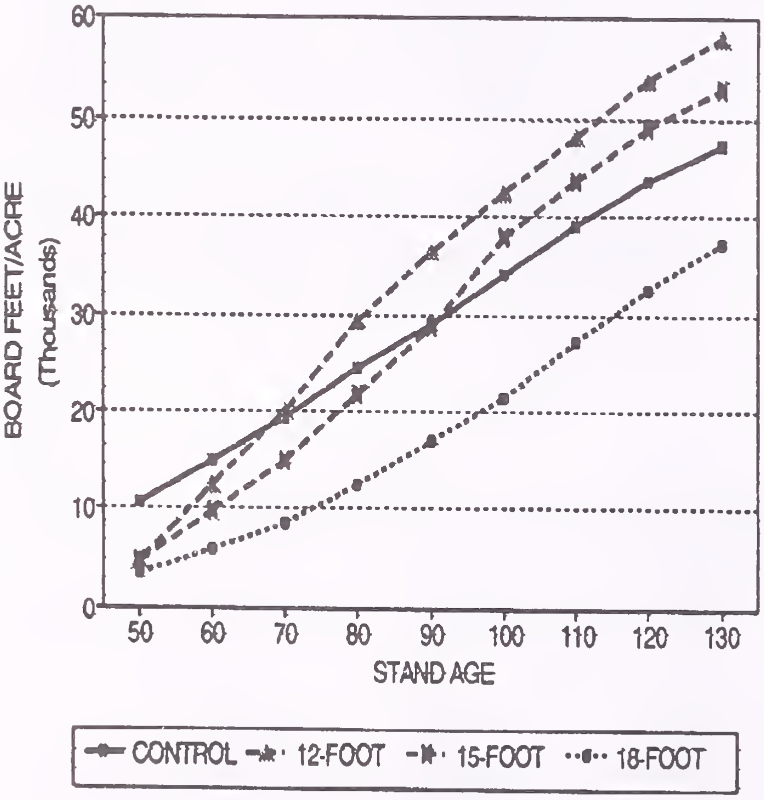

Figure 22—Projected board-foot yield for the Rattlesnake thinning trial. The projection begins at age 60; earlier values are actual yields.

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Western Larch Growth and Perturbations in Stands Regulated for 30 Years

Wyman C. Schmidt
Ward W. McCaughey
Jack A. Schmidt

Editor's Note: This is an abstract of a paper that will be published separately from this proceedings. Inquiries regarding the study and data may be made through the authors at the addresses listed at the bottom of this column.

Western larch is one of the most rapidly growing conifers in mountain forests of the Western United States and Canada. Overstocking is a common problem that can substantially reduce the potential growth of larch. It is one of the most significant problems in managing naturally regenerated forests. Thinning offers great silvicultural opportunities in young larch forests.

We established a long-term, permanent plot study in 1961 to determine the effects of different levels of regulated stand densities on individual tree and stand growth. Also examined was the relationship of these different stand densities to perturbations such as insect, animal, snow, and other types of damage to the trees. We now have 30 years of these measurements and observations.

Diameter growth of the shade-intolerant larch was very responsive to stand density, with the greatest individual tree growth in the least dense stands. Height growth was also related to stand density with the larch growing fastest in the less dense stands. However, height response on the different densities was far less pronounced than diameter.

Three major problems occurred during the 30 years. About 5 years after the 9-year-old stand was thinned a major storm of heavy wet snow in June flattened the young forest. Although crooks in the bole of the trees are still apparent in some trees 25 years later, overall the young forest had practically no mortality from the extreme snowbend and recovered remarkably well. Western spruce budworm can sever the terminal and upper lateral stems of larch. For several years we experienced relatively severe damage to form quality and some reduction in height growth due to budworm damage before budworm populations collapsed. Black bear can be a significant management problem in some areas, and this study helped identify the type and extent of damage and its relationship to stand density. Bear feed on the inner bark of larch in the spring and often kill the tree by completely girdling it. Bear damage was most severe where trees were largest and most vigorous in stands with the fewest trees.

These results help define appropriate management strategies in young western larch forests.

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Intermittent Long and Short Shoot Growth in Subalpine Larch Leaders

John Worrall

Abstract—Stem analysis of subalpine larch saplings growing at 2,000 m in southern British Columbia confirmed suspicions from observations of shoot morphology that the leaders of these trees grow as long shoots in only about 1 year in 4. Periods of up to 5 years of strictly short shoot activity are followed by less lengthy periods of long shoot growth of between 5 and 10 cm per year. Possible causes of this intermittent growth are discussed.

Several genera in the Pinaceae family exhibit a spur or short shoot habit of growth. Of these, the most familiar are in the *Larix* Mill. and *Cedrus* Trew. genera, with those in *Pinus* L. being a much more particular case. *Pseudolarix* Gord. is another example, as is *Ginkgo* L. in Ginkgoaceae. Numerous familiar hardwoods, such as *Betula* L. species also have this type of growth, as do less commonly encountered exotics such as *Davidia* Baill. and *Cercidiphyllum* Sieb. and Zucc. These latter two and *Betula alleghaniensis* Britt. have short shoots with seemingly indefinite longevity, which then become quite long.

Such species, in their first year have single spirally arranged leaves (opposite in *Cercidiphyllum*), separated by long internodes. In the axils of most of these in the Angiosperms, but only a small proportion in the Gymnosperms, apical meristems arise. Ordinarily these form lateral buds for next season's growth, though if conditions are favorable, they may instead grow directly into sylleptic shoots. Of these buds, in the following season, some, particularly the most acropetal and additionally the terminal bud (pseudoterminal in sympodial species), will grow into long shoots.

In *Larix*, these shoots will vary from perhaps 5 cm to more than a meter, depending on site, species, age and vigor, with internodes being in the 1-mm range. The majority of buds, though, will grow into short shoots, with increment perhaps 1 mm and internode lengths virtually zero. A short shoot may spontaneously assume the long shoot habit or may readily be induced to do so by the excision of the axis of the parent shoot distal to it. Powell has discussed these patterns of growth, particularly in *Larix laricina* (Du Roi) K. Koch, in numerous papers, such as these proceedings and 1987 and 1988, as have Owens and Molder (1979) for *Larix occidentalis* Nutt.

Occasionally, specimens of "short shoot species" planted without due care in unsuitable sites and conditions will show their displeasure, in that most buds, even the leading one, will grow as short shoots in the years before the plant gives up entirely. There is effectively no height growth. Can and does such a situation arise also in natural conditions in vigorous young plants?

MATERIALS AND METHODS

Subalpine larch (*Larix lyallii* Parl.) is a not-common tree occurring at or near the altitudinal limits for tree growth in parts of Alberta, British Columbia, Idaho, Montana, and Washington (Arno 1990; Arno and others, these proceedings). The north-northwesterly edge of its range is in Manning Park, BC, where at about 2,000 m in elevation on the northeastern flank of Mount Frosty, it is a pure all-age parklike stand. There would seem to be no between-plant competition, at least above ground.

In an attempt (Worrall 1990) to infer the ages of the larger trees, which are all hollow, data for a height/age curve were collected using a clinometer and breast height increment cores. These data are shown in figure 1. Trees with twice the diameter of those sampled do occur and are perhaps twice as old. To obtain the correction for age to reach breast height, a few young 2-m-tall trees were destructively sampled. These trees, of excellent monopodial form and, to somewhat inattentive observers such as myself, appearing to grow in height by 5 to 15 cm a year, proved to be about 75 years old by ring count at ground level. The slightly intriguing reason for the large difference between the actual ages of these plants and their "expected" ages should have been obvious. But this was obvious to me only

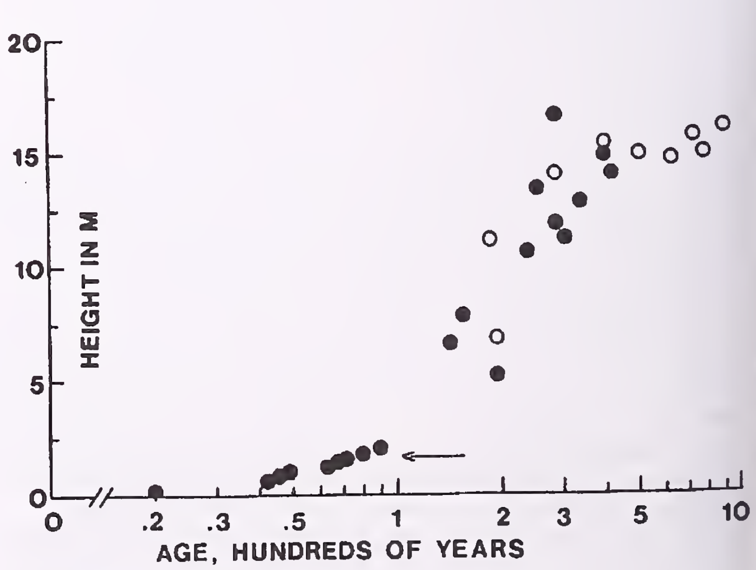

Figure 1—Height:age for subalpine larch. The hollow circles are data from hollow trees, whose age was interpolated from diameter and recent rate of diameter increment. The arrow indicates breast height.

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after I had discovered it by looking at the anatomy rather than the morphology of the phenomenon.

Growth of three of these 2-m saplings was investigated by the standard stem-analysis technique, except that the cross-sectional discs were cut at 1-cm intervals. Also, because the annual wood increments were so narrow, Larson's (1959) gambit of smoothing the cross-section with a razor blade and pressing into it a white powder (I used zinc oxide) had to be employed to detect them. This accentuates rings and reveals hitherto unsuspected ones to such a degree that individual cells and even the bordered pits between their lumens can be seen under a binocular microscope. An example is shown in figure 2 where the left-hand side did not receive the zinc oxide treatment. This method is far simpler and quicker than the preparation of microscope sections and can yield comparable results, depending on one's microtechnique. Stem analysis allowed the trees' height growth curves to be interpolated.

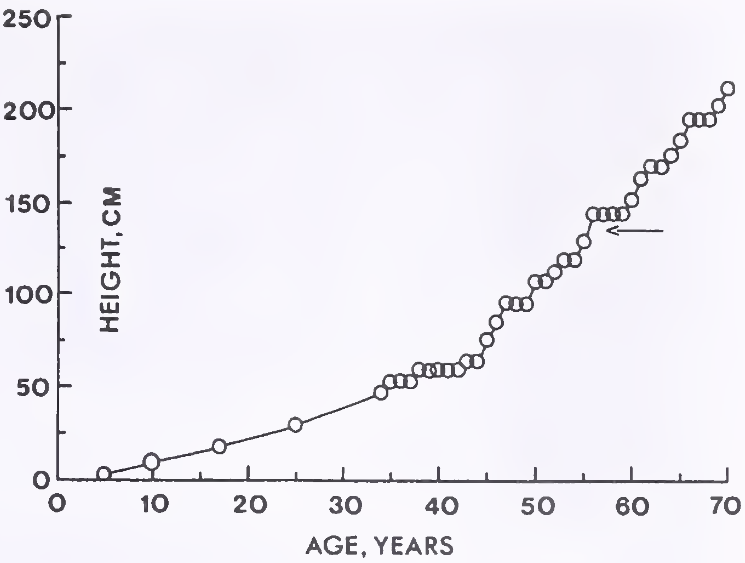

Figure 3—Height growth of a larch sapling, derived by stem analysis with a 1-cm sampling interval. The arrow indicates breast height.

RESULTS AND DISCUSSION

Figure 3 shows the height growth curve for one of the saplings. Toward the base, where most data are omitted, part of the slow height growth is due to loss of the leader by various causes, as was indicated by the arcs of compression wood in the turning-up lateral that is its replacement. In the top two-thirds of the plant this is not the case. There are several periods of up to 5 years duration when there is essentially no height growth, or to put it another way, opposite ends of 1-cm discs differed in ring count by as much as five. In another plant, sampled in the fall of 1991, the leader was free of lateral long shoots for more than 30 cm giving the illusion of fast growth rate.

The top 25-cm length of this plant is shown in figure 4, accompanied by cross-sections taken at the indicated levels in it. It is highly suggestive that just below the terminal bud where one growth ring is expected, there are in fact four. The innermost of these is fat, the outer three thin, though these terms are relative—the increments are all minute, having less than 10 tracheids in the radial files. About 5 cm farther down there are still four rings, with the pith and primary xylem being somewhat wider and the secondary xylem of the inner ring being a little wider. Clearly this long shoot grew in 1988 and has not grown since. The three outer rings were the cambium's response to the small amount of hormones produced by the growth of the 13 spur shoots on this length of stem.

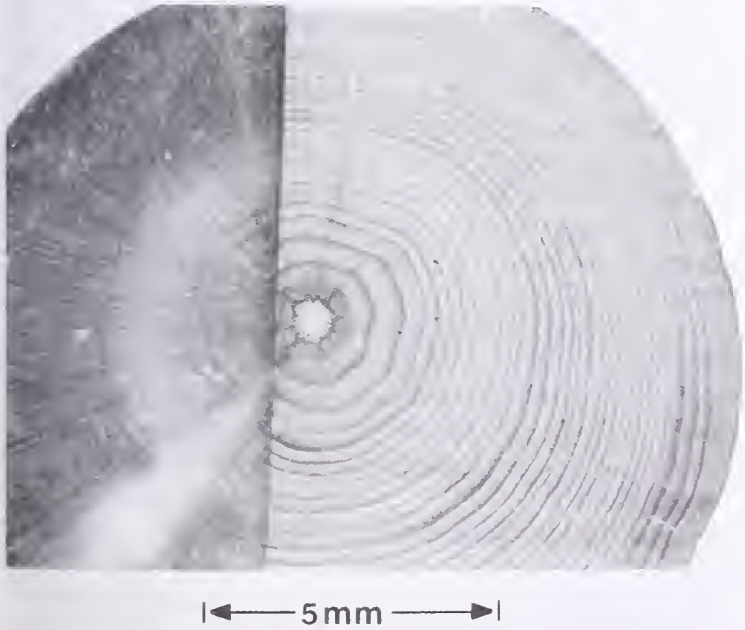

Figure 2—A cross-section showing accentuation of rings (right) by Larson's (1959) technique.

The third section, another 0.5 cm down, has nine wood increments. Growth of the long shoot must have been in 1983. Closer examination of the morphology of the top 6 cm of the plant would have indicated that this suspected 1991 increment did not in fact grow in that season. Not only were its lateral buds well on the way to being spur shoots, its surface was quite glabrous. One-year-old shoots have dense pubescence, most of which is gone by the end of the second season or before.

The final section in figure 4 is from the base of the shoot and has 19 wood increments. Forearmed with this knowledge, I carefully examined the shoot's bark morphology to judge from which points long shoot growth had proceeded. These points are indicated by the arrows in the figure, with the solidity indicating the basipetally rapidly diminishing level of confidence in them. Ring counts just above and below these points show these estimates to have been correct. The vertical double-ended arrows indicate the amounts (surprisingly invariable) of long shoot growth in the years they occurred. It seems remarkable that the 1988 long shoot has had no lateral long shoots from its 13 short shoots for 3 years, and that in 15 years there have been only four periods of long shoot growth, all in the first-order shoot, from the more than 60 buds from which such could have potentially occurred.

About 100 m farther down the mountain, on a better site, the top 60 cm of a wind-thrown closed-grown tree about 250 years old, and growing vigorously, had nearly 700 live short shoots on the leader and its two second-order long shoots. There were forty rings at its base, as shown in

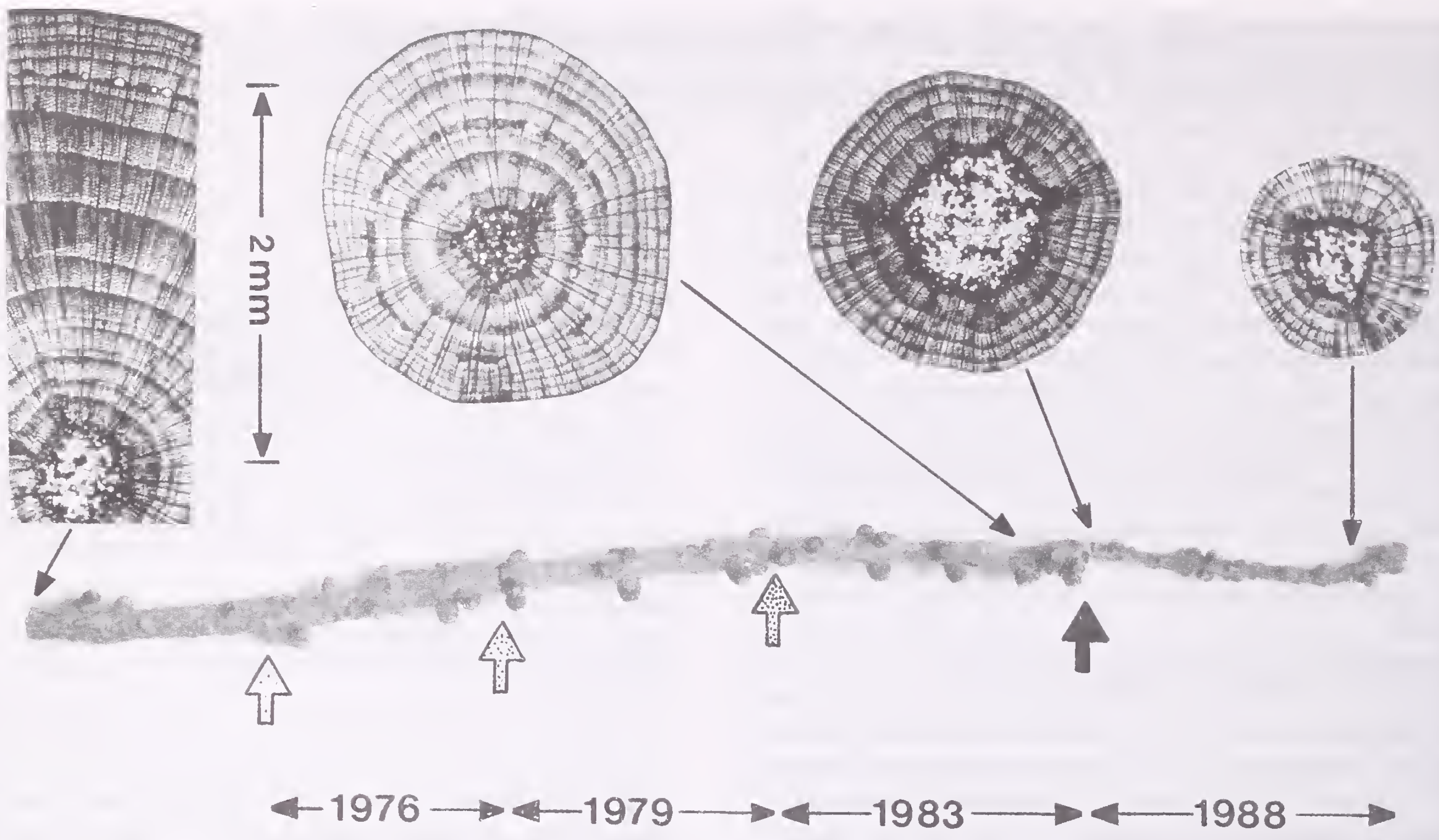

Figure 4—Left: the top 25 cm of a 2-m sapling. Right: cross-sections taken at the indicated levels in it.

figure 2. There had been two long shoots in 1992, none in 1991, and one in 1990. Beyond that it was not really possible to tell. It seems not unlikely that in old and nonvigorous trees, there are perhaps periods of dozens of years when there is no long shoot activity whatsoever, with shorter periods in younger trees and more particularly in their higher order shoots. The spur shoots, though, do have considerable longevity—well over 50 years in this species—and so do become quite long. This contributes to the craggy ginkgolike appearance of older trees.

The saplings whose growth is represented in figures 3 and 4 have somewhat different patterns of alternating long shoot/short shoot activity. In the former there are extended periods of long shoot activity. In the latter, there are only single seasons of such, separated by extended periods of nongrowth. The latter is the easier to attempt to explain. Does the plant, in this severe climate, build up its resources for a single debilitating spurt of growth? The lowest two photomicrographs of figure 4 do show at least two prominent rows of traumatic resin canals in the latewood, suggesting damaging frosts in August or even July (not an unexpected event at 2,000 m in elevation at 49° N.). Spring bud burst does vary widely in date (Worrall 1993).

Are some growing seasons too short for much long shoot growth to occur? A weather or climate explanation seems unlikely because in the (small) sample used, there was no synchrony among plants in the periods of shoot activity. There are some interesting cambial activity questions raised by these observations. Spur shoots do become thicker but not due to xylem increment, only phloem. The low levels of hormones produced by spur shoot activity do, by contrast, induce the long shoot cambia to produce wood increments.

What is the seasonal course of cambial activity in this species at the higher elevations? Presumably anyone who has the interest and fortitude to find out will have to be starting the study more than a month before the snowpack is gone because bud-burst usually occurs when there are still 2 m or more of snow on the ground.

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Growth of Western Larch Under Controlled Levels of Stocking

P. H. Cochran
K. W. Seidel

Abstract—Thinning pole-sized stands of larch to densities as low as 50 percent of "normal" results in little loss of basal area growth, a moderate loss in volume production, and a large increase in tree diameter. Thinning is necessary in many larch stands to maintain vigorous, rapidly growing trees. Thinning levels will greatly affect the appearance of future stands.

In Oregon and Washington, western larch (*Larix occidentalis* Nutt.) is a major seral species in the *Pseudotsuga menziesii* and *Abies grandis* zones in the Ochoco and Blue Mountains of northeastern Oregon and southeastern Washington, along the east-side Washington Cascade Range, and in the Okanogan highlands. Western larch is a minor but important species in these zones in the northern half of the Oregon Cascades and in the *Tsuga heterophylla* and *Abies lasiocarpa* zones of the east side of the Washington Cascade Range (Franklin and Dyrness 1973).

Larch has rapid juvenile growth and desirable wood properties. Even-aged stands generally become established after fire or other disturbances, and these stands often are heavily stocked. Larch is shade intolerant, and decreased vigor associated with reduced crown size usually occurs as stands develop so that stocking level control often is necessary. Questions about stocking level control include: (1) What spacings after precommercial thinnings allow the leave trees to develop into commercially sized stands with reasonable site occupancy most rapidly? (2) What is the relation between levels of growing stock and growth and yield of stands and individual trees in commercially sized stands? (3) What is the relation between mortality and stand density?

To aid in answering the last two questions, two studies on levels of growing stock have been established in the Blue Mountains of Oregon (Seidel 1986, 1987). These studies are also valuable because they provide field demonstrations of the influence of thinning and allow opportunities to study processes associated with stand development. Stand development influences all phases of forest management and greatly affects the ecology of forested or partly forested landscapes. This paper reports rates of growth over 25 years for one of these studies established in 1966.

STUDY AREA AND METHODS

This study is in sections 26 and 27 of T. 5 S., R. 11 E., Willamette Meridian, near Catherine Creek about 15 miles southeast of Union, OR, U.S.A., at an elevation of 4,000 feet. The soil is a Tolo silt loam (Typic Vitrandept) developing on 3 feet of ash originating from the eruption of Mount Mazama. The vegetation is a seral stage of the *Abies grandis/Calamagrostis* plant community (Johnson and Clausnitzer 1991). The stand, established after a fire, was 35 years old (28 years old at breast height) in 1966 when the study was started and has a site index of 70 feet (Schmidt and others 1976) or 90 feet (Cochran 1985). (The site index values of Schmidt and others are determined from average heights of dominants and codominants and their total age; site index values of Cochran are obtained from heights of the tallest five trees per acre and their age at breast height. The index age in both systems is 50 years.) Results of the study are directly applicable only to this particular stand; however, the soil and plant community have similar representatives over the range of western larch indicating corresponding results could be expected over a wide area.

The experimental design is completely randomized with two replicates of five levels of growing stock installed on 10 plots of 0.4 acre square each, and surrounded by a similarly treated buffer strip 33 feet wide. These 10 treated areas (each 0.9 acre) were distributed over the untreated larch stand. Thinning levels were assigned randomly to each plot. The treated areas containing each plot were then thinned from below to leave the required number of the largest and most vigorous trees as evenly spaced as possible. Two of the plots in the highest two density levels had about 40 percent of their basal area in lodgepole pine (*Pinus contorta* Dougl.) after the initial thinning. Lodgepole pine was discriminated against in each thinning. The eight other plots were pure larch. Values of stand density index (*SDI*) immediately after the first thinning for the five stocking levels were 57, 107, 152, 201, and 246 (table 1). These values are equivalent to 14, 26, 37, 49, and 60 percent, respectively, of an *SDI* of 410, the *SDI* for "normal" or "fully stocked" stands of western larch (Cochran 1985). The relation between trees per acre (*T/A*) and quadratic mean diameters (*Dg*) for "normal" western larch stands with bell-shaped diameter distribution curves is (Cochran 1985):

$$\log_e(T/A) = 10.001 - 1.73(\log_e Dg) \qquad (1)$$

The *SDI* (the number of trees that stands with bell-shaped diameter distributions would have at a standard *Dg* of 10 inches) is:

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Table 1—Stand characteristics per acre of western larch at Catherine Creek over the period of study

	Density							
Level[1]	*SDI*	Basal area	Number of trees	Average spacing	Quadratic mean diameter	Average height	Volume[2]	
		Square feet		*Feet*	*Inches*	*Feet*	*Cubic feet*	*Board feet*
After 1966 thinning (breast height age 28)								
1	52	26.0	96	21.3	7.0	48.4	474	48
2	101	49.6	215	14.2	6.5	46.2	902	0
3	148	70.9	355	11.2	6.1	46.5	1,272	193
4	204	96.4	546	8.9	5.7	42.9	1,616	0
5	240	109.8	745	7.6	5.2	42.0	1,847	0
1971 (breast height age 33)								
1	76	40.3	96	21.3	8.8	55.4	794	948
2	134	68.2	215	14.2	7.6	51.7	1,333	294
3	188	93.4	354	11.1	7.0	53.3	1,780	532
4	253	120.5	539	9.0	6.4	49.1	2,250	345
5	284	134.3	740	7.7	5.8	48.0	2,510	102
Before 1976 thinning (breast height age 38)								
1	102	56.3	96	21.3	10.4	62.7	1,222	3,654
2	164	86.1	215	14.2	8.6	56.6	1,870	2,366
3	227	114.8	354	11.1	7.7	58.2	2,471	1,464
4	288	143.9	534	9.0	7.0	55.5	3,103	1,168
5	325	155.7	734	7.7	6.2	53.6	3,317	706
After 1976 thinning (breast height age 38)								
1	61	34.2	51	29.2	11.1	64.9	760	2,876
2	112	59.3	129	18.4	9.2	62.8	1,301	2,368
3	161	82.7	225	13.9	8.2	62.7	1,808	1,464
4	202	104.0	333	11.4	7.6	60.9	2,248	1,168
5	247	121.0	464	9.7	6.9	61.7	2,621	706
1981 (breast height age 43)								
1	76	44.6	51	29.2	12.6	72.8	1,146	5,110
2	134	72.9	129	18.5	10.3	68.9	1,862	4,949
3	187	99.3	224	13.9	9.0	67.8	2,412	3,583
4	234	121.2	329	11.6	8.3	66.4	2,986	2,797
5	274	137.6	462	9.8	7.4	66.0	3,398	1,357
Before 1986 thinning (breast height age 48)								
1	89	52.7	51	29.2	13.8	74.7	1,514	7,583
2	150	82.9	128	18.6	11.0	69.6	2,294	8,915
3	209	110.9	220	14.1	9.6	68.7	2,962	7,253
4	251	132.9	318	11.8	8.8	67.9	3,625	5,628
5	270	137.8	408	10.4	7.9	69.4	3,858	3,028
After 1986 thinning (breast height age 48)								
1	60	36.4	32	37.4	14.7	78.6	1,065	5,463
2	108	59.9	87	22.5	11.3	71.3	1,671	7,197
3	148	81.5	148	17.2	10.0	71.5	2,206	6,200
4	190	101.7	218	14.3	9.4	70.0	2,776	5,269
5	220	115.1	313	11.9	8.2	71.3	3,241	2,899
1991 (breast height age 53)								
1	72	44.4	32	37.4	16.2	83	1,345	7,357
2	121	69.3	87	22.5	12.1	74	1,991	9,221
3	167	92	148	17.2	10.8	72	2,633	9,117
4	213	115.7	218	14.3	10.0	72	3,384	8,804
5	238	126.6	310	11.9	8.6	71	3,702	5,803

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[1] Two plots for each density level.

[2] Total cubic-foot volume—entire stem, inside bark, all trees; board-foot (International 1/4-inch rule) volume—trees 10.0-inch diameter at breast height and larger to a 6-inch top diameter inside bark.

$$SDI = (T/A)\ (Dg/10)^{1.73} \qquad (2)$$

All study plots were well stocked before the initial thinning; they contained about 1,300 trees per acre, averaging 4.5 inches in diameter and 45 feet in height. The study was designed to be rethinned to the initial stocking levels at 10-year intervals and has been rethinned twice (table 1). Slash from all three thinnings was left on the plots.

At the start and end of each 5-year measurement period, diameters at breast height of all plot trees were measured to the nearest 0.1 inch. Fifteen trees in each plot, proportionately distributed over the range of diameters, were measured with optical dendrometers. These measurements were used to fit models for each plot expressing board-foot volume (*V*), total cubic-foot volume inside bark (*V*1) (Husch and others 1972), and total height (*H*) as functions of diameter at breast height (*D*) (Clutter and others 1983):

$$\log_e V = a + b(\log_e D) + c(\log_e D)^2 \qquad (3)$$

$$\log_e V1 = a_1 + b_1(\log_e D) + c_1(\log_e D)^2 \qquad (4)$$

$$\log_e H = a_2 + b_2/D + c_2/D^2 \qquad (5)$$

New coefficients were determined by linear regression after each measurement and used to compute volumes and heights. The second degree terms were used only when they were significant ($p \leq 0.05$).

Annual tree mortality (R_m) was calculated as a negative interest rate for each plot-period combination by using (Hamilton and Edwards 1976):

$$R_m = 1 - (N2/N1)^{(1/n)} \qquad (6)$$

where *N1* is the number of live trees at the start of the period, *N2* is the number of live trees at the end of the measurement period, and *n* is the number of years in the measurement period. Mean diameters at the beginning of each period for trees that died during that period were divided by mean diameters of all live trees at the start of the period for all plot-period combinations where mortality occurred. These ratios were used to examine the size of the trees that died in relation to the average tree size.

Periodic annual increments (PAI) of gross and net volume, gross and net basal area, quadratic mean diameter, and average height were determine for each plot-period combination. The PIA's of diameter and height were determined for the trees surviving each period. Annual growth for gross and net basal area and volume were also determined for the 25-year period of study.

PAI's of basal area and volume were determined where possible for the 30 and 75 trees per acre with the largest diameters at the start of each period. After the second thinning in 1976, plots with the lowest stocking level did not have 75 trees per acre. The lowest stocking level after the third thinning in 1986 had only 32 trees per acre. These determinations aid in examining the influence of smaller trees on the growth of larger trees in the stand.

Split-plot-in-time analyses of variance were used to test for significance of treatment effects on all PAI's and mortality rates. A value of 1 was added to each mortality rate to avoid using zeros in the analysis of variance. Standard analyses of variance were used to test for treatment effects on annual growth rates. Tukey's test was used to determine significant differences among treatment means for annual growth rates and for differences in PAI's and mortality rates between stocking levels within each period. Because the lowest stocking level did not always have 75 trees per acre, the analyses of variance for PAI's of the 75 largest trees per acre used data from only the four highest density levels.

All PAI's and mortality rates for each treatment in each period were plotted as a function of midperiod *SDI*. Attempts were made to mathematically describe the relation of mortality rates or PAI's for mean diameter and height to stand density. Such descriptions did not appear, however, to aid in the interpretation of results and would not have wider application. Nonlinear regression analyses were employed to relate PAI's of gross volume and gross basal area to Cochran's (1985) site index (*S*), midperiod age at breast height (*A*), and midperiod *SDI* (*SDIm*), by using:

$$PAI = [\exp(b_0 + b_1 S + b_2 \log_e S + b_3 A + b_4 \log_e A)]\ [1 - \exp(b_5 SDIm)]^{b6} \qquad (7)$$

with combined data from all periods (50 observations) and assuming independence of each observation. The site index values used in (7) were values determined from the two tallest trees per plot in 1966 as outlined by Cochran (1985). The dependence among observations leads to a potential underestimate of experimental error that results in artificially high R^2 values and levels of significance that may not be real. Still, if examination of residuals and plots of actual versus predicted values demonstrates that the model does describe the results, then the model can aid in interpretation. Model (7) consists of two parts. The expression within the first set of brackets resembles the description of the gross PAI for a fully stocked stand (Cochran and Hopkins 1991). The expression in the second set of brackets defines the reduction of growth at lower stocking levels (Barrett 1982; Dahms 1983; Seidel 1987).

RESULTS AND DISCUSSION

Results covered mortality, periodic annual increments, and annual growth.

Mortality

Mortality was light for four of the five study periods. Twelve trees out of the 1,567 study trees died during the first period, seven during the second period, three during the third period, and one during the fifth period. The average mortality rate for all plots and all periods was 0.15 percent. No mortality occurred in the lowest stocking level. Still, density did not significantly ($p \leq 0.05$) affect mortality rates (tables 2 and 3). Mortality rates were highest during period 4 because an ice storm in 1984 broke 58 tree boles below the live crown and caused mortality rates averaging 1.15 percent for the highest density level. For other period-treatment combinations, average mortality rates did not exceed 0.64 percent. Mean diameters of trees that died on any plot during any period averaged 83 percent (range, 39 to 109 percent) of the mean diameter of all trees on the plot. No relation between this percentage and stocking level was evident although mortality occurred on so few plot-period combinations (18 out of 50) that no formal statistical test was performed.

Table 2—Sources of variation, degrees of freedom (df), and probability of greater *F* values for the repeated measures analyses of variance for the study at Catherine Creek

Source of variation	df	Mortality rates	Periodic annual increments					
			Basal area		Volume		Mean diameter	Average height
			Gross	Net	Gross	Net		
		Probability of larger F values						
Density	4	0.1313	0.0056	0.0011	0.0001	0.0003	0.0001	0.0024
error	5							
Period	4	.0058	.0001	.0001	.0001	.0003	.0001	.00001
Period x density	16	.6028	.0001	.0148	.7699	.8716	.0007	.8919
error	20							

Table 3—Values of stand density index at midperiod (*SDIm*), mortality rates, and periodic annual increments for each density level in each period for the study at Catherine Creek[1]

Density level	*SDIm*	Mortality rate	Periodic annual increments					
			Basal area		Volume		Mean diameter	Average height
			Gross	Net	Gross	Net		
		Percent	*Ft²/acre/yr*		*Ft³/acre/yr*		*Inches/yr*	*Ft/yr*
Period 1								
D1	64	0 b	2.9c	2.9c	64c	64c	0.35a	1.4
D2	118	0 b	3.7cb	3.7cb	86cb	86cb	.23 b	1.1
D3	168	.07ba	4.4 b	4.6 ba	102 b	101 ba	.18 c	1.2
D4	228	.33 a	5.0 a	4.8 a	131 a	127 a	.14 cd	1.4
D5	262	.28ba	5.1 a	4.9 a	136 a	133 a	.11 d	1.2
Average		.14	4.2	4.2	104	102	.20	1.3
Period 2								
D1	89	0	3.2c	3.2b	86b	86b	.32a	1.5
D2	149	0	3.6cb	3.6ba	108ba	108ba	.19b	1.0
D3	207	0	4.3cb	4.3ba	139ba	139ba	.15c	1.1
D4	271	.15	4.9 a	4.7ba	174 a	170 a	.13d	1.3
D5	304	.14	4.4 ba	4.3 a	164 a	162 a	.08e	1.1
Average		.06	4.1	4.0	134	133	.17	1.2
Period 3								
D1	68	0	2.1a	2.1c	78b	78b	.31a	1.2
D2	123	0	2.7ab	2.7cb	112b	112ba	.20b	1.3
D3	174	0	3.3 b	3.3 ba	121ba	121ba	.16c	.8
D4	218	.15	3.6 b	3.5 ba	148 a	147ba	.12cd	1.0
D5	261	.05	3.4 b	3.3 a	157 a	156 a	.10 d	.8
Average		.04	3.0	3.0	123	123	.18	1.0
Period 4								
D1	83	0	1.6c	1.6	74b	74	.22a	.9
D2	142	.18	2.1cb	2.0	88b	84	.14ab	.7
D3	198	.43	2.6 ba	2.3	118ba	110	.12 b	.7
D4	243	.64	3.0 a	2.4	144 a	128	.10 b	.6
D5	272	1.15	2.4cba	.4	148 a	92	.07 b	.7
Average		.48	2.3	1.7	114	98	.13	.7
Period 5								
D1	66	0	1.6	1.6	56b	56b	.30a	.9
D2	114	0	1.8	1.8	64b	64b	.16 b	.7
D3	157	0	3.1	2.1	86ba	86ba	.14 bc	.7
D4	202	0	2.8	2.8	122 a	122ba	.13 bc	.8
D5	229	.17	2.3	2.2	92ba	91 a	.08 c	.7
Average		.03	2.3	2.1	84	84	.16	.8

[1] Numbers followed by the same letter are not significantly different according to Tukey's studentized range test ($p \le 0.05$).

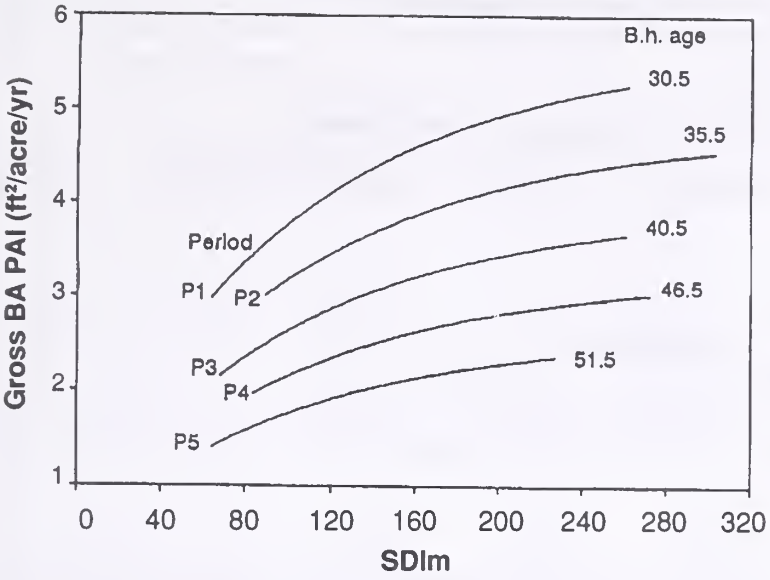

Figure 1—Periodic annual increment of gross basal area as a function of stand density (*SDI* at midperiod) and midperiod age calculated using the coefficients in table 7 with a value of 90 for site index.

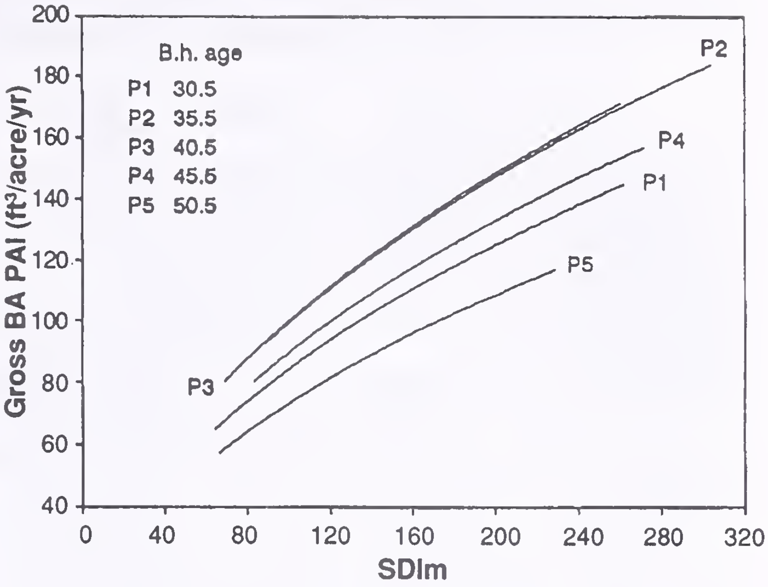

Figure 2—Periodic annual increment of gross cubic volume as a function of stand density (*SDI* at midperiod) and midperiod age calculated using the coefficients in table 7 with a value of 90 for site index.

Periodic Annual Increments

All PAI's differed significantly ($p \leq 0.05$) with density and period (or age) (tables 2 and 3). Gross basal area PAI decreased with increasing stand age except for the lowest density level, and significant differences ($p \leq 0.05$) between at least some of the density levels occurred in periods 1 through 4 (tables 2 and 3). Gross basal area PAI generally increased as *SDI* increased from 64 to about 205 (16 to 50 percent of "normal" stocking values) and then increased little with further increases in stand density (fig. 1). Gross volume PAI increased from the first to the second period (as midperiod breast height age increased from 30 to 35 years), was about the same for the second and third periods at comparable *SDI*'s, and then decreased (with further increases in age) over the succeeding two periods (table 3, fig. 2). Gross volume PAI's displayed a less pronounced leveling off at higher stand densities than for gross basal area PAI's. Because of the low mortality in this study, net PAI's differed with stand density and age in approximately the same manner as gross PAI's (table 3).

Quadratic mean diameter PAI's generally decreased with increasing stand density (tables 2 and 3), and differences between density levels varied with period, thereby resulting in a significant ($p \leq 0.05$) period-by-density interaction. PAI's for average height decreased with increasing age for the first 20 years of observation (tables 2 and 3), and response with changing density was erratic.

Annual Growth

Treatment averages for gross annual basal area growth ranged from 2.3 to 3.9 square feet per acre for 25 years of observation; the highest treatment mean for net annual basal area growth was 3.8 square feet per acre. Treatment averages for gross volume annual growth ranged from 71 cubic feet per acre to 147 cubic feet per acre, and the highest treatment average for net volume annual growth was 142 cubic feet per acre (table 4). No significant differences ($p \leq 0.05$) in annual growth of gross basal area occurred over the four highest stand densities. No significant differences in annual gross volume growth occurred over the three highest stand densities. No significant differences in net annual volume growth occurred between the two highest densities. Gross annual basal area growth was greater for stocking levels 3 and 4 than for stocking level 1, and gross annual volume growth for levels 4 and 5 was greater than for levels 1 and 2. Net annual volume growth for levels 4 and 5 was greater than for levels 1 and 2, greater for level 3 than for level 1, and greater for level 4 than for levels 1, 2, and 3. Net annual basal area growth tended to follow the same pattern as gross annual basal area growth (table 4).

Growth of Largest Trees

PAI's of basal area and volume for the 30 and 75 largest diameter trees differed significantly with period (table 5). These volume PAI's were highest during period 3 (table 6) after a thinning. Gross volume PAI for all trees was fairly high for this period (table 3), and the 30 and 75 largest trees made up a higher proportion of the growing stock following the thinning, thereby accounting for the high growth rates during this period. Corresponding PAI's for basal area differed more erratically (table 6), probably because gross PAI's of basal area for all trees decreased with succeeding periods or increasing age (table 3), but the amount of growing stock represented by the 30 and 75 largest trees increased after the two rethinnings. PAI's of basal area for the 30 largest trees were significantly

Table 4—Source of variation, degrees of freedom (df), probability of greater F-values from analyses of variance for annual growth of basal area and volume over the 25 years of study and treatment averages for these growth values[1]

Source	df	Gross basal area	Net basal area	Gross volume	Net volume
Density	5	0.0169	0.0522	0.0037	0.0017
error	4				
Total	9				

Density level	Average growth			
	Basal area		Volume	
	Gross	Net	Gross	Net
	- - - - - - *Ft²/acre* - - - - - -		- - - - - - - *Ft³/acre* - - - - - - -	
D1	2.3 b	2.3 b	71 b	71 d
D2	2.8 ba	2.8 ba	92 b	91 dc
D3	3.9 a	3.8 a	113 ba	110 cb
D4	3.9 a	3.7 a	147 a	142 a
D5	3.4 ba	2.6 ba	146 a	128 ba

[1] Values followed by the same letter are not significantly different ($p \leq 0.05$) according to Tukey's studentized range test.

greater ($p \leq 0.05$) for the lowest stand density than the four higher densities for all periods except period 4. Basal area PAI's for the 75 largest diameter trees tended to decrease with increasing stand density. Cubic volume PAI's for the 30 largest trees were higher for the lowest density levels than for the highest density levels. Although average cubic volume PAI's for the 75 largest trees per acre had highest average values for the lowest stand densities for all periods except period 2, these differences were not significant (table 5).

Growth Patterns

Fitting model (7) provides a way of generalizing the results (table 7). Site index values (Cochran 1985) for each plot ranged from 84 to 93 feet. Plotted residual values as functions of site, density, and age appeared balanced and reasonably small. Changes in gross PAI's with density and age (or period) differ for basal area (fig. 1) and volume (fig. 2). Increases in gross basal area PAI with increasing stand density are fairly small for *SDI*'s greater than 140.

Table 5—Sources of variation and probabiltiy of greater F-values for repeated-measures analyses of variance for periodic annual increments of basal area and volume for the largest 30 and the largest 75 trees per acre at the Catherine Creek study

Source	Probability of greater F-values			
	Basal area periodic annual increments		Volume periodic annual increments	
	Largest 30 trees	Largest 75 trees	Largest 30 trees	Largest 75 trees
Density	0.0005	0.0608	0.0053	0.3572
Period	.0013	.0001	.0001	.0001
Period x density	.0014	.2006	.1869	.4517
Density	**Average periodic annual increments over all periods**			
	- - - - *Ft²/acre/yr* - - -		- - - - *Ft³/acre/yr* - - - -	
D1	1.3	—	44.5	—
D2	.7	1.6	25.1	59.8
D3	.6	1.3	23.0	51.7
D4	.6	1.2	25.2	52.5
D5	.5	1.1	22.6	41.2

Table 6—Average periodic annual increments of basal area and volume by period for the 30 and 75 trees per acre with the largest diameters

	Periodic annual increments			
	Largest 30 trees/acre		Largest 75 trees/acre	
Period	Basal area	Volume	Basal area	Volume
	Ft²/acre/yr	*Ft³/acre/yr*	*Ft²/acre/yr*	*Ft³/acre/yr*
1	0.7	19.0	1.4	36.5
2	.8	25.0	1.3	46.2
3	.8	34.5	1.4	62.8
4	.7	31.5	1.2	46.8
5	.8	29.2	1.3	51.3

Although gross volume PAI does decrease with increasing stand density, it does not appear that the curve approaches an asymptote as normal density (*SDI* = 410) is approached. Examining how PAI's change with increasing stand density (fig. 3) shows the practical effects of thinning, assuming that the coefficients in table 7 reasonably describe growth rates to 100 percent of normal density. Stands at 25 percent of normal density produce 68 percent of the gross basal area PAI and 47 percent of the gross volume PAI grown by a "normal" or fully stocked stand. Stands at 50 percent of normal density produce 89 percent of the gross basal area PAI and 70 percent of the gross volume PAI grown by a fully stocked stand.

These estimates indicate that stands can be heavily thinned from below without sacrificing much basal area production, with only a moderate sacrifice in cubic volume production. This can be translated into a large increase in diameter growth and individual tree size. Heavy thinning probably produces an increase in board-foot production, too, but this possible result is not evident. The differing number of 10-inch trees (the designated diameter limit for a tree to have board feet) with time between treatments and between replications of individual treatments obscures the picture of board-foot production. The number of board feet at the end of the study seems to differ with treatment (table 1), but these differences are not statistically significant ($p \leq 0.05$).

Table 7—Coefficients from nonlinear regression analyses for $PAI = [\exp(b0 + b1(S) + b2(\log_e S) + b3(A) + b4(\log_e A))][1-\exp(b5 * SDIm)]^{b6}$ with gross periodic annual increments from the Catherine Creek study assuming independence of all periodic annual increment values

	Periodic annual increment	
Coefficient	Basal area	Volume
*b*0	−74.073	−143.513
*b*1	−0.240	−0.402
*b*2	21.426	36.736
*b*3	−0.0593	−0.201
*b*4	0.821	7.692
*b*5	−0.00896	−0.00125
*b*6	0.783	0.624
Approximate R^2	0.92	0.89

CONCLUSIONS

There is a tendency to leave too many trees after thinning for the future stand to have vigorous, fast-growing trees. Thinning commercially from below down to densities of 50 percent of normal is reasonable, and thinning to even lower densities may be proper where the object is to produce large-diameter trees in a short time. Thinning young western larch stands can greatly affect future tree diameters (and hence the appearance of the stand) without causing a severe change in wood production.

Managers have the opportunity to create a wide range of stand conditions. Mosaics of stands of dense, small-diameter trees and stands of large-diameter trees with an open, parklike appearance maintained by underburning are possible within the same landscape.

Decisions about the desired future condition and appearance of landscapes containing western larch stands and the silvicultural practices necessary to create and maintain these landscapes need to be made, probably with public input. The public needs to know what is biologically possible and silviculturally reasonable, and at the same time we need to obtain their concepts of the appearance of future forests. In this communication process, it should be possible to settle on management goals and methods to achieve these goals that would be supported by the majority of people with interests in future forests.

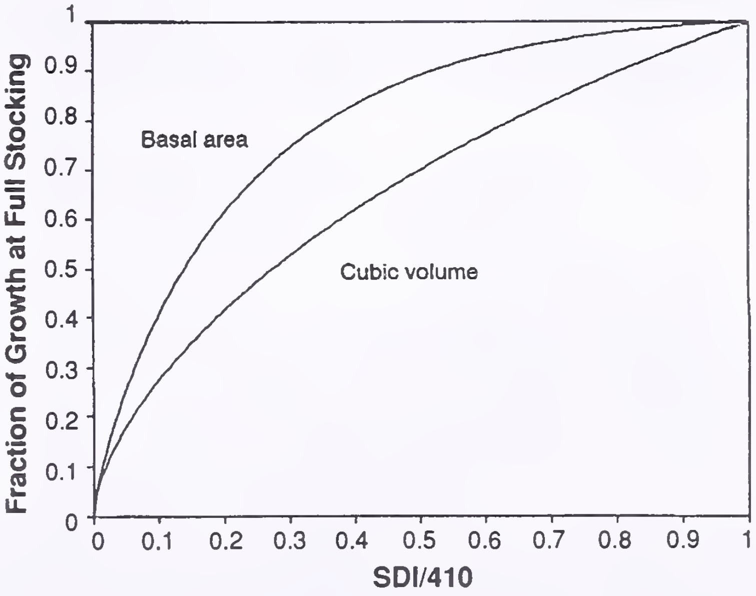

Figure 3—Estimates of the fraction of gross periodic annual increment at full stocking produced at various fractions of "normal" stand density. Curves were calculated assuming that the coefficients in table 7 adequately describe gross PAI's of cubic volume and basal area up to full stocking (*SDI* = 410).

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Exotic Larches: Experiences in Wisconsin

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Abstract—After 9 years, a provenance test of *Larix decidua* and *L. leptolepis* in central Wisconsin exhibited high survival and excellent growth and was outperforming *Pinus resinosa* on an adjacent site. Exotic larch plantations in 10 other Wisconsin counties resulted in some similar successes but also failures, the latter attributable to poor stock, needlecast disease, unfavorable soil or site preparation, late frost, or combinations. Avoidance of such conditions should assure exotic larches a bright future in parts of Wisconsin.

The economic history of Wisconsin has been intimately connected to forestry in general and conifers in particular. As this state's tree flora includes only nine indigenous coniferous trees, complications in the culture of any of the "bread and butter" species are seen as a threat. Notably the impact of blister rust (*Cronartium ribicola*) on eastern white pine (*Pinus strobus*) and the potential threat of Scleroderris canker (*Gremeniella abietina*) on red pine (*Pinus resinosa*) and jack pine (*Pinus banksiana*) have been viewed as such, prompting the search for alternative species such as exotic larches (*Larix* spp.) (Wyckoff 1982). These fast-growing trees also attracted attention in conjunction with the growing interest in forest tree improvement, leading to numerous trials in various parts of North America (Carter and Maass 1991).

After half a century of growth, a review of exotic larches in Wisconsin seems appropriate. This paper combines such an assessment with presentation of the results of one recent, particularly promising provenance trial in central Wisconsin.

MATERIALS AND METHODS

Central Wisconsin Plantation

In the spring of 1982, a small test plantation consisting of a single provenance of Japanese larch (*Larix leptolepis*) of German origin, and six of European larch (*Larix decidua*), two of German and four of Polish origin, was established in Portage County (Lee and Schabel 1989). The 2-0 stock was hand planted at 2.1 x 3 m spacing in furrows in an old alfalfa field on a north to northwest facing gentle moraine consisting of coarse loam. Subsequent management included one watering, and two mechanical weedings during the first, another weeding during the second growing season.

A randomized complete block design with seven replications (6 trees/plot x 7 plots/block x 7 blocks) was installed in the test. After five growing seasons in the field (1986), total height of all trees was recorded; total height was again assessed on the tallest tree per plot at the end of the ninth growing season (1991) in the field. According to Lee (1974), this procedure is convenient while resulting in only negligible loss in genetic information. All diameters at breast height were also measured in 1991. Plot means were used in an analysis of variance to test the significance of between-seedlot differences in growth characteristics, where the degrees of freedom were 6, 6, and 36 for seedlot (provenance), blocks, and error term, respectively. In order to correlate between height and diameter growth, simple correlation analyses were employed using seedlot means as items with 5 degrees of freedom. Tree health was monitored at frequent intervals.

Other Wisconsin Plantations

For comparison, major exotic larch plantations in the state were visited during the summer of 1992 (fig. 1). Field observations were supplemented by personal communications with field personnel, and a literature review.

RESULTS AND DISCUSSION

Central Wisconsin Plantation

After nine seasons in the field, height growth of dominants in this plantation ranged from 9.42 to 10.45 m, averaging 10.05 m (table 1). Five of the seven provenances remained at or near their earlier height growth ranking, while one (P2) advanced from fifth to second rank, and another (P3) dropped from second to fourth.

Between-provenance differences in this important growth trait were statistically significant at the 1 percent level. The range test shows that G3 grew significantly slower than the other provenances, which did not differ significantly from one another. Five randomly selected dominant red pines, which had been planted 2 years before the larches in the immediate vicinity, averaged 6.71 m, i.e. only 67 percent of the younger larches' height growth (fig. 2).

The 9-year versus 5-year height, and 9-year height versus 5-year shoot growth correlations were all statistically significant at the 1 percent level ($r = 0.936$ and 0.898, respectively, with 5 degrees of freedom).

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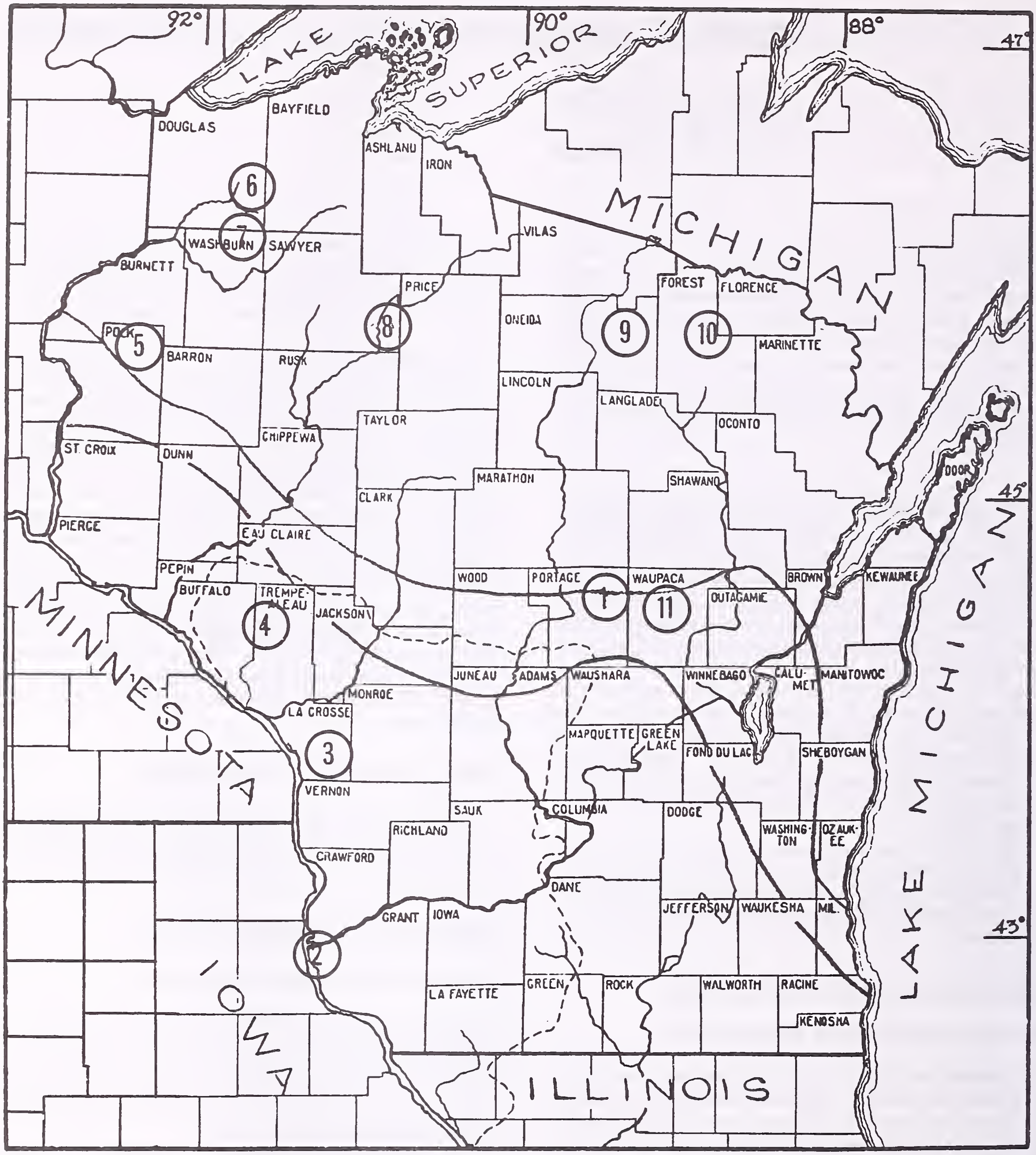

Figure 1—Location of major plantations of exotic larches in Wisconsin. The ribbon bisecting the state represents Curtis' tension zone.

Differences in diameters were also statistically significant among the seven seed sources, values ranging from 10.3 to 12.4, and averaging 11.5 cm (table 1). There appears enough room for further improvement on this growth trait through selection breeding.

As trees grow older and taller, height measurements become tedious, less reliable and more costly. If height growth can be reasonably predicted through diameter growth, greater efficiency in genetic measurement could be achieved. With the central Wisconsin test material, height-diameter correlations using data assessed in 1991 were nonsignificant (r = 0.65 with 5 degrees of freedom). Because height growth is not well correlated to diameter, each parameter should be assessed separately.

Table 1—Growth characteristics among seven larch seedlots in Central Wisconsin after five and nine field seasons.

Seedlot code	Source	Total height/cm 1986	Total height/cm 1991	Diameter/cm 1991
G1	Gahrenberg seed orchard	384	1,018	11.3
G2	Harbker	361	985	11.3
G3[1]	NW Deutsches Tiefland	321	942	10.3
P2	Skarzysko	381	1,028	11.9
P3	Lezajsk-Dabrowki	392	1,015	11.3
P4	Stary Sacz	381	1,006	12.4
P5	Bobolice	393	1,045	11.9
Plantation mean		373	1,005	11.48

[1] Japanese larch of unknown source introduced to Germany from Japan. Other seedlots are all European larch of German (G) and Polish (P) origin.

Because of greater sensitivity to frost, Japanese larch proved the least productive of the seven exotic larch seed sources tested in Portage County. It, nevertheless, outgrew neighboring 2-year-older red pine by 29 percent. Overall survival of all trees in this trial remained at 98 percent. In the sapling stage, minor damage by frost, grasshoppers, voles (*Microtus* sp.), and white-tailed deer (*Odocoileus virginianus*) occurred. In the winter of 1989-1990, extensive debudding of all materials by a flock of pine grosbeak (*Pinicola enucleator*) left conspicuous "windows" in the crowns of trees, but without discernible effects on subsequent growth. Defoliation by the larch sawfly (*Pristiphora erichsonii*) so far has been minor.

Figure 2—European and Japanese larch provenances outgrow two year older red pine on this Portage County site (1992).

Other Wisconsin Plantations

At least 10 other Wisconsin counties contain plantations of exotic larches (fig. 1). One of these trials in Forest County is part of a regional project on forest tree improvement, involving a twin plantation in Maine (Wyckoff and others 1992). The potential of larch as a long-rotation enrichment species in conjunction with various forest types, has apparently not been explored yet, just as timber stand improvement has barely received any attention to date.

The species employed, in decreasing order of emphasis, based on number of plantations and acreage, were European and Japanese larch, hybrids (*L. eurolepis*) between these two species, Siberian (*L. sibirica*) and Dahurian larch (*L. gmelini*). In one instance, Siberian larch had excellent survival but slow growth (Stoeckeler 1955); in another trial it ranked third in height among 37 seedlots of various species and provenances tested (Riemenschneider and Nienstaedt 1983). The single introduction of western larch (*L. occidentalis*), which took place as part of a study with needlecast disease (*Mycosphaerella laricina*), resulted in no survivals (Ostry and Nicholls 1989). The following remarks will focus on the two major species of exotic larch and their hybrids only, and attempt to explain often perplexing differences in performance.

European Larch—This most widely grown exotic larch in Wisconsin was apparently first established as part of a CCC planting on private land in La Crosse County in the early 1940's. Dominant trees in this plantation are now about 33 m tall and 60 cm in diameter (pers. comm. Adrian Hagen). Subsequent plantations (table 2) include everything from failure, to mixed performance between species, provenances and individuals on the same or neighboring sites, to unqualified successes. The most important factors limiting growth of European larch in Wisconsin were larch needlecast disease, late frost, unfavorable soil conditions, or poor planting stock.

Needlecast disease was first reported in a young plantation in La Crosse County in 1980 (Patton and Spear 1983), and has since been confirmed in other locations (table 2). While Alpine provenances of European larch tend to be highly susceptible to this disease, continental ones are considered resistant (Palmer and others 1986; Ostry and Nicholls 1989). *In vitro* screening of European larch for needlecast resistance is now recommended as a routine preliminary step to field screening (Ostry and others 1991). Other fungal problems observed in Wisconsin include *Meria laricis* needlecast, the larch needle rust (*Melampsora medusae*), and several woodrotters including *Armillaria* sp. None of these is of concern at this time.

Late frosts are clearly a complication in the culture of exotic larches in Wisconsin, at least during the juvenile stage, and in certain locations. All larch trials located in frost pockets and other sites with poor air drainage, especially north of Wisconsin's tension zone (fig. 1) (Curtis 1959), have experienced various degrees of damage by late frost.

The failure of European larch on swampy sites is clearly evident in several locations (table 2). On the other hand, European larch does not tolerate overly droughty conditions either. Almost all successful trials in Wisconsin took place on soils with intrinsically good water-holding capacity and nutritional status. However, south of the tension zone, larch may be subject to excessive evaporation during part of the year, especially on south to southwest slopes. But even in northern Wisconsin such as in Sawyer County, drought may have been an important contributor to plantation failure. During the establishment period of these plantations in the 1980's, a series of dry/hot summers prevailed, whose effect may have been further exacerbated by other stress factors and the site preparation procedure employed. Here, hardwood forests had been clearcut, then heavily bladed and windrowed, before planting into larch. Compaction and removal of much of the organic layer, almost certainly compromised healthy mycorrhizal relationships, known to be important for larch. It also invited an invasion of highly aggressive weeds such as goldenrod (*Solidago* spp.), typical for disturbed sites. Also, in several cases, stock was apparently outplanted after budbreak, resulting in serious losses.

Among pest insects, the larch casebearer (*Coleophora laricella*) and larch sawfly have to date been inconsequential in Wisconsin. In two instances, however, vertebrate pests did impact larch plantations tangibly. Once, meadow voles reduced sapling survival in a weedy plantation in La Crosse County to 29 percent (pers. comm. Adrian Hagen), while a 5-year-old very promising trial in Forest County suffered serious damage from porcupine (*Erethizon dorsatum*) (pers. comm. Dick Cutler).

Besides these various setbacks, there are notable successes in several plantations (table 2). Most of these were established on loamy soils, and on aspects other than south and southwesterly. Site preparation included furrowing and weeding, or scalping in conjunction with herbicide. Juvenile larch had been reported sensitive to herbicides (Knighton 1970), but at the rates and formulations tested by Netzer (1984), proved useful.

Most continental seed sources such as from Styria (Austria), Germany, and most notably Russia, Poland, and the Sudeten Mountains, were successful in Wisconsin. When growing on adjacent sites, European larch clearly outperformed native red pine not only in Portage County (fig. 2) but also in several other locations (table 2). In La Crosse County it also surpassed neighboring Norway spruce (*Picea excelsa*) and eastern white pine. When grown in mix with these, it eliminated the spruce, and suppressed the pine (Jacobs 1983). Based on its growth there, Gower and others (1991) consider European larch a viable candidate for the Driftless Area of Wisconsin. A minor spot market for larch poles for tobacco curing has already developed at this site since the early 1980's, apparently the only instance of marketing of exotic larches in the state to date. The lack of other demand at this time is probably only a reflection of the limited supply, and lack of awareness for the quality of larch wood. Jeffers and Isebrands (1974) recommended short rotation larch for pulp production, and according to Einspahr and others (1984), 18- to 23-year-old exotic larch can produce higher Kraft yield than 50- to 60-year-old jack pine.

Japanese Larch—Several trials of various provenances of Japanese larch were attempted in five Wisconsin counties. Among these, none exceeds the Portage County plantation in survival and growth. Three sources included in the Forest County regional trial, did not survive due to late frosts, while certain adjacent European sources performed

Table 2—Survey of major plantations of exotic larch in Wisconsin.

Map Code	Location	Species[1] provenances	Year planted	Rating[2]	Major problem(s)
1	Portage County				None
	T24NR9E, Sec. 22	EL Germany, 2 sources	1982	E	
		EL Poland, 4 sources	1982	E	
		JL Germany, source	1982	E	
2	Grant County				
	T6NR6W, Sec. 29	EL	1965	G	Needlecast
3	LaCrosse County				
	T16NR5W, Sec. 18 & 19	EL Styria	1961	E-G	Vole in one plot
	T16NR6W, Sec. 24		1962	E	
	T16NR5W, Sec. 30	EL Russia	1967	E	
	T16NR5W, Sec. 29 & 30		1971,1973		
	T16NR5W, Sec. 30		1976	E	
	T16NR5W, Sec. 19	EL	1978	F	Needlecast
	T16NR5W, Sec. 19	JL,HL XLL-LD9-81	1984	G	Dieback
	T16NR5W, Sec. 30	EL Russia	1985	E	
4	Trempealeau County				
	T23NR9W, Sec. 33	EL 1500 Boscobel	1968	G	Needlecast;
			1969	F	site too wet
5	Polk County				
	T37NR16W, Sec. 28	EL Sudeten(?)	1968	E	
	T37NR15W, Sec. 32	EL	1970	F	Needlecast; frost; wet
6	Douglas County				
	T45NR10W, Sec. 26	HL New York	1983	E	
		EL XLD-9-79	1983	G-F	Frost
7	Washburn County				
	T42NR11W, Sec. 4	EL Hayward	1973	F	Frost; deer browse; needlecast
8	Sawyer County				Drought? Site prep?
	T38NR3W, Sec. 23	EL + HL Hybrid	1981	G-F	Needlecast; wet
	T37NR3W, Sec. 6	EL Styria (LaCrosse)	1984	F	Frost; needlecast
	T38NR3W, Sec. 19	EL Commercial NY	1985	F	Frost
	T38NR3W, Sec. 25	EL Sudeten	1987	F	Frost
	T37NR3W, Sec. 2	EL Sudeten	1987	F	Frost
	T38NR3W, Sec. 26	Tatra	1988	G-F	Frost
9	Oneida County				
	T39NR10E, Sec. 31	HL (not Dunkeld)	1957	E-G	
		DL Asia	1958	E-G	
		EL Poland	1958	E-G	
		EL Austria	1958	E-G	
		JL	1958	G	
	T37NR10E, Sec. 32	JL 7 sources	1960	G-F	Sandy soil; frost
	T37NR7E, Sec. 20 & 21	EL,HL,JL,SL	1976	E-G	
	T36NR10E, Sec. 2	EL 3 Polish	1986	F	Frost; poor planting stock
10	Forest County				
	near Hiles	EL,SL	1950	?	?
	T38NR13E, Sec. 29	HL	1974	F	Site prep?
	T35NR16E, Sec. 24	EL,HL,JL,SL	1976	F	Porcupine; frost; deer
	T37NR14W, Sec. 26	EL Sudeten	1981	E-G	Frost
		JL 3 sources	1981	F	Frost
11	Waupaca County	EL,JL	1982	E	

[1] DL = *Larix gmelini*, EL = *Larix decidua*, HL = *Larix eurolepis*, JL = *Larix leptolepis*, SL = *Larix sibirica*,

[2] E = Excellent survival: growth surpassing native conifers; no major problems; G = Good survival and growth; some problems; F = Understocked stand with highly variable results or complete failure; major problems.

successfully. Another trial in Sawyer County had been abandoned early as a result of high mortality (Lester 1964). The most extensive trial with Japanese larch in Wisconsin, a replicated study including seven sources, was begun on a sandy site in Oneida County in 1960. This plantation generally grew well but exhibits substantial variability (Farnsworth and others 1972), and it lags behind adjacent red pine. In another Oneida plantation, Japanese larch ranked last in growth among 37 species and provenances (Riemenschneider and Nienstaedt 1983). Japanese larch is highly sensitive to frost, but is considered resistant to needlecast disease (Palmer and others 1986). However, a very promising young plantation in La Crosse County, including a few hybrid larch, was found to be affected by an undetermined dieback during this year's inspection.

Hybrid Larch—Trials including hybrid larches were established in five Wisconsin counties, including the northernmost site. In one trial in Forest County (Phipps and Noste 1976), first-year survival of these larch was 46 to 77 percent, probably due to unfavorable conditions resulting from site preparation which had removed much of the top layer of soil. In Douglas and Sawyer Counties, hybrids are among the few successful seed sources, outperforming adjacent European larch. This is most likely due to their rapid early growth which enables their early escape from the frost layer. In an Oneida County trial involving 37 sources of various species, hybrid larch ranked first and second in growth (Riemenschneider and Nienstaedt 1983). Zavitkovski and others (1982) and Zavitkovski and Strong (1984) confirmed the superior growth of these hybrids. Between 9 and 12 years the trees increased their height by an average of 1.3 m/year. Hybrids in Wisconsin have not experienced needlecast disease, and at least one source proved immune to larch needle rust under controlled conditions (Widin and Schipper 1978).

CONCLUSIONS

1. European and Japanese larches of Polish and German origin exhibit rapid juvenile growth and high survival in central Wisconsin, surpassing native red pine.
2. Generally, hybrid larch, and continental sources of European larch combine good growth with resistance to larch needlecast disease.
3. Atlantic sources (western and southern Alps) of European larch are generally not recommended for Wisconsin, and Japanese larch not for areas north of the tension zone.
4. Characteristics of a proper site include full light; well-drained, deep, loamy soils; and sloping topography facing east, north or northwest, excluding frost pockets.
5. Fall planting of container-grown stock tends to be successful in areas with reliable snow cover.
6. Spring planting tends to be most successful with large, branched seedlings prior to budbreak.
7. Site preparation should not excessively disturb the organic horizon, and must include control of competition.
8. For wider acceptance of exotic larches, markets need to be developed.
9. Experience with species other than European, Japanese, and hybrid larch is still too limited to allow conclusions.
10. Larches in Wisconsin deserve to not only be viewed as fast-growing species for plantation culture but also as silviculturally attractive, long rotation enrichment species in mix with various indigenous forest types.

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Management of Fungal Diseases of Western Larch Seed and Seedlings

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Abstract—Several fungal diseases adversely affect production of western larch in container and bareroot forest nurseries. Grey mold caused by *Botrytis cinerea* may cause widespread problems; chemical pesticide use should be limited. Seedling protection from the pathogen *Meria laricis* can be sought with fungicides. *Fusarium* and *Cylindrocarponn*, among other pathogenic fungi, cause damping-off, cotyledon blight, and root disease. Reducing pathogen inoculum, enhancing host resistance, encouraging competing and antagonistic organisms, and minimizing chemical pesticide use are included in an integrated pest management system.

Production of western larch (*Larix occidentalis* Nutt.) seedlings in Pacific Northwest, U.S.A., nurseries has been steadily increasing for several years in response to greater demand for larch seedlings to reforest many sites, particularly those with severe root diseases (Byler 1982). Production of stock in sufficient numbers and quality is an important goal of many nurseries. However, production may be restricted by limited quantities of high-quality seed and by diseases that affect amounts and quality of seedlings produced.

Western larch seedlings are grown as bareroot or container stock. Bareroot stock takes one to two growing seasons, whereas container stock can be grown in 6 to 8 months. Both stock types are usually satisfactory for most reforestation requirements, and both may become diseased during nursery production.

Organisms normally incapable of causing problems on natural forest sites may cause extensive damage in nurseries because of inherent differences between these two environments. Production conditions that might incite organisms toward disease include large areas of monoculture, agricultural production practices, and greenhouse environments. Natural buffers that limit pathogen buildup in forest ecosystems are often absent in more artificial growing environments of nurseries. Also, many pathogens that affect nursery seedlings do not affect young trees in forest areas because the pathogens are unique to nurseries.

Although many pathogens are capable of infecting western larch seedlings in nurseries, relatively few cause severe enough damage to warrant concern or corrective action. This paper focuses on three major groups of diseases—two that cause foliar or top necrosis and one that affects root systems. Approaches to managing these diseases vary. Most nursery growers use an integrated approach to disease control, using cultural, biological, and chemical alternatives. Integrated pest management involves establishing threshold levels of disease, monitoring pest populations before and after treatments, using efficaceous treatments to keep disease levels within established thresholds, and keeping adequate records for all pest management activities.

BOTRYTIS BLIGHT

Grey mold caused by *Botrytis cinerea* (Fr.) Pers. is a major disease of western larch seedlings, particularly those grown within containers in greenhouses (James 1984). The fungus may cause some damage in bareroot beds, particularly when seedlings are overcrowded. Presence of free moisture on foliage for several hours and prolonged cool temperatures of about 13 to 14 °C determine the severity of the infection (Blakeman 1980). Wounded or necrotic tissues are initially infected. The fungus may spread to healthy tissues under conducive environmental conditions (Sutherland and Van Eerden 1980).

Larch's extensive production of necrotic foliage at the end of the growing season greatly contributes to its disease susceptibility. Many primary needles formed on young seedlings are lost as seedling growth ceases; these needles tend to accumulate at the base of seedlings and are easily infected by *Botrytis* spores, which are usually airborne (Jarvis 1980). Once colonization of necrotic needles occurs, the fungus spreads to adjacent seedling stems, causing infection and often killing individual seedlings. Over time, groups of seedlings become infected, and the fungus produces vast amounts of spores that spread to nearby seedlings, continuing the cycle (James 1984).

Management approaches to *Botrytis* blight stress prevention because of the difficulty in keeping disease in

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check once it becomes established (Maude 1980). The best control approach is to avoid environmental conditions suited for disease buildup (James 1984). This includes reducing seedling density to improve air circulation (Cooley 1981a) and limiting irrigation during periods of high host susceptibility. Adding drying agents to irrigation water may also help reduce infection (James 1984).

Control of fertilization will also influence level of disease; excess or improperly applied fertilizer may cause foliage to burn, providing infection courts for the pathogen; and too little fertilizer may stress seedlings, making them more susceptible to infection (Sutherland and Van Eerden 1980).

Another important cultural practice is sanitation, aimed primarily at reducing inoculum. Sanitation practices include periodic removal of dead or infected plants and plant debris and cleaning interior greenhouse spaces with a sterilant between seedling crops (Cooley 1981a). A recent innovative approach to sanitation that shows promise in reducing disease impact is removal of necrotic foliage from the tops of containers with a vacuum (Dumroese and others 1992). Although this approach is somewhat labor-intensive, it works well and is cost-effective when compared with chemical pesticide applications.

Many nursery growers traditionally control *Botrytis* blight with preventive applications of chemical fungicides during periods when seedlings are susceptible to infection. This often results in many applications of several different chemicals. In some cases, fungicide applications have been effective; in others, the level of effectiveness decreases with continued application (James 1984). Investigations have shown *Botrytis* can readily develop resistance to chemical fungicides, especially if one particular chemical is reused several times (Cooley 1981a; Gillman and James 1980; Miller and Fletcher 1974; Webster and others 1970).

Most growers have reduced chances of developing resistance by alternating several chemicals during pesticide application (Powell 1982). This makes the fungus less likely to develop resistance. For example, some growers alternate chlorothalonil with captan, dicloran, and systemic fungicides such as vinclozolin and iprodione to adequately control disease (James 1984).

Benomyl, a systemic fungicide with wide-ranging efficacy, was initially effective against *Botrytis* blight. However, after use for only a couple of crop cycles, this fungicide often became much less effective (Bollen and Scholten 1971). The chemical was ineffective against most strains of the pathogen (Cooley 1981a; Gillman and James 1980). Fungal strains that developed benomyl resistance retained this resistance indefinitely, even in the absence of the chemical (Maude 1980). Such experiences have resulted in less reliance by many growers on chemical fungicides to control *Botrytis* blight.

Management has become more focused on prevention, sanitation, and possible introduction of biological control agents. This latter approach is only in the formative stage with regard to *Botrytis* blight. However, recent successes with other crops (Tronsmo 1991) have encouraged this approach on conifer seedlings. Environmental contamination as well as concerns over human exposure to pesticides will reduce the future use of chemicals in nurseries. Fortunately, effective alternatives to chemicals are available. Many growers are determined to replace chemicals with other, more environmentally benign alternatives.

MERIA NEEDLECAST

Needlecast caused by *Meria laricis* Vuill. is a common disease that occurs in many natural stands of western larch (Dubreuil 1982). This disease can also occur in forest nurseries and is most often detected on bareroot seedlings during their second growing season (Cooley 1981b, 1984; James 1985b). *Meria* has been detected much less frequently on container-grown stock and on bareroot seedlings in their first growing season (James 1985b). The pathogen infects young, succulent needles early in spring. Spores are disseminated throughout periods of cool, wet weather, and several cycles may occur during the growing season (Dubreuil 1982). When environmental conditions are favorable, pathogen buildup may be rapid. Although needles are initially attacked, stems may be colonized and, under extreme conditions, entire seedlings killed (James 1985b). However, once warm, dry weather occurs, disease severity diminishes. If wet weather persists, the disease may cause extensive damage in bareroot beds despite control efforts (James 1985b).

Meria needlecast is most effectively managed by application of protective fungicides during periods of high seedling susceptibility (Cooley 1981b, 1984). Most growers have traditionally applied chlorothalonil (or similar foliar protectant fungicides), commencing in early spring when needles are forming (James 1991). Fungicide applications are geared toward preventing infection; therefore, several applications are usually required while young foliage is susceptible to infection and cool, wet weather persists (Cooley 1981b). Fungicide applications may be terminated once warm, dry weather occurs.

Unfortunately, fungicides may be only marginally effective if favorable environmental conditions for disease development persist throughout much of the growing season (James 1985b). Other, nonchemical approaches to control are currently unavailable. Because pathogen spores are airborne and can be disseminated long distances (Dubreuil 1982), preventing inoculum introductions into the nursery is usually impossible. Once the disease occurs within a particular nursery, it seems to persist indefinitely (James 1991). The disease has less impact in greenhouses because environmental conditions can be more easily controlled. However, in bareroot nurseries, growers are at the mercy of ambient conditions. When conducive conditions persist for extended periods during spring, some level of disease usually occurs in second-year bareroot seedlings. The management goal is to keep losses within tolerable limits until weather conditions no longer favor disease.

ROOT DISEASES

Root diseases affect both bareroot and container-grown seedlings. Probably the most important group of root pathogens are in the genus *Fusarium* (James and others 1991). These fungi damage a wide range of host plants including many agriculturally important crops. Conifer seedlings, including western larch, are susceptible to several different *Fusarium* species, the most common being *F. oxysporum* Schlecht., *F. proliferatum* (Matsushima) Nirenberg, *F. acuminatum* Ell. & Ev., *F. sporotrichioides* Sherb., and *F. solani* (Mart.) Appel & Wollenw. (James and others 1991). These fungi attack young seedlings, causing preemergence and postemergence damping-off (James 1986a, 1987). They also cause root disease of older seedlings throughout the growth cycle (James and others 1991). Damage may be especially severe on older container-grown seedlings stressed to induce hardening and bud set (James and Gilligan 1985; James and others 1987).

Other major root pathogens of western larch seedlings include species of *Cylindrocarpon* and *Pythium*. *Cylindrocarpon* spp. are common rhizosphere inhabitants that often colonize cortical tissues on seedling roots (Booth 1966). They may become pathogenic under certain conditions, although they are not usually aggressive pathogens. *Pythium* spp. are especially damaging under conditions of poor soil drainage and may initiate disease by decaying fine roots (Hendrix and Campbell 1973). Normally, *Pythium* damage is limited to bareroot beds with poor drainage where water accumulates. Damage to container-grown seedlings is rare and may be associated with overwatering and using poorly aerated growing media (James 1992).

Root diseases are especially difficult to control because once seedling symptoms appear, their roots are usually extensively colonized with pathogenic fungi (James and others 1987). Chemical fungicide applications may be effective in controlling damping-off but ineffective in limiting root disease of older seedlings (James 1986b). Recent approaches to controlling root diseases have focused on prevention and using integrated pest management to reduce losses (James and others 1990).

Integrated pest management of western larch root diseases aims to reduce pathogen inoculum, enhance host resistance, encourage competing and anagonistic microorganisms, and minimize chemical fungicides.

Reduction of Pathogen Inoculum

To reduce root pathogen infection levels, it is important to limit pathogen inoculum within and adjacent to seedling growing environments. Seed is often an important inoculum source of root pathogens, particularly *Fusarium* spp. (James 1986a; 1987). Steps taken to reduce pathogen inoculum introduced into nurseries on seed are important. Soaking seed in common surface sterilants such as household bleach (active ingredient = sodium hypochlorite) and hydrogen peroxide are usually effective in reducing levels of pathogenic fungi (Advincula and others 1983; Barnett 1976; James and Genz 1981). Application of common fungicides to seed has limited utility because they may retard seed germination and young seedling growth (Dick and others 1958; Lock and others 1975; Peterson 1970). One of the most effective and least toxic treatments is tap water, either heated or applied over seed as a running water rinse (Dumroese and others 1988).

Seedling containers accumulate inoculum of root pathogenic fungi when repeatedly reused without adequate cleaning (James and Gilligan 1988a,b; Sturrock and Dennis 1988). Contaminated styroblock and Ray Leach® pine cells are important inoculum sources for new seedling crops (James and Gilligan 1988a,b). Most fungal inoculum resides near the container bottoms, probably existing on remaining organic debris such as pieces of growing media, roots, and algal growth inadequately removed during cleaning (James and others 1988). Recent investigations (James and Woollen 1989; Sturrock and Dennis 1988) have shown effective elimination of most pathogen inoculum on containers immersed in hot water (68 to 80 °C) for 3 to10 min. A soluble spreader such as R-11® or household detergent is often added to water to ensure that all container surfaces come into contact with hot water. Chemical sterilants such as sodium metabisulfite may also be used, although they have the disadvantage of being extremely caustic and somewhat dangerous (Sturrock and Dennis 1988). Hot water immersion of containers before reuse is the most satisfactory method.

Root pathogenic fungi may reside in nursery soil or growing media used to produce container seedlings. Nursery soil is often treated with broad-scale fumigants that kill all resident microorganisms, including pathogens (James 1989). Although expensive and dangerous to apply, these fumigants are effective in eliminating pathogens. However, the "biological vacuum" produced after fumigation may be invaded by the first introduced organisms. Care must be taken to ensure that pathogens are discouraged from introduction into newly fumigated soil. Soilless growing media used in container operations are pathogen-free, with some exceptions (James 1985a). The highly acidic nature of most growing media also discourages establishment by many pathogens. Media can be steam treated to eliminate potential pathogens while preserving desirable competing organisms (Baker and Olson 1959).

Keeping the growing environment clean is important in reducing problems from root pathogenic fungi. Many such fungi produce resting structures capable of surviving for long periods in the absence of suitable hosts (James and others 1987). Greenhouse interiors and the surface of implements used in bareroot seedling production may harbor these structures. Thoroughly cleaning these materials should reduce amounts of this inoculum introduced into new seedling crops.

Irrigation water may be an inoculum source for some root pathogens, particularly water molds such as *Pythium*. Nursery water from ponds, ditches, or streams may become contaminated with pathogens; deep wells are usually not contaminated (Landis and others 1989). Adequate filters or chemical treatment may be necessary to remove contaminants from water supplies.

Periodic inspections and sanitation procedures will go a long way in reducing pathogen inoculum in nurseries (James and others 1990). This is especially important in greenhouses where disease can spread and develop rapidly. Removal of diseased seedlings to prevent spread to surrounding, healthy seedlings is encouraged (Landis and others 1990). Sanitation coupled with the other procedures described above can be used to reduce pathogen inoculum and subsequent root disease.

Enhance Host Resistance

Some level of resistance to root pathogens undoubtedly exists in western larch populations. However, when a large number of seedlings are produced, often from a limited range of seed sources, little resistance occurs in nurseries. Many seedlings become infected with fungi capable of inducing disease. However, not all infected seedlings manifest disease symptoms (James and others 1990). Several factors probably influence the level of disease expression by infected seedlings. These might include seedling moisture stress, ambient and greenhouse temperatures, and nutrient levels within soil or growing media (Bloomberg 1985; Tint 1945a,b).

If infected seedlings are stressed for prolonged periods, they will probably become diseased. Temperature may be important in disease expression because most pathogenic *Fusarium* spp. are considered "warm weather" fungi, that is, they grow more rapidly and are more pathogenic when temperatures are high (Bloomberg 1976; Tint 1945b). Root disease in bareroot stock often occurs when ambient temperatures exceed certain thresholds in midsummer (Bloomberg 1976). In greenhouses, temperatures can be regulated during the growing season so that excessively high temperatures may be avoided.

Research on conifer root diseases has emphasized the importance of regulating nutrient applications during periods when young germinants are susceptible to damping-off fungi (Bloomberg 1976; Rathbun-Gravatt 1925; Tint 1945a). Adding nutrients (especially nitrogen) during seedling emergence but before stem lignification enhances damping-off losses by making seedlings more succulent. Added nutrients may also promote growth of pathogenic fungi (Landis and others 1989). Therefore, it is important to regulate fertilizer during the critical stage of seedling establishment and promote rapid lignification of germinant stems.

Encourage Competing and Antagonistic Organisms

To colonize, soil microorganisms usually compete with one another for nutrients, water, space, and organic matter. *Fusarium* spp. often occupy similar colonization niches of some other organisms (James and others 1990). If these niches are colonized by nonpathogens, exclusion of pathogenic *Fusarium* spp. may occur. Many soil microorganisms also produce antibiotics that may give them competitive advantages (Baker and Cook 1974; Papavizas 1985). Antagonism and competition are important in the balance of organisms colonizing organic substrates in soil (James and others 1990). If specific microorganisms that display both competitive and antagonistic properties can be introduced into nursery systems, it is possible to exert biological control on pathogenic organisms such as *Fusarium* spp. (Baker and Cook 1974).

Organisms having potential as biological control agents include bacteria in the genus *Pseudomonas*, actinomycetes in the genus *Streptomyces*, and fungi in the genera *Trichoderma* and *Gliocladium* (Baker and Cook 1974; Papavizas 1985). Several strains of these microorganisms successfully compete with, are antagonistic toward, or parasitize plant pathogenic fungi (James and others 1990). Special strains of *Trichoderma* have recently undergone genetic engineering to enhance their effectiveness as biological control agents (Stasz and others 1988). When introduced on seed or within the growing medium, these strains rapidly colonize the rhizosphere and may preclude host invasion by plant pathogens (Harman and Taylor 1988; Harman and others 1989). These biocontrol agents are yet to be tested on western larch seedlings to control *Fusarium* spp.

Inoculation of nursery seedlings with nonpathogenic strains of *F. oxysporum* offers another possibility for control (James and others 1990). These nonpathogens would occupy substrates to exclude pathogenic strains of the fungus. Saprophytic strains are well adapted to seedling root colonization and could exclude pathogen invasion. Such "cross protection" has been effective in several agricultural systems (Davis 1967). Pathogenicity tests of *Fusarium* spp. isolated from larch seedlings have yielded several nonpathogenic strains. However, these strains have yet to be tested for their ability to protect seedlings from pathogenic strains.

Ectomycorrhizal fungi may be antagonistic toward some plant pathogenic fungi (Marx 1972; Sinclair and others 1975). Ectomycorrhizal symbionts usually colonize fine root tips and provide a physical barrier to pathogen colonization (Marx 1972). These symbionts may also produce antibiotics that restrict development of some pathogens (Marx 1972; Stack and Sinclair 1975). Encouraging natural infection of nursery seedlings or introducing mycorrhizal inoculation into growing regimes may lessen the impact of root diseases (James and others 1990).

Minimize Chemical Fungicides

Many growers have attempted to control root diseases by using chemical fungicides once disease symptoms are apparent. Such an approach has been largely unsuccessful because once disease symptoms appear, seedling roots are usually compeletely colonized with pathogenic fungi (James and others 1987, 1990). Most fungicides are more effective in preventing infection rather than curing infected seedlings (Delp 1980). Therefore, it is easy to see why they have limited efficacy when applied after disease appears.

Another potential problem from fungicide usage is development of resistance to specific chemicals by pathogenic fungi (Dekker 1976; Delp 1980). Resistance has been demonstrated for several plant pathogenic fungi, especially those subjected to consistently high doses of a specific fungicide (James and others 1990). By minimizing exposure of pathogenic fungi to chemical fungicides, selection pressures for fungi to develop resistance are reduced.

Because experience has shown that much pesticide use is unnecessary and does not really reduce disease (Dumroese and others 1990), an integrated pest management program for root disease of western larch seedlings should discourage indiscriminate fungicide use. Fungicides should be used only for specific purposes, such as reducing levels of damping-off early in the crop cycle. Limiting fungicide use reduces cost of seedling production and problems with worker exposure to potentially toxic chemicals as well as potential environmental contamination.

CONCLUSIONS

Diseases affecting western larch seedlings in forest nurseries are best controlled by using principles of integrated pest management that minimize use of chemical pesticides. However, in some instances chemicals will be necessary to maintain disease losses within acceptable limits. This is especially true for *Meria* needle cast and sometimes for *Botrytis* blight.

Future emphasis on pest management in nurseries should focus on alternatives to chemicals whenever possible. This will result in greater emphasis on biological control. We have limited technology for biological control in forest tree nurseries. Few organisms are available for testing, and those that have thus far been tested have yielded disappointing results (James and others 1992).

We need development of more specific biological control agents for conifer seedlings that may be efficacious at particular sites. Satisfactory progress in this field will require increased commitment of resources for research of diseases and their control in forest tree nurseries. If such a commitment is made, the future should be bright for integrated pest management in nurseries.

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Effects of Thinning on Growth and Vigor of *Larix occidentalis* Infected With *Arceuthobium laricis* in Oregon

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Abstract—With increasing severity of dwarf mistletoe (*Arceuthobium laricis*) infection in western larch (*Larix occidentalis*), tree volume growth, and vigor (as estimated by cambial electrical resistance) decreased significantly. Growth and vigor of individual trees, however, was improved by commercial thinning, even if trees had light to moderate amounts of dwarf mistletoe. Method of thinning (above or below) greatly affected the results. Thinning from above led to increased mortality in infected trees from snow and ice damage.

Western larch (*Larix ocidentalis*) is an important tree species in central and eastern Oregon and Washington. Western larch is often retained in partial harvest units for seed trees or shelterwood. It is a valuable timber and wildife species and has obvious esthetic qualities. Western larch is resistant to many insect pests and diseases such as root diseases and therefore is valuable as a residual tree to increase the species as a component of the stand and for natural regeneration in root-diseased areas. However, dwarf mistletoe (*Arceuthobium laricis*) is responsible for most of the mortality of western larch either directly through parasitism or indirectly through stem breakage.

Dwarf mistletoe is a higher seed plant that parasitizes branches of western larch. This parasite infects 47 percent of the western larch type in Oregon and Washington (Bolsinger 1978) and 38 percent in Montana and Idaho (Drummond 1982). Larch normally has full-length branches, but mistletoe-infected branches form witches'-brooms that load up with snow and ice, leading to branch breakage and trunks that resemble telephone poles (Filip and others 1989). Often only adventitious branches remain.

Seidel (1986) showed that 55-year-old larch thinned from above (removal of dominants and codominants) or below (removal of suppressed, intermediates, and smaller codominants) increased in basal area and volume growth with increased stand density after 15 years. How larch, in relation to the absence or presence of dwarf mistletoe, responds to thinning has not been examined.

The objectives of our study were to examine 16 previously thinned larch plots and compare (1) volume growth in trees with increasing levels of dwarf mistletoe and (2) tree vigor as estimated by cambial electrical resistance in trees with increasing levels of dwarf mistletoe.

METHODS

Our research area was in northeastern Oregon, 6 miles northwest of Elgin at 3,000 feet elevation, with a site index of 80 feet at age 50 as reported previously (Filip and others 1989). The stand had been thinned at age 55 and 65 (Seidel 1975, 1986). Eight treatments were replicated twice in 16 plots of 0.3 acre each. Severity of dwarf mistletoe was recorded in 1986 using a six-class system (DMR) where 0 = no infection and 6 = the most severe infection (Hawksworth 1977).

Tree vigor was estimated by cambial electrical resistance (CER) as measured with a Shigometer Model OZ-67. Proportional cubic volume growth—[(1984 volume minus 1970 volume)/1970 volume] x 100—per tree was used rather than actual volume growth because of the wide range in initial tree sizes: 2.1 to 22.1 inches diameter at breast height. Frequency of tree mortality, CER, and volume growth were subjected to analysis of variance (SAS Institute 1987) to detect significant differences and interactions among dwarf mistletoe severity, thinning density, and thinning method.

RESULTS AND DISCUSSION

Of 737 sampled living and dead trees, 46 percent were either severely infected with dwarf mistletoe (DMR 5 or 6) or were dead or broken as a result of dwarf mistletoe brooms and snow loading (fig. 1). There was more severe dwarf mistletoe and associated stem breakage in plots thinned from above. Dwarf mistletoe seeds spread readily from dominant and codominant trees to intermediate and suppressed trees. Therefore, removal of infected dominants and codominants tends to leave severely infected residuals in the understory. These small, infected trees often cannot withstand wind, snow, and ice after the protection afforded by the larger trees is removed.

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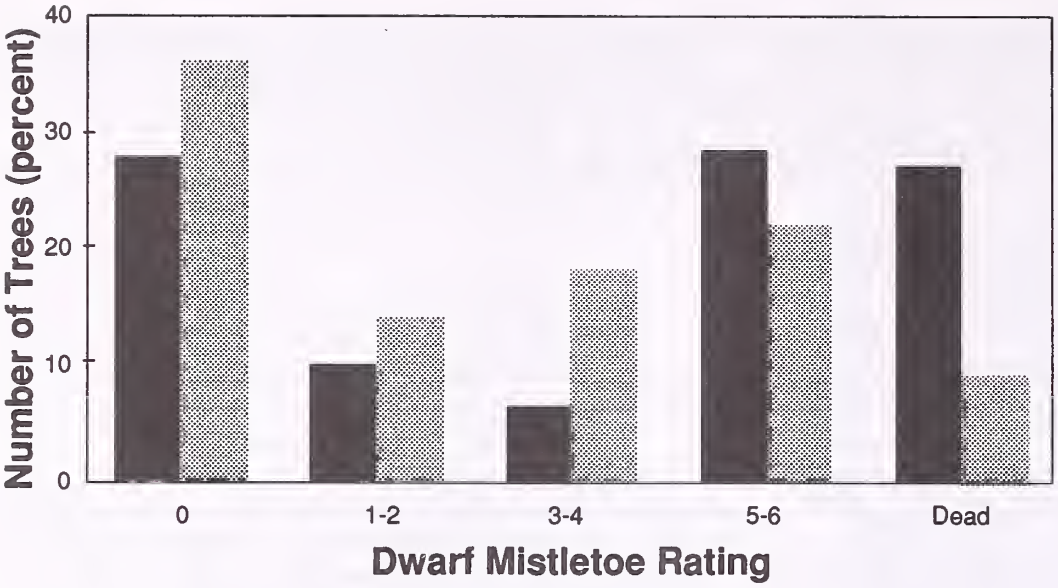

Figure 1—Percentage of western larch trees by dwarf mistletoe rating (0 = none, 5-6 = severe infection) in 16 plots of 0.3 acre each, thinned from above (black) or below (gray).

Tree volume growth and vigor decreased significantly ($P \leq 0.05$) with increasing severity of dwarf mistletoe infection in western larch (figs. 2 and 3). Growth of individual trees, however, was improved by thinning, even if trees had some dwarf mistletoe infections.

We recommend that larch stands of mean diameter at breast height 9 to 15 inches be thinned to basal area levels of about 90 ft^2 per acre to increase growth and vigor of uninfected or lightly infected trees (DMR = 0 to 2). This corresponds to the minimum stocking level curves for larch as proposed by Cochran (1985). Severely infected trees (DMR 5 or 6) should be removed because (1) thinning will not improve their growth or vigor, (2) they are the chief sources of infection in the stand, (3) they will probably die or be severely damaged before the next scheduled stand entry. Moderately infected trees (DMR 3 or 4) also should be removed during commercial thinning, if adequate stocking can be maintained. Moderate infections may intensify to severe infections by the time the stand is harvested, especially if the time between thinning and harvest exceeds 20 years. Previously unmanaged larch stands should be thinned from below rather than above, as this results in less residual tree mortality from snow and ice breakage.

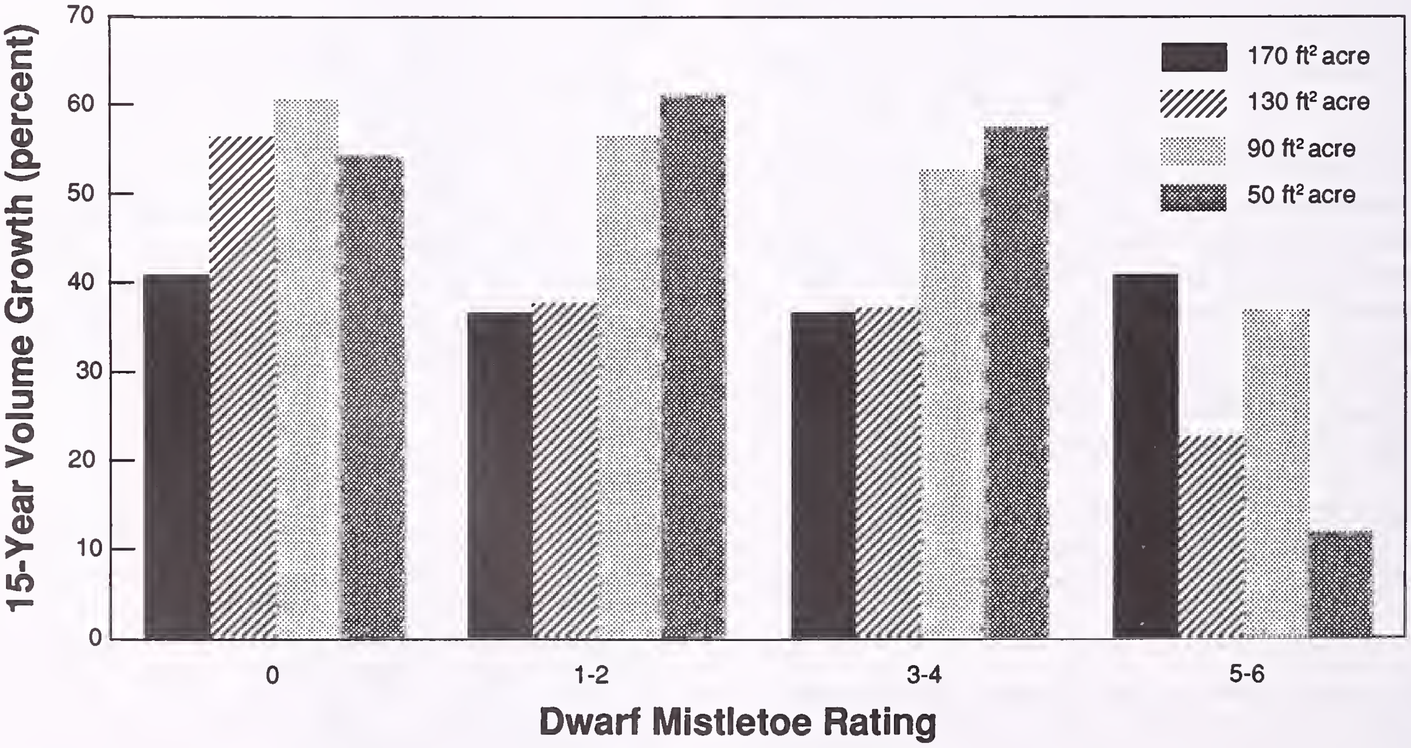

Figure 2—Percentage of proportional cubic volume growth in western larch trees after 15 years by dwarf mistletoe rating (0 = none, 5-6 = severe infection) in 16 plots of 0.3 acre each, thinned to four levels of residual basal area.

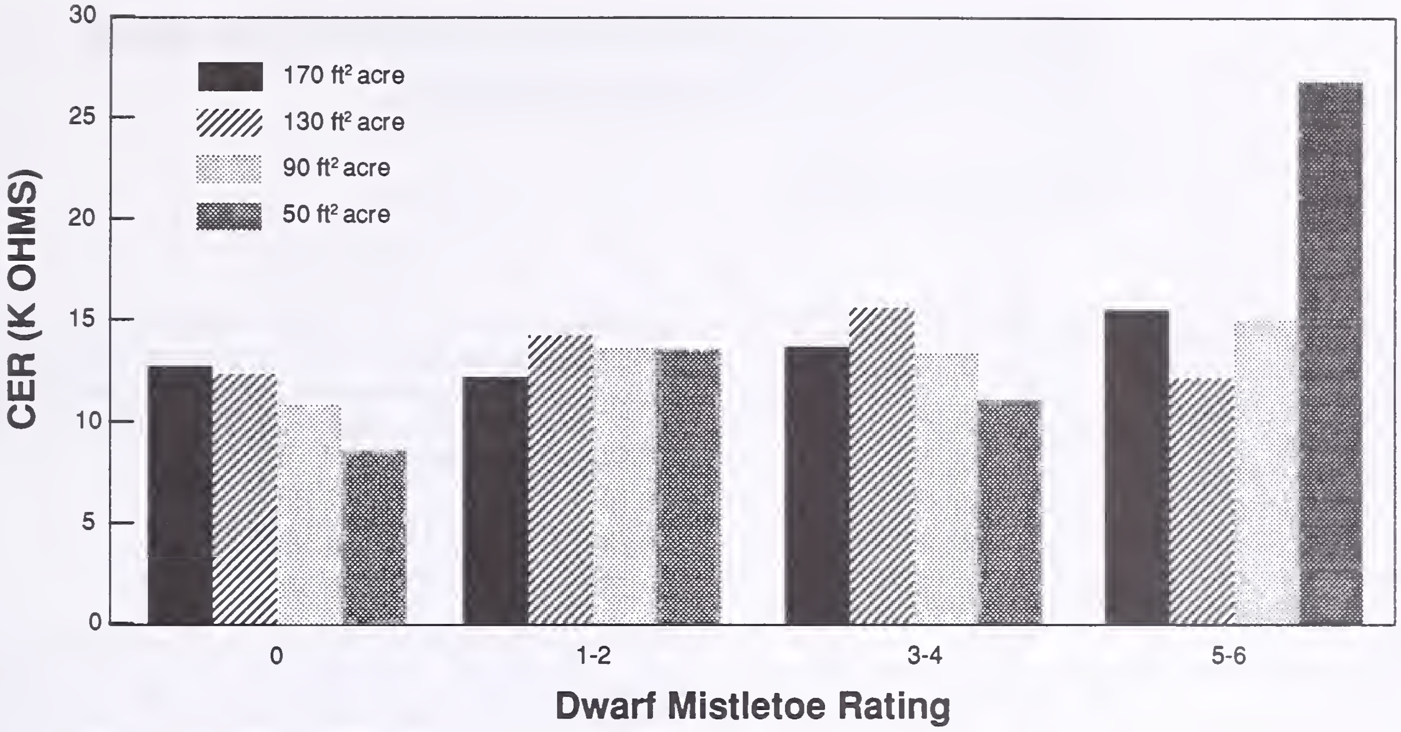

Figure 3—Tree vigor as estimated by cambial electrical resistance (CER) in western larch trees by dwarf mistletoe rating (0 = none, 5-6 = severe infection) in 16 plots of 0.3 acre each, thinned to four levels of residual basal area. High CER means low tree vigor.

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Western Larch Dwarf Mistletoe and Ecosystem Management

Jane E. Taylor

Abstract—Managers have traditionally emphasized dwarf mistletoe impacts on timber production and have viewed the parasitic plant as a pest that must be suppressed. In the ecosystem management context, larch dwarf mistletoe should be valued as an individual biological species and recognized as a functional component of western larch forest ecosystems. Dwarf mistletoe reduction may be warranted in stands where management goals emphasize timber production. In areas where management is not focused on timber, however, dwarf mistletoe control may not be desirable.

Larch dwarf mistletoe (*Arceuthobium laricis* (Piper) St. John) occurs generally throughout the range of western larch (*Larix occidentalis* Nutt.) in the Northwestern United States. Larch dwarf mistletoe infects approximately 35 percent of the western larch type in western Montana and northern Idaho (Drummond 1982; Dooling and Eder 1981) and 47 percent of the type east of the Cascades in Washington and Oregon (Bolsinger 1978). Dwarf mistletoes are parasitic plants that extract water and nutrients from living host trees causing decreased height and diameter growth, reduction in cone and seed crops, and direct mortality or predisposition to other pathogens and insects (Filip and Schmitt 1990).

Larch dwarf mistletoe is a native component of western larch forest systems, having co-evolved with its host for millions of years (Hawksworth and Wiens 1972). Because larch dwarf mistletoe only grows and reproduces on living trees, ecological forces that have patterned the development of western larch have also played important roles in influencing the ecology and biology of the dwarf mistletoe. Fire is one of these influential ecological forces. In general, any fire event that kills western larch trees also will reduce the population of larch dwarf mistletoe, at least in the short term. In many fire scenarios, older western larch individuals often escape death due to their high level of fire resistance (Barrett and others 1991). These individuals not only provide a seed source for the regeneration of western larch on the site, but if they are infected with dwarf mistletoe, an ideal situation is created for the perpetuation of the parasite as well. The dwarf mistletoe population is reduced immediately following the burn, but as the new larch regeneration develops, dwarf mistletoe seeds cast down from the overstory infect the new understory and the dwarf mistletoe population continues to increase throughout the stand until the next disturbance event. The greater the fire intensity and the larger the burn patch size, the greater the reduction in the dwarf mistletoe population.

TIMBER MANAGEMENT IMPLICATIONS

Although larch dwarf mistletoe is a native component of the western larch forest system, the significant effects that this parasite has on tree growth and survival are important issues when these systems are managed for resource production, especially the timber resource. Traditionally, dwarf mistletoe management has emphasized the reduction of the parasite to lessen the impact on timber growth and yield. Because it is an obligate parasite, dwarf mistletoe can be effectively reduced through the use of silvicultural treatments that emphasize the removal of infected trees. The most efficient treatments for dwarf mistletoe management are the even-age silvicultural systems such as clearcutting (20 acres or larger achieve best results) and seed tree or shelterwood operations using non-infected residuals or removal of all infected residuals before the newly developing understory reaches 10 years old or 3 feet tall.

Growth and yield simulation models have been developed which can be used in the planning of silvicultural decisions. One of the most widely used of such models throughout the USDA Forest Service in the Western United States is the Stand Prognosis Model (Stage 1973; Wykoff and others 1982). In recent years, a dwarf mistletoe impact model has been developed which links directly to Prognosis and allows the user to estimate dwarf mistletoe effects on yield in stands under different silvicultural treatments (Hawksworth and others 1992). An analysis of the effects of silvicultural treatments on the estimated volume reduction from dwarf mistletoe in infected western larch (using the northern Idaho variant of Prognosis) is presented in table 1. For the comparison, certain conditions were assumed: 120-year rotation, regenerated stand is 90-100 percent western larch, cutting unit edge contains infected larch residuals, leave-patches and reserve trees are infected, and no intermediate entries or sanitation treatments occur during the rotation. These simulations show that the impacts of dwarf mistletoe on merchantable cubic foot volume increase as the size of the cutting unit decreases and if infected residuals are left standing throughout the rotation. If cutting units are at least 20 acres in size and residual trees are removed before the regeneration is 10 years old, growth losses may be reduced to as little as 5 to 10 percent when compared to volume produced in a non-infected stand under similar conditions.

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Table 1—Effects analysis of silvicultural treatments on estimated stand volume yields in dwarf mistletoe-infected western larch. Analysis was done using the northern Idaho variant of the Stand Prognosis Model with a stand rotation of 120 years

Treatment	Percent of noninfected stand (MerCuFt)
2-acre group selection	60-65
5-acre clearcut	75-80
20-acre clearcut	90-95
40-acre clearcut	90-95
20-acre clearcut with reserves (3, 1-acre leave patches)	75-80
20-acre clearcut with reserves (3, 3-acre leave patches)	70-75
100-acre clearcut with reserves (15, 3-acre leave patches)	80-85
20-acre irregular shelterwood (16 trees/acre reserves left for rotation)	55-60
20-acre irregular shelterwood (30 trees/acre reserves left for rotation)	50-55
20-acre irregular shelterwood (16 trees/acre reserves, removed @ 20 years)	90-95

ECOSYSTEM MANAGEMENT

The USDA Forest Service has committed to implementing an ecosystem approach to land management. This approach involves the incorporation of forest management practices within a sound ecological framework that puts an emphasis on sustainability and places the production of values in an ecosystem context. The ecological approach considers the associations between ecosystems at various scales and focuses on the vital ecosystem elements of composition, structure, and function.

One of the important concepts in ecosystem management is that systems are dynamic and that all components and functions occur within natural ranges of variability at both the temporal and spatial scales. Components such as insects, pathogens, and fire have common or average ranges with occasional outbreak periods which, although are outside of the common range, are still within the natural range of variability. When components of forest ecosystems become imbalanced the health, integrity, and sustainability of the system may be threatened.

Dr. Sue Hagle (1992), Plant Pathologist, USDA Forest Service, defines forest health in an ecosystem management context: "Forest health is a condition typified by disturbance factors occurring within the natural range of amplitudes and periodicities. These functions provide for a natural rate of nutrient and energy flows within forest ecosystems. A healthy forest is a condition in which insects, pathogens, fire, and other agents function within limits set by the variability of natural ecosystems."

How do we approach dwarf mistletoe management in a manner consistent with the concepts of ecosystem management? Traditionally we have emphasized dwarf mistletoe impacts on timber growth and yield and viewed the parasitic plant as a pest that must be suppressed. Dwarf mistletoe management should no longer focus only on timber resource objectives and commodity production, but should also recognize the value of dwarf mistletoes as functional components of forest ecosystems in which they occur. Dwarf mistletoes have value as an individual biological species and can act as disturbance factors, influencing both structure and function of their forest communities (Bennetts and Hawksworth 1991; Tinnin 1984). For example, larch dwarf mistletoe may actually influence fire behavior in some situations. Small, dense witches' brooms develop on western larch as the result of dwarf mistletoe infection. The wood in these brooms is brittle and the broomed branches tend to break easily and fall from the tree. In heavily infected trees, most of the original crown is often removed and the dead brooms accumulate under the infected trees. During a fire, this accumulation of fuels around the base of the tree may increase the probability that the tree will be killed, but the sparse crown reduces the likelihood of a crown fire (Wicker and Leaphart 1976).

We do not have much information about benefits to wildlife specifically for larch dwarf mistletoe, but there is evidence regarding biological interactions associated with other *Arceuthobium* species and dwarf mistletoes in general. Bird species including black-capped chickadees, sparrows, ruffed grouse and blue grouse are reported to eat dwarf mistletoe seeds (Hawksworth 1975) and red squirrels and porcupines preferentially eat the bark associated with dwarf mistletoe infections (Baranay 1968; Kujit 1955). Dwarf mistletoe shoots can be an important winter food source for many animals including porcupines (Pierce 1960), mule deer (Urness 1969), Abert's squirrels (Hall 1981), and blue grouse (Severson 1986). Several species of insect are also reported to feed on various parts of dwarf mistletoe plants (Stevens and Hawksworth 1984). Trees killed by dwarf mistletoe are utilized by cavity-nesting birds, and witches' brooms provide cover and nesting sites for many different birds and small mammals (Bennetts and Hawksworth 1991; Nicholls and others 1984). Several owl species indicate an attraction to mistletoe brooms for nesting: long-eared, great gray (Bull and Henjum 1990;

Bull and others 1989), and northern spotted (Martin and others 1993).

Obviously, specific information on ecosystem functions of larch dwarf mistletoe is lacking. But it seems reasonable to speculate that dwarf mistletoes may play other roles in forest ecosystems that are not currently recognized, and these roles will probably never be fully known or understood. Nevertheless, it seems that the prudent approach would be to retain dwarf mistletoe in the landscape and maintain it within what we can best characterize to be the natural range of variability.

It also seems reasonable to ask two questions about the distribution of larch dwarf mistletoe now as compared to the "natural ecosystem" with regard to the conservation of biodiversity and retention of vital ecological processes:

1. What is the current abundance and distribution of the host? Larch dwarf mistletoe will probably not be within its historic natural range if western larch has been drastically reduced at certain elevations, stand age classes, or within certain habitat types as the result of certain logging practices or fire control.
2. What is the abundance and distribution of the pathogen and how has this been affected by past management practices? Perhaps larch dwarf mistletoe is now scarce in certain age classes, habitat types, elevation zones, or topographic positions that have been intensively managed. For example, dwarf mistletoe may be under-represented along ridge tops because that is where many logging roads have historically been located. Conversely, the severity of infection may be greater in some older age classes, at high elevations, or in inaccessible terrain because of fire suppression and lack of management.

These questions have obvious management considerations. They indicate a path to follow as we attempt to adjust our views of larch dwarf mistletoe in ways that better "mesh" with the ecosystem management effort.

Commodity production will continue to be a goal within some management units. In these stands, we may choose to emphasize the reduction of dwarf mistletoe populations even to levels below the natural range of variability. In areas where we are attempting to maximize timber production, it may be possible to manage larch dwarf mistletoe within an economic threshold rather than emphasizing complete eradication. In other stands where management is not focused on timber production, mistletoe control may not be warranted or desirable. We may choose to maintain, or even increase, dwarf mistletoe levels to meet specific desired resource objectives. Whatever management choices we make at the stand or site level, we hope to make these decisions with a better understanding of the effects on the function of the entire ecosystem. We should never depart so far as to threaten the future sustainability or integrity of the system.

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A Model of Photosynthesis During Autumn Foliar Senescence in Western Larch (*Larix occidentalis* Nutt.)

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Abstract—Western larch (*Larix occidentalis* Nutt.) seedlings were placed in cold frames under ambient conditions, 16-hour days, or soil temperature 10 °C above ambient, and changes were recorded in light-saturated photosynthetic rates and in pigments during autumn foliar senescence. From these data came a regression model explaining the sensitivity of photosynthesis to changes in date, air temperature, and chlorophyll content.

During autumnal foliar senescence nutrients are reabsorbed before leaf abscission occurs. Much of the literature on senescence is based on annuals (Nooden and Leopold 1988). The degree to which senescence in annuals and leaf senescence induced by darkness is similar to the autumn process is not well described, though studies on deciduous trees have begun to characterize events during autumn (Adams and others 1990; Bortlik and others 1987; Goodwin 1958).

Observations on perennials suggest that daylength, light levels, and temperature induce autumn color change. Although we know that daylength and temperature affect autumnal leaf senescence in trees and that species respond differently in the degree to which the environment affects the onset of senescence (Kozlowski 1973), few studies have quantified the relative importance of the weather variables nor examined the physiological changes during color change.

For many species, daylength is the trigger for senescence, with temperature modifying the influence of the photoperiod (Wareing 1956), but it is not known how temperature hastens the senescence process triggered by daylength. Although trees near street lights remain green longer (Matzke 1936), senescence is delayed but not prevented in these extended-daylight leaves because colder temperatures still induce leaf senescence. The onset of senescence is also based, in part, on the previous spring and summer weather (Addicott 1982; Worrall 1993). Consequently, there is year-to-year variation in the onset and intensity of the colors.

Studying the problem is made difficult because autumn senescence occurs only once a year, and seedlings always vary by the time they are measured because of differences in microhabitat and weather during the previous summer growth. In addition, simultaneous biochemical changes take place, making it difficult to determine the order of events. For example, as chlorophyll decreases, many proteins decrease, photosynthetic rates decrease, and RNA levels decrease (Stoddard and Thomas 1982). Autumnal leaf senescence in deciduous trees has been attributed to the action of shortened photoperiod on phytochrome and on plant hormones (Addicott 1982), both of which have a cascading effect on many biochemical pathways.

By altering the condition under which senescence occurs, it may be possible to separate processes occurring during senescence. We have focused on photosynthetic components during senescence to determine events that are sensitive to changes in autumn weather. This information will be useful in studies on the effect of planting trees of different genetic backgrounds in a greater diversity of climates.

We report here a method that allows examination of the influence of autumn weather on the senescence process in western larch (*Larix occidentalis* Nutt.) seedlings growing in outdoor cold frames under different temperature and day-length regimes. Regression analysis was used to analyze trends in photosynthetic data collected during autumn from seedlings growing in modified autumn conditions.

METHODS

One-year-old western larch seedlings from seedlot 5266, Grand Forks, British Columbia (Pacific Regeneration, Inc., Vernon, BC) were grown outdoors in Vancouver, BC, during the summer in peat/perlite 2:1 with lime. The seedlings were watered regularly and fertilized with 17-7-2 Osmocote. In September, trees were divided into treatment groups ($n = 50, 41, 29$) and placed in cold frames under a translucent roof. The lighted group (LONG DAY) received a 16-hour day from fluorescent lights (100 μmol/m^2/s). The temperature group (HIGH TEMP) had soil heating cables under the gravel. Soil temperature probes were placed in selected pots and data recorded using a CR10 datalogger (Campbell Scientific, Edmonton, AB), which also recorded air temperature and relative humidity. Soil heating cables maintained temperature 10 °C above controls by mid-autumn. A journal was kept on the appearance of each tree.

For 14 weeks from September through November, needles were harvested from side branches at approximately 10 a.m., placed into humid petri dishes, and brought into the lab. All measurements were completed

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within 2 hours of harvesting. Photosynthetic rates at saturation (1,000 µmol/m²/s) were measured immediately after harvesting using a LI-COR 6200 (LI-COR, Lincoln, NE) infrared gas analyzer. Chlorophyll was determined with acetone extractions (Lichtenthaler and Wellburn 1983).

DEVELOPMENT OF MODEL

In our initial analyses of changes in photosynthesis during autumn, photosynthetic rates were plotted separately against Julian date, air temperature, and chlorophyll, using a locally weighted scatterplot smoothing method in SYGRAPH (Wilkinson 1990a). However, graphical representation of the data limits analysis to two dimensions, which is problematic because photosynthetic rate is a function of several variables. Statistical analysis was used to determine significance in the decline of photosynthetic rate and difference among the treatment groups. In this paper we discuss our considerations in formulating a model to explain variation in photosynthetic rate attributable to weather and physiological variables.

We needed to choose variables unaffected by photosynthesis. For example, CO_2 concentration in the stomatal cavities could not be used to explain variation in photosynthetic rate because photosynthesis at a given moment influences internal CO_2. On the other hand, chlorophyll was exogenous with respect to photosynthesis at the time of measurement: a needle can be detached and frozen and still have the same amount of chlorophyll, but the photosynthetic rate would change. In addition, the selected variables should not be highly correlated with each other; otherwise, standard errors increase (causing *t*-ratios to fall), and a large data set would be needed to obtain reliable estimates of the coefficients.

The variation in photosynthesis on a given day is determined by many factors, including time of day, current weather conditions, history of the plant (that is, the cumulative stress received), age of the plant, and age of the needle. An ideal model would include variables for each of these possible contributors to the variation. Measurements were made at approximately the same time each day, so time of day was controlled through the sampling procedure. Needle age was considered a minor factor affecting senescence onset because seedlings kept in a warm, lighted greenhouse during autumn maintained green color and high rates of photosynthesis. This suggested that the onset of senescence was affected by the weather and not the age of the needle.

Air temperature and date were chosen as variables that best characterize current conditions that might affect senescence. We chose air temperature because it fluctuates daily (like relative humidity or light intensity), and we chose date to proxy conditions that change gradually, such as daylength, age of leaf, and cumulative stress received by a leaf. Using light intensity and relative humidity in the model instead of air temperature did not explain as much of the variation in photosynthesis as did air temperature. Additionally, these variables were too collinear to include all three in the model.

The choice of variable to best summarize the past condition of the plant was least obvious. Soil temperature was considered because it changes more slowly over time, but it is too highly correlated with air temperature. On the other hand, the amount of chlorophyll in a leaf is a good approximation of the past environment in which the plant has been growing. For example, a leaf growing in the shade will have different chlorophyll levels than one growing in the sun, or a nutrient-deficient leaf may have less chlorophyll than a healthy one. In addition, as noted earlier, the amount of chlorophyll in a leaf is exogenous of photosynthesis because the level of chlorophyll is unaffected by the level of photosynthesis at the time of measurement.

Given these arguments, we expressed photosynthesis as a function of chlorophyll, date, and air temperature. To further simplify the analysis, we assumed that these variables were linearly related and used ordinary least squares (Neter and others 1990) to explain the variation in the photosynthetic factor. Initially, the following model was estimated using SYSTAT (Wilkinson 1990b) where *AMAX* is photosynthesis, *CHL* is milligrams chlorophyll per square meter, *J* is Julian date, *AIRT* is air temperature (°C), b_0 is a constant, $b_1,\ldots,b_3$ are coefficients, e is an error term, and b refers to the population:

$$AMAX = b_0 + b_1CHL + b_2J + b_3AIRT + e.$$

The model was then expanded to include data from HIGH TEMP and LONG DAY treatments. Dummy variable (Zar 1984) T was set such that $T = 1$ for measurements from HIGH TEMP treatments, and otherwise $T = 0$. Similarly, the dummy variable D was set to $D = 1$ for LONG DAY treatment only, and otherwise $D = 0$. Using these variables it was possible to include the additional regressor *CHL*T*. The coefficient on *CHL*T* provided an estimate of the difference in the effect of chlorophyll between HIGH TEMP and CONTROL seedlings. Similar interactive variables were constructed for Julian date and air temperature:

$$AMAX = b_0 + b_1CHL + b_2CHL{*}T + b_3CHL{*}D + b_4J + b_5J{*}T + b_6J{*}D + b_7AIRT + b_8AIRT{*}T + b_9AIRT{*}D + e.$$

Interpretation of this equation would be: on average, a 1-mg decrease in chlorophyll for CONTROL seedlings would give a b_1 decrease in photosynthesis for any given date (*J*) and air temperature (*AIRT*). But a 1-mg decrease in chlorophyll for the HIGH TEMP seedlings would give a $b_1 + b_2$ decrease in photosynthesis, and for the LONG DAY seedlings a $b_1 + b_3$ decrease. Similar interpretation would hold for date and air temperature.

ASSUMPTIONS AND TESTS OF MODEL

The assumption that the function is linear was appropriate because the residuals were distributed symmetrically around zero (plot of residual as a function of the estimate). Further analysis suggested that the error terms are drawn from a normal distribution. A plot of the residual versus date showed that there was no correlation between error term over time. When the model was run with both independent and dependent variables transformed to log form, the coefficients remained significant and of the same sign as when the model was run with no log transformation (table 1). This suggests that the results are not sensitive to reasonable changes in functional form: although the true form may not be linear, no evidence suggests that a linear model is inappropriate as a first approximation toward analyzing the data. The final model contains only one constant: b_0. A preliminary model was run with two additional constants (b_{10} and b_{11}) for the treatment groups:

$$AMAX = b_0 + b_{10}{*}T + b_{11}{*}D + b_1CHL + b_2CHL{*}T + b_3CHL{*}D + b_4J + b_5J{*}T + b_6J{*}D + b_7AIRT + b_8AIRT{*}T + b_9AIRT{*}D + e.$$

However, in initial runs the constants b_{10} and b_{11} were not significantly different from zero (t-ratio –0.995 and –1.22, respectively) and were dropped from the final regression.

Table 1—Autumn 1991 western larch regression analysis, as explained in text

DEP VAR	AMAX	LOG AMAX	DEP VAR	LOG AMAX
CONSTANT	16.065 (3.955)[1]	3.610 (4.116)[1]	CONSTANT	15.581 (4.082)[1]
J	–462.747 (–3.852)[1]	–0.009 (–3.607)[1]	LOG J	–3.007 (–4.730)[1]
J*T	76.828 (2.223)[2]	0.002 (2.625)[2]	LOG J*T	0.369 (2.572)[2]
J*D	14.808 (0.420)	0.001 (0.861)	LOG J*D	0.224 (1.501)
CHL	94.674 (3.728)[1]	0.002 (3.557)[1]	LOG CHL	0.534 (4.852)[1]
CHL*T	–52.124 (–1.487)	–0.001 (–1.633)	LOG CHL*T	–0.361 (–2.293)
CHL*D	–32.948 (–0.950)	–0.001 (–1.060)	LOG CHL*D	–0.284 (–1.760)
AIRT	1399.640 (1.718)	0.029 (1.650)	LOG AIRT	0.116 (0.967)
AIRT*T	–385.343 (–0.400)	–0.011 (–0.510)	LOG AIRT*T	0.006 (0.037)
AIRT*D	–88.618 (–0.087)	–0.003 (–0.133)	LOG AIRT*D	0.102 (0.621)
Adj R^2	0.306	0.265		0.283
n	270	270		267
Res SS	1,699.669	79.240		76.830
F ratio	14.196[1]	11.795[1]		12.689[1]

Coefficients are given with the t-ratio in parenthesis; [1] $p < 0.01$ for 2-tail test; [2] $p < 0.05$ for 2-tail test; AMAX = apparent photosynthetic rate (µmol $CO_2/m^2/s$), coefficient x 10^{-4}; J = Julian date, J*T and J*D = interactive variables for HIGH TEMP and LONG DAY treatment groups; CHL = chlorophyll (mg chlorophyll m^2); CHL*T and CHL*D = interactive variables for HIGH TEMP and LONG DAY; AIRT = air temperature (°C), AIRT*T and AIRT*D = interactive variables for HIGH TEMP and LONG DAY.

The use of only one constant in the final model is consistent with the assumption that at the start of the experiment the treatment groups are all similar (on average, the photosynthetic rates were the same).

RESULTS

Preliminary analysis shows the usefulness of this approach in separating the effects of day length and temperature on the process of foliar senescence. From the regression analysis (table 1), a decrease in chlorophyll resulted in significantly lower photosynthetic rates ($p < 0.01$) for any given date and air temperature. An older leaf had lower photosynthetic rates ($p < 0.01$) than a younger one for any given level of chlorophyll and air temperature.

The treatment groups differed from the control. HIGH TEMP seedlings showed higher photosynthetic rates than CONTROL seedlings in late autumn for a similar amount of chlorophyll (table 1). Based on observations of each seedling, LONG DAY seedlings remained green significantly longer into autumn compared to CONTROL and HIGH TEMP seedlings ($p < 0.01$). In late autumn the sample of needles from the CONTROL seedlings included a greater portion of needles remaining green throughout the winter (Richardson and Bliss 1986) compared to LONG DAY needles, which were green because senescence was delayed. Thus, the physiology of the needles remaining green later into autumn in the LONG DAY treatment cannot be compared to CONTROL needles in this data.

DISCUSSION

Because many variables influence photosynthesis, we have used a statistical model to understand trends occurring during autumn leaf senescence in western larch seedlings. We easily interpreted results from regression analysis of CONTROL seedlings, thus increasing confidence in the regression model: photosynthesis decreased as leaves age and as leaves lost chlorophyll. Photosynthetic rates decreased during autumn for a given level of chlorophyll and air temperature. This is consistent with the hypothesis that older leaves are not as productive as younger leaves, even though they may have the same amount of chlorophyll.

HIGH TEMP seedlings were able to lengthen their growing season by higher photosynthetic rates late in autumn. The fact that chlorophyll loss was not delayed suggests that cytokinins, which are mostly synthesized in the roots and transported to the leaves, may not be important in regulating the autumnal senescence process even though they are involved in delaying leaf senescence in annuals (Stoddard and Thomas 1982). The delay in senescence of seedlings receiving a long photoperiod during autumn is consistent with the literature on several other deciduous trees (Matzke 1936).

The data reported here suggest correlations between weather conditions and photosynthesis during senescence of autumn deciduous leaves. Future work will use this method to analyze additional photosynthetic components such as stomatal conductance, quantum efficiency, and amount of ribulose bisphosphate carboxylase/oxygenase. The sensitivities of the measured factors to autumn conditions can be used to formulate hypotheses on the effect of day length and temperature on specific pathways during leaf senescence.

For example, based on these data showing that light levels delayed yellowing, it could be hypothesized that the light intensity and duration used in this experiment initially affect pathways leading to chlorophyll degradation. In contrast, soil temperature influences pathways initially affecting enzymes involved in carbon fixation because warm soil kept photosynthetic rates high, but higher photosynthetic rates were not able to delay the yellowing process. Analyzing additional photosynthic components using the method described here will provide further data to determine how day length and temperature interact to trigger the senescence process.

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Phenology and Growth of Nine Larch Species and Hybrids Tested in New Brunswick, Canada

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Abstract—Several provenances or seedlots of nine species or hybrids were tested in a temperate climate at latitude 45°52' N., longitude 66°32' W., and 120 m elevation. *Larix gmelini, occidentalis,* and *sibirica* initiated height growth earliest (April 20 to 22), and the same species plus *L. gmelini* var. *olgensis* also terminated growth earliest (by August 2), several weeks before the first fall frost. *Larix laricina, decidua, polonica, eurolepis,* and *kaempferi* grew and survived best.

In 1738 the German forester Fockel, working in the service of Czarina Anna of Russia, established plantations of Siberian larch (*Larix sibirica* Ledeb.) near Raivola on the Ladoga Peninsula northwest of St. Petersburg for the purpose of producing ship-building material. When the resulting forests were measured 180 years later by Dr. Lauri Ilvessalo of the Finnish Forest Research Institute, the results were sensational: the best sample plot carried a volume of 1,825 m^3/ha, a figure ranking among the highest ever measured in northern forests (Ilvessalo 1923). Two-thirds of this volume consisted of Siberian larch and one-third of natural Norway spruce (*Picea abies* [L.] Karst.), which had grown into the stand from below. The results demonstrated the potential of Siberian larch for fast growth, to grow in mixtures, and its suitability for long rotations.

In North America we have had many experiments with larches, but with some exceptions their potential in practical silviculture has not been realized. Few reports indicate that larches are grown on an operational scale in plantations. A certain reluctance to accept the wood still exists among pulp mill managers. Seed is scarce, and knowledge of some exotic species (such as *L. sibirica* and *L. gmelini* [Rupr.] Kuzeneva) is insufficient. Many reports state that exotic species grew poorly but do not explain why. Clearly, much more research and development work needs to be done (Boyle and others 1989; Loo-Dinkins and others 1992; Martinsson 1992; Weisgerber and Sindelar 1992).

The objective of this study was to compare the phenology and growth of a native and several exotic species in eastern Canada. The results demonstrate a good correlation between phenology and growth and indicate why some of the exotics are not well adapted.

MATERIALS AND METHODS

Plant Material

Seed of nine species, varieties, or hybrids was supplied by the National Tree Seed Centre at Chalk River, ON, in 1986, and 2-year-old transplants were outplanted in 1988. The origin of the 33 provenances is given in table 1. Most seedlots came from natural stands; some seedlots were obtained from planted stands grown in Denmark, Germany, or Canada, where the species involved is not native, but records of original sources had been kept.

Species abbreviations used throughout this paper are as follows:

DEC – European larch, *Larix decidua* Mill.
EUR – hybrid larch, *L. eurolepis* Henry (*L. decidua* x *leptolepis*)
GME – Dahurian larch, *L. gmelini* (Rupr.) Kuzeneva
OLG – Manchurian larch, *L. gmelini* var. olgensis (Henry) Ostenf.
KAE – Japanese larch, *L. kaempferi* (Lamb) Carr. (*L. leptolepis*)
LAR – Eastern larch, *L. laricina* (Du Roi) K. Koch
OCC – western larch, *L. occidentalis* Nutt.
POL – Polish larch, *L. decidua* var. *polonica* (Racib.) Ostenf.
SIB – Siberian larch, *L. sibirica* Ledeb.

Test Site

Each provenance was generally represented by a rectangular plot of 15 trees (3 rows of 5 trees at 3- by 3-m spacing) in each of the 2 blocks of the Larch Arboretum in the University of New Brunswick Forest. The location is south of Fredericton at 45°52' N. latitude, 60°32' W. longitude, and 120 m elevation. The soils consist of well-drained sandy loams derived from acidic Pennsylvanian sandstones of medium fertility. The area is in the Harvey-Hartcourt Site Region, which has a cool temperate, moderately continental climate (Zelazny and others 1989).

Variables Measured

In April 1991, the trees began their sixth growing season and were measured and observed from then on until late October. Only 6 of a total of 10 characteristics will be reported here; the remaining characteristics have been discussed elsewhere (Carswell 1992).

1. *Growth initiation.* Growth initiation, measured by bud burst, was monitored every second day beginning

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Table 1—Origin of the 33 provenances in the University of New Brunswick larch arboretum

Species	Place and country of origin	Lat. (°.' N.)	Long. (°.')	Elevation (m)
DEC	CSR[1] via Eur. Bundesstr., Germany[2]	50.00	18.00 E.	600
DEC	European Alps via Farum, Denmark[2]	47.00	13.00 E.	1,200
DEC	CSR[1] via Jagersborg, Denmark[2]	50.00	18.00 E.	600
DEC	CSR[1] via Ottawa, Canada[2]	50.00	18.00 E.	600
DEC	Frenstat, Czechoslovakia	49.32	17.37 E.	320
DEC	Brnicko, Czechoslovakia	49.54	17.00 E.	420
DEC	Albrechtice, Czechoslovakia	50.10	17.33 E.	600
EUR	Holbaek, Denmark	—	—	—
EUR	Jap. Braak, Germany	—	—	—
EUR	Cartegory 3, Germany	—	—	—
GME	Heilongjiang, China	47.00	127.00 E.	500
GME	Hu-Lun-Pei, China	50.00	124.00 E.	200
GME	Amur, China	52.45	123.12 E.	1,200
OLG	Jilin Prov., China	43.00	126.00 E.	400
OLG	Jilin Prov., China	43.00	126.00 E.	400
LAR	Petawawa, ON, Canada	45.58	77.25 W.	168
LAR	Petawawa, ON, Canada	45.58	77.25 W.	168
LAR	Ignace, ON, Canada	49.25	91.40 W.	450
LAR	Ignace, ON, Canada	49.25	91.40 W.	450
KAE	Hokkaido Prefecture, Japan	43.00	141.30 E.	700
KAE	Central Honshu, Japan	35.00	136.00 E.	600
KAE	Japan via Burrrits Rapids, Canada[2]	37.00	140.00 E.	1,500
OCC	Flathead Valley, Canada	49.04	114.24 W.	1,500
OCC	Flathead Valley, Canada	49.04	114.24 W.	1,500
SIB	Russia via Indian Head, Canada[2]	60.00	60.00 E.	500
SIB	Kambja, Estonia	58.10	26.51 E.	150
SIB	Baskirskaya Region, Russia	55.00	55.00 E.	150
SIB	Baskirskaya Region, Russia	55.00	55.00 E.	150
SIB	Krasnoyarskiy Region, Russia	55.00	95.00 E.	1,500
POL	Poland via Petawawa, Canada[2]	51.00	21.00 E.	600
POL	Poland via Petawawa, Canada[2]	51.00	21.00 E.	600
POL	Poland via Petawawa, Canada[2]	51.00	21.00 E.	600
POL	Meidzylesie, Poland	50.15	16.30 E.	500

[1] CSR = Czechoslovakia.
[2] Sources not obtained from original sites (secondary sources).

April 15. Each tree in a plot was examined by searching for the presence of new recognizable needles in its upper branches. Average heat-sum requirements for bud burst of each species or hybrid were calculated. These were based on hourly temperatures measured by a thermograph connected to a datalogger. Daily averages of degree-hours above the 3 °C threshold were accumulated and related to the mean date of growth initiation of each plot (Edey 1977).

2. *Spring frost damage.* On May 29, the approximate date of the last spring frost, each plot was inspected for evidence of damage. Damage was rated on a scale of 0 (no damage) to 3 (20 percent of foliage affected).

3. *Growth cessation.* Beginning on July 22 and ending in early September, each plot was examined weekly for the presence of brown buds at the shoot apex.

4. *Total height.* Each tree was measured for 6-year height with a pole to the nearest 1 cm.

5. *Root-collar diameter.* Each tree was measured for root-collar diameter with a caliper to the nearest 0.5 cm.

6. *Survival.* The percentage of trees surviving in each plot at the end of the sixth growing season was determined.

Statistical Analysis

Plot means were used for analyses of all characters. From the plot means, provenance and species means were calculated for correlation among all variables including geographic origin. A nested analysis of variance was conducted using the sources "species," "provenances in species," and "within provenances." "Species" was considered a fixed and "provenances" a random effect. Survival percentages were transformed by arcsine before analysis, but actual percentages are reported in the tables. Significant differences between means were determined using Duncan's multiple range test (Steel and Torrie 1980).

Provenance means were used to calculate correlations between all characters observed and heat sum at the test site and latitude at the place of origin. The hybrids (*L. eurolepis*) were excluded from correlation analysis.

RESULTS

Growth Initiation and Cessation

All species initiated growth within 7 days as indicated by species means, that is, between day 110 (April 20) and day 117 (April 27). The sequence from earliest to latest was: *L. gmelini, occidentalis, sibirica, polonica, decidua, laricina, olgensis, eurolepis,* and *kaempferi* (fig. 1).

The range in cessation dates was much greater and extended over 38 days, from day 203 (July 22) to day 241 (August 29). The sequence from earliest to latest was: *L. sibirica, occidentalis, olgensis, gmelini, laricina, decidua, polonica, eurolepis,* and *kaempferi* (fig. 1).

Analysis of variance revealed differences that were significant at the 1 percent level among species as well as among provenances within species (table 2). The Duncan test suggests that there are up to five different species groups for the six observed characters (table 3).

Frost Damage and Survival

Although spring frost damage was not severe, it affected the earliest flushing species, particularly *L. gmelini* and *L. occidentalis*, to a moderate degree (about 10 percent of needles), and the remaining species less.

Survival of *L. gmelini* var. *olgensis, L. occidentalis, L. gmelini,* and *L. sibirica* ranged from 68.8 to 81.0 percent, in that order, while all the other species were above 90 percent (table 3). Provenance differences were not significant even at the 5 percent level for these two characteristics (table 2). According to the Duncan test, there were three groups for frost damage and five for survival (table 3).

Total Height and Root-Collar Diameter

These characteristics were well differentiated, but provenances within species differed significantly only for height (table 2). Heights and diameters of *L. sibirica, occidentalis, gmelini,* and *olgensis* were substantially smaller than for the remaining five species or hybrids (table 3).

Correlations

The correlations of major interest that were statistically significant were those between initiation and heat sum, cessation and latitude, and cessation and height. These correlations were significant at the 1 percent level. Several other correlations were found (table 4).

DISCUSSION

The performance of the nine species or hybrids in the University of New Brunswick Larch Arboretum differs greatly, and the species may be separated into two distinct groups. One group includes the four exotic species or varieties *L. sibirica, occidentalis, gmelini,* and *olgensis*. They originated in far northerly latitudes or high elevations and were moved to lower latitudes and elevations where their growth potential was not realized. They

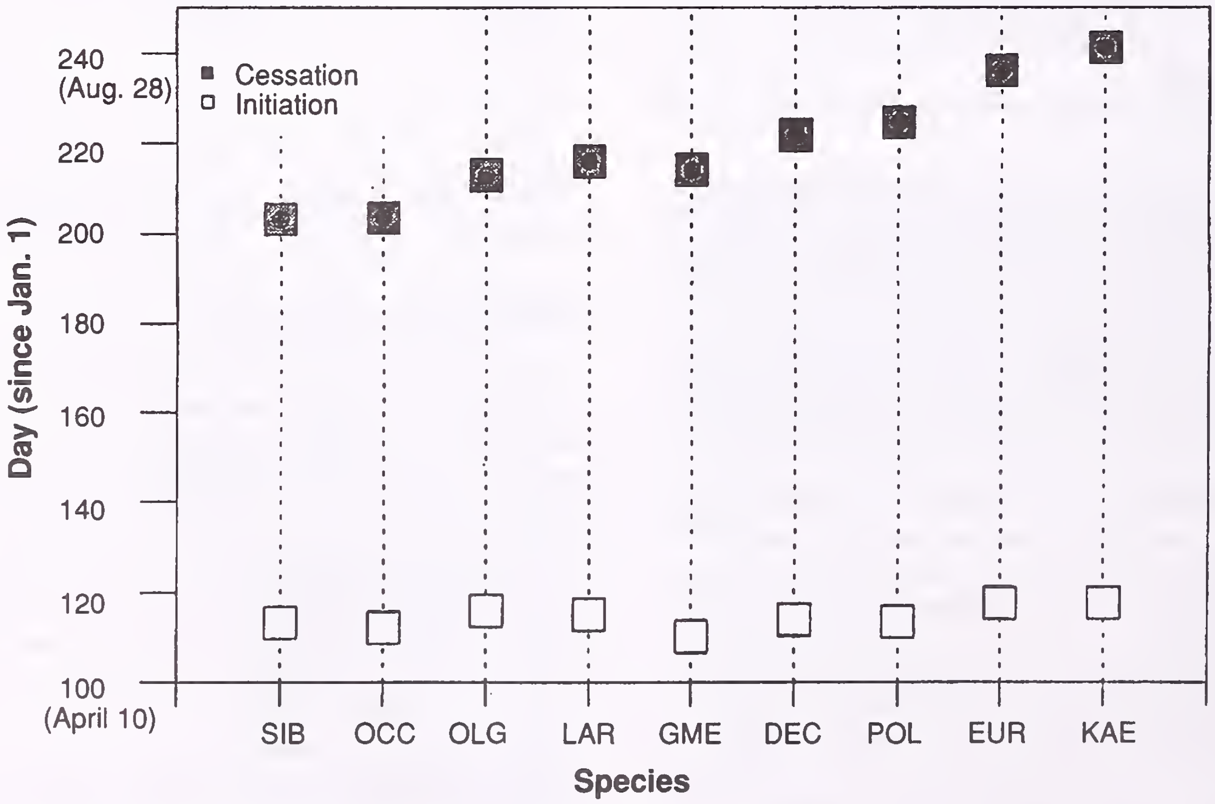

Figure 1—Dates of initiation and cessation of growth of the nine species or hybrids.

Table 2—Analyses of variance for all six characteristics

Source	d.f.[2]	Mean squares[1]					
		Initiation	Cessation	Frost damage	Survival	Height	Diameter
Species	8	34.0**	1,022.3**	1.79**	797.6**	313,505**	10.55**
Provenances in species	24	4.1**	26.3**	.23	143.3	2,171**	.88
Within provenances	35	1.4	11.1	.16	120.1	731	.55

[1] Significance levels: **, 1 percent.

[2] d.f. for "within provenances" is larger than expected due to a third plot for some provenances.

Table 3—Species means and Duncan test[1] results for all characteristics

Initiation		Cessation		Frost damage		Survival		Height		Diameter	
KAE	117.4a	KAE	241.2a	GME	1.91a	KAE	100.0a	EUR	258a	EUR	5.27a
EUR	117.3a	EUR	236.0b	OCC	1.78a	POL	98.0a	LAR	255a	DEC	4.83ab
OLG	115.8b	POL	224.5c	POL	.83b	LAR	95.6b	KAE	240a	POL	4.59ab
LAR	114.9bc	DEC	221.7c	DEC	.83b	DEC	93.4b	DEC	235a	KAE	4.58ab
DEC	113.7cd	LAR	216.0d	OLG	.78b	EUR	93.36	POL	233a	LAR	4.16b
POL	113.7de	GME	214.1d	SIB	.77b	SIB	81.0c	OLG	151b	OLG	3.14c
SIB	113.1de	OLG	213.0d	KAE`	.65bc	GME	78.3c	GME	143b	GME	3.03c
OCC	112.0e	OCC	203.5e	EUR	.59c	OCC	72.5d	OCC	119bc	OCC	2.35cd
GME	110.0f	SIB	203.1e	LAR	.23c	OLG	68.8e	SIB	90c	SIB	1.92d

[1] Species means followed by the same letter do not differ significantly at the 5 percent level.

Table 4—Correlation coefficients based on provenance means (d.f. = 28)[1]

	Variable	x_1	x_2	x_3	x_4	x_5	x_6	x_7
x_1	Initiation date	—	0.61**	–0.57**	0.51**	0.45**	0.80**	–0.41*
x_2	Cessation date		—	–.32	.57**	.74**	.57**	–.55**
x_3	Frost damage			—	-.42*	–.54**	–.22	.08
x_4	Survival				—	.59**	.50**	–.16
x_5	Height					—	.28	–.37*
x_6	Heat sum at test site						—	–.34
x_7	Latitude at place of origin							—

[1] Significance levels: *, 5 percent; **, 1 percent.

began to grow too early, tended to suffer from spring frost damage, and then formed terminal buds and ceased growing in midsummer, several weeks before there was any danger of fall frost. They are utilizing the growing season poorly and have relatively low survival.

The second group consists of the native species *L. laricina* and the introduced species or varieties *L. decidua, polonica, kaempferi,* and the hybrid *eurolepis,* all of which perform well. They begin to grow a few days later in the spring, suffer less frost damage, and cease to grow later in the autumn than the first group. Their survival is above 90 percent, and height and diameter growth are better. With the exception of *L. kaempferi,* this group has been moved shorter latitudinal distances from the place of origin to the test site, and therefore they are better adapted. Although the observation period here includes only the first 6 years after sowing, these species or hybrids are expected to grow well during their whole life.

The sample of provenances or hybrid seedlots tested for each species is small, but the literature supports the idea that the responses observed here may be typical for test sites in north-temperate climates. Unfortunately, phenological studies have been rare so that this aspect of performance is not easily compared. On the other hand, reports on growth characteristics agree that *L. sibirica* and *gmelini* and their varieties or subspecies have usually been slow growing when tested in midlatitudes, that is, about 45° to 50° N. in western Europe or eastern North America (Boyle and others 1989; Schenck 1939). *Larix occidentalis*, too, when observed at Petawawa, ON, grew slowly, and survival after 10 years was less than 10 percent (Boyle and others 1989).

In more northerly regions, as in Iceland, Finland, northern Ontario, and Saskatchewan, *L. sibirica* grew much better (Bloendal and others 1986; Boyle and others 1989; Ilvessalo 1923; Schroeder 1987). It is also possible that southern provenances of *L. sibirica* from the Altai Mountains in Russia and northern Mongolia (latitude 48° to 52° N.) have greater potential than the northern provenances tested here.

The better performance of the second group was no surprise and is well supported by the literature. *Larix decidua* and *L. kaempferi* and their hybrids have usually grown well in Europe and North America, and in North America they have often outgrown native species (Farnsworth and others 1972; Genys 1980; Hattemer 1969; Morgenstern and Vallée 1986). At Acadia Forest Experiment Station near Fredericton, *L. kaempferi* was the most productive species and produced wood of lumber quality 25 years after planting (Fowler and others 1988; Park and Fowler 1983). In the Arboretum, the hybrid *L. eurolepis* ranked first in height, followed by *L. laricina,* but *L. laricina* was fifth in diameter. In the Acadia test, initial height superiority of *L. laricina* was not maintained for long. The same change in rank may occur here. Overall, the species ranking observed here is similar to that in other experiments in eastern Canada. Phenology explains a good part of the species differences.

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The Role of Epicormic Branches in the Life History of Western Larch

Ronald M. Lanner

Abstract—As a western larch (*Larix occidentalis*) tree matures, its first-order branches decline, die, and are replaced by clustered epicormics that form a replacement crown. These epicormics grow from dormant buds at first-order branch-bases, appearing at successively higher positions in the crown, eventually making up entire crowns of old trees. Crown replacement is a normal life-history trait which prolongs the life span, not an injury response. It occurs in *Larix, Pseudotsuga, Abies, Picea, Tsuga, Sequoia,* and *Sequoiadendron.*

The first-order branches of larch originate from the elongation of axillary buds formed on the leading shoot. As leader growth continues over the years, a first-order branch that was at the time of its formation the uppermost branch in the crown finds itself progressively lower in the crown and eventually becomes the lowermost live branch. After a period of decline, it may die and eventually fall from the tree. During this process of crown formation and recession, a branch's characteristics change, as well as its position in relation to other branches. It grows longer, it spreads laterally by producing one or more additional orders of branching, and it grows in diameter. Its orientation changes from an acute angle to a right angle. The stress at its junction with the bole is increased not only by the weight of new biomass but by snow-loading, rain-soaking, wind-torque, birdnests, mistletoe witchesbrooms, and epiphytic lichens. Each year's suite of foliage is farther from the source of its water and more exposed to drying winds. In the meantime its light environment is changing from unshaded to progressively more heavily shaded.

In this paper I maintain that those changes set limits on the size, and therefore the age, that a branch can attain, and they eventually lead to its death. The death of a branch, however, is not detrimental to the tree as a whole because larch is equipped with embryonic replacement branches whose release mitigates the effects of the loss. These replacements are of epicormic origin—they result from the outgrowth of dormant buds located at the base of the first-order branches. Finally, the new replacements, which eventually dominate the crown, prolong the tree's life.

This argument is based on preliminary data and observations reported here, through analogy with Douglas-fir (*Pseudotsuga menziesii*), and on speculation.

MATERIALS AND METHODS

Observations of standing western larch have been made at several Montana locations: Seeley Lake and vicinity, Morrell Lake Trail (Lolo National Forest), and Coram Experimental Forest. Stands at Coram were aged 45 years, 60 to 70 years, and 350 to 500 years (residual old growth) (Shearer 1992). Trees at the other locations were old growth, aged 300 to 500 years. Elevations of the observed stands ranged from 900 to 1,375 m. Associated species at Coram Experimental Forest were white spruce (*Picea glauca*), Douglas-fir, western white pine (*Pinus monticola*), and lodgepole pine (*P. contorta*). Associates on the Morrell Falls Trail were Engelmann spruce (*P. engelmannii*), subalpine fir (*Abies lasiocarpa*), Douglas-fir, and lodgepole pine. Trees were measured with an Abney level and diameter tape, and branches were viewed with 10 x binoculars.

RESULTS

The 45-year-old stand on the South Fork of Abbott Creek had been thinned about 30 years prior to examination. A sample of four typical trees was 20 to 25 cm diameter at breast height (d.b.h.) ($\bar{x} = 23$) and 20 to 23 m in height ($\bar{x} = 20.9$). Height to the first live branch (base of live crown) was 2 to 5 m ($\bar{x} = 4.1$). These trees and 16 others were examined for the presence of epicormic shoots arising from the bole and from lower first-order branch bases. About half the trees had such shoots, the longest of which were about 0.3 m in length (fig. 1). Several of these had sprouted 2 years previously and were unbranched. Some of the epicormics arose from the bole and some from branch bases. Due to the difficulty in seeing where all of them originated, however, the percentages of each category cannot be stated. None were in clusters. The first-order branches that made up the crowns were in distinct whorls and appeared evenly spaced around the circumference of the bole.

The trees in the 65 to 70-year-old stand were widely interspersed among Douglas-firs and lodgepole and western white pines. Four typical trees ranged from 38 to 46 cm d.b.h. ($\bar{x} = 41.9$) and from 24 to 26 m in height ($\bar{x} = 24.6$). Some of these sample trees were adjacent to a meadow and had live branches to within 30 cm of the ground surface. On one tree an epicormic shoot about 45 cm long had sprouted several years previously from the stub of a 7.6-cm diameter branch that had been broken off at a height of 5 m. In several instances epicormic shoots emerged singly or in groups of two or three from the bases of lower limbs that were still alive. The first-order branches

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Figure 1—Epicormic shoots arising from the base of a first-order branch on a 45-year-old western larch on the Coram Experimental Forest, MT.

composing the tree crowns tended to be evenly spaced around the circumference of the boles and in distinct whorls.

The old-growth western larches are along the South Fork Road at the southwest corner of the Coram Experimental Forest Natural Area. The stand consists of emergent, scattered larches with an understory of lodgepole and western white pines, white spruce, and northern black cottonwood (*Populus trichocarpa*). Six typical trees (table 1) ranged from 76 to 99 cm d.b.h. ($\bar{x}$ = 82.5) and 44 to 49 m in height ($\bar{x}$ = 46.6). Heights to base of live crown were 9 to 18 m ($\bar{x}$ = 14.1). In most of these trees' crowns, two distinctive branch types could be discerned. The lower limbs of all the trees emerged from the bole in clusters of usually two or three contorted or drooping branches. Many of these were associated with the conspicuous stubs of fallen first-order branches. The upper limbs of all but one tree appeared to be relatively straight first-order limbs emerging singly from the bole. The only tree lacking these limbs had a 9-m long dead spike-top and a crown below the spike made up entirely of clustered branches. Due to visibility problems (parallax, epiphytic lichen growth, dense branching) it was never possible to be certain of the height of the uppermost clustered branches or the lowermost single first-order limbs. In all cases, however, the clustered branches made up the major part of the crown (table 1), and in all trees except the one with a dead spike, there was a zone in midcrown in which both categories of branches occurred (fig. 2).

DISCUSSION

If we interpret the branching characteristics of these trees of various ages to represent a developmental continuum, an interesting pattern emerges. Apparently, the original first-order branches eventually die and are replaced by clusters of epicormics that often emerge from the bases of those first-order branches ("primaries") while the primaries still live. This process of primary branch replacement begins at the crown base and continues gradually upward. When carried to completion, the replacement process results in a crown comprised entirely of branches of epicormic origin. Thus, trees living on into old age would eventually be totally supported by replacement crowns whose components originated as epicormic branches.

An interesting physiological question is: What triggers the emergence of these epicormic branches? Epicormics are often symptoms of injury or stress that result from the release of inhibited buds in the tree bole or on major limbs. Release has been variously attributed to thinning shock (Fowells 1965), pruning (Cosens 1952), or air pollutant stress ("Angsttriebe," Westman and Lesiński 1985). The mistaken notion that epicormics are rare in conifers has long persisted (Harlow and others 1979). In an earlier study on epicormic branching in Douglas-fir, Bryan and Lanner (1981) were unable to find any evidence that such branching depends on perturbations for its expression. Instead, they regarded the appearance of epicormics as "a routine event in the normal life cycle of the tree" and speculated that no exogenous triggering mechanism was required.

My observations reported here shed no new light on this question. The 45-year-old stand and the old-growth stand had been previously thinned or partially cut, so we cannot exclude the possibility that a change in stand density stimulated epicormic branching. Such an influence does,

Table 1—Crown characteristics of six 350- to 500-year-old western larches on the Coram Experimental Forest, MT

		Height			
Tree	Diameter at breast height	Total	To first epicormic cluster	To highest epicormic cluster	To first live primary branch
	cm	*Meters*			
1	99	48.2	9.1	39.6	24.4
2	76	46.3	17.7	39.0	46.5
3	81	43.9	12.8	34.8	29.3
4	81	46.6	12.8	37.2	32.3
5	79	48.8	17.1	39.6	28.0
[1]6	79	45.7	15.2	36.6	none
Mean	82.5	46.6	14.1	37.8	32.1

[1] Uppermost 9 m is dead.

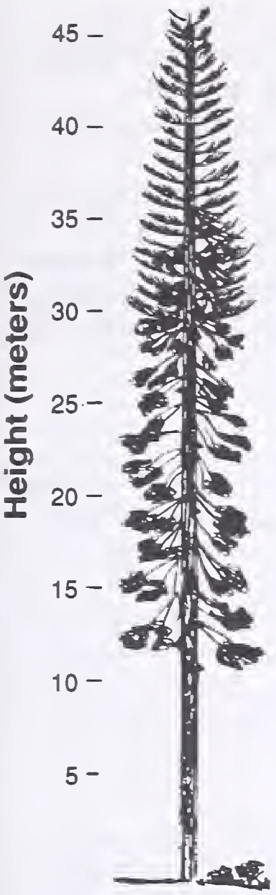

Figure 2—A typical old-growth western larch with its crown of first-order branches being replaced by clusters of epicormic branches, from the crown base upward. The dimensions of this tree are mean values of trees 1 through 5 in table 1.

however, seem extremely unlikely in the old-growth stand, where 75 percent of the total crown lengths of the six sampled trees consists wholly or in part of epicormic branches and where spacing was wide even before partial cutting. Further, similar observations in unthinned old-growth stands, as along the Morrell Lake trail, disclose the same behavior pattern in old larches.

Epicormic branching is not necessarily induced in larch by exogenous effects but may indeed occur routinely even in the absence of such effects. For example, Nairn (1958) reported "adventitious branches" on tamarack (*L. laricina*) following sawfly attack, and Burns and Honkala (1990) stated that western larch responds to release by producing "sprouts from adventitious buds on the upper bole." But according to Pierce (1960), western larch produces epicormics upon self-pruning, the replacement process that is the subject of this paper.

An obvious question from the standpoint of evolutionary ecology might be: What possible advantage is there in replacing established branches with new ones? This offers fertile ground for speculation.

Big persistent limbs have several liabilities. They are heavy, especially when loaded with rain-soaked lichens, snow, birds nests, and witchesbrooms. Thus, they require for support a large woody mass with its considerable need for maintenance respiration. If they cannot create that necessary support they may break off, leaving a large wound on the trunk and broken branches.

Big limbs high in the crown act dangerously like sails in the wind, increasing susceptibility to windthrow. Limbs like those of western larch, which frequently and systemically become infected by dwarf mistletoe, can act as conduits for the parasite into the tree's bole. The longer an infected limb persists, the greater a threat it is for its parent tree. Weir (1916) called attention to the "secondary crown" of epicormics that results after infected branches, laden with brooms, are "lopped" from larch crowns by the wind. He illustrated a trunk cross section showing four "generations" of a regenerating branch base. Heaps of fallen witchesbrooms were often found at the base of infected larches.

It is thus advantageous for western larch to allow its primary limbs a limited life-span, replacing them with clusters of wiry little branches that emerge from long-dormant buds residing within the bases of the very branches they are replacing, that are economical to maintan, and that could be shed when they start to become liabilities. I have recently observed this process occurring commonly on European larch (*L. decidua*) in the Swiss Alps and in alpine larch (*L. lyallii*) in northwestern Montana.

In addition to the widespread occurrence of epicormic replacement branches in Douglas-fir (Bryan and Lanner 1981) and larch, I have also observed it in *Abies, Tsuga, Picea, Sequoiadendron*, and *Sequoia*.

Thus, a genetically programmed "ontogenetic shift" in branch formation appears among several important coniferous genera. Not surprisingly, ontogenetic changes occur in these long-lived organisms. During its early years, a tree is in competition for the atmospheric volume it needs to grow into, so its growth strategy must emphasize "shoots of exploration," rapidly elongating axes that capture volume. Later, its major need is to produce less energetically demanding "shoots of exploitation" that bear masses of foliage on minor axes (Edelin 1977; Thiebaut and others 1981). A better understanding of this shift can only emerge from detailed study of old trees—a category of research that has been sorely neglected in forestry.

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Nitrogen-Fixing Processes in Western Larch Ecosystems

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Abstract—Nitrogen deficiency limits tree growth in most habitat types in the Intermountain West, including those where western larch (*Larix occidentalis* Nutt.) occurs as a major seral species. Both symbiotic and nonsymbiotic nitrogen fixation play key roles in adding nitrogen to western larch ecosystems. Practitioners have the opportunity to develop and use silvicultural systems that minimize nitrogen losses and maximize nitrogen addition from both symbiotic and nonsymbiotic sources.

Western larch occurs as a major seral species in at least 30 habitat type series in northern Idaho, central Idaho, and Montana. It rarely grows in pure stands and most commonly associates with Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) and less frequently with grand fir (*Abies grandis* [Dougl. ex D. Don] Lindl.) or ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.). Western larch is sometimes found with subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), lodgepole pine (*Pinus contorta* Dougl. ex Loud), Engelmann spruce (*Picea engelmannii* Parry ex Englem.), western white pine (*Pinus monticola* Dougl. ex D. Don), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), and western redcedar (*Thuja plicata* Donn ex D. Don) (Schmidt and Shearer 1990; Shearer 1980). Western larch attains its best development in western Montana, northern Idaho, and eastern Washington in the United States, and in southern British Columbia, Canada (Schmidt and Shearer 1990; Schmidt and others 1976).

Nitrogen deficiency limits tree growth in many habitat types of the Intermountain West, including those where larch occurs. Forest nitrogen capital is composed of nitrogen accrued during ecosystem development. Forest ecosystems are typified by a large nitrogen capital, but with only small amounts available for vegetation uptake. The atmosphere represents an almost unlimited potential nitrogen source, but rates of transfer are extremely low in most forest ecosystems (Carlyle 1986).

NITROGEN CYCLING IN FOREST ECOSYSTEMS

The total pool of nitrogen found in most forest soils is large. However, the growth-limiting factor is usually nitrogen's unavailability to the forest vegetation (Mikola and others 1983).

Western larch uses nitrogen efficiently and retranslocates nitrogen well from senescing foliage. This in turn reduces its reliance on the soil for its annual nitrogen requirement (Gower and others, these proceedings). This ability is probably a key factor in making the species an effective pioneer in the largely infertile, disturbed environments of the Inland Northwest.

Fire is a major force in the nitrogen cycle. It regulates soil nitrogen either directly, through volatilization and oxidation of nitrogen present in soil organic matter (particularly the forest floor horizons), or indirectly by altering soil chemical and physical properties. These alterations in turn affect nitrogen transformations (Mroz and others 1980; Wells 1971). Volatilization of nitrogen begins at relatively low temperatures (300 °C) (Hungerford and others 1991). Because the amount of nitrogen lost is proportional to the amount of organic material consumed, nitrogen losses from wild or prescribed fires can be large.

Although trees respond quickly to fertilizer nitrogen, the uptake process is inefficient (Mikola and others 1983). Fertilization must be repeated often, resulting in potentially unaffordable expense. The probable rise of nitrate levels in ground water is a problem associated with fertilizer application (Mikola and others 1983), as are the complications of increasing stress sensitivity and root disease problems with associated, highly susceptible conifers (Miller and others 1992). Because of these problems, the application of nitrogen fertilizers is not considered a desirable management option in much of the inland Mountain West. Therefore, the natural sources of nitrogen concentrated in organic matter (forest floor, soil wood, woody residue, and dispersed organics in mineral soil) are critical to maintaining and enhancing site productivity. Manipulation of the nitrogen cycle to increase forest production, such as by altering nitrogen-fixing associations, is theoretically possible, but more research is needed to refine the practicality (Carlyle 1986).

The four possible sources of nitrogen additions to western larch forest are: (1) precipitation and dry deposition from sources such as dust and pollen, (2) symbiotic biological nitrogen fixation by microorganisms living in plant

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roots, (3) nonsymbiotic nitrogen fixation by free-living soil microorganisms, and (4) nitrogen fertilizers (Jurgensen and others 1991). Recently managers in the Inland Northwest have begun to apply nitrogen fertilizer on some sites (personal communication, James A. Moore, University of Idaho). Managers have no control over precipitation and dry deposition. The remainder of this paper focuses on symbiotic and nonsymbiotic nitrogen fixation.

SYMBIOTIC NITROGEN FIXATION

Nitrogen-fixing plants found in western larch ecosystems fall into two groups: (1) plants in the family Leguminosae and (2) other nodulated but nonleguminous vegetation. Table 1 shows the co-occurrence of several nitrogen-fixing plants with western larch in climax forests of northern Idaho, central Idaho, and Montana. The greatest potential for exploiting biological nitrogen fixation in forestry is in managing symbiotic nitrogen-fixing plants (Jurgensen and others 1991).

Arnalds (1979), as cited by Turvey and Smethurst (1983), reported excellent growth of larch when planted with Alaskan lupine (*Lupinus nootkatensis*). While there has been little nitrogen-fixation research specifically related to western larch, a moderate amount of research has been done on nitrogen fixation in ecosystems where larch is present.

In forest ecosystems, 5 to 10 percent of the nitrogen cycled annually is by nitrogen fixation; usually this is much more than nitrogen input associated with precipitation (Granhall and Lindberg 1980). In the Pacific Northwest, rain contains only small amounts of nitrogen, ranging from 0.5 to 5 kg per ha per year (Bormann 1988).

Forest soil acidity strongly influences symbiotic nitrogen fixation. Nodule formation in legumes is inhibited when soil pH falls below the range of 4.5 to 5.5 and optimum pH for nodule formation is 7.0 (Carlyle 1986). Burning generally raises soil pH due to ash production, and following fires, forest soil can be pH 7.0 (Jurgensen and others 1981). Soils in the inland Mountain West where western larch occurs generally have a pH range of 4.1 to 6.1 (Feidler and Lloyd, these proceedings), indicating that legumes growing in conjunction with western larch may be fixing nitrogen at less than optimum.

Succession/Plant Distribution

Nitrogen is often in short supply in the early stages of primary succession (Vitousek and Walker 1987) and is a crucial factor in ecosystem development (Marrs and others 1981). Ecosystem studies have suggested that biological nitrogen fixation may be a major source of the nitrogen accumulated both in forest biomass and in the forest floor during succession (Cushon and Feller 1989).

As a pioneer species, western larch requires disturbance, such as fire, to establish. Fire also plays a significant role in the establishment of *Ceanothus*, a major nitrogen-fixing plant. *Ceanothus* seed stored in the forest floor and surface mineral soil remains viable in the soil for up to 200 years and needs a heat treatment to break dormancy. The more complete and intense the burn, the greater the development of *Ceanothus* from buried seed (Noste and Bushey 1987; Orme and Leege 1976).

Fire can also influence the development of other important nitrogen-fixing plants. Some studies in northern Idaho cedar-hemlock habitat types reported *Alnus* was increased after burning while others reported it was more restricted (Mueggler 1965; Stickney 1986; Wittenger and others 1977). *Lupinus* species are colonizers of disturbed soils (Kenny and Cuany 1990), and some are fire survivors that can maintain themselves in the initial stages of plant succession following fire. Lupines are deep-rooted species that likely store seed in the soil and can probably survive burning disturbance (Steele and Geier-Hayes 1987). In southwestern Montana, species of *Lupinus* were abundant after wildfire (Jurgensen and others 1991; Lyon and Stickney 1976). However, canopy coverage of *Lupinus* remained about the same after wildfire in a northern Idaho cedar-hemlock stand (Stickney 1986). The improvement of soil nitrogen status by nitrogen-fixing colonizers of disturbed soils paves the way for later succession.

Table 1—Co-occurrence of nitrogen-fixing plants and western larch in forest climax series in Idaho, central Idaho, and western Montana

	Habitat type series[1]				
N-fixing plant	**PSME**	**THPL**	**TSHE**	**ABGR**	**ABLA**
	Region where plant is found				
Nonlegumes					
Alnus rubra			NI[2]		
Ceanothus sanguineus	NI, M	NI		NI, CI, M	
C. velutinus	NI, M		NI	NI, CI, M	
Shepherdia canadensis			NI, M	NI, CI, M	M
Legumes					
Lathyrus nevadensis	NI, M	NI		NI, CI, M	CI
Thermopsis montana	NI, M	NI, M	NI, M	NI, CI, M	NI, CI, M
Vicia americana	NI, M	NI		NI, CI, M	NI, CI, M

[1] PSME = Douglas-fir, THPL = western redcedar, TSHE = western hemlock, ABGR = grand fir, ABLA = subalpine fir.
[2] NI = northern Idaho, CI = central Idaho, M = western Montana.

Nitrogen Input

Substantial amounts of nitrogen could be added by nitrogen-fixing plants in seral forests where western larch occurs. On highly productive sites in western Oregon and Washington up to 100 kg of N per ha per year were added by *Ceanothus* and *Alnus* (Conard and others 1985; Kimmins and others 1985). The amount of nitrogen fixed by symbiotic nitrogen fixers depends on plant density, plant vigor, percentage of plants nodulated and environmental conditions (Everett and others 1991). However, the mere presence of nitrogen-fixing plants does not guarantee that they will fix nitrogen because symbiotic nitrogen fixation is dependent on the amount of light reaching the soil surface and soil moisture levels during the growing season (Sprent and Sprent 1990).

NONSYMBIOTIC NITROGEN FIXATION

When nitrogen-fixing plants are scarce, nitrogen fixation by free-living soil microorganisms may be the only source of biological nitrogen. In addition to fixation in the soil, nonsymbiotic nitrogen fixation also occurs on leaves, twigs, bark, glands, buds, and epiphytic plant parts, and in association with lichens (Dawson 1983).

Organic matter is the energy source for most free-living, nitrogen-fixing microorganisms (Jurgensen and Davey 1970). Therefore, nonsymbiotic nitrogen fixation rates correlate well with soil organic matter content and are generally higher in woody residue and surface organic layers than in mineral soil (table 2). Woody residue decay may enhance soil nitrogen status by providing a long-term environment for nitrogen-fixing microorganisms. The amounts of nitrogen fixed in woody substrates are often small but can last hundreds of years and help minimize nitrogen losses from timber harvest and postharvest site preparation (Harvey and others 1987; Jurgensen and others 1984).

Nonsymbiotic nitrogen-fixing microorganisms do not increase soil nitrogen levels to the point that nitrogen is no longer limiting for plant growth. This is due in part to the high amount of energy required for nitrogen fixation. Nitrogen fixation is highly energy expensive, requiring about 18.8 g C per gram nitrogen fixed or 10 to 100 g of glucose per gram of nitrogen fixed (Bormann 1988; Bormann and Gordon 1989). Thus, energy sources available in the organic matter of most soils are not adequate to fix large amounts of nitrogen (Jurgensen 1973).

Nitrogen Input

Nitrogen-fixation values cited in the literature range from <0.1 to 55 kg N per ha per year, but in the Western United States rates are <2 kg N per ha per year (Boring and others 1988; Dawson 1983; Jurgensen and others 1991; Kimmins and others 1985). Nitrogen fixation by nonsymbiotic sources in ecosystems where western larch is present generally reflects site productivity (table 2). Values are highest in the most productive cedar-hemlock stands of northern Idaho and lower in Montana. However, all these values are lower than most reports of symbiotic nitrogen fixation in the Northwest.

Harvesting Impacts

Harvesting is probably the single most influential management factor that impacts soil nitrogen supplies. Bormann and Gordon (1989) cautioned that short-term forest productivity may be enhanced by silvicultural practice. However, long-term loss increases when a greater proportion of the total biomass is harvested, rotation length is reduced, planting densities are increased or fast-growing species are cultured.

The removal or destruction of organic matter by harvesting and site treatments also results in reductions of nitrogen storage and nonsymbiotic nitrogen fixation (table 3). A prescribed burn after timber harvesting a cedar-hemlock site in northern Idaho removed 62 percent of the forest floor, soil wood, and woody residue, resulting in a 63 percent decrease in nitrogen fixation. Intensive slash removal reduced nitrogen fixation by 48 percent. Clearcutting, without site preparation, reduced nitrogen fixation by only 16 percent. However, where large amounts of woody residue were maintained, nitrogen fixation was 33 percent greater than in a comparable uncut stand. Harvesting and site preparation removed the forest floor on all treatments, except the heavy slash treatment.

Table 2—Nonsymbiotic nitrogen-fixation in old-growth forests containing western larch as a significant stand component (Jurgensen and others 1991)

Soil component	Subalpine fir (Montana)		Cedar-hemlock (Montana)		Cedar-hemlock (Idaho)	
	ng N/d[1]	*g N*[2]	*ng N/d*	*g N*	*ng N/d*	*g N*
Woody residue	21.0	515	15.6	230	35.2	1,428
Forest floor	32.5	328	15.7	192	14.0	88
Soil wood	26.3	250	7.0	91	19.1	178
Mineral soil	.7	379	.6	326	4.0	1,197
Total	—	1,472	—	839	—	2,891

[1] Nanograms (10^{-9}) of N fixed/g of soil/day from June-October 1977 as measured by the acetylene reduction technique using a 3:1 ethylene to N conversion ratio.

[2] Total N fixed/ha over a 180-day period. Mineral soil sampled to a depth of 30 cm.

Table 3—Nonsymbiotic nitrogen fixation on a cedar-hemlock stand containing western larch in northern Idaho after timber harvesting and woody residue removal (Jurgensen and others 1992)[1]

Soil component	Residue treatment									
	None		Burn		Intensive removal		Heavy residue		Uncut	
	Mg[2]	*g N*[3]	*Mg*	*g N*	*Mg*	*g N*	*Mg*	*g N*	*Mg*	*g N*
Woody residue	146.0	984	57.9	177	10.6	111	249.8	1,483	154.3	1,428
Forest floor	16.7	110	5.5	26	13.3	73	34.5	326	23.2	88
Soil wood	50.9	109	22.4	47	51.6	195	50.3	430	47.9	178
Mineral soil	—	1,218	—	826	—	1,125	—	1,608	—	1,197
Total	213.6	2,421	85.8	1,076	75.5	1,504	334.6	3,847	255.4	2,891

[1] Site was clearcut to a 12.7-cm diameter top. Residue treatments: none = residue left; burn = broadcast burned in the fall; intensive removal = residue removed by blading with a crawler tractor; heavy residue = residue removed by blading was added to residue left on another area.

[2] Dry weight (metric tonnes/ha) of organic material on top of mineral soil.

[3] Total N fixed/ha over a 180-day period, 1977. Mineral soil sampled to a depth of 30 cm.

Decayed wood in the soil was less affected by logging and consequently became a more valuable source of nitrogen fixation than the forest floor in harvested stands.

Woody residue provided a major source of nonsymbiotic nitrogen fixation in the cedar-hemlock stand before harvesting (table 4). However, a significant amount of the woody residue was removed or destroyed by the prescribed burn and intensive harvesting (table 3). This, in turn, resulted in low posttreatment nitrogen-fixation rates in both the intensive harvest and burn treatments. The nitrogen-fixation input from woody residue on this site was directly related to the amount and type of woody material left after harvest. The largest amounts of nitrogen fixation occurred in large logs in advanced decay stages. Most of these were destroyed during the harvesting operations (Jurgensen and others 1992).

SILVICULTURAL IMPLICATIONS

Many early and midseral stages of plant succession in the Inland Northwest include symbiotic nitrogen-fixing species (Steele and Geier-Hayes 1987, 1989, 1992). However, density and diversity of nitrogen-fixing plants diminish during later seral/climax development where light is limiting (Bormann and Gordon 1989). Because western larch is an early seral species that is shade intolerant, it has the opportunity to grow in association with nitrogen-fixing plants that would most likely stimulate growth. Understory plants will likely fix significant amounts of nitrogen if they can be encouraged during early stand establishment or after heavy thinning (Gadgil 1976). However, nitrogen fixers, especially shrubs, compete with larch seedlings for moisture, nutrients, and light during establishment. If western larch is overtopped, its crown rapidly deteriorates and its vigor declines (Dawson 1983; Schmidt and Shearer 1990). But once western larch becomes established it has excellent juvenile growth (Haig and others 1941; Schmidt and others 1976), and competition from nitrogen fixers should not be a serious problem.

Western larch can be perpetuated by using prescribed fire in conjunction with other silvicultural practices (Arno and Fischer, these proceedings). Fire is also essential for *Ceanothus* regeneration, which probably presents the best management opportunity to encourage nitrogen input on western larch sites. Even though *Ceanothus* can be a strong competitor, better initial establishment of some conifer seedlings under *Ceanothus* has been reported (Conard and others 1985).

Dawson (1983) and Jurgensen and others (1979, 1992) discussed various forest management practices that would encourage high rates of nonsymbiotic nitrogen fixation. Dawson (1983) stressed leaving slash in close contact with the soil to ensure more rapid decomposition. This practice should increase bacterial nitrogen fixation by increasing the amount of decaying wood. Although annual nitrogen input by nonsymbiotic nitrogen-fixing bacteria is not large, it may be highly significant over a stand rotation, particularly on sites with low densities of symbiotic nitrogen-fixing vegetation (Jurgensen and others 1992).

SILVICULTURAL PRESCRIPTIONS

Contributions of nitrogen from nitrogen-fixing plants have been compared to nitrogen fertilization of forest stands. Gordon (1983) listed significant advantages and disadvantages resulting from introducing or maintaining a nitrogen-fixing plant species as part of the development of silvicultural prescriptions.

Advantages:

1. The species produce a regular supply of available nitrogen over a longer time.
2. Nitrogen will less likely volatilize and leach.
3. Public concern about chemicals added to forests will likely decrease.
4. The plants are a source of increased organic matter.

Disadvantages:

1. Enhancement of biological nitrogen fixation is limited by knowledge of nitrogen-fixing species.
2. Biological nitrogen fixation is likely to be more expensive on a unit applied nitrogen basis than applied fertilizer nitrogen.
3. The plants are a possible source of competition to tree seedlings.
4. The species will likely produce a managerially more complex ecosystem.

Table 4—Contribution of surface soil organic materials to nonsymbiotic nitrogen fixation in three old-growth forests containing western larch (Jurgensen and others 1991)

Soil component	Subalpine fir (Montana)		Cedar-hemlock (Montana)		Cedar-hemlock (Idaho)	
	Mg[1]	*% N fix*[2]	*Mg*	*% N fix*	*Mg*	*% N fix*
Woody residue	145.7	35	83.2	27	154.3	49
Forest floor	36.0	22	49.7	23	23.2	3
Soil wood	35.9	17	50.5	11	47.9	7
Mineral soil	—	26	—	39	—	41

[1] Dry weight (metric tonnes/ha) of organic material on top of mineral soil.
[2] Percentage of total nitrogen-fixation shown in table 3.

Natural sources of nitrogen are much less likely to induce the adverse impacts often derived from short-term pulses in nitrogen availability. Possible negative impacts of nitrogen pulses include increased shoot-to-root ratios, sensitivity to drought stress, and susceptibility to insect and disease problems. Thus, in contrast to disadvantage 4 cited above, effects of natural biological sources of nitrogen may be easier to predict than those of fertilizer applications, although they may be difficult to achieve.

Nonsymbiotic nitrogen fixation should not be overlooked in the silvicultural prescription. The two primary sites for nitrogen-fixation—surface organic layers and woody residue—need to be protected and preserved. If proper planning and care are not taken during timber harvesting, slash disposal and site preparation, considerable damage to the nonsymbiotic nitrogen-fixation system can occur. To reduce damage it is vital to avoid intensive slash removal. For example, if prescribed burning or mechanical site preparation is part of the prescription, a balance must be struck. An intensive burn that ensures mineral soil for western larch seed germination could be controlled to avoid extensively destroying the nitrogen-fixing environment in the forest floor, soil wood, and woody residue.

Knowledge of how biological nitrogen fixation interacts with other ecosystem processes should be viewed as a basis for developing silvicultural tools for forest managers who are now faced with the challenge of working at the ecosystem level. Biological nitrogen fixation and nitrogen management information should be included in silvicultural prescriptions because of their critical interactions with ecosystem processes (Gordon 1983; Jurgensen and others 1992).

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Distribution of Nutrients in the Stem of Eastern and European Larches

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Abstract—Internal reserves of nutrients in a stem are an important part of the biochemical cycle of elements, especially during spring flush of needles. Nutrient pattern and distribution zones were established for European larch (*Larix decidua* [Mill.]) and eastern larch (tamarack) (*L. laricina* [Du Roi] K. Koch). Concentrations of mobile elements (P and K) were the highest in the external part of the xylem, while the concentrations of immobile elements or elements of intermediate mobility (Ca, Mn, Mg, and Zn) were the highest in the internal part of the xylem. There were five distribution zones identified with P.

Larch stemwood consists of three zones. The first, total bark, includes cambium, phloem (cortex), phellogen (phellem and phelloderm), and outside bark. The second zone, commonly referred to as sapwood, contains the living component of the xylem tissue, is found in the external zone of the xylem, and has a yellowish-white color. The final zone, the heartwood, has a russet-brown color and is in the inner rings of the xylem. The heartwood contains a central zone, the pith, that can be distinguished from the other annual rings by its position and color. These zones correspond to the ones proposed by Frey-Wyssling and Bosshard (1959), according to various cytological and physiological characteristics of the ray cells. The distinctions between each of these zones, however, are not always obvious, especially the transition zone.

The sapwood contains living cells and reserve materials and has three physiologically important functions: (1) it conducts water and salts in solution to the cambium and leaves; (2) it assures structural support to branches, thus providing proper position of foliage for air and light; and (3) it serves as a reservoir for water, food reserves, and nutrients (Hillis 1987; Hook and others 1972). Heartwood is characterized by the presence of arabinogalactan, an extractive, which is absent in the sapwood (Côté and others 1966). It contains no living cells, as reserve materials have been removed or converted (Hillis 1971, 1987). Possibly under genetic control, the heartwood of larch starts to form during the fifth or sixth year (Hirai 1951, 1952; Schober 1953; Trendelenburg and Mayer-Wegelin 1955), but an average of 19 sapwood rings has been reported for a 58-year-old eastern larch (tamarack) (Yang and others 1985). Although the number of sapwood rings decreased with height, the sapwood cross-sectional width remained relatively constant at different levels in the tree until approximately 12 m in height (Yang and others 1985).

The concentrations of several nutrients have been found to exhibit systematic variations on both sides of the sapwood/heartwood transition zone (Gilbroy and others 1979). In general, concentrations of N, P, and K are higher in the sapwood than the heartwood, while the opposite is true for Ca, Mg, and Mn. However, this pattern can vary with species, site, environment, and other local factors. Not only does each species have its own distribution pattern, but individuals growing on the same site may show differences in concentration values (Beadle and White 1968).

Most studies report a higher concentration value for P in the external zone of the xylem. Differences between sapwood and heartwood concentrations of P are generally so pronounced that this distinction has been used to delimit sapwood area (Bondietti and others 1990), to discriminate distribution zones in the xylem (Clément and Janin 1976; Janin and Clément 1972), and to define a functional zone or biologically active zone of the xylem (Clément and Janin 1976; Maurer and others 1986; McClenahen and others 1989; Ranger 1981). In view of this constant pattern, P can be seen as one of the best discriminants to delimit the distribution zones of nutrients in the stem. Lower concentrations of P and K in the heartwood supports the hypothesis of a retranslocation during heartwood formation (Bowen 1984; van den Driessche 1984). Specifically, the analysis of P, K, Ca, Mg, Mn, and Zn in the annual rings of both European and eastern larches was conducted to (1) establish patterns of nutrient distribution in the stem for every year of growth and (2) delimit, using P, the distribution zones of nutrients in the different parts of the stem.

MATERIAL AND METHODS

Two 18-year-old plantations, one of European larch (*Larix decidua* [Mill.]) and one of tamarack (*L. laricina* [Du Roi] K. Koch), less than 300 m apart, were selected near Chartierville, Province of Québec, Canada (45°19' north, 71°6' west, 500 m elevation). These sites receive between 1,000 and 1,300 mm of precipitation yearly. The trees were planted in 1973 at a spacing of 2 to 3 m, and no treatment has been applied since. The European larch plantation is on an orthic humo-ferric podzol (Canada Soil Survey Committee 1978) originating from a glacio-fluvial outwash deposit. The texture is a loamy sand in the solum and gravelly sand in the IIC horizon, with rapid drainage.

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In the tamarack plantation, an eluviated dystric brunisol has developed on till of loam texture and has a moderate drainage. This soil is more fertile than that of the European plantation (table 1).

Four representative trees were cut in each plantation between November 15 and 18, 1989.

Sampling and Analysis Procedures

Disks 3 to 4 cm thick were cut at every 20 cm along the stem for four trees of each species. An additional disk was cut at the 10-cm level from the ground. Disks were frozen the same day and were kept frozen during all measurements and separation of rings. Each disk was cut into a cross shape to ensure samples from all directions. The end of each cross was separated into annual growth rings; the material was dried at 70 °C for 36 hours and ground to 2 mm with a Wiley Mill, equipped with stainless sieve and cutters. Because each year of growth was represented by two or more disks, and mean annual height growth was more than 50 cm a year, the material representing the same year of growth was pooled to form one sample. Of this composite sample, 2 to 3 g were redried at 70 °C for 2 h and kept in the dessicator until weighing. Then 1 g of material was dry ashed for 5 h at 500 °C in a muffle furnace, and ashes were recuperated with 10 mL HCl 2 M. Analysis of solutions for P, K, Ca, Mg, Mn, and Zn was done on a plasma emission spectrophotometer (ICP) (Perkin Elmer's Plasma 40). Aluminum and copper concentrations were determined in two stems for both species.

Data Analysis

Ratios for P, based on the relationship between the concentrations for two contiguous annual rings, were calculated starting at the external part of the stem. The higher the value, the higher the difference between the concentrations of two adjoining annual rings. The ratios are reported in a triangle figure representing the 151 points of sampling, with age on the *Y* axis and annual rings on the *X* axis.

RESULTS

Although concentration values differ between European larch and tamarack, nutrients follow the same three distribution patterns in the xylem from sapwood to heartwood: (1) a decreasing/constant gradient of concentration of P for both species, and K for European larch, with a sharp decrease in the transition zone; (2) a constant/increasing gradient of Ca, Mg, and Mn in both species, and K for tamarack, with maximum values in the heartwood and pith area; and (3) stable values of Zn, Cu, and Al for both species in all zones of xylem, except pith area, and maximum values in bark (fig. 1). For both species, there was an evident vertical distribution of P throughout the stem, increasing from the base of the stem to the crown. Potassium, and to a lesser extent Mg, showed the same vertical pattern for European larch. Other nutrients had no vertical gradient (Myre 1992).

In larch, the distribution patterns of P can be divided into four zones: (1) apical (last 6 years); (2) bark; (3) external xylem (one to seven annual rings); and (4) internal xylem (fig. 2 and 3). Vertical and horizontal limits can be established with P concentrations. The ratios between concentrations of P between contiguous annual ring delimit five major distribution zones of the stem (fig. 4 and 5). In the sapwood, ratios decrease to a low value, increase to a maximum and then decrease again. This pattern enables the establishment of a fifth zone, the transition zone. Apart from this, these zones correspond almost exactly with those established by concentration values. The ratios do not distinguish a central zone (pith area). These zones are similar to those obtained with factorial scores determined by principal component analysis (Myre 1992).

Table 1—Physio-chemical properties of horizons of the orthic humo-ferric podzol (European larch plantation) and of the eluviated dystric brunisol (tamarack plantation)[1]

Species	Horizon	Depth	pH	Sand	Silt	Clay	C (org.)	P (Bray II)	K	Ca	Mg	CECE
		cm	*$CaCl_2$*	*- - - - - - - - - - - - -Percent - - - - - - - - - - - -*				*mg/kg*	*- - - - - - - - - - - -cmol(+)/kg- - - - - - - - - - -*			
European larch	LF	2-0	4.2	—	—	—	33.4	—	3.18	48.2	10.3	74.2
	Ap	0-8	3.9	64	23	13	8.56	9.20	.39	3.43	1.05	14.5
	Bf	8-21	4.3	75	14	11	3.64	6.90	.02	.38	.03	3.77
	BC	21-32	4.6	77	13	10	1.26	15.0	.01	.20	.01	2.05
	IIC	32^+	4.7	89	4	7	.46	24.2	.01	.09	.01	1.90
Tamarack	LF	2-0	3.9	—	—	—	39.6	—	3.54	49.9	9.86	80.9
	Ap	0-9	3.6	43	35	16	1.30	1.93	.33	7.08	1.23	18.6
	Bf	9-15	4.3	46	31	24	4.45	6.30	.02	1.12	.06	5.59
	BC	15-23	4.5	47	42	22	2.76	6.20	.02	.51	.03	3.49
	C	23^+	4.6	36	35	19	1.35	13.2	.03	.41	.02	2.31

[1] pH was determined with $CaCl_2$ 10 mM with a soil:solution ratio of 1:10 for LF horizons and 1:2 ratio for mineral horizons. The texture was determined by the Bouyoucos method. Organic carbon was determined by oxidation with potassium dichromate. Exchangeable cations were extracted with NH_4NO_3 1M (Stuanes and others 1984). Acidity was determined by titration of the extract, and the other cations were analyzed with ICP. Effective CEC (CEC_E) represents the sum of and the acidity and of other cations.

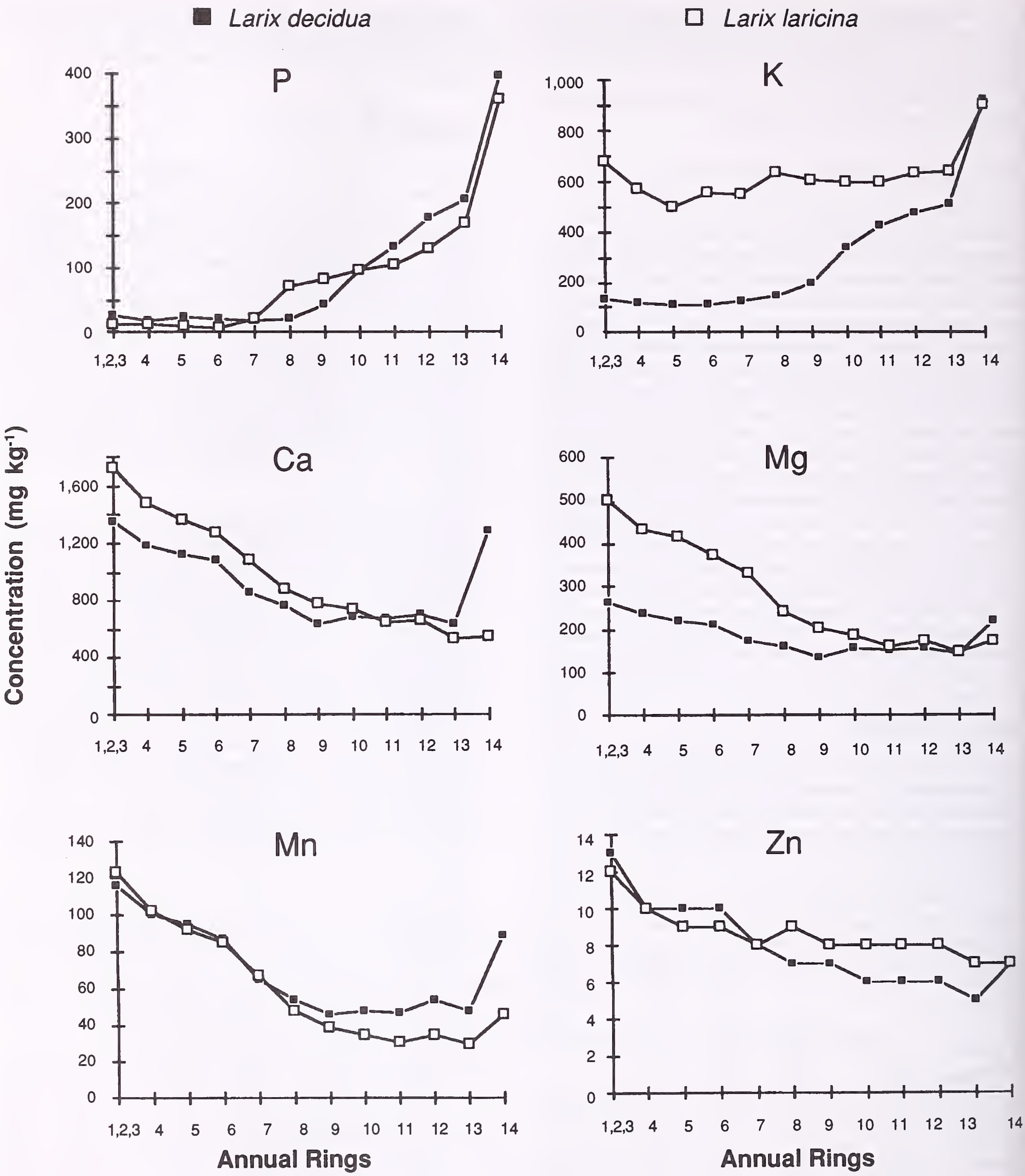


Figure 1—Distribution of nutrients in annual rings of European and eastern larches at the d.b.h. level (1.4 m). 123**: one sample for the three first annual rings.

DISCUSSION

Distribution Patterns of Elements

The distribution pattern of nutrients for *Larix* spp. is similar to that reported for other species, including *Eucalyptus* spp. (Baker and Attiwill 1985; Lambert 1981), tropical and subtropical species (Beadle and White 1968; Grubb and Edwards 1982; Lambert 1981; Wright and Will 1958), deciduous species (Berish and Ragsdale 1985; Clément and Janin 1976; Frelich and others 1989; Janin and Clément 1972; Merrill and Cowling 1966; Tout and others 1977), and coniferous species (Frelich and others 1989; Merrill and Cowling 1966; Tout and others 1977; Wright and Will 1958). Nutrient distribution patterns follow three gradients in larch stems, depending on the specific elements. The first distribution pattern is a gradient similar to the one proposed by Merrill and Cowling (1966): maximum values for the last formed annual ring, gradual elution (five or six annual rings), and stabilization of concentrations in the heartwood. Maximum values in the last formed annual ring has been reported for other species (Hampp and Häll 1974; Queirolo and others 1990). Transport of these ions is dependent on plant metabolism (Sutcliffe 1976).

The second type of distribution follows an inverse pattern, although the last formed annual ring also contains high values. The lowest values are found in the sapwood, while the heartwood contains the highest values, with maximum concentrations in the pith area for most elements. Transport of these ions is dependent on transpiration (Sutcliffe 1976).

The third type of distribution, typical of heavy metals, is characterized by constant concentrations for all annual rings (Al, Cu, and Zn). No retranslocation or accumulation is noticeable for these elements.

Distribution Zones

The distribution patterns of the elements and ratios established with P allows a regrouping of nutrients into four or five distribution zones (fig. 2 through 5). The first, the apical zone, is characterized by high concentrations of P and K and relatively low values of Ca and Mn. Stored water is mainly located in the tree crown (Schulze and others 1985), and therefore the nutrient reserve in this zone can be regarded as essential during the establishment of tree water potential.

Age	123**	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Bark
17-18*	1551																
16	761																
15	135	382	1203														
14	75	193	439	1081													
13	52	124	256	599	1045												
12	21	74	143	235	410	932											
11	23	19	91	164	217	413	946										
10	22	17	46	128	179	207	346	912									
9	31	24	14	44	138	166	226	381	854								
8	26	19	16	21	82	157	174	205	403	846							
7	27	20	15	17	31	98	141	176	199	388	736						
6	24	26	21	16	21	44	112	148	181	220	355	745					
5	27	19	25	21	18	21	43	96	133	178	206	398	706				
4	28	22	20	22	22	24	29	46	91	153	195	236	412	709			
3	27	22	20	19	18	20	22	43	73	105	156	202	267	427	616		
2	30	30	17	19	14	12	12	34	54	105	143	227	243	280	476	553	
1	25	25	21	14	10	10	10	12	27	72	120	183	203	230	274	501	552

Annual rings

Figure 2—Distribution's gradient of phosphorus (mg/kg) for European larch ($n = 4$). 17-18*: one sample for both ages. 123**: one sample for the three first annual rings.

Age	Annual rings																
	123**	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Bark
17-18*	1856																
16	1298																
15	289	809	1992														
14	173	362	674	2004													
13	61	139	247	615	1828												
12	30	95	129	218	519	1567											
11	16	60	94	134	207	485	1355										
10	17	25	79	104	134	183	467	1319									
9	14	15	57	87	112	133	187	478	1337								
8	16	10	16	65	84	112	132	186	444	1277							
7	14	11	9.0	46	75	101	113	138	190	442	1159						
6	14	9.0	8.0	13	58	79	99	108	132	186	410	1111					
5	13	11	10	8.0	21	72	83	96	106	132	169	363	1069				
4	18	11	9.0	9.0	8.0	34	82	79	93	115	121	180	379	1033			
3	14	12	12	11	10	14	39	82	89	87	109	118	163	395	1062		
2	18	15	13	11	11	10	16	48	84	98	92	107	139	185	395	1009	
1	29	29	17	14	12	10	11	25	63	111	151	124	145	162	207	419	1067

Figure 3—Distribution's gradient of phosphorus (mg/kg) for eastern larch ($n = 4$). 17-18*: one sample for both ages. 123**: one sample for the three first annual rings.

The second, the external zone, is characterized by maximum values of P for both species and of K for European larch. This zone contains between four to eight annual rings and is the most permeable part of the xylem. These two zones represent the internal nutrient reserve of the stem, susceptible to be retranslocated to active parts of the plant.

The third, the internal zone, is characterized by the highest concentrations of Ca, Mg, and Mn. Most of the annual rings in this zone are russet-brown, and the moisture content is considerably lower than in the external and apical zones (Rudman 1966).

The fourth, the bark, is characterized by high concentrations for every nutrient. A fifth zone, the transition zone, can be delimited with the ratios.

The use of phosphorus ratios permits a quantitative evaluation of the limits of each zone, in comparison to limits defined by concentration values alone. This method is simple and reflects the modulations in each distribution pattern. These zones correspond to the ones proposed by Clément and Janin (1973, 1976) and Janin and Clément (1972), based on the distribution of P, for a 15-year-old poplar (*Populus trichocarpa* "Fritzi-Pauley"). These zones are also comparable to the ones delimited by the horizontal and vertical distribution of P, K, and Mg in a 15-year-old black pine (*Pinus nigra* Arn) by Ranger (1981). For larch and these other species, the distribution zones of nutrients are similar during this stage of development, and only the number of annual rings pertaining to each zone may differ.

The external and apical zones, containing between four to eight annual rings, could serve as an internal reserve of nutrients for the plant. On a daily basis, because transpiration occurs 2 to 3 hours earlier than the stem flow for larch (Schulze and others 1985), demands for nutrients are probably met by the most proximal internal reserve of mobile elements. Also, these reserves can almost entirely support the early shoot growth when the soil is frozen in spring (Jonasson and Chapin 1985), as well as compensate for temporary deficit during the growing season when uptake is insufficient (Bormann and others 1977; Bowen 1984; Ernst 1983). For *Eucalyptus obliqua* (L'Hérit.), between 46 and 54 percent of gross annual demand of P is supplied by internal redistribution (Baker and Attiwill 1985). Retranslocation during the transition from sapwood to heartwood was estimated to be 15 percent of total redistribution.

Furthermore, the external and apical zones are likely the most susceptible to correspond to the first and second levels of storage in the stem proposed by Miller and others (1979) and could explain the long-term response of a plant after a fertilizer treatment.

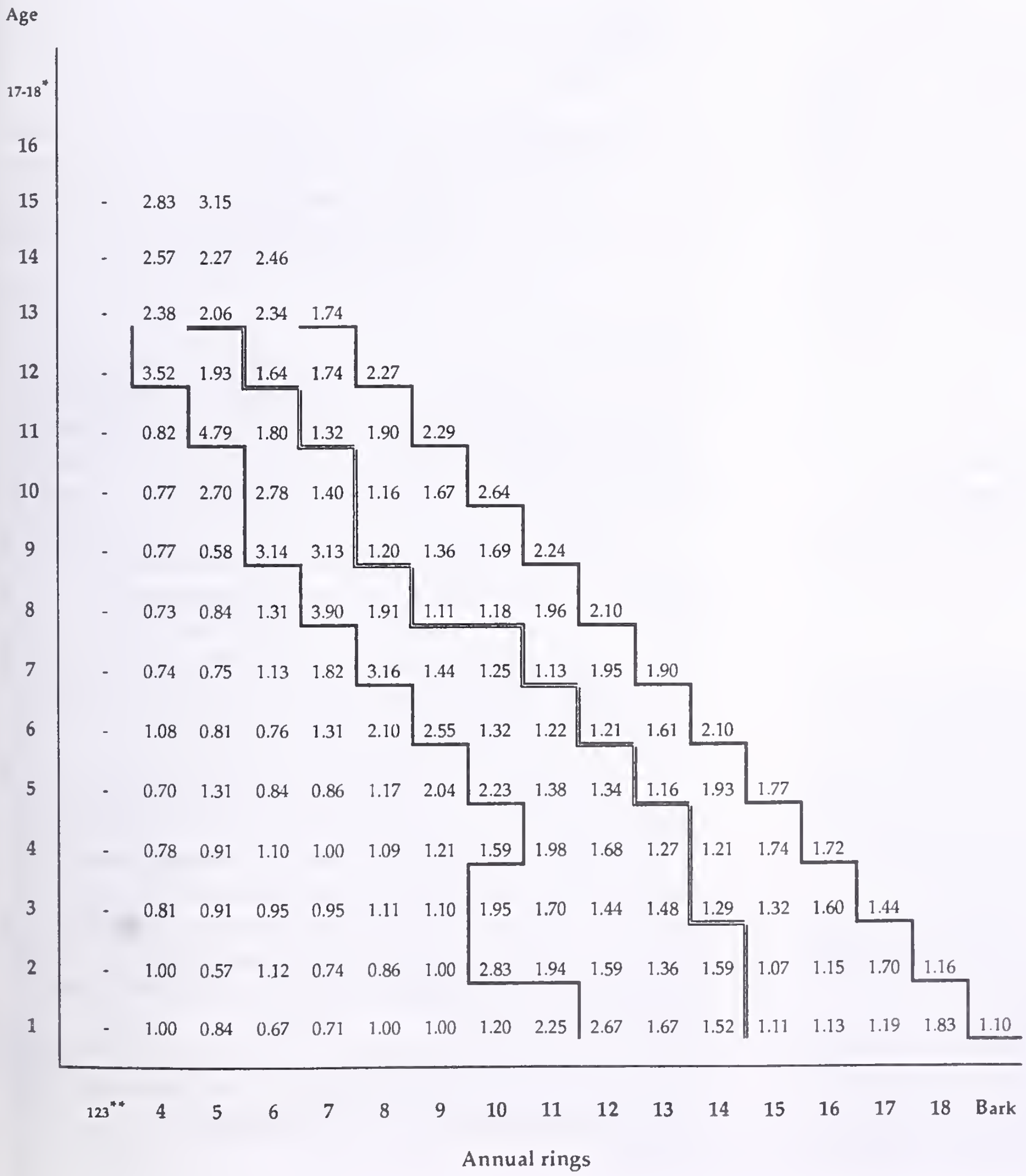
For larch and other species, the apical and external zones are especially important for P. During the first phase of development of the buds, P in the xylem sap is provided by the parenchyma cells, not from the roots (Burström 1948). Mutoh (1972) reported that 55 percent of P from perennial parts is redistributed to active parts during the spring flush for Japanese larch (*Larix leptolepis* Gord.). At the beginning of needle growth, more than 92 percent of P retranslocated to needles came from internal reserves. During this period, more than 85 percent of P uptake was retained by the root system. These results are similar to those from Meyer and Tukey (1965), who reported that 75 and 50 percent of P utilized by new growth came from the internal reserves for *Taxus media* Cl. and *Forsythia intermedia* Cl., respectively. In general, between 27 and 70 percent of the demand for P is met by internal reserves (Gosz 1981; Nihlgard 1972; Switzer and Nelson 1972; Turner 1977). Assuming that the importance of stored mobile nutrients is related to vigor of the initial growth, this could be advantageous for larch in terms of light competition with other species during the spring flush (Mutoh 1972).

CONCLUSIONS

Xylem can be divided into different zones according to cytological and physiological characteristics, as well as by nutrient distribution. All of these criteria delimit the same four to five zones in the stem. Only the limits and the number of annual rings in each zone differ. However, the results of this study may not apply to larch at older ages or under different site conditions.

The external and apical zones of the xylem can be regarded as an important nutrient reserve, especially for P, and favor larch as a species for plantation on low fertility sites.

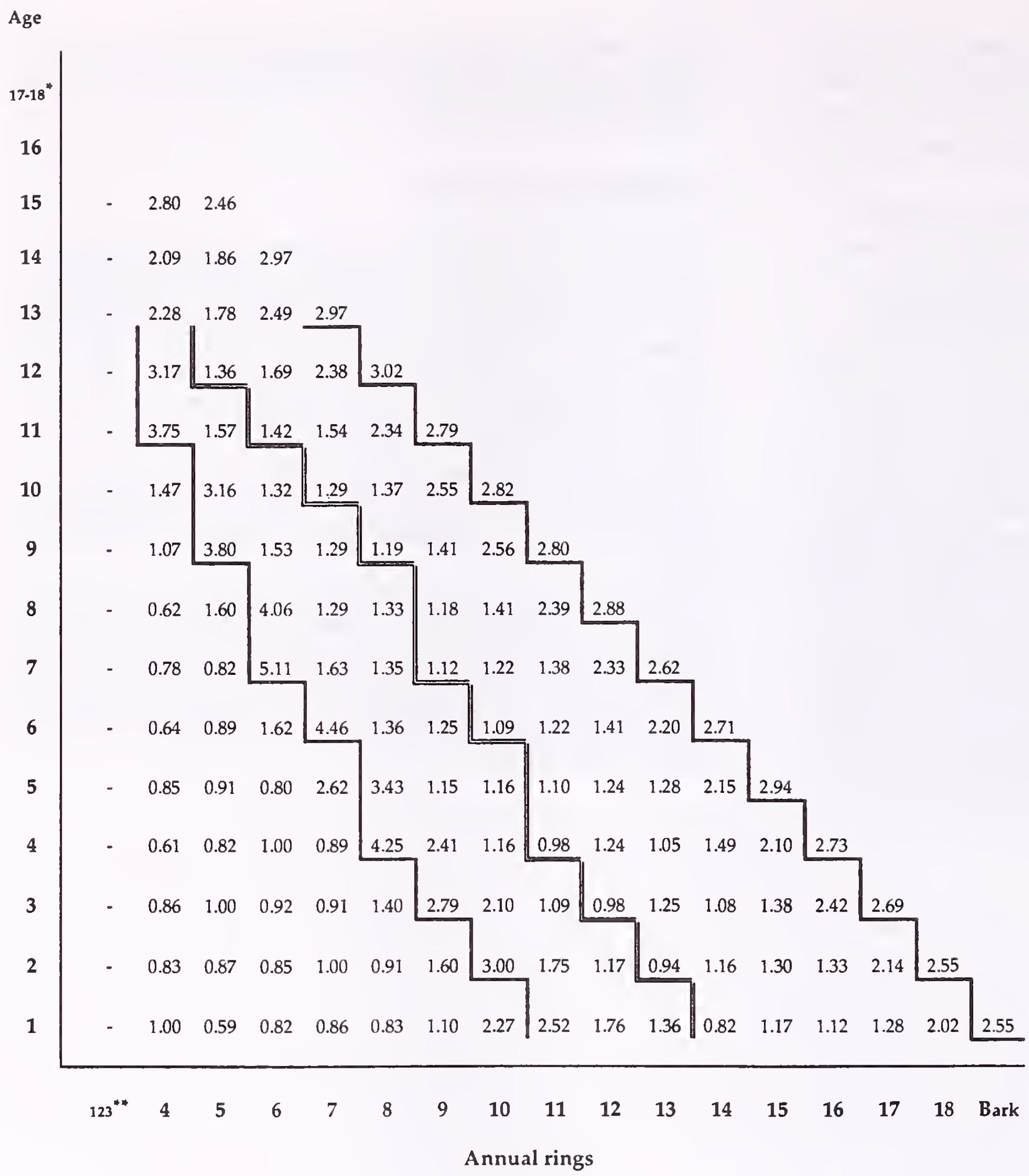
Fertilizer experiments would be useful to assess the capability of larch to retain nutrients in the biologically active xylem zone and the effect of such a treatment over a long period. Evaluation of nutrient removal during harvest could be more precise if these distribution zones were taken into account.



Age	123**	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Bark
17-18*																	
16																	
15	-	2.83	3.15														
14	-	2.57	2.27	2.46													
13	-	2.38	2.06	2.34	1.74												
12	-	3.52	1.93	1.64	1.74	2.27											
11	-	0.82	4.79	1.80	1.32	1.90	2.29										
10	-	0.77	2.70	2.78	1.40	1.16	1.67	2.64									
9	-	0.77	0.58	3.14	3.13	1.20	1.36	1.69	2.24								
8	-	0.73	0.84	1.31	3.90	1.91	1.11	1.18	1.96	2.10							
7	-	0.74	0.75	1.13	1.82	3.16	1.44	1.25	1.13	1.95	1.90						
6	-	1.08	0.81	0.76	1.31	2.10	2.55	1.32	1.22	1.21	1.61	2.10					
5	-	0.70	1.31	0.84	0.86	1.17	2.04	2.23	1.38	1.34	1.16	1.93	1.77				
4	-	0.78	0.91	1.10	1.00	1.09	1.21	1.59	1.98	1.68	1.27	1.21	1.74	1.72			
3	-	0.81	0.91	0.95	0.95	1.11	1.10	1.95	1.70	1.44	1.48	1.29	1.32	1.60	1.44		
2	-	1.00	0.57	1.12	0.74	0.86	1.00	2.83	1.94	1.59	1.36	1.59	1.07	1.15	1.70	1.16	
1	-	1.00	0.84	0.67	0.71	1.00	1.00	1.20	2.25	2.67	1.67	1.52	1.11	1.13	1.19	1.83	1.10

Annual rings

Figure 4—Zones delimited with phosphorus ratios for the European larch (*n* = 4). 17-18*: one sample for both ages. 123**: one sample for the three first annual rings.



Age	123**	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Bark
17-18*																	
16																	
15	-	2.80	2.46														
14	-	2.09	1.86	2.97													
13	-	2.28	1.78	2.49	2.97												
12	-	3.17	1.36	1.69	2.38	3.02											
11	-	3.75	1.57	1.42	1.54	2.34	2.79										
10	-	1.47	3.16	1.32	1.29	1.37	2.55	2.82									
9	-	1.07	3.80	1.53	1.29	1.19	1.41	2.56	2.80								
8	-	0.62	1.60	4.06	1.29	1.33	1.18	1.41	2.39	2.88							
7	-	0.78	0.82	5.11	1.63	1.35	1.12	1.22	1.38	2.33	2.62						
6	-	0.64	0.89	1.62	4.46	1.36	1.25	1.09	1.22	1.41	2.20	2.71					
5	-	0.85	0.91	0.80	2.62	3.43	1.15	1.16	1.10	1.24	1.28	2.15	2.94				
4	-	0.61	0.82	1.00	0.89	4.25	2.41	1.16	0.98	1.24	1.05	1.49	2.10	2.73			
3	-	0.86	1.00	0.92	0.91	1.40	2.79	2.10	1.09	0.98	1.25	1.08	1.38	2.42	2.69		
2	-	0.83	0.87	0.85	1.00	0.91	1.60	3.00	1.75	1.17	0.94	1.16	1.30	1.33	2.14	2.55	
1	-	1.00	0.59	0.82	0.86	0.83	1.10	2.27	2.52	1.76	1.36	0.82	1.17	1.12	1.28	2.02	2.55

Annual rings

Figure 5—Distribution of phosphorus ratios for eastern larch ($n = 4$). 17-18*: one sample for both ages. 123**: one sample for the three first annual rings.

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Ectomycorrhizal Relationships in Western Larch Ecosystems

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Martin Jurgensen
Russell Graham

Abstract— Ectomycorrhizae depend on soil organic materials for successful colonization and activity in larch ecosystems of the Intermountain West, U.S.A. Western larch (*Larix occidentalis* Nutt.) and three other conifer species were evaluated to assess the role of site disturbances and organic horizons on root growth and ectomycorrhizal activity. All species use organic horizons and principal growth substrates. Use of mineral horizons varies by species. Soil types with the greatest organic matter supported the greatest fungal and root growth.

Ectomycorrhizal fungi predominate in temperate forests of the Intermountain West (Molina and Amaranthus 1991). Conifers in western larch *(Larix occidentalis* Nutt.) ecosystems form an obligate, usually mutually beneficial, relationship with ectomycorrhizae. Ectomycorrhizal fungi, in general, may allow trees to successfully compete with grasses and herbs for resources (Bowen 1980), and their hyphae can connect plants of different species to facilitate the transfer of carbon and nutrients (Bjorkman 1960; Francis and others 1986; Kropp and Langlois 1990). In return, the fungi receive simple sugar energy sources from host plant roots (Bjorkman 1962; Marx and others 1977). Ectomycorrhizal associations depend on environment, particularly soil fertility (Bjorkman 1962) and organic matter content (Harvey and others 1978), and play a critical role in soil development and plant nutrition. Ectomycorrhizal tip formation is dependent on rhizosphere conditions such as moisture content, pH, temperature (Slankis 1974), and the content and type of organic matter (Bjorkman 1970; Harvey and others 1979). Harvey and others (1976, 1978, 1987) and Harvey (1982) have demonstrated that humus and brown cubical decayed wood are major substrates for ectomycorrhizal root-tip growth. Organic horizons also have a direct effect on tree root development (Coutts and Philipson 1977; Page-Dumroese and others 1989). Organic soil horizons, such as humus, decaying wood, and charcoal, are positively correlated with root growth because of their high moisture contents, high gas exchange, and low bulk densities.

Reforestation success depends on seedlings using site resources quickly. On relatively fertile sites, competition for nutrients, space, and water is keen. On droughty, nutrient-depleted, or stressful sites, only a brief period exists for favorable growth and, if a seedling fails to establish during that time, survival is unlikely (Amaranthus and Perry 1987, 1989). Ectomycorrhizal root structures help provide greater drought resistance than nonectomycorrhizal roots (Parke and others 1983). Microbial populations shift in response to the loss of organic matter, nutrients, and decaying root systems (Kozlowski and Ahlgren 1974; Perry and Rose 1983). On harsh sites, these alterations may jeopardize reforestation (Pilz and Perry 1984), because without a living host, ectomycorrhizal fungi do not persist long (Amaranthus and Perry 1987; Hacskaylo 1973). Total elimination of ectomycorrhizal roots was reported 1 year after clearcutting a high-elevation site in western Montana (Harvey and others 1980).

The effect of ectomycorrhizae on seedlings is not consistent (Kropp and Langlois 1990). Ectomycorrhizae are generally thought to be crucial for acceptable growth and survival (Perry and others 1987), and failure of afforestation efforts in absence of ectomycorrhizal inoculum (Meyer 1973) demonstrates their importance. However, Harvey and others (1991) point out that the "cost" of maintaining an active complement of these fungi may be high. Seedling growth responses vary according to soil chemical and physical characteristics as well as the fungal inoculum present (Danielson 1988; Marx and Cordell 1988).

This paper discusses comparative root growth and ectomycorrhizal colonization on four conifer species common to western larch ecosystems of the Intermountain West, U.S.A.

METHODS

Two studies of western larch ecosystems in the Northern Rocky Mountains have been conducted to assess the potential role of disturbance types and organic horizons on root growth and ectomycorrhizal formation and distribution. This entailed (1) evaluation of natural conifer regeneration associated with undisturbed and harvested forests, and (2) the development of planted conifer regeneration associated with four postharvest site preparation treatments.

The Natural Regeneration Study

This study was conducted on 11 different sites (fig. 1). Six sites were in northwestern Montana, three within the

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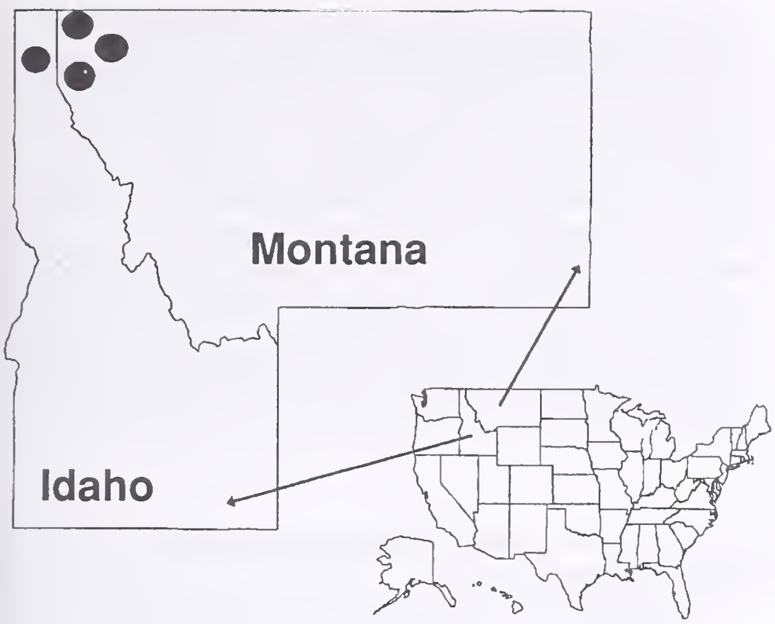


Figure 1—Location of natural regeneration study sites.

boundaries of the Coram Experimental Forest, one within the Lubrecht Experimental Forest, and two on the Miller Creek Watershed. The other five sites were within the Priest River Experimental Forest in northern Idaho. For further information on site location and characteristics see Harvey and others (1976). Site treatments included undisturbed forests, clearcuts with broadcast burns, and underburned partial cuts. Tree species examined were western larch, Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco), western white pine (*Pinus monticola* Dougl. ex D.Don), and Engelmann spruce (*Picea engelmannii* Parry).

Samples consisted of 10- by 30-cm soil cores (Jurgensen and others 1977) taken randomly, five from around each plot center, 10 plot centers total, scattered evenly over 1 ha of uniform conditions on each study site. Samples were taken during late spring and early summer over several years (1978 to 1982) to obtain maximum seasonal ectomycorrhizal activity for each site (Harvey and others 1978). Roots were separated from soil cores and active ectomycorrhizal tips counted with the aid of a dissecting microscope (10-50x). Each active tip was counted, even though in many cases it was part of a complex structure. From the core, total root length was also measured.

Analysis of variance was used for testing the effects of site, soil component, ectomycorrhizae, and root length. If significant differences were found, Duncan's multiple range test was used to evaluate significance of differences between means.

The Planted Regeneration Study

This study was conducted on two sites at different elevations within the Priest River Experimental Forest. For more information about site characteristics and soil chemical and physical properties from this study see Page-Dumroese and others (1986, 1989). A randomized complete block experiment was established at each site.

Both sites were mechanically prepared in the summer of 1982 by concentrating the forest floor and mineral soil from the top 10 cm of a 1.5-m wide area and forming mounds. Treatments on these sites consisted of (1) mounded soil beds with competing vegetation left in place, (2) mounded soil beds with competing vegetation removed manually in year 1, (3) a scalped area where the top 10 cm of organic matter and mineral topsoil were removed, and (4) an area essentially undisturbed after harvesting. At the low-elevation site, there were four treatments with four replications in one large block. A higher elevation, midslope site consisted of four treatments with three replications.

In May 1983, the treatments were planted with locally adapted, 1+0 container-grown Douglas-fir, western white pine, and western larch on a 1- by 1-m spacing.

Forty-five Douglas-fir and western white pine and five western larch seedlings were excavated from each treatment replication four times during the growing season for 2 consecutive years (1983 and 1984). Ectomycorrhizal root tips were counted on the entire seedling root system using a dissecting microscope. Seedling rooting depth and longest lateral roots were also measured.

An analysis of variance was conducted on the data, utilizing a randomized complete block design. The treatment means were separated using Duncan's multiple range test.

RESULTS AND DISCUSSION

Natural Regeneration Study

Species morphology and soil moisture were factors expected to influence ectomycorrhizal colonization of seedling roots, especially for natural regeneration (Harvey and others 1980). Generally, those habitat types with the largest amounts of soil organic matter (from Harvey and others 1987) supported the greatest numbers of ectomycorrhizae (table 1). In general, soil organic matter depth increased as precipitation and elevation increased.

Table 1—Total number of ectomycorrhizal root tips on naturally regenerated seedlings growing on a variety of habitat types (Cooper and others 1991)

Habitat type[1]	Western white pine	Engelmann spruce	Western larch	Douglas-fir
PSME/PHMA	[2]40a	—	—	10b
PSME/VAGL	—	—	93a	54a
ABLA/CLUN	2a	14b	—	14b
ABLA/XETE	17a	272a	14b	20b
THPL/PAMY	88a	—	27b	23b
TSHE/CLUN	—	39b	13b	55a

[1] PSME/PHMA = *Pseudotsuga menziesii/Physocarpus malvaceus*
PSME/VAGL = *Pseudotsuga menziesii/Vaccinium globulare*
ABLA/CLUN = *Abies lasiocarpa/Clintonia uniflora*
ABLA/XETE = *Abies lasiocarpa/Xerophyllum tenax*
THPL/PAMY = *Thuja plicata/Pachistima myrsinites.*
TSHE/CLUN = *Tsuga heterophylla/Clintonia uniflora.*

[2] Different letters indicate significant differences ($P \leq 0.05$) across habitat types.

Harvey and others (1980) noted that the quantity of ectomycorrhizal root tips in random soil samples directly reflect relative ecosystem productivity. In addition, each seedling species produced abundant ectomycorrhizae in specific habitat types. For example, Engelmann spruce seedlings produced the greatest number of ectomycorrhizae in the ABLA/CLUN habitat type, larch produced the most in the PSME/VAGL habitat type and western white pine was most prolific in the TSHE/CLUN habitat type. Douglas-fir appeared more of a generalist, producing about the same numbers of ectomycorrhizae in all habitat types.

Site treatments altered both location of seedling ectomycorrhizae and greatest root length (tables 2 and 3). In undisturbed conditions, neither Engelmann spruce nor western larch had longest roots or ectomycorrhizae in mineral or humus horizons. After a clearcut and burn, all four species had lateral roots and ectomycorrhizae in the mineral soil and decayed wood horizons. On the burned sites, lower pH values may have made the mineral soil more suitable for ectomycorrhizal activity.

In clearcut and burned sites, Douglas-fir used mostly decaying wood for ectomycorrhizal development. Western white pine and larch, conversely, formed most of their

Table 2—Total number of ectomycorrhizae root tips on naturally regenerated seedlings as affected by site treatment and soil horizon. Values are averages across habitat types (*n* = 114)

Treatment	Soil horizon	Western white pine	Engelmann spruce	Western larch	Douglas-fir
Undisturbed	Mineral	[1]43a	—	—	36a
	Humus	—	—	—	19b
	Decayed wood	23a	15a	13a	14b
Clearcut and burn	Mineral	88a	39a	16a	19a
	Humus	—	75a	—	6a
	Decayed wood	66a	39a	10a	41a
Partial cut and underburn	Mineral	—	—	98a	30a
	Humus	—	—	18a	64a
	Decayed wood	—	—	—	30a

[1] Different letters indicate significant differences ($P \leq 0.05$) across soil horizons within treatment.

Table 3—Total root length within random core samples as affected by site treatment and soil horizon. Values are averages across habitat types (*n* = 114)

Treatment	Soil horizon	Western white pine	Engelmann spruce	Western larch	Douglas-fir
		cm			
Undisturbed	Mineral	[1]17.0a	—	—	11.7a
	Humus	—	—	—	12.8a
	Decayed wood	14.5a	24.0a	18.4a	14.6a
Clearcut and burn	Mineral	17.7a	16.2ab	14.1a	14.8a
	Humus	—	11.0b	—	11.5a
	Decayed wood	19.1a	25.5a	19.5a	12.2a
Partial cut and underburn	Mineral	—	—	12.5a	13.5a
	Humus	—	—	13.3a	11.1a
	Decayed wood	—	—	—	5.0a

[1] Different letters indicate significant differences ($P \leq 0.05$) across soil horizons within treatment.

Table 4—Root length in random soil cores as affected by soil horizon. Values are averages across habitat types and treatment ($n = 243$)

Soil horizon	Western white pine	Engelmann spruce	Western larch	Douglas-fir
	- - - - - - - -	- - - - - - - - *cm*	- - - - - - - -	- - - - - - - -
Mineral	[1]17.7a	16.3a	13.3b	12.7b
Humus	—	—	25.0a	—
Decayed wood	17.8a	13.7a	18.9ab	14.8a
Charcoal	—	11.0a	13.3b	11.2c

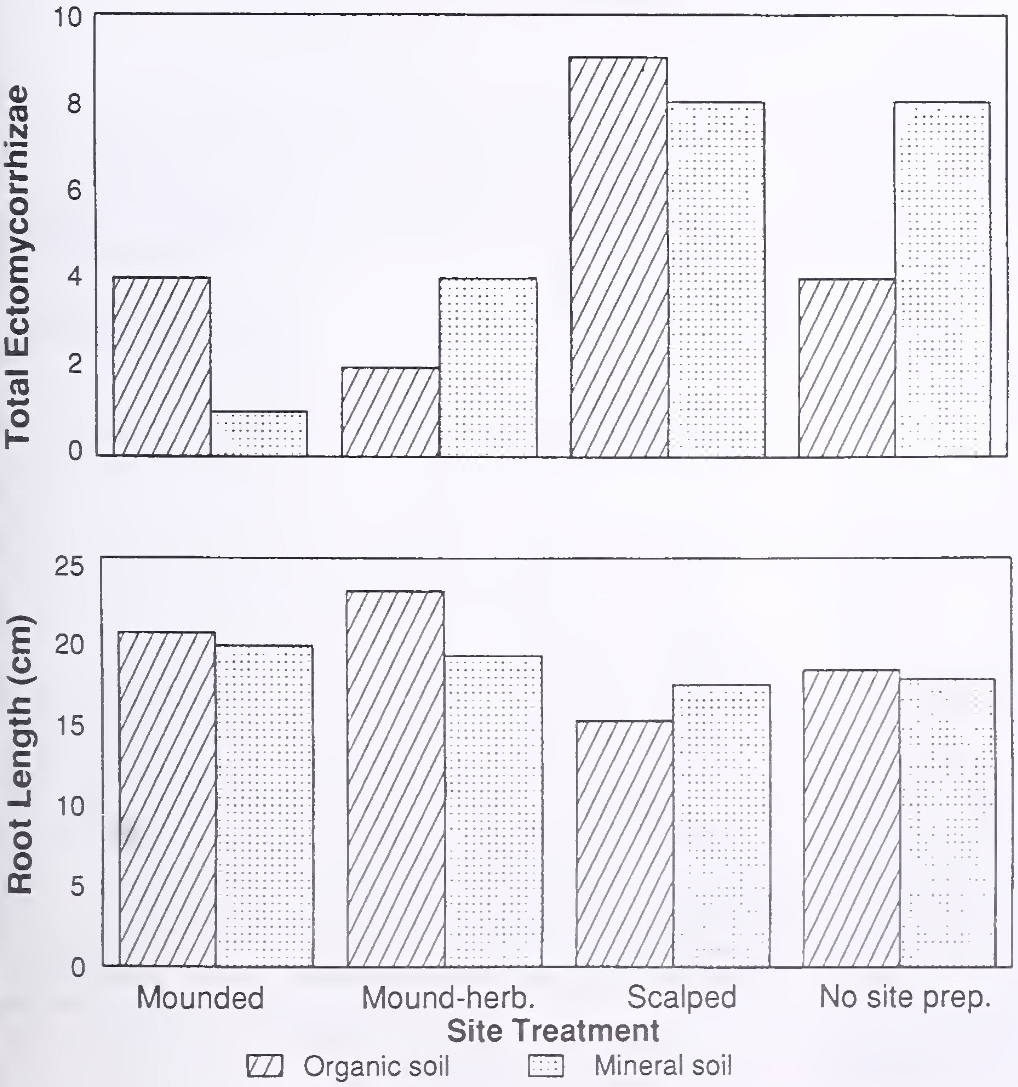
[1] Different letters indicate significant differences ($P \leq 0.05$) across soil horizons.

ectomycorrhizae in mineral soil. This may have been because postharvest organic horizons depths were relatively shallow (Harvey and others 1978). A partial cut with underburning seemed to be more detrimental to organic horizons, as evidenced by high ectomycorrhizal development in mineral horizons. The large volume, general distribution, and high moisture content of decayed wood throughout the soil profile probably contributed to its ability to retain and support ectomycorrhizal activity when compared to other soil components. Irrespective of site treatment, organic horizons, and in particular decayed wood, were the locations of greatest root length (table 4). When humus horizons were present, western larch was notably adept in exploiting them.

No specific attempts were made to identify particular ectomycorrhizal fungi associated with these seedlings. However, Harvey and others (1976) noted that fruiting structures of *Russula brevipes* Pk. and the distinctive morphology of *Cenococcum graniforme* (Sow.) Ferd. et Winge were often associated with Douglas-fir seedlings during sampling. Douglas-fir is also host to *Rhizopogon vinicolor* Smith, *Laccaria laccata* (Scop. ex Fr.) Berk and Br., and *Hebeloma crustiliniforme* (Bull ex St. Am.) Quel. (Perry and others 1987). Estimates indicate that Douglas-fir may form ectomycorrhizae with over 1,500 fungal species over its entire range (Trappe and Strand 1969). Far fewer fungi are estimated to form ectomycorrhizae with western larch. Some that have been noted include: *Suillus cavipes* (Opat.) Smith et Thiers, *Suillus grevellii* (Kl.) Singer, *Cenococcum graniforme, Laccaria laccata,* and *Pisolithus tinctorious* (Pers.) Coker and Couch (Amaranthus 1992; Chakravarty and Chatarpaul 1990; Harvey and others 1976).

Planted Regeneration Study

Western larch seedlings planted in raised planting beds formed fewer ectomycorrhizae than seedlings growing in scalped treatments (fig. 2a). Seedlings growing in treatments considered stressful (such as mounding with no competition control or scalping) formed most of their



Figures 2a and 2b—Total number of ectomycorrhizae and length of longest lateral root of planted western larch as affected by site treatment.

ectomycorrhizae in the mineral horizons. Seedlings in the mound with weed control and the no-site-preparation treatment formed most of their ectomycorrhizae in organic soil horizons. These latter two treatments also had the greatest height growth (see Graham and others, this proceedings). There were few differences in western larch root length among these treatments (fig. 2b).

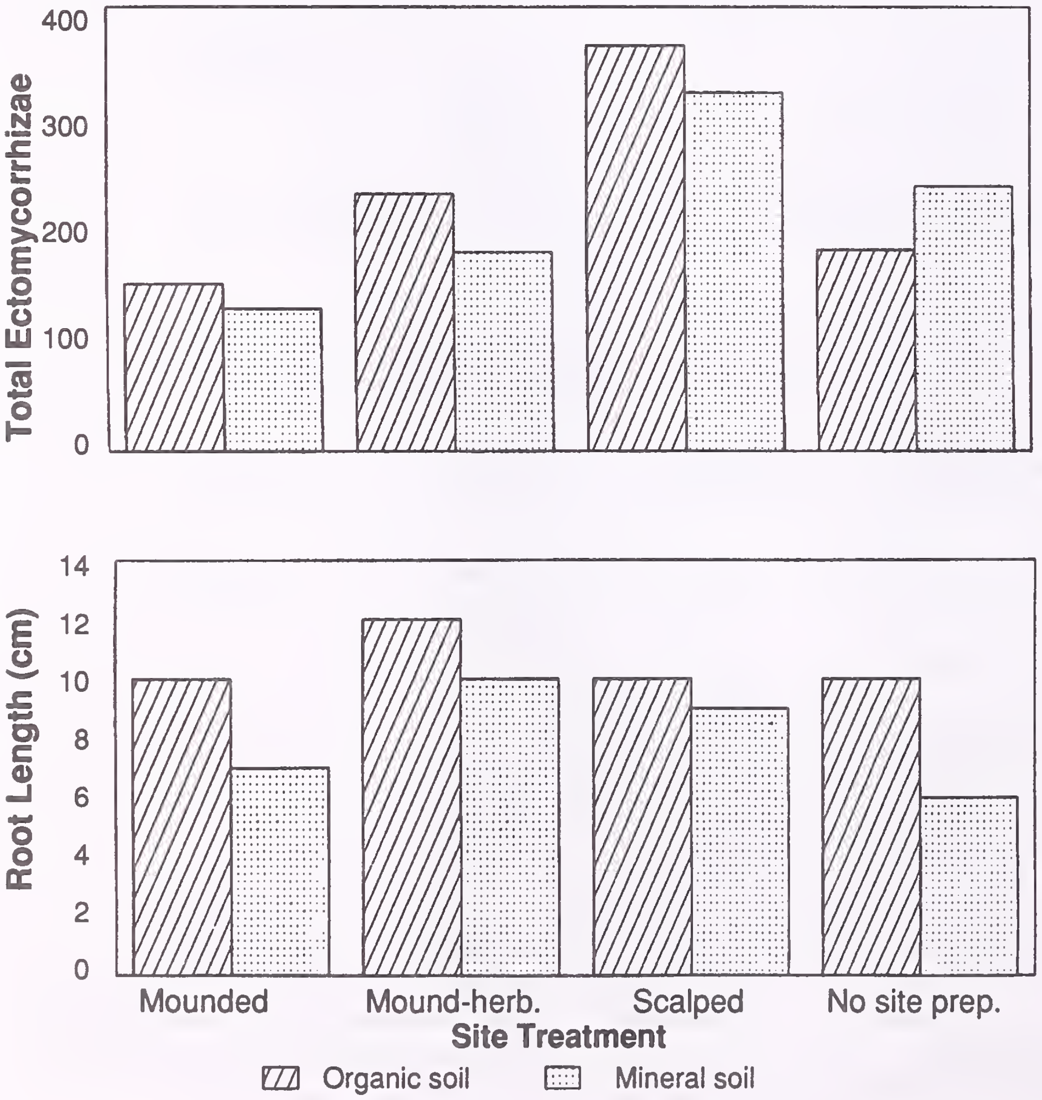
Western white pine and Douglas-fir seedlings exhibited similar trends in ectomycorrhizal colonization in these treatments (figs. 3a and 4a). Seedlings in mounded, mounded with competition control, and scalped treatments had more ectomycorrhizal tips in organic than mineral soil. However, the no-site-preparation treatment showed an opposite trend; more ectomycorrhizal tips in mineral soil. This may be because the soil had intact soil horizons after harvesting and only a shallow surface organic horizon. After three growing seasons, both species growing in the mound-competition control treatment had the greatest biomass and height (Page-Dumroese and others, in press).

Western white pine seedlings produced the longest laterals in organic soils for every treatment (figs. 3b and 4b). Douglas-fir used the organic soil horizons more when competition or compaction created unfavorable growing conditions elsewhere.

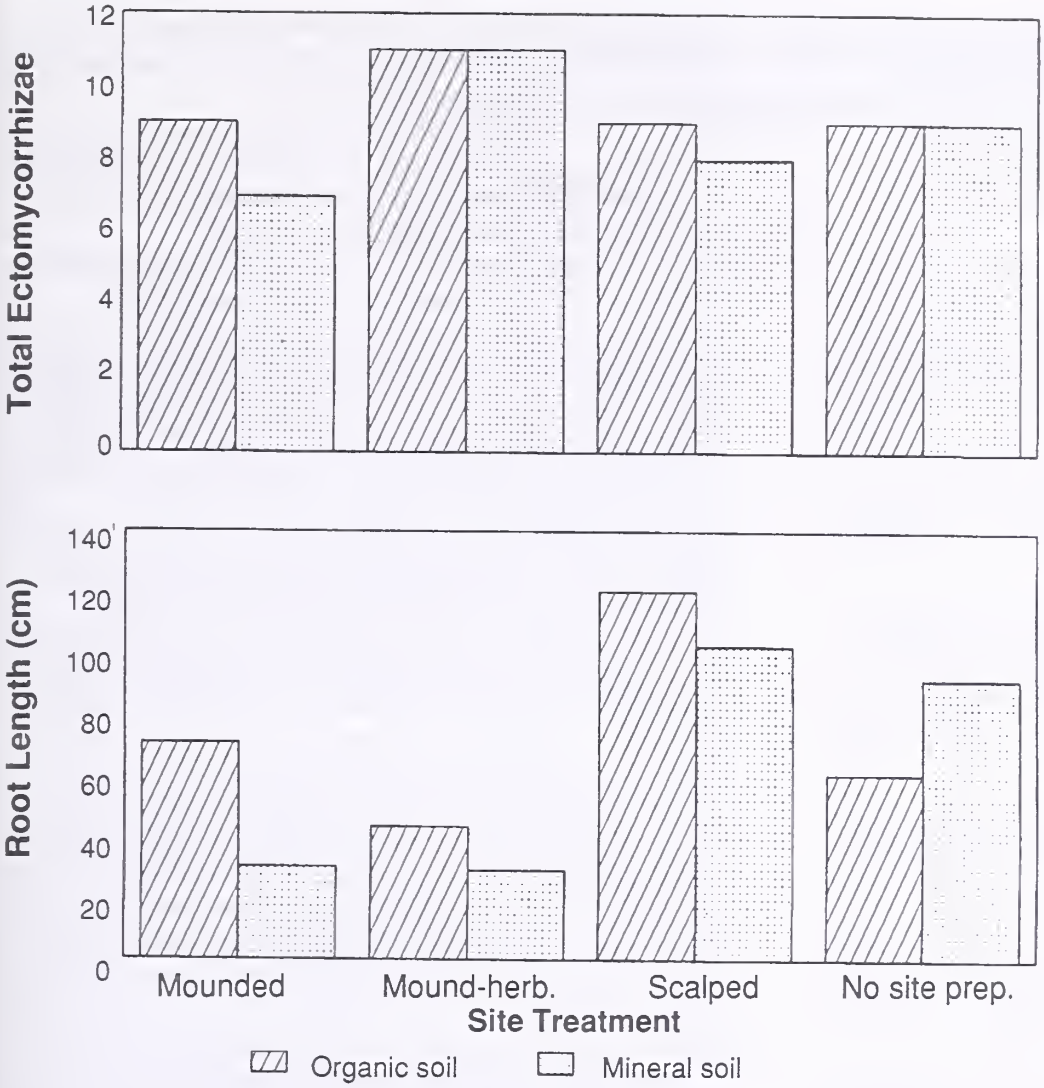
In this study, organic horizons were important for all three of these western conifers. Harvey and others (1991) noted that both Douglas-fir and western white pine responded similarly in these treatments. There was significantly more ectomycorrhizal colonization in the scalped treatment than in the other three treatments. Despite high numbers of ectomycorrhizal short roots on these seedlings, growth was not improved after 3 years (Harvey and others 1991; Page-Dumroese and others, in press). Seedlings growing in more fertile environments tend to have fewer ectomycorrhizae than those growing in harsher conditions (Brainerd and Perry 1987; Page-Dumroese and others 1990). Under fertile conditions, ectomycorrhizae may represent a carbohydrate cost to seedlings deficient in factors unimproved by colonization (Reid 1979) or perhaps unavailable in low organic matter soils (Harvey and others 1991).

CONCLUSIONS

Ectomycorrhizae play an important role in maintaining healthy forest ecosystems in the Intermountain West. In most habitat types they are dependent on organic horizons for successful colonization. Western larch is well known for its ability to thrive in areas devoid of organic matter. However, it and most other western conifers benefit from intact organic horizons. The critical nature of ectomycorrhizae and organic matter in these ecosystems present many opportunities for land managers.



Figures 3a and 3b—Total number of ectomycorrhizae and length of longest lateral root of planted western white pine as affected by site treatment.



Figures 4a and 4b—Total number of ectomycorrhizae and length of longest lateral root of planted Douglas-fir as affected by site treatment.

With careful management these soils can be protected or even improved. Recognizing the importance of organic horizons and ectomycorrhizal colonization for seedling establishment and growth provides the basis for restoration of damaged soils.

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Distribution and Site Ecology of Eastern Larch in Newfoundland, Canada

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R. S. van Nostrand

Abstract—The distribution and mensurational characteristics of eastern larch (*Larix laricina* [Du Roi] K. Koch), were studied in relation to physiognomic and ecological sites in Newfoundland. A forest site classification based upon a biophysical soils approach was adopted. Classification was: (1) bog and fen areas (mesotrophic and eutrophic types); (2) alluvial areas (carex-alder, lycopodium-alder, and typical alder types); and (3) upland areas (herb and moss rich, and ericaceous types). The herb and moss rich type is the most productive. Stands on this type have the best height-age and height-diameter relationships.

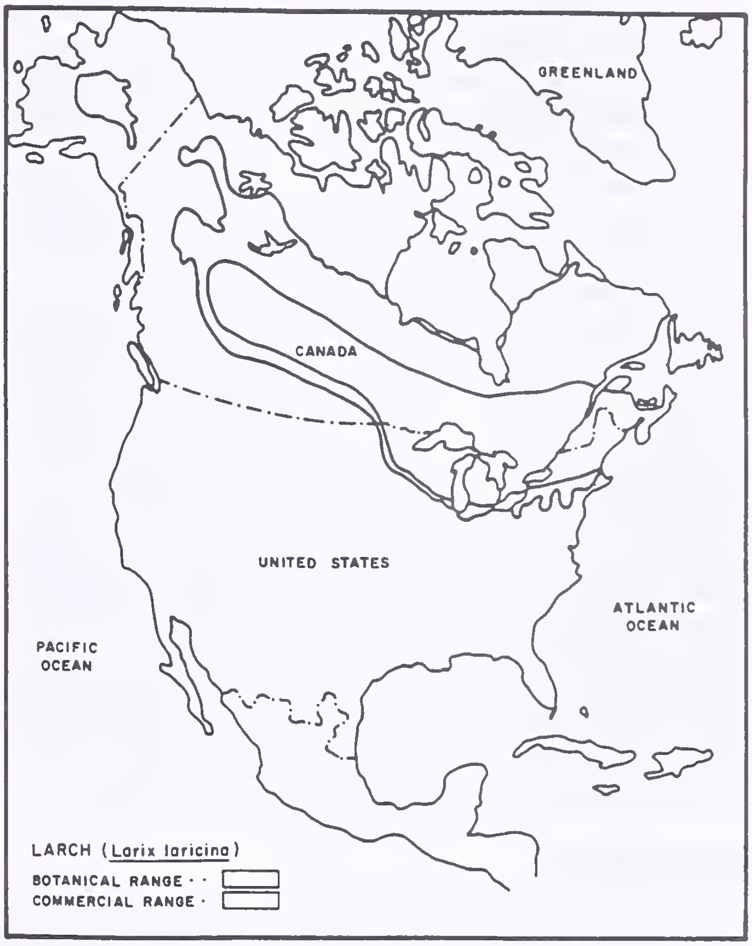

Figure 1—Range of larch in North America.

Eastern larch, *Larix laricina* (Du Roi) K. Koch, has the widest range of any American coniferous tree species. It is found farther north than either white spruce, *Picea glauca* (Moench) Voss, or black spruce, *Picea mariana* (Mill.) B.S.P., and remains arborescent, whereas the other tree species do not (Johnston 1990; Roe 1957) (fig. 1). Ostenfeld and Larsen (1930) had earlier described the range of eastern larch in North America, and Zoltai (1973) reported an extension of its range into the northern Yukon territory. Zoltai and Zalasky (1979) have found and identified postglacial fossil larch wood even beyond this range.

This paper presents the distribution and the site ecology of larch in Newfoundland. The conditions for the initial establishment of larch and its subsequent growth are described using a forest site classification approach. Some preliminary aspects of this paper have already been described (Roberts 1980; Roberts and Bajzak 1984; Roberts and van Nostrand 1984).

REVIEW OF LITERATURE

Probably the most complete summary of the silvical characteristics of larch was that of Roe (1957) who reviewed most of the North American work up to that period. Although this work was later revised (Fowells 1965), site and mensurational data from the eastern part of Canada for both reports are noticeably lacking. Clausen and Kozlowski (1967) and Clausen (1970) studied seasonal growth characteristics of long and short shoots of larch. MacGillivary (1969) reported on the reforestation and tree improvement potential in Eastern Canada, and this stimulated further work. Tilton (1975) presented a doctoral thesis on "The growth and nutrition of tamarack (*Larix laricina*)" and subsequently a later paper (1977) on seasonal growth and foliar nutrients of *Larix laricina* in three wetland ecosystems from Minnesota. Earlier Duncan (1954) studied some of the factors affecting the natural regeneration of larch in Minnesota forests.

Larix seed characteristics have been summarized by Rudolf (1974) and Hall and Brown (1976). Farmer and Reinholt (1986) have reported on the reproduction, phenology, and potential seed yield of *Larix*, and subsequent further investigation on microsporogensis (Hall 1979, 1981, 1982). Studies by Hall (1977) and Wright (1978) show the value of larch in plantation forestry and intensive forest management and as a pulping species. In biochemical studies, Niemann (1976, 1980a,b) and Niemann and Baas (1978) have reported the phenolics from *Larix* and the chemical composition of needles mainly from the species *Larix leptolepis*.

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In 1983, a larch symposium (Graham and others 1983) "Potential for the future" reviewed much of the tree improvement, pests of larch, nursery practice, and related work for the Canadian central region.

The nitrogen (N) availability beneath mixed larch stands, the importance of larch litter, and understory processes have been recently reported by Carlyle and Malcolm (1986a,b,c,d) and Roberts and Bajzak (1984).

Several site types have been described from Newfoundland and Labrador in which larch is the dominant component. Damman (1967) described a *Larix*-alder community that consisted of understocked stands of larch, a few white spruce and balsam fir (*Abies balsamea* [L] Mill.) and some alder (*Alnus rugosa* [Du Roi] Spreng.) growing on an imperfectly drained carbonated Orthic Gleysol (Wells and others 1972). Roberts (1977) reported a *Larix-Abies-Picea* shrub forest type from eastern Newfoundland located on a moderately well-drained Lithic Humic Podzol. Mercer and Bajzak (1973) gave an ecological description of a larch forest type for the Lake Melville area in Labrador and reported its mensurational characteristics. The Labrador larch types grow mostly on poorly drained Organic and moderately well-drained Gleyed Ferro-Humic Podzols. Living larch trees over 60 years of age (Wilton 1965) do not occur in these forests but some older dead trees occurred in this area. Most likely these Labrador larch stands were killed by the large Northeastern North America larch sawfly outbreak in the late 1880's. Tree ring evidence for endemicity of the larch sawfly in North America using a 300-year tree-ring series (1682-1989) has been presented by Jardon and others (1994). The larch sawfly was probably present as early as 1744, (Jardon and others 1994), more than a century before its presumed accidental introduction from Europe to North America. However, its populations certainly intensified around 1880.

METHODS

The study area was the island portion of Newfoundland and was divided into three regions: (1) Eastern, (2) Central, and (3) Western. From 1977 to 1987, 143, of $\frac{1}{25}$ ha plots each were established in all three regions using the criteria that larch stands sampled had greater than 75 percent larch by basal area (fig. 2). The mensurational characteristics (stump age, d.b.h., age, height, volume, site index) were measured and recorded initially and the site classification assigned after all plots were established. A complete plot tally of all species greater than 1 cm as well as height/diameter data for all species were measured. At least 10 dominant and codominant trees were measured for stump and breast height age. Total aboveground biomass was calculated using tree mass equations from 243 local larch tree samples (Lavigne 1982), throughout insular Newfoundland. A representative number of plots were revisited 10 years after establishment to assess growth conditions and to observe changes. The major site data collected included:

1. Landform/land type, micro topography, slope/aspect/ position.
2. Major and minor vegetation (abundance/cover sociability), exposure, origin and stand disturbance.
3. Complete soil profile description including horizon sequence, depth, color, structure, texture, seepage, pH, rooting depth, stones, parent material, soil drainage, depth to water table, depth to bedrock. In addition, soil samples were collected on a horizon basis for laboratory determination of chemical and physical characteristics.

Figure 2—Range of larch in Newfoundland and location of plots.

Plots were grouped into physiognomonic sites and larch types were classified on the basis of:

1. The abundance of indicator ground species.
2. Soil type and soil drainage.
3. Climatic exposure, slope, and stand history.

RESULTS

Fen Sites

Two fen types, mesotrophic and eutrophic, were identified and separated on the basis of abundance of ground cover, pH values, and soil properties (table 1).

Mesotrophic Fen Type—The mesotrophic sites that contained productive stands of larch were not as common as the richer eutrophic type especially in central and western Newfoundland (fig. 3).

The ground flora is usually dominated by *Betula michauxii*, *B. pumila*, *Potentilla fruticosa*, *Myrica gale*, and *Spiraea latifolia* in the shrub layer with *Sanguisorba canadensis*, *Scirpus cespitosus*, *Carex livida*, and *Aster nemoralis* dominant in the herb layer. *Sphagnum papillosum*, *S. magellanicum*, and *S. rubellum* are the dominant mosses. The soils are poorly drained Typic Mesisols.

Table 1—Site classification: larch forests, Newfoundland Region.

Forest type	Succession	Forest capability*	Soil parent materials & landforms	Soil drainage**	Soil subgroup**
Larch Forest					
1. Mesotrophic Larix-fen (Lfm)	?	6W	Organic	5 - 6	Typic Mesisol
2. Eutrophic Larix -fen (Lfe) A	?	6W	Organic/base rich till	5 - 6	Typic Humisol, Fera Gleysol, Mucky Orthic Gleysol
3. Carex Larix - alder (Lc) A	?	6W	Alluvium	5 - 6	Mucky Orthic Gleysol, Typic Humisol, Typic Mesisol
4. Lycopodium Larix-alder (L1) A	?	5W	Alluvium	4 - 5	Orthic Gleysol, Gleyed Humo-Ferric Podzol
5. Typic Larix-alder (Lt) A	?	5-6W	Alluvium	5 - 6	Mucky Orthic Gleysol, Typic Humisol
6. Ericaceous Larix (Le)	Stable ?	6F/M	Mv, Mh	2 - 3	Orthic Humo-Ferric & Ferro-Humic Podzols, coarse
7. Herb & Moss rich Larix (Lh)	?	4F	Mp, Cx	2 - 4	Orthic & Gleyed Humo-Ferric & Ferro-Humic Podzols

*Canada Land Inventory (CLI) Forest Capability Class; F - fertility limitation to growth; M - moisture limitation to growth; W - wetness limitation to growth

** Canadian Soil Classification System 1978

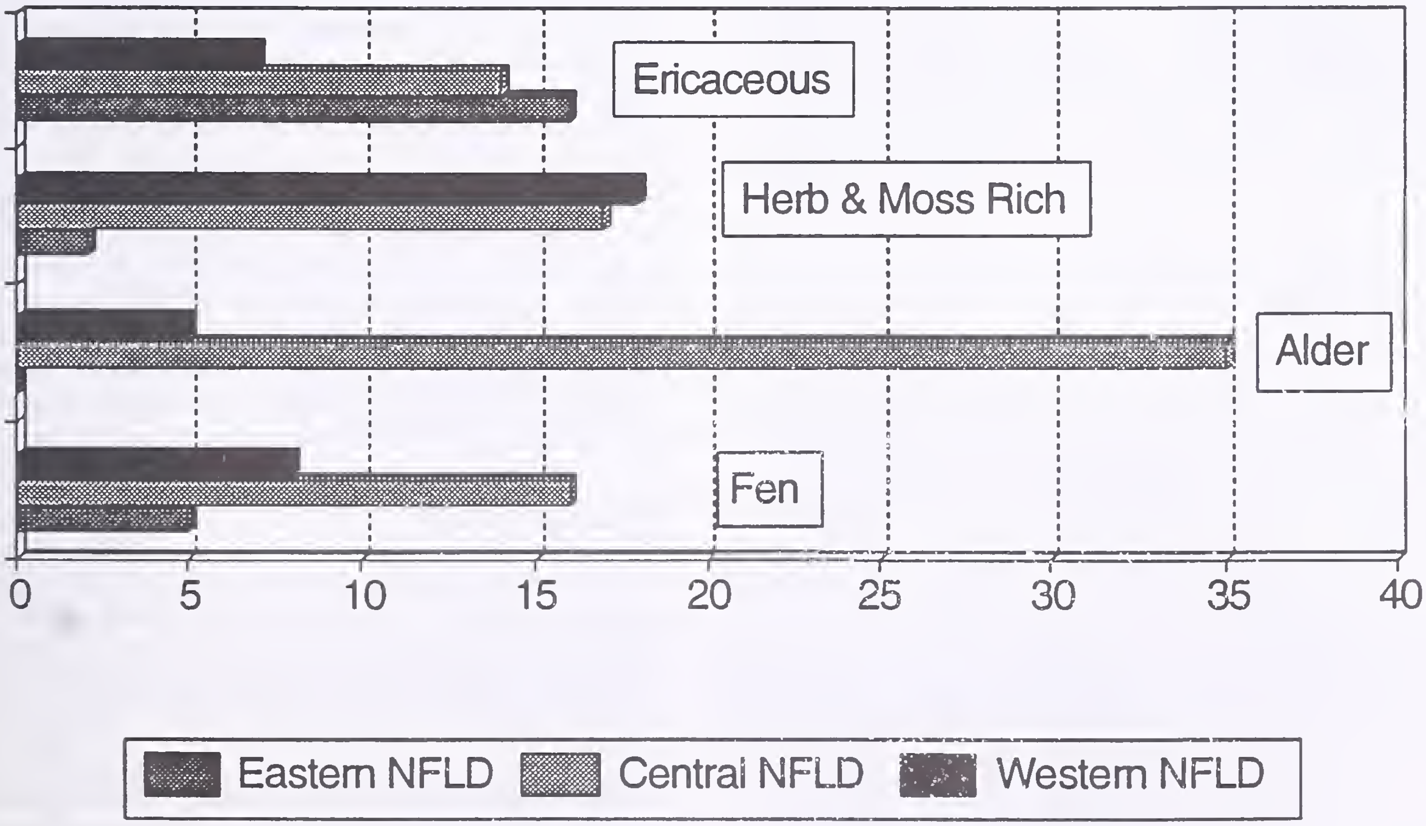

Figure 3—Larch types and number of plots per region.

Eutrophic Fen Type—The eutrophic fens have a greater dominance of larch and fen indicator species such as *Betula pumila*, *Potentilla fruticosa*, *Cornus stolonifera*, *Myrica gale*, *Thalictrum polygamum*, *T. alpinum*, *Carex scirpoidea*, and *Sanguisorba canadensis*. The moss layer was composed mainly of brown mosses (*Campylium stellatum*), and *Sphagnum* mosses were rare or absent.

The soils of this type were Typic Humisols, Fera Eluviated, and Orthic Gleysols from organic and base rich deposits and were all poorly to very poorly drained. Appendix A gives typical soil textures and pH values.

The growth curves height/age (fig. 4) and height/diameter (fig. 5) shown are the averages of both types. The eutrophic fen type shows a consistently better site index and height/diameter relationship in all plots on this site type.

Alluvial Alder Sites

The alder site type was most common in central Newfoundland (fig. 3). The three subtypes (table 1) were assigned mainly on the basis of ground indicator species and soil drainage. All types had a shrub coverage (0.5 to 4 m height) of 10 to 95 percent of speckled alder (*Alnus rugosa*).

Carex Alder Type—The *Carex* alder subtype was not very common and was encountered only a few times during the course of field sampling. It consisted of moderately stocked stands of larch with clumps of alder, *Alnus rugosa* in the shrub layer. The herbs *Cornus canadensis*, *Coptis groenlandica*, *Linnaea borealis*, and *Clintonia borealis* are common but cover was less than 10 percent. In groups or tuffs with a coverage of 25 to 50 percent are *Carex irisperma*, often *C. irisperma* var. *billingsii*, *C. intumescens*, and *C. leptoneuria*.

The soils were eutrophic muck (30 to 40 cm) over gleyed alluvium parent material and poor to very poorly drained. Textures are silt loam to coarse loamy sand; pH values for a typical profile are given in appendix A. Sites as indicated are usually less acidic than the ericaceous types.

The growth characteristics of height/age and height/diameter (figs. 4, 5) show that this larch type is the poorer of the three alder types, and the site index is lower than shown for the typical alder.

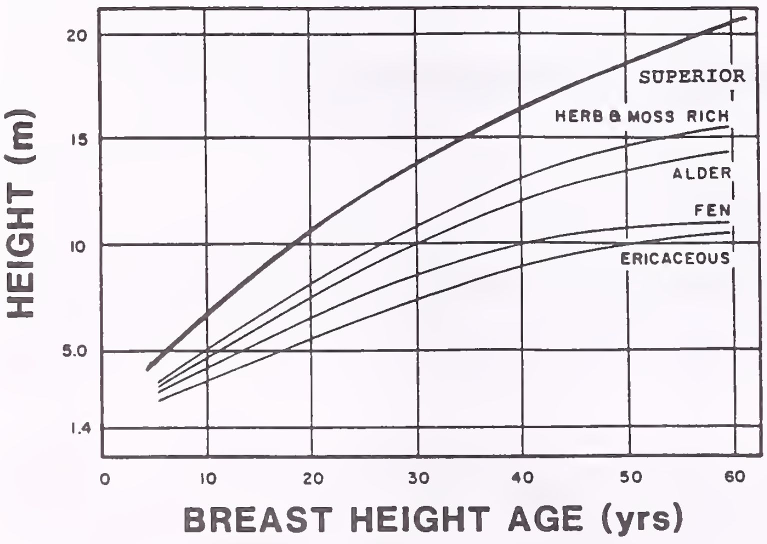

Figure 4—Height versus age for larch.

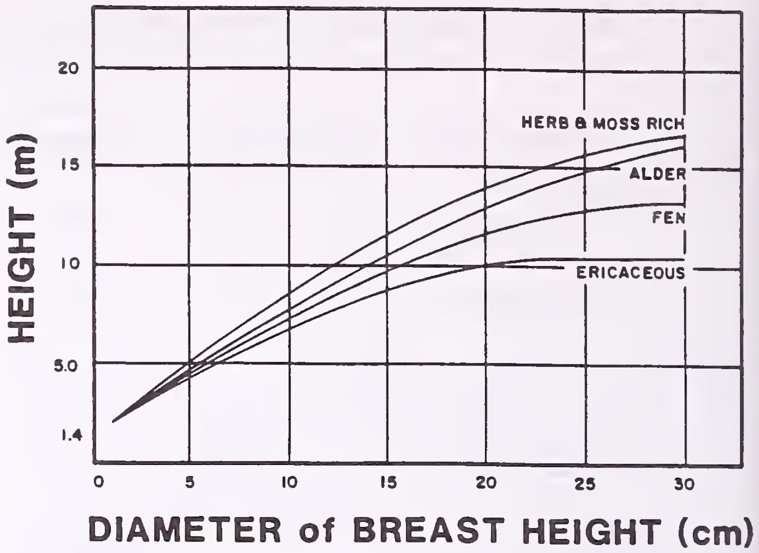

Figure 5—Height versus diameter for larch.

Typical Alder Type—In the course of the study, a number of sites were definitely members of the alder type, but no characteristic species in the ground vegetation was dominant. The density of *Alnus rugosa* greater than 90, prohibits shrub on herbaceous growth.

Soils are poorly to very poorly drained Mucky Orthic Gleysols or poorly drained Typic Humisols on Alluvium.

The height/age curve for alder (fig. 4) is the average curve shown for all the three alder types.

Lycopodium Alder Type—This subtype is the most common of the alder type. The characteristic ground cover is *Lycopodium annotinum* and more rarely *L. lucidulum* with *Dryopteris spinulosa*, *Ribes lacustre* dominant in the herb layer. In the drier segments small patches of *Rhytidiadelphus triquetrus* are common and in the wetter microdepressions small patches of *Sphagnum capillaceum* occur. Common throughout this subtype but lacking the dominance of the species above are *Trientalis borealis*, *Aster puniceus*, *Mittella nuda*, *Linnaea borealis*, and *Cornus canadensis*.

The soils associated with this subtype are imperfectly to poorly drained Orthic Gleysols, Gleyed Humo-Ferric, Humic Podzols, and Typic Humisols all on alluvial parent materials. Textures range from silt loam to coarse sandy loam, and pH values for typical profiles are given in appendix A.

This alder type is the richer of the alder sites and shows a slightly higher site index than the typical alder.

Upland Sites

These larch types are typical shrub, herb, and moss rich forests but have a dominance of larch instead of the usual balsam fir or black spruce cover. The larch is the result of fire or cutting practices removing the fir or spruce leaving a few scattered larch that quickly seed in to form a small stand.

Herb and Moss Rich Type—The ground vegetation is dominated by such herbs as *Cornus canadensis*, *Linnaea* *borealis*, *Clintonia borealis*, and occasionally *Dryopteris spinulosa*. Mosses are chiefly the feather mosses *Hylocomium splendens*, *Pleurozium schreberi*, and *Ptillium crista-castrensis*, but *Rhytidiadelphus loreus* and *Dicranum majus* are often present.

The soils are well to moderately well-drained Orthic Humo-Ferric and Ferro Humic Podzols, occasionally gleyed in the lower B horizon. Parent material is glacial till, and typical textures and pH values are given in appendix A. The height/age and height/diameter curves (fig. 4, 5), are highest for this site type.

Ericaceous Type—The ground vegetation of the ericaceous type was dominated by *Kalmia angustifolia*, *Ledum groenlandicum*, *Rhododendron canadensis*, *Vaccinium vitis-idaea*, and *V. angustifolium*, all members of the ericaceous or heath family in the heavy shrub layer, which covers 50 to 100 percent of the site. *Nemopanthus mucronata* is also a shrub that appears consistently in this type. The herb layer includes *Cornus canadensis*, *Trientalis borealis* as dominant members, and the lichens (*Cladonia alpestris*, *C. rangiferina*, and *C. mitis*) are always present, and mosses *Pleurozium schreberi* and *Dicranum scoparium* form scattered patches.

The soils associated with the ericaceous type were well to moderately well-drained Orthic Humo-Ferric Podzols and Orthic Ferro-Humic Podzols with almost equal numbers of each per site investigated. The parent materials were stony glacial tills derived from noncalcareous sedimentary and igneous rocks giving a range of textures from silt loam to sandy loam pH values for typical profiles (appendix A). The thick ericaceous humus sometimes impedes regeneration, and growth in terms of height and diameter was the lowest of the site types assigned.

Other larch habitat types commonly found in Newfoundland are the immediate roadside borders that are now often dominated with larch. The seven types described are well represented on these road right of ways and are an important seed source.

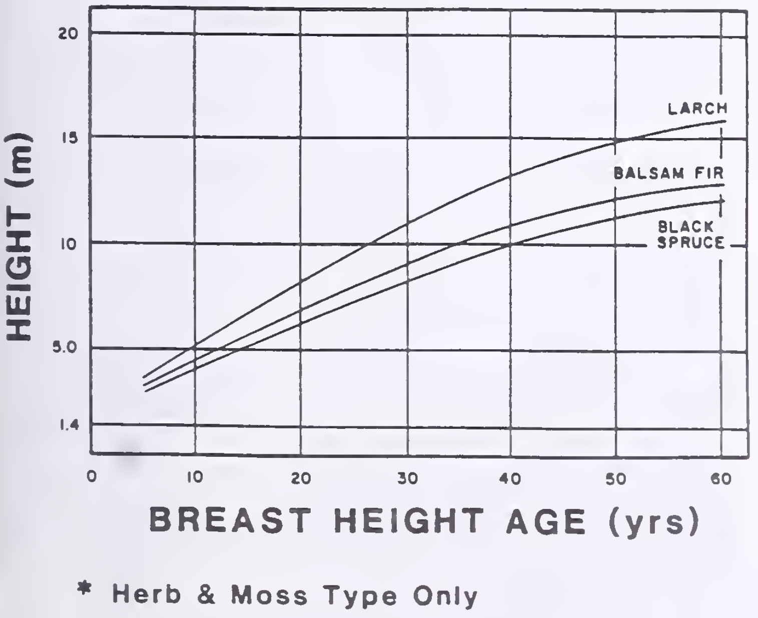

Figure 6—Height versus age for larch (herb and moss type only), black spruce and balsam fir.

Old field succession to larch on previously cleared land similar to white spruce was also encountered a few times during the survey. The most unusual larch habitat is an ericaceous larch type on soils derived from serpentinized rocks. Larch is the only tree species to reach 5 to 12 m on these sites, which are known to have toxic quantities of magnesium, lack of major nutrients, and possible toxic heavy metals but in a natural setting (Roberts 1992). The ability of larch to exclude the uptake of heavy metals and to survive and grow on soils with chemical imbalances suggests this species could have potential in the stabilization of mine spoils and tailings.

SUMMARY OF LARCH GROWTH CHARACTERISTICS

Height/age and height/diameter curves were constructed for each of the seven larch site types (figs. 4, 5). The best growth occurred on the upland herb and moss type, averaged site index 16 M at 60 years. The height/age growth of superior stands, plotted separately was also best for this site type (fig. 4). The alder types (averaged site index 14 M) showed the next best growth followed by the fen types (averaged site index 11.7 M) and the ericaceous type (averaged site index 11 M). The growth data of three Larix alder types was similar. The carex alder had the lowest site index, the lycopodium alder the best the typical alder type was very close to the average curves shown figs. 4 and 5 when the complete data set was analyzed. Larch showed better height/age relationships than *Abies balsamea* or *Picea Mariana* on the same herb and moss type (fig. 6).

The number of trees, total volume, and total aboveground biomass for the herb and moss type, the averaged alder type, the averaged fen type, and the ericaceous type are given in table 2. The data also show the same site trend as shown by the growth curves. Stem density varied in all types from 800 to 6200 stems/ha. The mean values for the herb and moss, alder, fen, and ericaceous types were 2340, 3050, 3100, and 1940 per ha, respectively (table 2). Mean basal area and total volume varied from a low of 9.9 m^2 and 42.4 m^3 per ha in the ericaceous type, to 23.8 m^2 and 128 m^3 in the herb and moss type. The highest recorded total volume in this survey was from the lycopodium alder type, which exceeded 157 m^3 per ha. Total aboveground biomass showed similar trends and on the better quality sites was greater than 100 ton per ha. Mean values for the ericaceous, fen, alder, herb and moss types were 35.7, 46.8, 78.8, and 101.2 ton per ha, respectively. The lycopodium alder and the herb and moss types had highest ton per ha of 124.5 and 121.8, respectively, for the best quality sites (table 2). Figures 7 shows photographs of each type.

DISCUSSION

Although larch currently occupies less than 5 percent of the tree volume in Newfoundland its numbers are increasing yearly by natural regeneration after logging disturbance and wildfire. It is not used for local pulpwood even though there are reports (Wright 1978) that it can make suitable pulp, especially from the younger age classes. The heart wood of older larch currently leads to color problems in the

Table 2—Mensurational characteristics for stands 35 to 55 years.

Type	No. stems/ha			BA-m²/ha			Total volume-m³/ha			Biomass-T/ha		
	H	L	M	H	L	M	H	L	M	H	L	M
Herb and moss rich	4100	1220	2340	27.7	18.0	23.8	153.0	84.4	128.0	121.8	70.5	101.2
Alder	4550	1580	3050	32.1	8.7	20.9	157.5	30.4	101.6	124.5	27.6	78.8
Fen	6200	1680	3100	22.0	4.7	13.9	91.2	14.0	54.8	70.5	19.7	46.8
Ericaceous	4080	800	1920	14.0	5.8	9.9	75.6	18.5‘	42.4	62.4	17.4	35.7

H = High
L = Low
M = Mean
T = Ton of total aboveground, over-dry, tree biomass
No., basal area and volume - all stems 2 cm > d.b.h.

pulping process. The species is used mostly as fuelwood and as lumber for fencing. In eastern Newfoundland it is widely cut for fuelwood along with black spruce to meet demand there. More than 1 million m^3 of fuelwood are needed annually (Roberts and Titus 1994), with white birch the preferred species in the central and western regions. Significant quantities of birch are also transported to eastern Newfoundland suggesting that energy plantations from eastern Larch or other larix species certainly would help the fuelwood industry here.

This project has shown that larch is really the only species in the exposed land areas that will produce a merchantable crop on the poorest sites, while at the same time at age 50 years and on better quality sites, larch will produce greater

Figure 7—(A) Herb type; (B) moss type; (C) typical alder type; (D) ericaceous type; (E) mesotropic fen type; and (F) eutrophic fen type.


C


D


E


F

height growth and biomass than other local species (Hall 1986). There is a current revised interest in site classification (Meades and Roberts 1992). Matching species to site, optimizing growth, and species diversity indicate a future interest in larch. Individual tree and stand response to spacing appear to be similar to other conifers (Stiell 1984) and thus early precommercial thinning in dense stands (greater than 3000 stems/ha) appears to be a good management option.

One of the main concerns of increasing the percentage of larch forest type has been the threat of insect infestations such as the eastern larch beetle (Langor and Raske 1989) and the larch sawfly. The masked shrew was introduced to Newfoundland in 1958 (Warren 1970) and has appeared to be effective in reducing populations of several forest insect pests including the larch sawfly, one of its preferred foods in the cocoon stage. The shrew is now well distributed throughout Newfoundland, and sawfly populations have not reached outbreak levels since the introduction. Five major pests of larch are recognized in Newfoundland (Schooley and Pardy 1981), but at least 55 insect species have been recovered on larch. The European larch canker is a disease of larch that has caused concern in eastern Canada (Magasi 1983) and is currently being studied.

In terms of genetic improvement and plantation management, Lavigne (1982) and Hall (1986) indicate 8 to 43 percent increase in larch biomass over black spruce in mixed stands from central Newfoundland, which can be further doubled if Japanese larch (*L. kaempferi* [Lam.]) is used in plantation. In medium quality sites with exposure, hybrid larches and eastern larch show the most promise and are recommended in reforestation programs. In a recent review of tree breeding strategies (Vallee and Stipanicic 1993), present a synopsis of programs for larch species from Canada including Newfoundland where there appears more interest now than a decade earlier.

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APPENDIX A

Typical soil subgroups, depth, pH and texture of soil horizons for each site type.

CSSC Soil Subgroup	Horizon	Depth (cm)	pH	Texture
1. Ericaceous site type				
Orthic humo-ferric podzol	L	-6	5.25	
	F+H	6-0	4.30	
	Ae	0-8	4.75	Sandy loam
	Bfh	8-18	4.90	Loam
	Bf	18-47	5.00	Loam
	C	47+	5.10	Sandy loam
Orthic ferro-humic podzol	L	14-11	4.30	
	F+H	11-0	3.60	
	Ae	0-13	4.15	Sandy loam
	Bhf	13-23	4.85	Silt loam
	Bfc	23-28	5.00	Loam
	Bf	28-36	5.15	Sandy loam
	BC	36-44	5.20	Sandy loam
	C	44-51+	5.20	Sandy loam
2. Alder site type				
A. Carex-alder subtype				
Mucky orthic gleysol	L	32-22	4.50	
	Oe	22-0	6.05	
	Bg	0-9	6.00	Silt loam
	Cg	9-23+	6.00	Fine sandy loam
B. Lycopodium-alder subtype				
Orthic gleysol	L	15-10	4.80	
	F+H	10-0	4.20	
	Aeg	0-15	5.70	Loam
	Bg	15-30	5.90	Loam
	C	30-41+	6.30	Loamy sand
C. Typical alder subtype				
Typic humisol	L	100-95	5.35	
	Oh	95-60	6.20	
	Oh	60-0	5.25	
	C	0-10+	5.45	Sandy loam
3. Fen site type				
A. Mesotrophic fen subtype				
Typic mesisol	L	68-11	5.15	
	Om	61-26	4.40	
	Om	26-0	4.90	
	C	0-7+	5.30	Sandy loam
B. Eutrophic fen subtype				
Typic humisol	L	0-5	4.80	
	Oh	5-20	6.00	
	Oh	20-25	5.30	
	Oh	4+50	6.20	
	Oh	4+100	6.80	
Fera eluviated gleysol	Oh	30-20	6.65	
	Oh	20-0	6.90	
	Aeg	0-6	7.40	Loam
	Bfg	6-16	7.30	Loam
	Bg	16-41	7.45	Silt Loam
	Cg	41-50+	7.70	Loam

(con.)

APPENDIX A (Con.)

CSSC Soil Subgroup	Horizon	Depth	pH	Texture
		(cm)		
4. Herb & moss site type				
Orthic humo-ferric podzol	L	22-12	4.90	
	F+H	12-0	3.70	
	Ae	0-12	4.50	Sandy loam
	Bfh	12-20	4.60	Loam
	Bf	20-32	4.95	Loam
	C	32-46+	5.20	Sandy loam
Orthic ferro-humic podzol	L	17-9	5.60	
	F+H	9-0	4.10	
	Ae	0-2	4.20	Sandy loam
	Ah	2-4	—	—
	Bhf	4-14	4.50	Silt loam
	Bf	14-19	4.90	Loam
	BC	19-26	4.95	Sandy loam
	C	26-40+	5.00	Sandy loam

Distribution and Variation of *Larix Principis-Rupprechtii* Forest in Shanxi Province

Li Wenrong
Qi Liwang
Han Youzhi
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Abstract—Growth and characteristics of the needle, cone, and seed have been investigated in 41 natural populations of *Larix principis-rupprechtii* in China. As climate becomes dry and cold, the number of needles per fascicle in short shoot and the number of cone scales increases in a mono-directional cline. The annual height growth increased from northeast to southwest. Diameter at breast height was positively correlated with elevation. Latitude, mean annual temperature, and mean January temperature were the main factors affecting the height growth. Latitude and mean July temperature influenced the number of needles per fascicle in short shoots.

Larix principis-rupprechtii Mayr. is a unique species in high elevations of northern China. The natural forests of this species are mainly distributed in Shanxi and Hebei provinces. Shanxi has been known as the home of *Larix principis-rupprechtii* forests with about 29,678 hectares, mainly growing in the mountains of Guandi, Guanqing, Wutai. There are small stands in Hengshan of northern Shanxi and Taiyue of southern central Shanxi. Elevational distribution is from 1,400 to 2,800 m, with most stands growing from 1,600 to 1,900 m.

Because the natural forests are widely distributed with a great variation in topography, there might be a considerable variation among individuals which are subjected to natural selection. Although studies have concentrated on the variation in growth and seed quality in the central range of *Larix principis-rupprechtii* (Liu 1984; Chang and Liu 1984), none of these studies have focused on geographic variations in the overall range of this species.

In order to clarify the geographic distribution and the variation among natural populations, which provide better understanding of the gene resources and the potential utilization of the current natural variation, we investigated 41 populations across the natural range in Shanxi province during the period from 1983 to 1985. The main objectives of this study were: (1) to determine the relationship between the horizontal and vertical distributions of *Larix principis-rupprechtii* and its geographic positions; (2) to determine the relationship between natural condition and larch distribution; (3) to evaluate the pattern of population variation along a geographical gradient; and (4) to establish the multiple linear models to find out the predominant ecological factors influencing the variation of growth or morphological traits.

METHODS

This investigation combined literature review with field survey. Information on the distribution status of *Larix principis-rupprechtii* was first obtained through reviewing literature of the previous investigation, followed by the field survey, during which forest distribution map and a forest phase map of the individual forest regions were confirmed.

In the field survey, the number of sites and locations of the sampling were determined according to the distribution of the natural forest. Relatively fewer sampling sites were arranged in the places with continuous distribution; but in the discontinuous distribution of forest, we assigned at least a site for each population even though the population was small. Meanwhile, all populations were chosen from the middle-aged and healthy stand with 41 populations between 32 forest farms throughout the Shanxi province.

In each population, mean height and diameter at breast height of the forest were estimated from the measurements of more than 30 representative trees which were all from a randomly selected sampling plot. The trees with the average height and DBH were selected for determination of the volume per tree and the volume per unit area. Five dominant or sub-dominant trees with pest-free and erect trunks were chosen as sample trees. To avoid the influence by close parentage, distance between sample trees was no closer than 60 meters. Cones, needles, and seeds were collected from the sample trees and tested as follows: (1) needle: fascicles were collected from 2-year-old branches located on the southwest of the central crown for the measurement of the length and width of individual needle and the number of needles per fascicle; (2) cone and seed: from directions of east, west, south, north of the central crown of each sample tree, four cones were collected for measurement of the length, width, and the number of cone scales. Seed length, width, and weight per 1,000 seeds were measured from 25 populations.

Climatic data was obtained from the meteorological stations adjacent to sampling sites (Shanxi Meteorology Bureau 1982). Temperature of the sampling sites was

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estimated by a decrease of 0.5 °C for every 100 m rise in elevation. The annual precipitation was estimated by isohyetal line map of Shanxi (The Mapping Commission of Shanxi Province 1984). The degree of aridity and warmth in spring were calculated based on the air temperature and precipitation of the period. Banguls and Ganssen (1970) suggested use of the ratio of precipitation to the double air temperature to measure the moisture supply. If the precipitation of a given month exceeds the doubled value of the mean air temperature, moisture supply is sufficient; otherwise, water deficit occurs. Meigs (but see Goor and Barney 1976) considered an area arid if the precipitation of a given month was less or equal to the doubled mean temperature. We used this ratio as an index for spring aridity in April, May, and June. The warmth index was calculated by summing up the monthly average temperature above 5 °C of a year after subtracting 5.

GEOGRAPHIC DISTRIBUTION OF THE NATURAL *LARIS PRINCIPIS-RUPPRECHTII* FOREST

Horizontal Distribution

The natural forest of *Larix principis-rupprechtii* in Shanxi province is distributed in the geographic locations from 36°39' to 39°52' latitude from the North and from 111°22' to 114°20' longitude from the East. The boundaries are north to the Hualinbei Forest Farm in Yanggao county, the branch range of Hengshan Mountain, and south to Qiliyu Forest Farm in Huozhou county of Taiyue Mountain. The western boundary lies in the Nanyunding Mountain in Fangshan county of Guandi Mountain Forest Region and the eastern boundary is in Lingqiu county. Larch mainly grows with evergreen conifers at high elevations in Guandi, Guanqing, Wutai, and Hengshan Mountains. Some are found in the subalpine meadow belt (1,900-2,347 m above sea level) in the central south area of Shanxi province.

Guanqing Mountain Forest Region—*Larix principis-rupprechtii* in this region extends about 60 km from the west in Wangjiacha village of Kelan county to the east near to the peak of Yunzhong Mountain. The north of this region starts from the Shanchunlin Forest Farm in Shenchi county, the northwest slope of the ridges of Luliang Mountain and ends up in the Dujiacun Forest Farm in Jingle county down to the south, with a distance of about 50 km.

Larch in this region is of continuous distribution. There are 14 forest farms covering 16,353 hectares, accounting for more than half of the total natural larch forest in Shanxi. Furthermore, there is high productivity as well as large pure stands in this region.

Guandi Mountain Forest Region—This region covers the area west to Nanyunding Mountain in Fanshan county, east to the boundary between Loufan and Jiaocheng counties in Beiyunding Mountain, with a distance of about 20 km. The north starts from Zhoujiagou in Fangshan county and south ends up in Guji Mountain, with a distance of about 30 km. The total area of *Larix principis-rupprechtii* is 6,413 hectares in this region, centered in Mount Xiaowen of Guandi Mountains. Most larch stands in the south of Mount Xiaowen are of excellent quality with site index of I_a or I.

Wutai Mountain Forest Region—Larch grows on the north and south slopes of the peak of Wutai Mountains, covering an area of 4,300 hectares. Kuantan and Boqiang Forest Farms are the largest. Natural pure stands are in Chantanmiao, Dadonggou, Xiaodonggou, and Erqielan in Fanci county and Shaluoshu in Wutai county.

Around Hengshan Mountain, the total area of the natural *Larix principis-rupprechtii* forest is 2,080 hectares. Within this area 1,793 hectares of larch grows on sites with indices of II or III. About 60 hectares in discontinuous stands are in Hualinbei Forest Farm, the northern boundary of this region. In addition, larch also grows in scattered stands in Guanling and Linqiu counties. Another 533 hectares of larch grows in Xinzhou.

Taiyue Mountain Forest Region—Larch is dispersed around the ridges of the east and west slopes of Taiyue Mountain in this region. The forest farms, including Haodifang, Jiangtai, and Wangtao in Qinyuan county, Jiemiao and Shigaoshan in Lingshi county, Mianshan in Jiexiu county, and Qiliyue in Huozhoue county, cover a total area of 133 hectares. Most of the forest grows in Haodifang Forest Farm, about 87 hectares. Although temperature and moisture are superior in this region, the growth of forest is slow because soils are calcarious and site index is only graded II or III. Moreover, most stands are in spotted or scattered plots in this region, 400 years old, more than 25 m tall, and up to 1 m DBH.

Vertical Distribution

The upper and lower limits of *Larix principis-rupprechtii* increase gradually from east to west in Shanxi (table 1).

Table 1—The geographic information of *Larix principis-rupprechtii* in Shanxi

Location	Upper limit	Lower limit	Latitude	Longitude
	(m)	*(m)*	*(N)*	*(E)*
Hualinbei	1,850	1,600	39°50'	113°47'
Hengshan	2,150	1,400	39°34'	113°41'
Wutai Mountains	2,600	1,750	39°04'	113°29'
Guanqing Mountains	2,700	1,750	38°45'	111°08'
Guandi Mountains	2,800	1,600	37°54'	111°28'
Taiyue Mountains	2,300	1,850	36°45'	112°00'

Table 2—Population variation in the characteristics of needle, cone and seed

Variable	Mean	Range	F-value
Number of needles	53.54	39-80	4.38**
Cone length (cm)	2.87	2.40-3.38	3.28**
Cone width (cm)	1.89	1.45-2.45	14.80**
Cone length/width	1.55	1.20-1.99	4.47**
Number of cone scales	39.83	28-49	4.28**
Seed length (mm)	4.70	4.42-5.06	0.89
Seed width (mm)	2.89	2.54-3.27	2.23**
Seed length/width	1.64	1.37-1.76	1.72
Wt. per 1,000 seeds (g)	6.01	4.89-7.49	39.43**

Note: ** statistically significant at $P = 0.01$

The correlation coefficients are –0.73 and –0.43 between the upper limit and longitude and between the lower limit and longitude respectively. Although none of the correlation coefficients are statistically significant at the 0.05 level, the trend is clear. Such an increase in distribution with an increase in longitude is related to climate (except Wutai Mountains) that becomes colder from the east to the west.

The correlation coefficients between the upper and lower limits with latitude are –0.39 and –0.60 respectively. Such distribution agrees with the general growing pattern of forest species and is related to the geomorphological and climatical conditions in Shanxi. From the south to the north, the topography becomes flatter, but the climate becomes colder. As long as the ecological requirements of larch are met, natural forest will be present.

The edges of Dahuangcaoliang in Guanqing Mountains, with an elevation of 2,700 m, is a subalpine meadow formed because of clear-cutting and overgrazing. However, from the residual stumps, it can be seen that this elevation is not the upper limit of larch. In Mount Xiaowen of Guandi Mountains, with an elevation of 2,830 m, larch still grows along its north-facing slopes, stretching to the top of the peak. On the northern plateau of Wutai Mountains, although the elevation is 3,058 m, spruce has replaced the vegetation bordering the subalpine meadow on the upper parts of the north-facing slopes. The south-facing slopes of the mountain summits in Shanxi are blocked by cliffs and larch grows only in patches.

The elevational difference of the vertical distribution is 750 to 1,200 m in the central and northern parts of Shanxi, while the difference between the northern-most and the southern-most is only 250 to 450 m. Such distribution indicates that the range in which the tree grows well can be greatly extended, which has been proven by species introduction practices in Shanxi and other provinces.

POPULATION VARIATION

Needle, Cone, and Seed Traits

Significant differences were detected among populations in the number of needles per fascicle on short shoot, cone length and width, the number of cone scales, seed width, and weight per 1,000 seeds (table 2). The number of needles was significantly correlated with latitude ($r = 0.35$, $P<0.05$), longitude ($r = 0.40$, $P<0.01$), and annual precipitation ($r = 0.31$, $P<0.05$) (table 3), indicating that the number of needles increases from the south to the north as latitude increases, and from the west to the east as longitude increases. However, the less precipitation there was, the more needles per fascicle. The number of needles is one of the important indexes in this study, which is in accordance with the results of our 7-year experiment. This probably resulted from the long-term adaptability of larch to the changes of geographic and climatic environment.

The mean of the length of cones was 2.87 cm, varying from 2.40 to 3.38 cm. The width of the cones was 1.89 cm, ranging 1.45 to 2.45 cm. The average number of cone scales was 39.83 ranging 28 to 49 (table 2). The number of cone scales was the only variable correlated significantly with longitude, elevation, and annual precipitation (table 3). The size of cone was not correlated with any environmental variable. On the other hand, the number of scales was correlated with the latitude ($r = 0.38$, $P = 0.1$). All indications are that as latitude increases, precipitation decreases and climate becomes colder, the number of scales per cone tends to increase; whereas, as the elevation increases, the number of cone scales decreases. It is found from the overall analysis that annual precipitation has been a predominant ecological factor in conifer forests.

Although a pronounced difference was found among populations in seed length and the ratio of length to width

Table 3—Correlation coefficients between the morphological traits and geographic variables

Variables	Latitude	Longitude	Elevation	Precipitation
Number of needles	0.35*	0.40**	–0.11	–0.31*
Cone length (cm)	0.16	0.28	–0.20	–0.32
Cone width (cm)	0.21	0.26	–0.24	–0.33
Cone length/width	–0.12	–0.13	0.12	–0.16
Number of cone scales	0.38	0.54**	–0.48**	–0.64
Seed length (mm)	0.10	–0.05		
Seed width (mm)	0.12	0.02		
Seed length/width	–0.01	0.20		
Wt. per 1,000 seeds (g)	–0.29	–0.25		

Note: * statistically significant at $P = 0.05$
** statistically significant at $P = 0.01$

of seed, all seed characteristics were not significantly correlated with geographical and climatic variables (data not shown), which is possibly due to the improper time of seed collection and heterogeneity of the distribution.

Growth Traits

The investigation indicates that under different natural conditions the growth is quite different; the general trend is that annual growth slows down from southwest to northeast. Height, DBH, and volume per tree were negatively correlated with latitude and longitude (table 4). The growth decreased from the west to the east, and from the south to the north. These trends are probably explained by the fact that annual precipitation has a positive correlation with height, DBH, and volume (table 4).

REGRESSION EQUATION AND ANALYSIS

Establishment of Regression Equation

Growth and morphological traits investigated are the fundamental factors reflecting the growth of the forest and population variation. Therefore, growth and morphological characteristics of needle, cone, and seed are selected as dependent variables (Y_n), and nine other variables which have a considerable influence on growth of forest are independent variables (X_i). A multiple linear model is proposed as:

$$Y_n = b_0 + \sum_{i=1}^{9} b_i X_i$$

where: b_0 = intercept;
b_1 = partial regression coefficient;
n = 1, 2, ..., 8;
i = 1, 2, ..., 9.

Through the significance test for the equations (Zhang and Hu 1985), we found that the equations are statistically significant only in the case of the combination of ecological factors with the height, DBH, volume, number of needles per fascicle, and the number of cone scales. The reliability reaches 95 percent or higher.

Table 4—Correlation coefficients between growth and climatic variables

Variable	Height	DBH	Volume per tree
Latitude	–0.36*	–0.57**	–0.62**
Longitude	–0.42**	–0.42**	–0.47**
Elevation	0.28	0.31*	0.30
Mean January Temperature	–0.00	0.13	0.19
Mean July Temperature	–0.30	–0.25	–0.28
Annual Mean Temperature	–0.09	–0.01	0.04
Spring Aridity	–0.26	–0.30	–0.34*
Warmth Index	–0.17	–0.17	–0.16
Annual Precipitation	0.39*	0.48**	0.40**

Note: * statistically significant at $P = 0.05$
** statistically significant at $P = 0.01$

Partial Regression Coefficients

Through the significance test for the partial regression coefficients and stepwise regression, some of the non-significant independent variables are removed. At a confidence level of 70 percent, factors that have significant influence on the dependent variable are selected to establish the regression equation:

$$Y_1 = 6.3608 - 0.0489X_1 - 0.0427X_2 + 0.0901X_5 + 0.2124X_7 - 0.0216X_8$$
$$Y_2 = 4.2599 - 0.0937X_1 - 0.0227X_5 - 0.0258X_6 + 0.3773X_7$$
$$Y_3 = 0.2161 - 0.0011X_1 - 0.0014X_2 + 0.0004X_4 - 0.0006X_5 - 0.0019X_6 + 0.0197X_7$$
$$Y_4 = 67.125 + 7.3671X_1 - 16.174X_5 - 33.837X_7 + 2.9858X_8$$
$$Y_7 = 478.468 - 2.9865X_1 + 5.308X_2 - 2.1599X_4 + 2.1874X_6$$

where Y_1 = mean annual height, Y_2 = mean annual DBH, Y_3 = the average volume per year per tree, Y_4 = the number of needles, and Y_7 = the number of cone scales.

All partial regression coefficients of the 5 selected dependent variables in the above equations have reached a significant level, while the interactions among the independent variables are very small. The variables with larger partial regression coefficients contribute more to the dependent variable.

Analysis of Predominant Factors

From table 5 it is seen that for the five established regression equations, in which the non-significant independent variables have been removed, all the multiple correlation coefficients have reached a significant level, indicating that these traits are closely related to the ecological factors. However, the determination coefficients (R^2) show the order of the direct influence of the ecological factors on the 5 dependent variables Y_1, Y_2, Y_3, Y_4, and Y_7: 14.66 percent, 39.61 percent, 39.72 percent, 33.67 percent, and 42.81 percent, respectively. The rest (1- R^2) percent comes from other unknowns.

Partial correlation analysis is further conducted for the ecological factors and the selected traits (table 6) to find out the predominant ecological factors determining the variations of the forest characters.

The factor that has the greatest influence on the height is longitude, followed by latitude, mean January temperature, mean annual temperature, elevation, annual precipitation, spring aridity, mean July temperature, and warmth index.

Latitude is the most important factor to the DBH, followed by mean annual temperature, mean January temperature, precipitation, longitude, spring, aridity, elevation, mean July temperature, and warmth index.

The factor with the greatest influence on the volume is latitude, followed by mean annual temperature, mean January temperature, precipitation, longitude, spring aridity, warmth index, elevation, and mean July temperature. Mean temperature has the greatest influence on the number of needles per fascicle, followed by elevation, latitude, warmth index, spring aridity, mean January temperature, mean annual temperature, precipitation, and longitude.

Table 5—Test of the partial regression coefficients and the multiple correlation coefficients of the equations

	Y_1	Y_2	Y_3	Y_4	Y_7
*t*1	1.751*	15.934**	1.599*	14.691**	2.717*
*t*2	−2.838**		−5.060*		−11.028**
*t*4			1.053*		3.401**
*t*5	−5.197**	−11.783**	11.587**	−43.512**	
*t*6		2.068*	−503.640**		−3.356**
*t*7	−5.588**	−30.741**	−111.980**	−38.929**	
*t*8	1.260*			6.444**	
R	0.497*	0.629	0.630**	0.580*	0.654*
*R*2	0.247	0.396	0.397	0.337	0.428

Note: * statistically significant at $P = 0.05$
** statistically significant at $P = 0.01$

Table 6—Partial correlation coefficients between the measured variables and climatic variables

Variable	Y_1	Y_2	Y_3	Y_4
Latitude	−0.31	0.43	−0.44	0.28
Longitude	−0.42	0.17	−0.08	0.06
Elevation	−0.17	0.04	−0.02	−0.28
Mean January Temperature	0.23	−0.20	0.12	0.12
Mean July Temperature	0.11	0.02	−0.02	−0.38
Annual Mean Temperature	−0.20	0.23	−0.12	−0.09
Spring Aridity	0.11	−0.09	0.06	−0.21
Warmth Index	−0.00	−0.01	0.04	0.24
Annual Precipitation	−0.14	−0.20	0.08	0.07

CONCLUSIONS

1. The natural *Larix principis-rupprechtii* forest in the Shanxi province mainly grows in the area of Guanqing and Guandi Mountains, with a small amount in the Wutai Mountains and the Hengshan Mountains. Down in the southern part of Shanxi in the forest farms of Jiangtai, Jiemiao, Haodifang, and Qiliyu, small patches of larch forest are found. There are no natural larch forests to be found in the southern area of the Taihang Mountains and the Zhongtiao Mountains. The vertical distribution of larch is generally in the 1,600 to 1,900 m elevation range, with a relative elevation difference of 250 to 1,200 m. The upper limit reached 2,800 and the lower limit can be down to 1,400 m. The upper limit does not significantly shift from the south to the north, but the lower limit descends.

2. The distribution of *Larix principis-rupprechtii* is greatly determined by climatic factors. The correlations between its distribution and temperature, precipitation, warmth index and spring aridity were all statistically significant. Types of soil and vegetation also influence the distribution of larch. *Larix principis-rupprechtii* usually grows on mountainous brown soil or leached cinnamon soil of the north-facing slopes; scarcely on the south-facing slopes. Most larch forests are pure, although occasionally they are mixed with spruce, aspen and birch.

3. Population variation is mainly influenced by geomorphological and climatic factors, and closely related to precipitation and latitude. The number of needles per fascicle on the short shoot shows an increasing tendency in a pattern of mono-directional cline from the southwest to the northeast as the climate becomes dry and cold. Cone sizes do not differ among population; it seems to decrease with the increase in precipitation. The number of cone scales increases from the south to the north as the latitude increases and the climate becomes dry and cold.

4. The growth of larch slows down from southwest to northeast as the climate becomes dry and cold. The mean annual increment of the DBH is significantly correlated with elevation. The volume is significantly negatively correlated with spring aridity.

5. The reliability of the regression equations with the growth indexes reaches 95 percent or higher, with the number of needles per fascicle 99 percent and the number of cone scales 95 percent. The multiple correlation analysis reveals close relationships among height, DBH, volume, number of needles, and number of cone scales with all the effecting factors. The established equations reflect the real situations.

6. Predominant factors affecting the growth traits have been found. The most important factors influencing the height, DBH, and volume are latitude, mean annual temperature, and mean January temperature, which reveals that at different latitudes, the growth is different due to the differences in geological positions and the conditions of moisture and temperature. The factors influencing the number of needles include mean July temperature and latitude. Changes of the number of needles follow the genetic variation pattern of mono-directional cline.

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Spatial Distribution of Tamarack Cones Damaged by the Larch Cone Maggot and Lepidoptera

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Abstract—Spatial distribution of tamarack cones and of insect damage were determined in trees at Thunder Bay, ON, in 1990. A total of 5,900 cones were collected by tree, north and south crowns, and crown level. All cones were attacked. The proportion of cones damaged by the larch cone maggot was more variable than by the eastern spruce budworm and four other Lepidoptera. Numbers of cones infested by larch cone maggot and Lepidoptera were greatest in the upper crown of the south face; while for budworm the numbers were greatest in the middle crown of the south face.

In tamarack (*Larix laricina* [Du Roi] K. Koch), viable seed production is low where up to eight seeds per cone can be extracted, but generally only two to five seeds are present (Amirault and Brown 1986; Etheridge 1986; O'Reilly and Farmer 1991; Smith 1981; Tosh 1986). Low production of viable seeds in conifers can be due to a variety of factors that include pollination (Di-Giovanni and Kevan 1991), fertilization (Hall and Brown 1976, 1977), and insect feeding (Hedlin and others 1980). Self-pollination (Farmer and Reinholt 1986; Hall and Brown 1977), poor pollination and fertilization (Hall and Brown 1976, 1977; O'Reilly and Farmer 1991), and insects severely limit viable seed production in tamarack (Amirault and Brown 1986; Eavy and Houseweart 1986; O'Reilly and Farmer 1991; Prévost, in press; Turgeon 1989).

Insects that feed in cones and seeds of tamarack belong to the Diptera, Lepidoptera, Hymenoptera, and Homoptera (Hedlin and others 1980). A review of tamarack cone and seed insects and some biological notes can be found in Amirault (1989), Amirault and Brown (1986), Eavy and Houseweart (1986), Prévost (in press), and Rose and Lindquist (1980).

Evaluation of cone and seed characteristics of tamarack in northwestern Ontario indicated that seed damage could be as high as 97 percent (O'Reilly and Farmer 1991). This level will be an obstacle to tamarack tree improvement programs. Consequently, studies were initiated to determine the importance of insects to cone and seed production in wild tamaracks near the tamarack provenance plantations in Thunder Bay (Prévost, in press).

Besides knowledge of insect damage, understanding the distribution of cones and damage within and between trees is necessary if effective protection programs are to be implemented. Annual intertree and intratree variation in cone production and insect damage poses problems for seed orchard management because there is usually not enough lead time between cone crop monitoring, insect monitoring, and when action is required. Forecasting tools for cone crop production and insect damage would allow proper planning for the coming field season. Knowing the distribution of the larch cone maggot (*Strobilomyia* sp.) and of Lepidoptera cone damage between and within trees is a valuable step in developing these forecasting tools. This knowledge would determine where and how much to sample for evaluating damage that could be correlated to pheromone trap and sticky trap catches of adult insects.

Development of forecasting tools has been initiated by Roques (1988) in France and by Turgeon (1989) in northeastern Ontario to determine the relationship between cone production and damage by larch cone maggots. And both Lepidoptera and Diptera have been deemed important in reducing seed production in tamarack (Amirault and Brown 1986; Eavy and Houseweart 1986; Prévost, in press). The objective of this study was to determine the intertree and intratree variation of cone distribution and damage by both larch cone maggot and Lepidoptera at Thunder Bay, ON, Canada.

METHODS AND MATERIALS

During May 1990, five upland open-grown trees 8 to 10 m tall and about 25 years old were selected based on the presence of current-year female strobili. During the third week of August all 5,900 entire cones and those chewed by eastern spruce budworm (*Choristoneura fumiferana* [Clem.]), were collected by tree, north or south crown, and crown level. Access to tree tops was gained by a 9-m extension ladder stabilized using guy ropes (Yeatman and Nieman 1979). Cones were stored at 4 °C until they were assessed within 6 months of collection.

External feeding was classed as present or absent. Spruce budworm was the only lepidopteran feeding externally on the cones. The damage included lacerations, truncations, hollowing out, and near-complete consumption of the cone. Internal feeding was assessed by peeling back cone scales from the cone base to apex. Larch cone maggot damage was recognized as tunneling around the cone axis through seeds and cone scales, whereas internal

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Lepidoptera feeding was recognized by the irregular-shaped feeding patch containing fecal pellets and silken webs.

Untransformed mean number of cones per tree and arcsin-transformed percentages of cones were analyzed by one-way analysis of variance (ANOVA) for the effect of cardinal direction and crown level on the following dependent variables: number of cones and damage to cones by the larch cone maggot, spruce budworm and Lepidoptera using the statistical analyses program, Minitab (Ryan and others 1985). I also tested for the interactive influence of crown level and cardinal direction on the dependant variables by using two-way ANOVA. When ANOVA showed significant differences, Duncan's Multiple Range Test was used to indicate which means were different.

RESULTS AND DISCUSSION

Intertree Variation

The number of cones per tree for the five trees ranged from 395 to 2,614 (table 1). There was a tendency for taller trees to have more cones, as Turgeon (1989) also found. This can be explained generally in that tall trees have more sites for the formation of female reproductive buds. In contrast, Powell and others (1984) found that the shortest tree in their study carried the most cones. Cone production is dependent not only on tree height, but also on tree age, light intensity, photoperiod, temperature, and soil nutrients (Duncan 1954; Owens and Blake 1985), which also influence the periodicity of cone production.

Generally in years of good cone production, the percentage damage to the cone crops is light (Annila 1981; Cameron and Jenkins 1988; Fogal 1989; Mattson 1971; Prévost 1990). In 1990, cone production in tamarack was light at this site; only five trees of 40 examined had greater than 100 cones. Consequently, the percentage damage to the cone crop was expected to be high, and it was (table 1). All 5,900 cones were damaged by at least one insect.

The percentage of cones attacked by all insects was not related to the total number of cones per tree (table 1). Larch cone maggot likely attacked a greater proportion of cones than indicated here. But cones destroyed by budworm were not counted if they did not reveal (upon cone dissection) if a maggot feeding had taken place (table 1). Nevertheless, this study and that of Turgeon (1989) suggest that the larch cone maggot attack is not greater in trees with more cones.

Table 1—Total cones and percentage attacks by the larch cone maggot, eastern spruce budworm, and Lepidoptera in five tamaracks at Thunder Bay, ON, in 1990

Tree	Height	Total cones	Larch cone maggot	Spruce budworm	Lepidoptera
	Meters		*- - - - - - - - Percent attacks - - - - - - - - -*		
1	9.0	1,127	75.2	23.8	80.1
2	9.0	1,154	67.9	22.4	87.2
7	8.4	610	78.7	18.9	94.2
9	10.1	2,614	41.2	42.5	83.1
10	8.1	395	48.1	22.8	84.8
Means	8.9	1,180	62.2	26.1	85.9
(S.D.)	(0.8)	(990)	(16.7)	(9.4)	(5.3)

Even though eastern spruce budworm was not a major pest on tamarack, like the western spruce budworm (*Choristoneura occidentalis* Free.) is on western larch (*Larix occidentalis* Nutt.) (Fellin and Shearer 1960), eastern spruce budworm can be an unanticipated problem. Eastern spruce budworm damage was more or less constant at about 21 percent except for tree 9 where the damage observed was double that of the others (table 1). It may be that two white spruce (*Picea glauca* [Moench] Voss) near tamarack 9 harbored eastern spruce budworm, which dispersed to it. Other tamaracks were not in the immediate vicinity of white spruce.

Lepidoptera damage consisted of that by eastern spruce budworm and four other species: brown larch tubemaker (*Spilonota laricina* Heinrich), larch needle worm (*Zeiraphera improbana* [Walker]), larch casebearer (*Coleophora laricella* [Hubner]), and the orange larch tubemaker (*Coleotechnites laricis* [Freeman]). Although in the fourth to sixth instar, damage by eastern spruce budworm was external, second and third instars mined the cones like the four other Lepidoptera, and their damage characteristics were not sufficiently different to separate them from the others. Damage by these miners was greater than 80 percent in all trees and should be considered a potential menace to tamarack seed production (table 1).

Intratree Variation

Tamarack cones were not distributed evenly in the crown (table 2). Mean number of cones and percentage of total cones on the south face of the trees were not significantly ($P = 0.05$) greater than on the north face. About 63 percent of the cones were in the south crown, whereas 37 percent were in the north crown. In contrast, Turgeon (1989) had a significantly greater mean number of tamarack cones in the south face than in the three other cardinal directions. In red pine (*Pinus resinosa* Ait.) (Mattson 1979) and jack pine (*P. banksiana* Lamb.) (Rauf and Benjamin 1983) the south face also had a significantly greater mean number of cones. Where these other studies have found differences, the lack of difference in this study is probably due in part to the limited number of trees and the large variation among them.

The number of tamarack cones in a given crown level was not significantly different at $P = 0.05$ except in the northern lower crown (table 2). About 49 and 47 percent of the total cones were in the upper and middle crowns, respectively, whereas only about 4 percent were in the lower crown. Cone numbers greater in the middle crown than in upper and lower crowns have been found in tamarack (Turgeon 1989), European larch (*L. decidua* Mill.) (Roques 1988), red pine (Mattson 1979), and jack pine (Rauf and Benjamin 1983).

Larger number of cones tend to grow on exposed branches (Mattson 1979; Roques 1988). In our study,

Table 2—Distribution of cones in five tamarack trees by crown level and cardinal direction at Thunder Bay, ON, in 1990. Similar alpha (crown level) and numerical (cardinal direction) designations indicate no significant differences at $P = 0.05$ as determined by one-way analysis of variance and Duncan's Multiple Range Test

	North			South		
Crown level	Number in five trees	Mean (S.D.) cones per tree	Mean % (S.D.) of 5,900 cones	Number in five trees	Mean (S.D.) cones per tree	Mean % (S.D.) of 5,900 cones
Upper	1,127	a1 225.4 (150.5)	a1 19.1 (9.0)	1,762	a1 352.8 (275.7)	a1 29.9 (9.4)
Middle	1,031	a1 206.2 (121.1)	a1 17.5 (6.4)	1,766	a1 353.2 (372.6)	a1 29.9 (12.1)
Lower	28	b1 5.6 (7.7)	b2 0.5 (0.3)	186	a1 37.2 (31.7)	b3 3.1 (2.1)

we found it difficult at times to distinguish whether the cone-bearing branch was on the north or south side because the crown in a tamarack is not compact as in a white spruce. Some branches that distinctly originated on the north side of the bole were sufficiently long enough to be exposed to the sun for the major part of the day. This was especially true in the top third of the crown and may explain in part why in our study we did not find significant differences in cone numbers between cardinal and vertical directions, except in the north bottom side where sun exposure was limited.

Larch cone maggot attacked significantly ($P = 0.05$) more cones in the top and middle crowns where the greatest number of cones were located (table 3). However, the proportion of cones infested between the three crown levels was not significantly different ($P = 0.05$). As well, the number of cones infested in the south face was not significantly ($P = 0.05$) greater than in the north face, while the proportion of cones infested in the two faces were similar. This resembles Roques' (1988) and Turgeon's (1989) findings except they found significantly more cones attacked in the south than the north face.

Tree height and cone numbers per tree appear unimportant to the level of infestation by the cone maggot, which depends more on the fecundity of the flies and the number of flies ovipositing. The cone fly may select any tamarack bearing current-year cones and then oviposit preferentially in the upper and middle crown where there are the most cones. Larch cone maggot damage distribution was generally parallel to the cone distribution in the tree (tables 2 and 3), but the percentage damage per tree can be variable (table 1).

Eastern spruce budworm did not damage significantly ($P = 0.05$) more cones or a greater percentage of cones in any crown level of the south face, while in the north face significantly more cones were damaged in the upper and middle levels than in the lower (table 4). This damage pattern by eastern spruce budworm is not similar to that of budworm distribution in balsam fir where the greater proportions are in the upper crown (Régnière and others 1989). It is possible that greater damage observed in the middle crown is due to more larvae displaced to lower branches because the upper branches were whipped in the wind.

Collectively the Lepidoptera damaged the greatest number of cones in this study (tables 1 and 5). The number of cones damaged was not significant from the upper to lower crown except in the lower north face when it was significantly ($P = 0.05$) less than the other two levels due to the low number of cones in this part of the crown (table 5). As with spruce budworm (table 4), in the upper two levels there were no significant differences ($P = 0.05$)

Table 3—Distribution of cones tunneled by the larch cone maggot in five tamaracks by crown level and cardinal direction at Thunder Bay, ON, in 1990. Similar alpha (crown level) and numerical (cardinal direction) designations indicate no significant differences at $P = 0.05$ as determined by one-way analysis of variance and Duncan's Multiple Range Test

	North			South		
Crown level	Number in five trees	Mean (S.D.) cones per tree	Mean % (S.D.) of total crowns in crown level	Number in five trees	Mean (S.D.) cones per tree	Mean (S.D.) of total crowns in crown level
Upper	813	a1 162.6 (109.8)	a1 72.1 (12.8)	1,248	a1 249.6 (159.6)	a1 72.3 (12.6)
Middle	685	a1 137.0 (93.1)	a1 66.4 (15.3)	1,051	ab1 210.2 (202.2)	a1 59.5 (18.0)
Lower	14	b1 4.8 (6.9)	a1 50.0 (33.6)	112	bb1 22.4 (23.7)	a1 60.2 (44.2)

Table 4—Distribution of cones fed on by spruce budworm in five tamaracks by crown level and cardinal direction at Thunder Bay, ON, in 1990. Similar alpha (crown level) and numerical (cardinal direction) designations indicate no significant differences at $P = 0.05$ as determined by one-way analysis of variance and Duncan's Multiple Range Test

	North			South		
Crown level	Number in five trees	Mean (S.D.) cones per tree	Mean % (S.D.) of total crowns in crown level	Number in five trees	Mean (S.D.) cones per tree	Mean (S.D.) of total crowns in crown level
Upper	299	a1 59.8 (44.5)	a1 26.5 (15.0)	447	a1 89.4 (133.9)	a1 25.8 (14.1)
Middle	318	a1 63.6 (36.9)	a1 30.8 (18.7)	633	a1 126.6 (188.5)	a1 35.8 (20.0)
Lower	3	b1 0.6 (0.5)	a1 10.7 (21.0)	66	a1 13.2 (14.4)	a1 35.5 (37.0)

between the north and south faces in the mean number of cones damaged and the proportion of cones damaged.

There was no interactive effect between crown level and cardinal direction on the number of sound cones and those attacked by larch cone maggot, eastern spruce budworm, and Lepidoptera. One-way and two-way ANOVA's yielded similar differences.

Where other studies have found differences, the lack of significant differences in this study is probably due to the small number of trees examined, the large intertree variation, the sun exposure of branches on the north side, and the masking of damage of one insect by another. Although more extensive studies are required to recommend how to sample operationally for the larch cone maggot and Lepidoptera damage to tamarack cones, this study and those of Turgeon (1989) and Roques (1988) indicate that the most practical crown sector to sample would be the south middle crown. The recommendation is based on intratree density of cone production, location of larch cone maggot and Lepidoptera damage, and accessiblity of sample unit. The most immediate steps toward developing a monitoring system for tamarack cone and seed protection are relating pheromone trap catches of budworm to damage and developing pheromone traps for the other Lepidoptera and sticky traps for the North American larch cone fly species as has been done by Roques (1988) in France.

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Table 5—Distribution of cones mined by the Lepidoptera in five tamaracks by crown level and cardinal direction at Thunder Bay, ON, in 1990. Similar alpha (crown level) and numerical (cardinal direction) designations indicate no significant differences at $P = 0.05$ as determined by one-way analysis of variance and Duncan's Multiple Range Test

	North			South		
Crown level	Number in five trees	Mean (S.D.) cones per tree	Mean % (S.D.) of total crowns in crown level	Number in five trees	Mean (S.D.) cones per tree	Mean (S.D.) of total crowns in crown level
Upper	1,002	a1 220.4 (134.3)	a1 88.9 (11.6)	1,559	a1 311.8 (266.1)	a1 90.3 (15.3)
Middle	925	a1 185.0 (106.4)	a1 89.7 (10.5)	1,333	a1 266.6 (289.2)	a1 75.5 (12.2)
Lower	12	b1 4.4 (5.6)	b1 42.8 (48.4)	151	a1 30.2 (32.0)	a1 81.2 (23.8)

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Woody Residue and Soil Organic Matter in Western Larch Ecosystems

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Abstract—Woody residue and surface organic layers are important components of soil organic matter in western larch (*Larix occidentalis* Nutt.) ecosystems. These organic materials provide physical, chemical, and biological functions for sustaining these forests. Historically, forest management practices have removed much of the woody residue and surface soil organic matter when establishing western larch. Forestry practices need to balance organic matter removals, by leaving adequate amounts of organic materials to sustain western larch site productivity.

Western larch (*Larix occidentalis* Nutt.) is an important commercial tree species in Northern Rocky Mountain forests (Schmidt and others 1976; Schmidt and Shearer 1990). This species is an aggressive seral, which is adapted to fire and resistant to attack by insects and disease. Western larch is widely distributed throughout the region, showing its greatest development in eastern Washington, northern Idaho, western Montana, and southern British Columbia, Canada (Schmidt and Shearer 1990). It is particularly well represented in the wetter habitat series: grand fir (*Abies grandis* [Dougl ex D. Don] Lindl.), western redcedar (*Thuja plicata* Donn ex D. Don), western hemlock (*Tsuga heterophylla* [Raf.] Sarg.), moist end of Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco). In these areas it occurs extensively in 19 habitat types (table 1). Soil organic matter is an important component of site productivity in these forest types. It provides a framework for soil physical, chemical, and biological functions, which have integral roles in soil nutrient cycling, mycorrhizal root development, seedling establishment, and soil water availability (Harmon and others 1986; Harvey and others 1987; Page-Dumroese and others 1993; Tonn and others 1993).

SOIL ORGANIC MATTER

Because western larch occurs in many Northern Rocky Mountain forest ecosystems, the amount of soil organic matter among stands can be quite variable. Although western larch is well adapted as a pioneer species on disturbed soils low in organic matter, the productivity of western larch forests generally increases as the amount of soil organic matter increases, except on cold, wet soils at high elevations (Page-Dumroese and others 1991). The type and distribution of soil organic matter on western larch sites differs widely, depending on tree species present, stand age, and fire history. However, the majority is found in woody residue and in surface organic layers (soil wood and forest floor) (table 2).

Woody residue can be of any size, but material larger than 7.5 cm in diameter has the potential to become a long-term component of the functioning soil ecosystem. Wood less than 7.5 cm in diameter usually decays quite rapidly, or is consumed readily by both natural and prescribed fires (Edmonds 1991; Reinhardt and others 1991). Woody residue is a major part of most western larch ecosystems, and may equal or surpass other organic biomass in the forest floor (table 2). In some habitat types woody residues can exceed 500 Mg per ha (Brown and See 1981). Dead wood in these western conifer forests has a major role in soil carbon cycling, nitrogen fixation, stream ecology, erosion control, and the incidence of tree disease (Harmon and others 1986; Jurgensen and others 1992; Sollins and others 1980, 1987).

Downed logs are also important for seedling growth, mycorrhizae development, and protection of seedlings from wildlife and domestic livestock damage (Graham and Kingery 1992; Harvey and others 1987).

When decayed wood is incorporated into the forest floor and covered by litter, it can be termed "soil wood". In western larch ecosystems soil wood can comprise over

Table 1—Occurrence of western larch as a major seral in habitat types of northern Idaho and western Montana

Habitat series	Total number habitat types	Habitat types larch present[1]
Douglas-fir	15	5
Grand fir	10	4
Englemann spruce	8	2
Western hemlock	4	2
Western redcedar	6	2
Mountain hemlock	5	2
Subalpine fir	19	2

[1] Western larch present as a major seral in all or certain areas of habitat type (Cooper and others 1987; Pfister and others 1977).

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Table 2—Organic matter components of forest soils in western larch ecosystems of the Northern Rocky Mountains

Site	Yield capability	Woody residue	Forest floor	Soil wood	Mineral soil[1]	Total	Proportion in mineral soil
	Organic matter component						
	$m^3 ha^{-1} yr^{-1}$	-----------	-----------	$Mg\ ha^{-1}$	-----------	-----------	Percent
Cedar/hemlock (Montana)	7.7	83	50	51	145	329	44
Subalpine fir (Montana)	7.7	146	36	36	153	371	41
Cedar/hemlock (Idaho)	9.5	154	23	48	201	426	47
Douglas-fir (Montana)	4.9	45	26	37	133	241	55

[1] Sampled to a depth of 30 cm. These values do not include root weights.

15 percent of the organic matter in the surface 30 cm of soil and can equal or surpass organic matter contents of the forest floor (table 2). Virtually all soil wood is produced by brown-rot fungi from large residues having appreciable amounts of heartwood (Larsen and others 1980). Soil wood is usually wetter and cooler than the surrounding forest floor and can remain buried in the soil for hundreds of years (Harvey and others 1979, 1981; McFee and Stone 1966). Consequently, root activity and conifer regeneration are favored, particularly on dry sites (Harvey and others 1987).

Western larch does not appear to be a major source of soil wood in habitat types where it occurs (table 3). This could be due to a low larch component in the current or previous stand, or to the possible formation of less resistant decay products during larch wood decomposition.

The forest floor is a combination of three recognizable layers: (1) the litter layer (O_i), consisting of freshly fallen needles, twigs, and other debris having only slight decomposition, (2) the fermentation or duff layer (O_e), plant materials undergoing active decomposition but are still identifible, and (3) the humus layer (O_a), unrecognizable, amorphous organic material that is highly decomposed. The extent of forest floor development is a function of litter inputs and decomposition rates, fine root turnover, previous stand management, and fire history (Edmonds 1991).

Mineral soil horizons in western larch forests also contain large amounts of organic matter, especially if the soil has a significant volcanic ash content (Page-Dumroese and others 1991). The surface 30 cm of mineral soil is the zone of greatest importance because root numbers and root activity decrease rapidly below this depth (Kimmins and Hawkes 1978).

HARVESTING AND SITE PREPARATION

Soil organic matter is an important factor in the continued productivity of western larch forests. Harvesting these forests greatly affects levels of woody residue on a site, the forest floor integrity, and amounts of surface organic matter incorporated into the mineral soil. All of these factors can have important implications for seedling survival and growth, root development, and nitrogen cycling (Harvey and others 1987).

Most western larch stands in the Northern Rocky Mountains contain adequate organic reserves (Brown and See 1981) and are not considered highly sensitive to soil organic matter depletion following harvesting. However, mechanical site preparation methods often used on western larch sites (such as dozers and grapple pilers) can remove most woody residue or displace the forest floor and surface mineral soil over large areas. Such extensive machine piling, windrowing or soil scarification could have significant impacts on seedling establishment and growth (Graham and others 1992b). Prescribed burning for site preparation can also favor organic matter conservation on most western larch sites, even when using seed-tree and

Table 3—Tree species of decayed wood in soils of four old-growth forests in the Northern Rocky Mountains

Habitat series[2]	Total samples	DF	WWP	WL	LPP	WH	SAF	ES
		Species[1]						
		----------	----------	----------	Percent	----------	----------	----------
Western Montana								
Douglas-fir	22	100	0	0	0	0	0	0
Subalpine fir	101	77	0	8	3	2	6	4
Western hemlock	16	63	0	0	6	19	6	6
Northern Idaho								
Western hemlock	153	45	31	16	1	4	1	2

[1] Species codes are DF = Douglas-fir, WWP = western white pine, WL = western larch, LPP = lodgepole pine, WH = western hemlock, SAF = subalpine fir, and ES = Engelmann spruce.

[2] Climax type as described by Pfister and others (1977).

shelterwood cuttings (Schmidt and Shearer 1990). But care is needed to ensure that the slash disposal and site preparation objectives of burning are met without adversely affecting soil organic reserves.

Studies worldwide show that high levels of organic matter removal from forest sites are linked to substantial long-term growth reductions of various conifer species (Ballard and Will 1981; Farrell and others 1986; Ginter and others 1979; Graham and others 1992b; Smith 1985; Weber and others 1985). Clearcut harvesting, which is used to manage for early successional species, such as western larch, cause greater losses of soil organic matter than other harvesting systems. Substantial losses in site productivity have been reported in the Northern Rocky Mountains 15 to 25 years following clearcutting as a result of forest floor/surface soil displacement and soil compaction (Bosworth and Studer 1991; Clayton and others 1987).

Losses of organic matter from undisturbed forest floor and mineral soil after timber harvesting are generally a result of increased organic matter decomposition by soil microorganisms (Hendrickson and others 1982). Higher levels of soil moisture, temperature, and alkalinity after harvesting, especially if fire is used for slash disposal (table 4), increases microbial activity (Hungerford 1980; Jurgensen and others 1981). Mixing of the forest floor into the mineral soil during harvest and site preparation also increases organic matter decomposition rates (Salonius 1983).

The amount of large woody residue left on the soil surface after timber harvesting is dependent on stand species composition, amount of decay and defect, wood utilization levels employed, and site preparation techniques. However, in some cases, woody residue levels after harvesting are less than was originally present before the stand was cut. This was especially evident on a clearcut cedar/hemlock site in northern Idaho, where woody residue loadings after prescribed burning and intensive harvesting were reduced by more than 90 percent (table 5). The amount of residue remaining after clearcutting was nearly the same as in the uncut stand, but the type of woody material was quite different. Nearly 60 percent of woody residue on the clearcut was in the solid rot or crumbly rot stage, and 40 percent was undecayed. Woody residue in the solid rot stage is sound enough to remain intact during logging operations, while crumbly rot residue is easily destroyed (Benson and Schlieter 1980). In contrast, most woody residue on the uncut site was large decayed logs in the crumbly rot stage, many of which were broken apart during harvesting operations. These disturbed and fragmented logs would have much less impact on soil nutrient and biological processes than before the harvest (Harmon and others 1986; Jurgensen and others 1987).

Table 5—Surface organic matter contents following clearcutting and site preparation

Soil component	Residue treatment[1]			
	None	Prescribed burned	Intensive removal	Uncut
	Mg[2]	*- - - - - - - - - - Mg*	*- - - - - - - - - -*	
Cedar/hemlock (Idaho)				
Wood residue	146.0	57.9	10.6	154.3
Forest floor	16.7	5.5	13.3	23.2
Soil wood	50.9	22.4	51.6	47.9
Total	213.6	85.8	75.5	225.4
Subalpine fir (Montana)				
Wood residue	—	55.2	43.7	145.7
Forest floor	—	30.2	35.8	36.0
Soil wood	—	37.6	43.2	35.9
Total	—	123.0	122.7	217.6

[1] Site was clearcut to a 12.7 cm diameter top. Residue treatments: none-residue left; prescribed burned-broadcast burned in the fall; intensive removal-residue removed by blading with a crawler tractor.

[2] Dry mass ha^{-1} of organic material on top of mineral soil.

MANAGEMENT IMPLICATIONS

Historically, even-aged management systems of shelterwood, seed-tree cuttings, and clearcutting followed by prescribed burning or scarification provide adequate microsite conditions for establishing western larch from seed (Cole and Schmidt 1986; Schmidt and Shearer 1990; Shearer and Stickney 1991). All of these silvicultural systems stress forest floor removal, exposing mineral soil, and controlling competing grasses, shrubs, and trees (Schmidt and Shearer 1990; Schmidt and others 1976). Consequently, these operations remove much of the woody residue and surface soil organic matter present on a site, but the amounts vary according to the intensity of treatment and the distribution of organic matter in the soil (Graham and

Table 4—Soil moisture content and temperature on a cedar-hemlock site in northern Idaho following clearcutting and site preparation treatments

Soil component	Residue treatment[1]							
	None		Prescribed burned		Intensive removal		Uncut	
	H_2O Percent	*Temp °C*	*H_2O Percent*	*Temp °C*	*H_2O Percent*	*Temp °C*	*H_2O Percent*	*Temp °C*
Forest floor	88	15.4	43	14.3	104	15.3	90	11.7
Soil wood	158	13.4	122	12.8	206	12.4	232	11.4
Mineral soil[2]	47	12.0	38	11.5	61	10.7	41	10.5

[1] Site was clearcut to a 12.7 cm diameter top. Residue treatments: none-residue left; prescribed burned-broadcast burned in the fall; intensive removal-residue removed by blading with a crawler tractor.

[2] Mineral soil to a depth of 30 cm.

others 1993; Minore and Weatherly 1988; Page-Dumroese and others 1991). Soils having a higher proportion of organic matter in woody residue and the forest floor would be more affected by these operations than soils having greater amounts in surface mineral layers.

Burned-over soil surfaces or exposed mineral soil with minimal competing vegetation is desirable when establishing western larch from seed (Haig and others 1941; Schmidt and Shearer 1990). However, the removal of large amounts of soil organic matter to expose mineral soil for adequate seed germination is not required if the site is planted with nursery stock. Normally, site preparation methods used prior to planting seedlings would be less intensive and have less impact on soil organic levels than those used for seedbed preparation (Harvey and others 1987). In such situations, site preparation should provide planting sites that ensure good root to soil contact. This may involve clearing litter and twigs to prevent these materials from entering the planting hole, rather than the removal of all surface organic layers.

After timber harvesting a large amount of woody residue is added to the soil surface. How much should be left to become part of the soil organic supply will depend on site conditions and wildfire potential. In general, greater amounts of woody residue can remain on the cooler, moister habitat types occupied by western larch (western hemlock and western redcedar) than on the warmer, drier ones (Douglas-fir). A minimum value of 22 to 36 metric tons per ha of residual woody material has been recommended to maintain long-term site productivity in western larch forests of northwestern Montana and northern Idaho (Harvey and others 1987). Leaving greater amounts of wood can benefit many sites, but might create a significant fire risk. However, after considering fuel reduction and various other site preparation objectives, Reinhardt and others (1991) established a fairly wide range of allowable woody residue loadings (22 to 125 metric tons per ha) for mixed conifer forests in the Northern Rocky Mountains. With such guidelines, site-specific woody residue management can become a realistic goal.

CONCLUSIONS

With the current interest in forest ecosystem management, simply using silvicultural practices that ensure the natural or artificial regeneration of western larch is insufficient. An equally important management objective for sustaining western larch forests is the maintenance of adequate soil organic reserves. Many western larch ecosystems are fire dependent, so the amount and cycling of organic matter may be more critical on dry sites than on wet sites where fire is less frequent. Woody residues and surface soil organic matter are key components for the function and maintenance of western larch ecosystems. How much postharvest organic matter to leave will be influenced by whether western larch is established by planting or by natural regeneration. However, when using natural regeneration, forest managers must always be aware of the risk that extensive seedbed preparation may have on soil organic matter reserves needed for subsequent stand growth and development.

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Vegetation Responses to Silviculture and Woody Residue Treatments in a Western Larch Forest

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Editor's Note: This is an abstract of a paper that will be published separately from this proceedings. Inquiries regarding the study and data may be made through the authors at the addresses listed at the bottom of this column.

Western larch forests commonly have luxurious understory vegetation that protects the site and provides significant habitat for various wildlife species. Knowing how various forest management practices affect the response of shrub, forb, and grass components of the understory was one of the subjects of a multidiscipline study in a larch-Douglas-fir forest. This report describes 10-year response to the harvest cutting treatments: (1) clearcut, (2) shelterwood, and (3) group selection and residues disposal treatments. The third group included: (1) moderate level of woody residues followed by broadcast burning, (2) heavy amount of residues followed by broadcast burning, (3) intense removal of all residues, and (4) understory tree protected with moderate removal of woody residues.

Residues treatments were superimposed on the three harvest cutting treatments, resulting in 12 combinations. There were two replications. Also included for comparison were identical understory vegetation measurements in adjacent virgin natural forests.

Understory vegetation responded substantially in the first 10 years following treatments. The initial harvest cutting and residues treatments reduced volumes of live shrubs to as little as 3 percent of the preharvest volumes on the clearcut and burned treatments. The average for all treatments 2 years after treatment, however, was about 20 percent of preharvest level. Ten years after treatment, shrub volumes averaged 50 to 70 percent of preharvest levels with shrubs on the group selections and clearcuts responding the most and those in the shelterwoods the least. Residues treatments, particularly prescribed fire and protected understory tree treatments, also affected understory response.

The two burning treatments reduced shrub volume the most, and the treatment that attempted to protect the understory trees resulted in the least reduction in shrub volume. Herb cover and volume generally increased to greater than preharvest levels during the first 4 years after treatments. After that these values generally declined. At about 10 years they had declined to near preharvest levels. Ten years after treatment the number of different species found on the study plots exceeded that in the original mature forest. All of the increases were in the herb component of the understory vegetation.

Understory vegetation in larch-Douglas-fir forests is responsive to various combinations of harvest cutting and residues removal treatments. Vegetation responses are rapid for the first 2 to 4 years. This is followed by a gradual approach toward the levels found in mature forests. Long-term multidisciplinary studies such as this help define the trajectory of the gradual changes in understory and the relationship to other forest values and ecological processes.

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At the time of the study, Wyman C. Schmidt (retired) was Project Leader and Research Silviculturist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, located at the Forestry Sciences Laboratory, Montana State University, Bozeman, MT 59717-0278, U.S.A. Carl E. Fiedler is Research Silviculturist, Montana Forest and Conservation Experiment Station, University of Montana, Missoula, MT 59812, U.S.A. Ward W. McCaughey is Research Forester, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Forestry Sciences Laboratory, Montana State University, Bozeman, MT 59717-0278, U.S.A.

Old-Growth Western Larch Forests: Management Implications for Cavity-Nesting Birds

B. Riley McClelland

Abstract—This paper discusses the role western larch plays in the habitat requirements for cavity-nesting birds. The pileated woodpecker's importance as a "pathfinder" species, the importance of old-growth western larch, and the need for management strategies that feature optimal ecological values are emphasized.

Characteristics of nest trees and surrounding habitats were documented for more than 300 cavity nests used by 28 bird species in northwestern Montana between 1975 and 1991. Study areas included the Coram Experimental Forest and Glacier National Park. Forests of western larch (*Larix occidentalis*) and Douglas-fir (*Pseudotsuga menziesii*) were studied most intensively.

There were more nests in western larch and fewer in Douglas-fir than expected, based on availability. Forest stands characterized as old growth (with trees large and old relative to species and site, large snags and logs, and a high incidence of broken tops and heartwood decay) supported the highest density and diversity of cavity nesters.

A "PATHFINDER" SPECIES AND ITS NESTS

The study focused on the pileated woodpecker (*Dryocopus pileatus*), a "pathfinder" species that creates nesting, roosting, and feeding opportunities for many birds and small mammals incapable of excavating in the dense wood of western larch. Fifty-three pileated woodpecker nests were in western larch; only one was in Douglas-fir. Mean diameter at breast height of larch nest trees was 80 cm; 72 percent were snags.

Nearly all larch nest trees had visible evidence of heartwood decay: conks (primarily *Phomitopsis officinalis*) or white pocket rot in the wood chips from the cavity excavation. Because undecayed larch wood is dense and difficult to excavate, woodpeckers selected trees with heartwood decay. Such trees usually were more than 200 years old. Western larch may have been preferred because the sapwood is slow to decay, leaving a cylinder of relatively firm and protective sapwood surrounding a core of decaying heartwood. In Douglas-fir snags, the sapwood and heartwood decay nearly concurrently as the snag ages.

Considering its pathfinder role and need for large decaying trees, the pileated woodpecker is appropriately identified as a sensitive species, dependent on the old-growth component in western larch forests. However, the pileated woodpecker is not a meaningful management indicator for a diverse range of old-growth forests; the pileated woodpecker does not nest in all tree species (e.g., Engelmann spruce or subalpine fir) and it rarely nests in high elevation forests. Additionally, attributes of old growth are site specific. Use of a single bird species as an indicator for a complex and diverse array of old growth is illogical.

BIOLOGICAL DIVERSITY

Where retention of biological diversity is important in western larch forests, old growth is an essential component. This will require subordinating maximum timber production on selected low elevation, productive sites and planning on a landscape scale—not simply one cutting proposal at a time. Heartrot, for example, may decrease timber production, but it is an indispensable process in cavity-nesting habitat. So called salvage and sanitation sales can destroy cavity-nesting habitat even while leaving substantial volume on site.

Rather than focusing on minimum habitat standards for cavity nesters (e.g., nest tree size and density of snags) management strategies should emphasize optimum ecological values (Conner 1979).

Historically, extensive stands of old-growth western larch were shaped by lightning, wildfire, insects, disease, and decay. However, in recent decades the extent of old-growth larch forests in northwestern Montana has been diminished primarily by logging. In the future, regardless of how eloquently "New Forestry" and biodiversity jargon dominate forest planning rhetoric, the terms will be canards unless a biologically objective perception of diversity is applied. The roles of all native flora and fauna including insects, decay organisms, snags, old growth, and pathfinders need to be recognized and incorporated into long-term management strategies for western larch forests.

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Silvicultural Treatments Influence Water Use in Western Larch Forests

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Editor's Note: This is an abstract of a paper that will be published separately from this proceedings. Inquiries regarding the study and data may be made through the authors at the addresses listed at the bottom of this column.

Water is considered the most limiting factor for growth of most western larch forests. The amount and pattern of water use by the forest are important criteria for forest management decisions.

The study describes soil water use differences in a larch-Douglas-fir forest subjected to different forest management treatments. Included were the harvest cutting treatments: (1) clearcut, (2) shelterwood, and (3) group selection and residues disposal treatments. The third group included: (1) moderate level of woody residues followed by broadcast burning, (2) heavy amount of residues followed by broadcast burning, (3) intense removal of all residues, and (4) understory tree protected with moderate removal of woody residues.

Residues treatments were superimposed on the three harvest cutting treatments, resulting in 12 combinations. There were two replications. Also included for comparison were identical soil water measurements in adjacent mature uncut forests. Soil water was measured with a neutron probe.

Harvest cutting treatments increased the total amount of precipitation that reached the ground, most in the clearcuts and group selections, and least in the shelterwoods. Differences in snow accumulation accounted for much of the difference. Soil water was gradually depleted during the growing season with the upper soil depleted first. The mature uncut forest used more soil water than any of the treated areas.

Of the harvest cutting treatments, clearcuts used the least water, group selections a moderate amount, and shelterwoods the most. Of the residues disposal treatments, prescribed burned treatment areas used the least soil water, and the understory protected treatment the most. Water use on all treatment areas is gradually returning to that of the mature forest.

Water is a key resource in western larch forests. This study helps define water use as it relates to a variety of forest management practices.

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At the time of the study, Wyman C. Schmidt (retired) was Project Leader and Research Silviculturist, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, located at the Forestry Sciences Laboratory, Montana State University, Bozeman, MT 59717-0278, U.S.A. Jack A. Schmidt is Forester, Intermountain Research Station, Forest Service, U.S. Department of Agriculture, Forestry Sciences Laboratory, P.O. Box 8089, Missoula, MT 59807, U.S.A.

Influence of Interspecies Competition on Growth of Larch in Beech Thickets

Milan Saniga

Abstract—In forests of Slovakia, determining competition relations between beech (*Fagus*) and larch (*Larix*) would help determine the degree to which larch should be introduced into the nutrient-rich beech stands. The root system of larch was more than 100 percent larger than that of beech. In stands of three beech trees or less per square meter, height growth of larch showed no competition relation, but at six beech trees per square meter, height growth of larch slowed significantly and lost its dominance.

The forests of Slovakia are mostly created from the original ecosystems. The prevailing tree species is beech (*Fagus*) with a representation of 30.1 percent. It occurs in both the pure and mixed stands. In pure stands, which represent the growth optimum of beech, this species competes vigorously with other species. Because sites of pure beech stands are rich in nutrients, typologists recommend that economically desirable species, mainly spruce (*Picea*) and larch (*Larix decidua*), be introduced into natural beech stands that originate from natural regeneration. This silvicultural practice enables an increase of total volume production in pure beech stands by 15 to 20 percent at the felling age.

The representation of larch in beech stands is already decided in the early growth stage of natural seedings and thickets. Due to strong competition of beech, it is necessary to support larch, and to better understand the competition relations between beech and larch, it is necessary to quantify this problem. Many authors have dealt with the modeling of competition relations. Different mathematical formulas expressing competition are convenient for silvicultural problems. The works of Bella (1969) and Gillepsie and Hocker (1986) express the competition influence of neighboring individuals on the investigated individual by measuring the zone of crown overlapping. Other works dealing with the mathematical function of competition take into consideration the ratio of heights of the neighboring trees to their distance from the individuals that they affect from the viewpoint of competition (Adlard 1977; Alemdag 1978; Breaathe 1984; Daniels 1976; Gerrard 1969; Spurr 1962). The given indexes express the influence of competition on the growth characteristics of the investigated individual, especially on its height and later on its diameter and volume growth.

Based on the investigations of Leibundgut-Kreutzer (1958) ex Köstler and others (1968) competition for nutrients and water also takes place in the ground. How much of the supply of water and nutrients from the various layers of the soil profile is available depends on the type of the root system. According to Kern and others (1961), roots thinner than 2 mm find their share in various layers of the soil profile. Thus, the type of root system decides the supply of nutrients and water from the soil.

The quantification of the final extent of competition is difficult and greatly depends on the amount of measurings, variability of species, form of their mixture, and their requirements as to ecological and pedological factors.

The objective of this paper is to assess the height growth of larch in its individual mixture in a beech thicket by using the height competition index and obtaining the root system information for both species.

MATERIALS AND METHODS

The basis for analysis was the network of permanent experimental plots (PEP) covering 0.12 ha in various geographical units of Slovakia (Small Carpathians and Kremnica Mountains). These plots were in mixed spruce-beech thickets where beech had originated by natural regeneration (number of individuals per hectare, 80,000 to 100,000 pieces). Larch of the same height had been introduced into natural beech stands by planting (this being confirmed by the *t*-test).

Since the beginning of the experiment in 1981, current total height (h) and annual height increments (i_n) have been measured on beech and larch trees every year. In 1990, in addition to the mentioned biometric values, crown widths (b) of larch and beech were measured. Also, the distance (d) of beech from larch trees that influenced them was measured. All the data were measured to the accuracy of 1 cm.

The height competition index (*HCI*) was used to assess the influence of competition of beech on the height growth of larch. The given relationship approximates the dependence between the height competition index (x) and the current height increment for years, expressed in percentage of its maximum of 3 years current height increment (y). Numerous curves (24) were used to establish the objective dependence. One of these, whose correlation dependence was characterized by a high index of correlation and a minimum residual dispersion, was selected. The following formula was used:

$$HCI = \sum_{i=1}^{m} \left[\frac{h}{d_{ij}} + \frac{(r_i + r_j) - d_{ij}}{r_j} \right]$$

Although unable to attend the symposium, the author contributed this paper for the proceedings of the Symposium on Ecology and Management of Larix Forests: A Look Ahead, Whitefish, MT, U.S.A., October 5-9, 1992.

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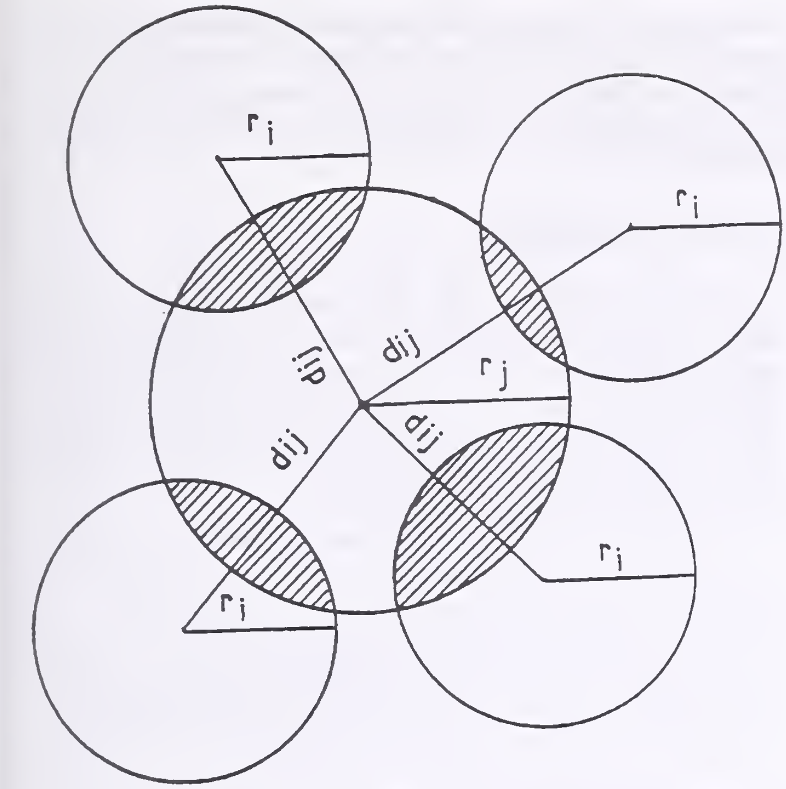

Figure 1—Characteristics of the height competition indices.

where

HCI = height competition index
h_i = height of the *i*th individual beech acting in the *b* zone of larch
b = diameter of the crown of larch
d_{ij} = distance of the *i*th beech stem from the *j*th larch one
r_i = radius of the crown of the *i*th beech
r_j = radius of the crown of the *j*th larch with the validity of $(r_i + r_j) \geq d_{ij}$ (fig. 1).

Data have been divided into two subgroups. With a density of four beech trees per square meter and less, no correlation dependence seems to exist, with larch in a dominant height position. The second subgroup represented the density of beech trees when they exceeded four trees per square meter. Here, a close correlation dependence has been confirmed.

For the analysis of roots, two individuals each of beech and larch of average height were selected from each series of experimental plots. These two individuals of both beech and larch were examined by the method of gradual exposure according to the procedure of Kern and others (1961) where only roots thinner than 2 mm in individual layers of the soil profile were analyzed.

RESULTS

Competition Index

The plotted points of the competition index (*HCI*) and the 3-year current height index, expressed in percentages of the maximum 3-year current height increment of larch, were dispersed. Because the correlation indices were low—0.1 and 0.13, respectively—only the biometric characteristics of both species are given in table 1. The table illustrates that larch had a dominant position in beech thickets in both geographical units.

Figure 2 illustrates the relationship of the height increment of larch with the density of beech (four trees and more per square meter) on the height competition index in both geographical units.

The correlations have been approximated by the curves:

$y = 91.4 - 10.2 \cdot n\,x$ (Kremnica Mountains)
$y = 89.1 - 9.8 \cdot n\,x$ (Small Carpathians)

with correlation index $I_{x,y} = 0.81^{++}$ and 0.94^{++}, respectively. These are close correlations. Both curves have the same shape. With height competition indices of 50 and 55 and higher, the curve decreases only slightly. The density of a beech thicket per square meter increases from this value to the number of six to 10 trees per square meter. To ensure the eventual survival of enough larch thickets, in later growth stages of beech and larch stands, larch maintain a dominant height position. To meet this silvicultural requirement, larch must grow at least as fast as the 3 years of maximum height increment of beech.

The heights of larch sample trees varied from 291 to 307 cm, and for beech from 201 to 219 cm (table 2). This represents the value of 51.1 and 51.4 percent, respectively,

Table 1—Biometric characteristics of beech and larch with the density of three beech trees per square meter and less in the growth stage of thicket

Biometric characteristics	Kremnica Mountains		Small Carpathians	
	Larch	Beech	Larch	Beech
	-----------	cm	-----------	
$h \pm s_x$	409.0±62.1	47.8±57.8	326.2±53.2	220.6±59.4
$3i_h \pm s_x$	173.1±40.2	98.3±28.2	151.0±29.6	84.6±22.4
$b \pm s_x$	232.9±15.7	89.3±27.3	183.6±19.2	81.3±21.1
$3i_h$ max	243.0	121.0	198.0	107.0

Legend: $3i_h$ = Average current height increment for 3 years
$3i_h$ max = Maximum current 3-year height increment.

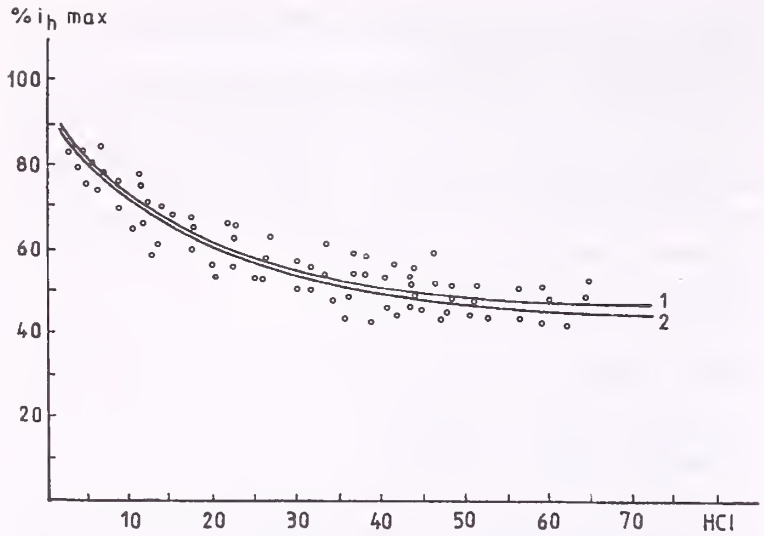

Figure 2—The relationship between the height competitions index (*HCI*) and the 3-year current height increment expressed in percentage of its maximum 3-year current height increment (percent i_h max) (1 - Kremnica Mountains; 2 - Small Carpathians).

of the maximum height increment of larch for years with *HCI* = 45 for the Kremnica Mountains and *HCI* = 36 for the Small Carpathians. The density for beech in the vicinity of larch representing five to six trees per square meter corresponds to the value *HCI* = 45 and 36, respectively. This information is significant for practical silvicultural measures in mixed larch-beech thickets. These measures must aim at reducing beech in the vicinity of larch to the appropriate value.

Root Analysis

Information on physiologically important roots of beech sample trees is given in table 3. The total length of roots thinner than 2 mm is significantly bigger, by 100 percent on the average, in 9-year-old larch trees than the total length of the roots of comparable beech.

Interesting is the distribution of the roots of this category in various layers of the soil profile. In the case of larch, 50 to 60 percent of roots thinner than 2 mm occur in the humus layer. In the case of beech it is only 20 to 30 percent.

CONCLUSIONS

The interspecies competition of beech and larch has been investigated on the basis of the relationship of 3-year height increment of larch to the magnitude of the height competition index. This was supplemented by the analysis of the root systems of four sample trees of each species. The root system of sample trees of larch was more than 100 percent larger than that of beech.

The competition influence of beech in stands with three beech trees or less per square meter on the height growth of larch as measured by the height competition index showed no relationship using correlation analyses. At the value of *HCI* of 45 and more (density of beech of six trees per square meter), the height growth of larch slows down significantly and gradually loses its dominant position.

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Table 2—Biometric characteristics of beech and larch with the density of beech at four trees per square meter and more in the growth stage

Biometric characteristics	Kremnica Mountains		Small Carpathians	
	Larch	Beech	Larch	Beech
	cm			
$h \pm s_x$	328.6±66.2	211.3±51.2	290.6±51.4	220.3±52.6
$3i_h \pm s_x$	156.1±38.2	105.8±31.6	109.6±27.3	82.6±27.4
$b \pm s_x$	167.5±35.7	72.6±20.3	160.2±31.6	73.4±20.2
$3i_h$ max	213.0	109.0	181.0	93.0

Legend: $3i_h$ = Average current height increment for 3 years
$3i_h$ max = Maximum current 3-year height increment.

Table 3—Analysis of the root systems of samples of larch and beech

Trees	Layer of the soil profile														
	1-10		11-20		21-30		31-40		41-50		50-60		Together		Weight of root systems
	Roots thinner than 2 mm														
	cm	*%*	*cm*	*%*	*cm*	*%*	*cm*	*%*	*cm*	*%*	*cm*	*%*	*cm*	*%*	*g*
Larch I	151	62	59	24	19	8	16	6	—	—	—	—	245	100	517
Larch II	163	59	60	22	34	12	21	7	—	—	—	—	278	100	625
Larch III	125	61	30	14	30	14	21	11	—	—	—	—	206	100	531
Larch IV	113	41	95	35	31	11	24	9	10	4	—	—	273	100	523
Beech I	23	20	31	27	22	19	19	16	15	13	6	5	116	100	275
Beech II	35	30	27	23	19	16	14	12	13	11	9	8	117	100	281
Beech III	29	24	34	28	20	16	15	12	10	9	13	11	121	100	279
Beech IV	31	24	35	27	24	19	20	16	11	8	7	6	128	100	264

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Architecture of European Larch With Special Reference to Flowering

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Dieter Lüscher

Abstract—The objective of the study was to qualify and, to a lesser extent, to quantify the mode of branching of European larch (*Larix decidua* Mill.) in order to understand the basic principles of the formation of short and long shoots, the flower formation and its impact on the mode of branching, and the role of dormant buds. A practicable method for the dating of any long shoot, especially in high order branches, proved to be the age of the short shoots branching from the long shoot, and this could be determined after removal of the bark.

During the past decades plant morphology has rather been neglected, and it is only in the past few years that tree botanists have begun to take it seriously. The discussion and the controversies in connection with forest decline have made it apparent that there is a regrettable lack of basic information on many aspects of tree morphology. Before talking about symptoms we must know the scope of "normal" behavior of a plant. In morphology this implies basic architecture and possible modifications. Our experience has shown that all features of a plant vary, some of them considerably. Even with careful observation we only look at one individual at a time, and we should only generalize if we are sure to have covered the whole range.

European larch (*Larix decidua* Mill.) occurs naturally in several disjunct and scattered areas of central Europe, mainly in mountainous regions (Alps, Sudeten, Tatra). The trees show marked differences in the different regions. Accordingly, the species has been subdivided into various sub-species, varieties, forms, and races, respectively (Vidakovic 1991). In the Swiss Alps, where this study was undertaken, larch grows naturally in the subalpine forest of the inner Alpine valleys, normally between about 1,500 and 2,300 m elevation where it often forms the timberline. It can be grown at lower altitude, provided competition by other plants is reduced. However, for economic reasons other provenances of European larches have been introduced into the lower altitude regions, so that today there is a mixture of provenances.

European larch is a deciduous tree. On low altitude habitats it can reach a height of up to 50 m, in subalpine forest up to 40 m, a diameter at breast height of 2 m. It is a light demanding species, resistant to drought (especially low atmospheric humidity), and can grow on raw soils as long as it is not in competition with other vegetation (mosses, grasses, dwarf shrubs) (Mayer and Ott 1991). It is thus a typical pioneer species in regions with a continental climate.

Larch has a monopodial branching pattern (fig. 1). The branches are not arranged in whorls, though, due to apical dominance and apical control respectively, they can show a trend towards a formation resembling whorls. There is a clear differentiation into long and short shoots. To understand the basic patterns of branching it is important to follow the development of short and long shoots from the youngest buds. At the beginning of a growing season the buds of a previous year's long shoot grow into short shoots, each one bearing a cluster of needles. After a resting period of several weeks some of them grow further into a long shoot with solitary needles. After needle fall there are long shoots with terminal and lateral buds and short shoots with a terminal bud only.

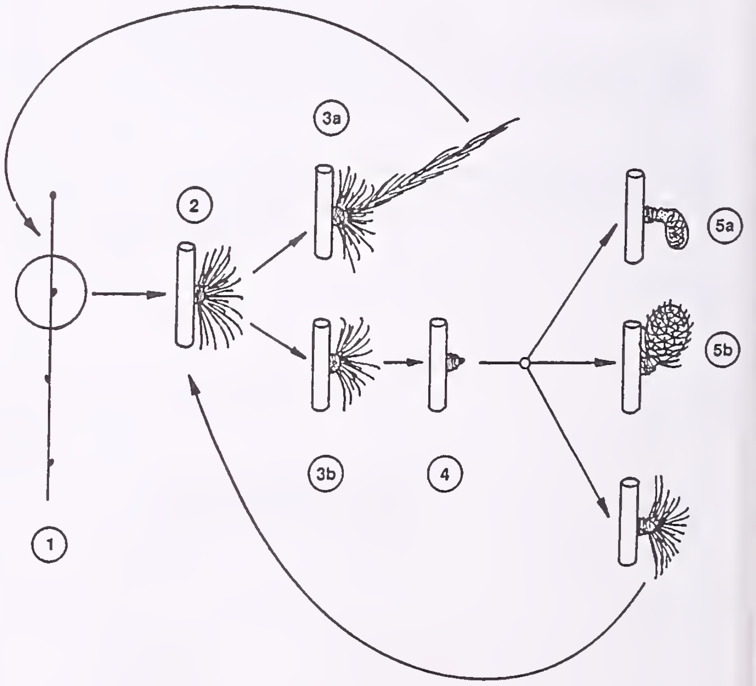

Figure 1—Basic pattern of branching: (1) winter aspect of previous year's long shoot with terminal and lateral buds; (2) short shoot during early part of first growing season; (3) state during late part of first growing season; "a" with long shoot formation, "b" without long shoot formation; (4) winter aspect of short shoot; (5a) male flower; (5b) female inflorescence.

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In the second growing season the previous year's long shoots behave as described above, whereas the short shoots have three possibilities: they may form (a) a male flower, (b) a female inflorescence, or (c) remain vegetative and behave like those short shoots that have been formed during the previous year. The production of female inflorescences from lateral buds of 1-year-old long shoots, as described for *Larix laricina* (Johnston 1990), does not seem to occur in European larch. Formation of long shoots means an addition of buds or branching. Formation of flowers means loss of buds, since the short shoots die after flowering and fruiting, respectively. It depends entirely on the behavior of the short shoots whether there is formation of needles, new long shoots, or flowers.

Observations on other European tree species have revealed that flowering had a very strong impact on the mode of branching and on the amount of biomass produced (Lüscher and Sieber 1988; Lüscher 1989, 1990). Since larch flowers frequently and abundantly the question arose whether the same was true for this species.

The main aim of the project was to find out the following:

- Time and place of formation of long shoots
- Flower formation
- Life span of short shoots
- Ability of short shoots to form long shoots after a long short shoot state
- Spontaneous formation of short shoots from dormant buds

MATERIALS AND METHODS

In a preliminary study, the crown architecture of old trees was assessed (compare to Salzmann 1989). For quantitative analysis, 19 first order branches were collected in May 1989 from the median portion of the crowns of nine trees 120 years old. The location was Lenzburg (Swiss Central Plateau, 415-615 m elevation). The segments of the years 1984 through1988 were identified, and the elements growing from them (long shoots, short shoots, male, and female flowers) counted. The flowers were only considered for the year 1989. Using the results of the above preliminary study as a basis, the authors focussed on detailed botanical aspects, including the determination of age of short shoots and their morphogenesis. For this purpose branches and twigs were collected from about 50 trees on various habitats at altitudes between 400 and 2,400 m elevation (Swiss Central Plateau, and Valais). The methods for the detailed observations on branches, twigs, and short shoots were developed gradually as many of the problems became only apparent when the first results were available.

Estimation of the age of short shoots was done both indirectly and directly. Indirectly it was done by counting the growth rings of the long shoot bearing the short shoot in question.

A direct method was to count the segments of annual growth in length of a short shoot. These became distinctly visible as nodes after removal of the bark (fig. 2). The nodes were counted with the help of a stereo microscope at a magnification of x10, the object being illuminated more or less parallel to its axis. By choosing a suitable angle of illumination, even very small structural differences could be made visible. To estimate the accuracy of this method, 100 short shoots from different parts of different trees were analyzed and the number of nodes compared with the number of growth rings of the respective long shoots.

Bark peeling was also used for the reconstruction of the morphogenesis of long and short shoots branching from main branches. Before peeling, the branches were softened in water in an autoclave at a temperature of 110 °C and a pressure of 2 bar for about 2 to 4 hours, depending on the dimension of the branch. Branches that were collected during the first few weeks of the growing season did not need softening. By removing the bark from a branch or twig and from all the elements branching from it, it was possible to see small structures like dormant buds and traces of dead long or short shoots. On the peeled branches the relevant spots were chosen for further examination. The lateral organs were traced by planing or splitting the respective portion of the branch, and, on a bigger scale, by turning on a lathe. For the latter purpose pieces 20 to 25 cm long of first order branches were chosen. Crooked and very excentrically grown pieces were not suitable. The pieces were shaved 1 mm at a time down to a minimum radius of 3 mm, the pith being

Figure 2—Short shoot after removal of the bark. The secondary xylem does not form a cylinder, but a series of nodes and constrictions, each node representing 1 year's growth in length. The basal part is not structured distinctly. Length of short shoot about 15 mm.

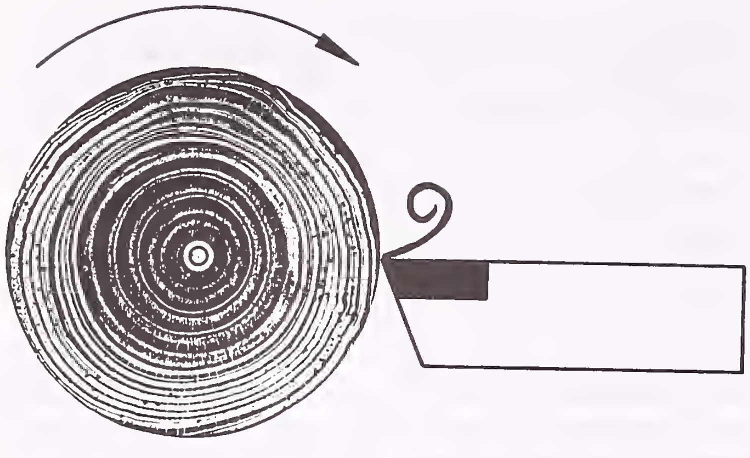

Figure 3—Setup for turning on a lathe. The pith was used as the turning centre. The cutting tool was advanced 1 mm at a time. The arrow indicates the direction of turning.

the geometrical centre (fig. 3). After each step the traces of all lateral organs visible on the surface of the wood cylinder were drawn on tracing paper. This allowed reconstruction of the morphogenesis of the lateral organs and, if necessary, their identification (dormant bud, short shoot, long shoot).

For more detailed studies razor blade sections were made for observation under a microscope.

RESULTS

General Morphology

Long Shoots—The majority of long shoots (about 80 percent) grew from those short shoots that were just a few weeks old; that is, on previous year's long shoots (table 1, fig. 4). About 75 percent of all the long shoots grew from short shoots on first and second order branches, and practically none on fourth or higher order branches (table 2, fig. 4).

Flowers—Practically all male flowers 1989 were on second and on third order branches (table 3, fig. 4). The female inflorescences showed the same trend, though not quite as extreme (table 3, fig. 4). No flowers were observed on the 1988 long shoots.

Short Shoots—The average number of living vegetative short shoots per segment decreased steadily from 19 on the 1-year-old segments to 7 on the 5-year-old segments.

Detailed Morphology

Accuracy of Age Determination of Short Shoots—The comparison of peeled short shoots growing on first order branches of various ages with the number of growth rings of the respective segment showed that the two corresponded very well; that is, the number of nodes was equal to the number of growth rings of the bearer shoot minus one. However, on short shoots over 12 years old (low altitude) and over 25 years old (high altitude) the basal part was not structured very distinctly, thus making counting difficult (fig. 2). Estimates of the age of such old short shoots were usually 10 percent below those reached by counting annual rings of the bearer shoot. The comparison described above was not possible on high order branches, since the growth ring structure was not clear. This may be illustrated by the example of a 25-year-old short shoot growing on a long shoot of a diameter of 2.5 mm below bark. Even with the help of a microscope it was not possible to distinguish clear annual rings in the peripheral portion of the transverse section, thus arriving at an age of about 6 to 8 years.

Table 1—Distribution of long shoots according to the age of the short shoots producing them

Age of short shoot	Proportion of long shoots (percent)
Some weeks	78
1 year	14
2 years	5
3 years	3

Maximum Age of Short Shoots—Generally speaking, trees on high altitude habitats had older short shoots than those on low altitude sites. Ages above 12 years were not very common in trees from low altitude sites, though short shoots of up to 30 years of age were found in some cases. The trees growing in their natural habitat at 2,340 m elevation (Valais) had much older short shoots. Ages of over 45 years were very common. In trees from high altitude sites over 25-year-old short shoots that grew into long shoots as vigorous as those growing from the youngest short shoots were frequently observed. In addition the axes of many second order branches remained in short shoot stage for as long as 25 years and resumed longitudinal growth as long shoots.

Morphogenesis of Old Short Shoots—On old first order branches short shoots were either solitary or arranged in clusters. The pattern revealed by turning the bearer shoots on a lathe clearly indicated that the solitary ones were usually original (formed at the earliest time possible), and the clusters were the result of the formation and subsequent branching of a long shoot, usually two to three short shoots per long shoot (fig. 5). Short shoots were often arranged around the trace of a former long shoot, indicating that the long shoot producing them had died and was now overarched due to secondary growth of the branch bearing it.

Table 2—Distribution of long shoots according to the branching order of the long shoots bearing them

Branching order	Proportion of long shoots (percent)
1	22
2	54
3	23
4	1

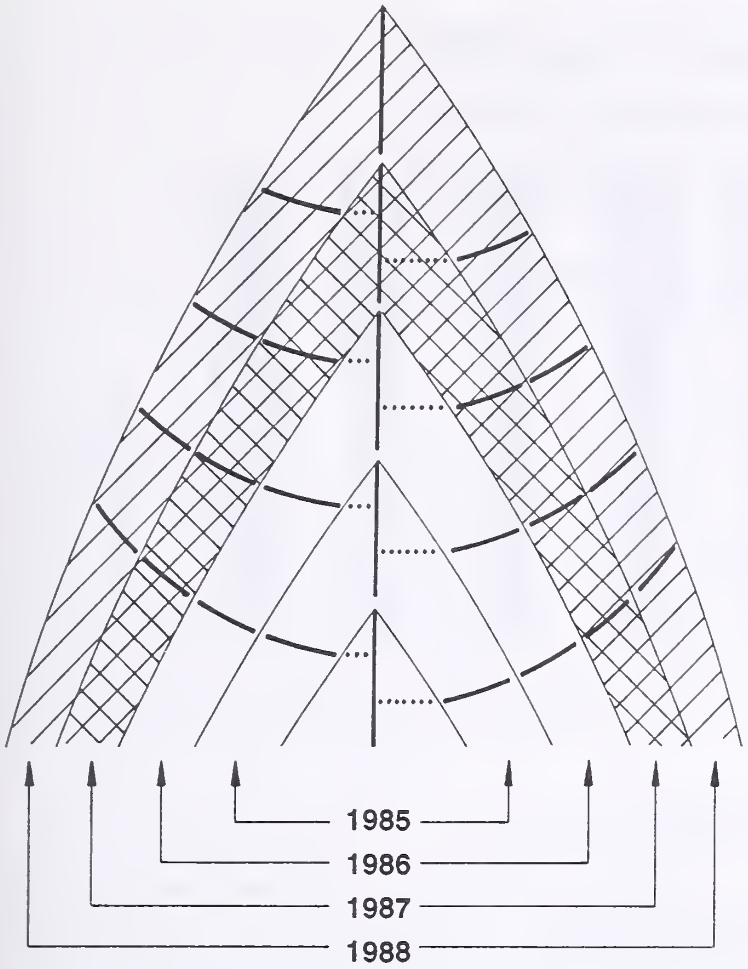

Figure 4—Distribution of the different elements on a 5-year-old first order branch. Most of the long shoots 1989 were formed on the 1-year-old long shoots (hatched) of second and third branching order. Most of the flowers 1989 were formed on 2-year-old long shoots of third branching order (cross hatched). Vertical axis: first order branch.

Table 3—Distribution of flowers 1989 according to the branching order of the long shoots bearing them

Branching order	Male flowers	Female flowers
	Percent	
1	4	7
2	76	60
3	20	31
4	0	2

Dormant Buds—Dormant buds were only found in few trees. Though they may not be prominent, they nevertheless exist.

DISCUSSION

The results of the analyses show definite trends, though the restricted amount of material examined does not allow precise quantitative conclusions.

It is quite obvious that long shoots and flowers are formed at the expense of the short shoots. However, since the long shoots will bear new short shoots, the overall number of short shoots will increase for each short shoot growing into a long shoot. The new organs are mainly formed at the periphery, while there is a decrease in the inner part of the crown.

Contrary to long shoot formation, flowering happens entirely at the expense of the short shoots. Each flower and inflorescence respectively means a loss of a short shoot and thus of a potential long shoot. This should result in a substantial loss of potential long and short shoots. However, the majority of the new long shoots are formed on the previous year's long shoots (on such shoots where flowering does not occur). In consequence, flowering, though reducing the number of short shoots in the inner parts of the crown, does not greatly influence the number of newly formed long shoots. Though the total number of long and short shoots is not affected, there is a shift, that is, the inner (older) parts of the tree crown bear distinctly fewer short shoots than before. However, this trend can be compensated by the activity of some of the remaining short shoots. Since short shoots can keep the ability to form long shoots throughout their entire (often very long) life, there is an almost unlimited potential reserve of meristems in the inner part of the crown. Even a very short long shoot growing out of an old short shoot will have several lateral buds which in turn will grow into short shoots. It seems that this ability has been underestimated in the past, with reference to both the maximum life expectancy of short shoots and their ability to grow into long shoots. Büsgen (1927) puts the maximum age of a short shoot of European larch at 4 years, and Fink (1980) between 3 and 5 years. Even if the age determination by counting the annual growth segments of the peeled short shoots may be inaccurate by 10 percent, the figures at a magnitude of 50 years are strikingly higher than the ones given by the authors quoted above.

Peeling a short shoot for age determination is much less destructive than cutting the long shoot and can be applied for the indirect age determination of long shoots of any branching order, where the growth ring structure is somehow erratic.

The direct method of age determination raises the very basic question as to how short shoots keep up with the secondary growth of the bearing long shoot. If their longitudinal growth were exclusively apical, the basal part of the secondary xylem of the short shoot would be overgrown due to secondary growth of the bearing long shoot, and the secondary phloem would be compressed longitudinally. However, the number of nodes visible and the regular arrangement of the longitudinal elements of the secondary phloem, as seen in radial sections, are strong indications that there must be some elongation in the basal part of short shoots or possibly in the cambial region of the bearing long shoot.

Two other factors also have to be borne in mind: larch can make up for needle loss during the growing season by proleptic short shoots as late as August, and on favorable habitats it can form a large proportion of sylleptic long shoots (Schill 1989).

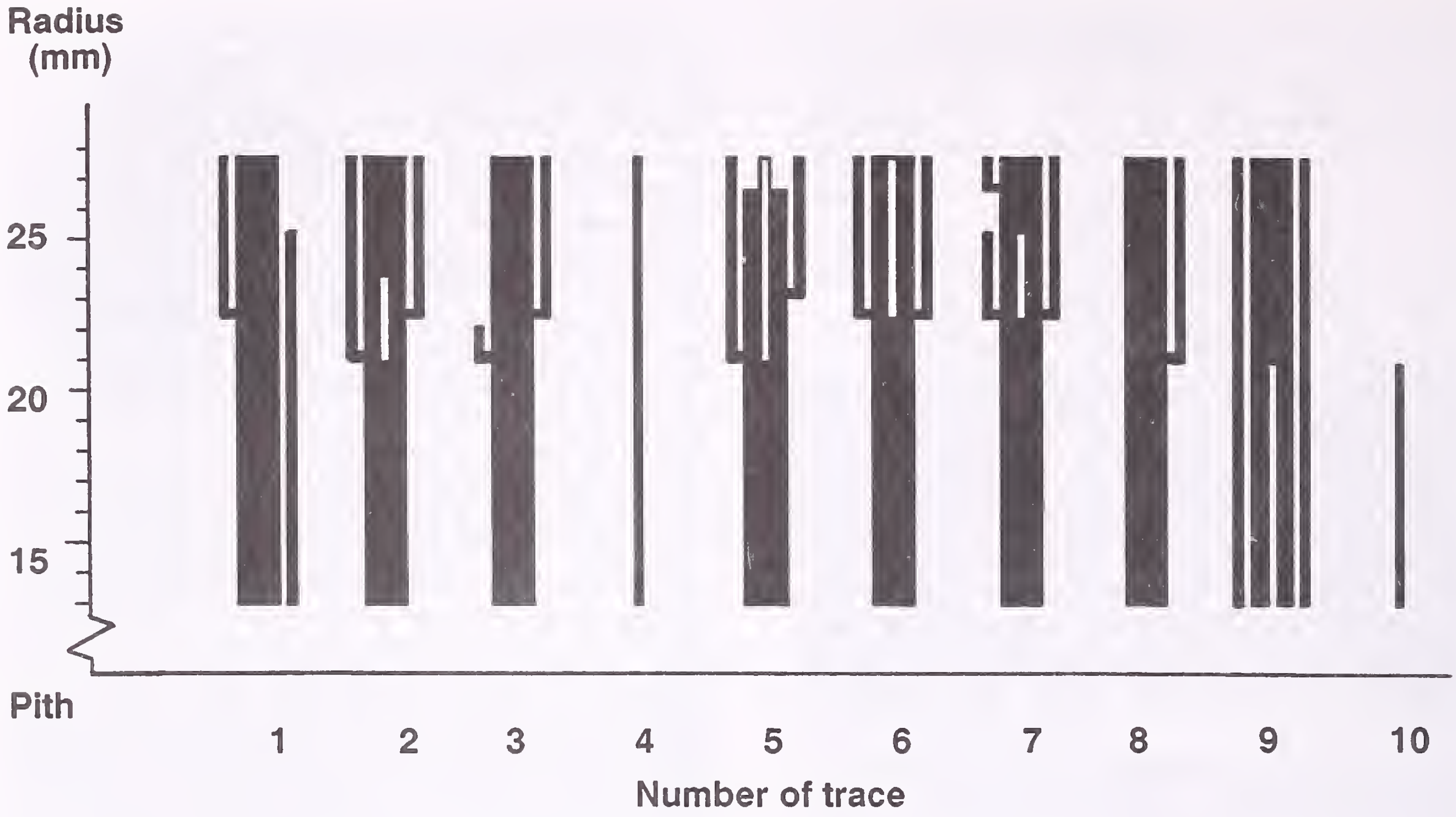

Figure 5—Morphogenesis of lateral organs branching from a first order branch. Broad lines = long shoots, narrow lines = short shoots. For convenience's sake all long and short shoots are arranged in one plane. The distances between the traces are not true to scale. On this particular length of branch, only short shoots and no second order long shoots were visible from the outside. After removal of the bark, and especially after turning down to a radius of 22 mm, it became apparent that the majority of the short shoots originated from second order long shoots.

CONCLUSIONS

European larch is obviously a very flexible species. Long shoots form the skeleton of the tree, whereas short shoots are for main foliage and flowering. Long shoots are mainly produced at the periphery of the crown, where flowering does not occur. Though flowering reduces the short shoots in number, their number can increase again by one or several remaining short shoots growing into a long shoot and thus producing several short shoots each.

Short shoots ensure foliage in the inner parts of the crown, a feature that is particularly important in small-leaved deciduous trees. At the same time they act as a kind of reservoir for future formation of long shoots, thus having a function similar to that of dormant buds. This characteristic may be the reason for the scarcity of dormant buds.

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Within-Crown Patterns of Shoot Development and Their Relationship to Cone Production in Young Tamarack

Graham R. Powell

Abstract—On young tamarack (*Larix laricina* [Du Roi] K. Koch), sylleptic and proleptic long and short shoots, and extensions thereof, and positioning of cones on shoots, each show vigor-related patterns. Lateral seed cones predominate on young trees, and terminal ones on older trees. Most pollen cones are terminal. Cones predominate on lower and side surfaces of parent long shoots. Cones are positioned more distally along single parent long shoots in successive years. Understanding these patterns is vital in studying tree crowns and functional status.

In 1982, two related studies of development of crowns of young tamarack (*Larix laricina* [Du Roi] K. Koch) began. The first study involved development of shoot and branch structure (crown architecture). The second involved the start and year-to-year progression of seed-cone and pollen-cone bearing and how these related to shoot development and reproductive potential. The former was designed to quantify for simulation the spatial and temporal relationships among long shoots and short shoots (Clausen and Kozlowski 1967, 1970) and thereby to gain understanding of production of the two kinds of shoots, their populations and apparent functions. The latter was designed to quantify early seed-cone and pollen-cone production on young trees, as available information dealt only with seed cones on older trees (Dow 1951; Duncan 1954; Wile 1981), and to extend knowledge of reproductive biology of *Larix* (Chandler 1959; Fujimoto 1978; Hall and Brown 1977; Longman and Wareing 1958; Owens and Molder 1979a,b). Both investigations led quickly to new insights (examples are Powell and others 1984; Remphrey and Powell 1985) and to exploration of additional aspects of development. To date, this research has resulted in 15 refereed journal or conference papers (McCurdy and Powell 1987; Powell 1987, 1988a; Powell and Hancox 1990; Powell and Tosh 1991; Powell and Vescio 1986; Powell and others 1984; Remphrey and Powell 1984a,b, 1985, 1987, 1988; Tosh and Powell 1986, 1991; Yip and Powell 1991), and others are in preparation. This paper synthesizes the work that relates to patterns of shoot development and to patterns of seed-cone and pollen-cone production.

TYPES OF SHOOTS

I define a shoot here as a leaf-bearing axis that extends in a single growing season. Shoots of tamarack occur terminally or laterally on their parent axes (table 1). Morphologically, shoots may be long or short or associated with seed cones (table 1). Rarely, leaves may be associated with pollen cones (Tosh and Powell 1986), but such occurrences will not be considered here. A single shoot borne laterally on a tree's main stem may be termed a branch. More commonly, a branch comprises the complex of successive shoots borne at such a position. Shoots (and subsequently the main axes of branches) arising laterally from the main stem are designated as first order: shoots borne laterally on first-order shoots are of second order, and so forth.

Long Shoots

The morphological descriptor "long shoot" is variously applied but is often used for shoots that are partly preformed in a scaly resting bud and partly neoformed (produced by elements that, from initiation, expand to mature size without undergoing a period of rest). The terms "preformed" and "neoformed," and "prolepsis" and "syllepsis" are used in this paper in the manner defined for universal use for trees by Hallé and others (1978). Many long shoots of tamarack comprise preformed and neoformed segments, but other shoots with extended leaf internodes may be wholly preformed or wholly neoformed and are here also termed long shoots.

The partly preformed/partly neoformed long shoot is the most common form of long shoot on tamarack (Clausen and Kozlowski 1967, 1970; Remphrey and Powell 1984b). It has at its base a cluster of preformed leaves (basal leaves) where leaf internodes remain minute, and then an axial section with well-extended leaf internodes (fig. 1C). The proximal leaves on the axial section are preformed in the resting bud (preformed axial leaves), and the distal leaves are neoformed (neoformed axial leaves).

Basal and axial preformed leaves are distinct within the resting bud. The basal-leaf primordia are well developed and relatively large. The preformed axial-leaf primordia are small, scarcely developed, and borne spirally on a conical axis below the shoot apical meristem and within the surrounding and overarching basal-leaf primordia (Remphrey and Powell 1984b). On expansion following rest (and usually winter quiescence), the basal-leaf primordia elongate rapidly to form the cluster of basal leaves

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Table 1—Occurrence of types of long shoots, short shoots, and shoots associated with seed cones, according to position on their parent axis

Position on parent axis	Long shoot			Short shoot		Seed cone	
	Wholly neoformed	Preformed/ neoformed	Wholly preformed	Wholly neoformed	Wholly preformed	Stalk preformed	Proliferation neoformed
Terminal	No[1]	Yes	Probably	No	Yes	Yes	Yes[2]
Lateral	Yes[3]	Yes	Probably	Yes[3]	Yes	Yes	Yes[2]

[1] Except the epicotyledonary axis of a first-year seedling.

[2] The cones are terminal or lateral, the proliferated shoot is terminal on the cone.

[3] Neoformed lateral long shoots and short shoots are sylleptic by definition (Hallé and others 1978).

(Clausen and Kozlowski 1967; Powell 1988a). The preformed axial-leaf primordia elongate more slowly. As their internodes begin to elongate, the shoot apical meristem begins to initiate more lateral-appendage primordia that differentiate as leaves. These neoformed leaves add to the complement of axial leaves, and their production continues until late in the season when the latest lateral appendages are differentiated as bud scales, rather than as leaves, and a terminal bud forms (Powell 1988a).

Axial elongation is slow at first, the product remaining hidden within the cluster of basal leaves for several weeks. But axial elongation increases exponentially and then reaches a relatively steady state that is held for several weeks before decreasing rapidly and stopping as the terminal bud is formed (Powell 1988a). It is this form of growth that provides the long period of annual height growth typical of the species (see Cook 1941; Mitchell 1965; Powell 1988a; Powell and Vescio 1986).

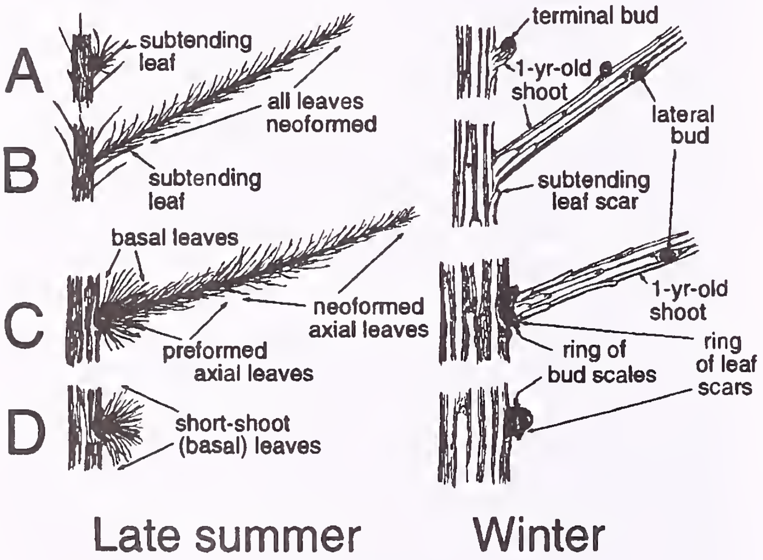

Figure 1—Types of long and short shoots in late summer and winter (enlarged relative to late-summer depiction, bases only for long shoots) arranged in approximate order of occurrence down the main stem: (A) sylleptic short shoot, (B) sylleptic long shoot, (C) proleptic long shoot, and (D) proleptic short shoot. Sylleptic shoots elongate during the same growing season as does their parent axis. Proleptic shoots usually elongate during the subsequent growing season so are usually 1 year younger than their parent axis.

Wholly preformed long shoots probably occur on tamarack (Remphrey and Powell 1984b), but their existence has not been confirmed. Such shoots would be the weakest of the shoots extending from long-shoot buds (with basal and axial preformed leaves). In them, the first post-rest lateral appendages initiated from the apical meristem would differentiate as scales. Thus, terminal-bud formation would start immediately. Wholly preformed "long" shoots have been observed in *Acer* (Powell and others 1982) in which other shoot types are similar to those of tamarack.

Wholly neoformed long shoots are usually sylleptic (lateral) shoots. The exceptions to this are the terminal epicotyledonary axis of a first-year seedling and the terminal proliferated shoot of a seed cone (table 1, discussed later). Sylleptic long shoots arise from new lateral-axis apical meristems that arise in axils of certain leaves on the parent axis. From the apical meristems, lateral appendages form, differentiate as leaves, and grow to full size, all without an intervening period of rest. As the leaves formed on these shoots elongate, their associated leaf internodes also elongate considerably so that the shoots lack clusters of leaves at their bases (fig. 1B). Neoformed-element production and development continues until bud scales are initiated from the shoot apical meristem instead of leaves, and terminal buds are formed.

Short Shoots

Preformed short (or dwarf) shoots arise from scaly resting buds. Each of these buds contains well-developed leaf primordia and a shoot apical meristem. As the new season advances, the leaf primordia begin to elongate, burst through their enveloping bud scales, and continue to grow to mature leaves. These leaves remain in a tight cluster as there is virtually no leaf-internode expansion (Powell 1988a). As leaf growth occurs, the shoot apical meristem produces bud scales. The resulting terminal bud is situated deep in the cluster of leaves (fig. 1D). Such preformed short shoots may be situated terminally on weak long shoots, terminally on short shoots, or laterally along second-year long shoots (table 1).

Neoformed (sylleptic) short shoots arise in axils of certain leaves on current-year long shoots (fig. 1A). Remphrey and Powell (1985) and Powell (1987) used lengths of up to

5 mm to characterize sylleptic short shoots and to separate them from the weakest sylleptic long shoots. Sylleptic short shoots may bear only one or two leaves (the prophylls), or several leaves before their apical meristems differentiate bud scales and form terminal buds. Often the leaves are more evident on the abaxial than the adaxial surface of the shoot (fig. 1A). The terminal buds of sylleptic short shoots comprise more bud scales and leaf primordia than do nearby lateral buds on the parent axis (Powell 1987). They thus have greater potential for subsequent development.

Shoots Associated with Seed Cones

All seed cones differentiate distal to a series of leaf primordia, which, in the bud, appear comparable to short-shoot leaf primordia or to basal-leaf primordia in a long-shoot bud. On expansion, the leaves below the cone grow to lengths less than those of nearby short shoots (Powell and Tosh 1991). The leaf internodes extend somewhat, and distinct decurrent ridges become evident below the leaves making the shoots more like the axial portions of long shoots than like short shoots that have leaves packed closely together and not associated with decurrent ridges. The shoots that subtend and provide the "stalks" for the seed cones are thus distinct from both short shoots and preformed long shoots. Furthermore, the leaves they bear are the first to turn color and abscise as the season progresses (Powell and Tosh 1991).

Although production of shoots from the tips of seed cones (proliferation) is common in tamarack, it is associated more with certain trees than with others. The neoformed shoots (table 1) extend as do the distal portions of long shoots (Tosh and Powell 1986). The leaves borne are spaced normally but remain relatively short. Lateral buds occur in some leaf axils, and terminal buds form. However, these shoots invariably die with the cones that subtend them. They thus constitute only a passing addition to the structure of the crown.

DISTRIBUTION OF SHOOTS ALONG PARENT SHOOTS

The pattern of shoot distribution along parent long shoots is well established when tamarack trees are 4 or 5 years old (figs. 2 and 3). On sapling leaders, this often includes sylleptic long shoots (Powell 1987). But the propensity for sylleptic long-shoot production is genetically controlled (Powell 1988b; Shaotang 1990), and some vigorous saplings lack or produce few sylleptic long shoots. Sylleptic long shoots typically occur between the lower 10 and 50 percent of the length of the leader, and their lengths tend to decrease acropetally (fig. 2; Powell 1987; Remphrey and Powell 1985). Sylleptic short shoots occur among and on either side of the sylleptic long shoots. Their distribution is wider, occurring between the lower 5 and 70 percent of the length of the leader (Powell 1987). Some leaders bear sylleptic short shoots but lack sylleptic long

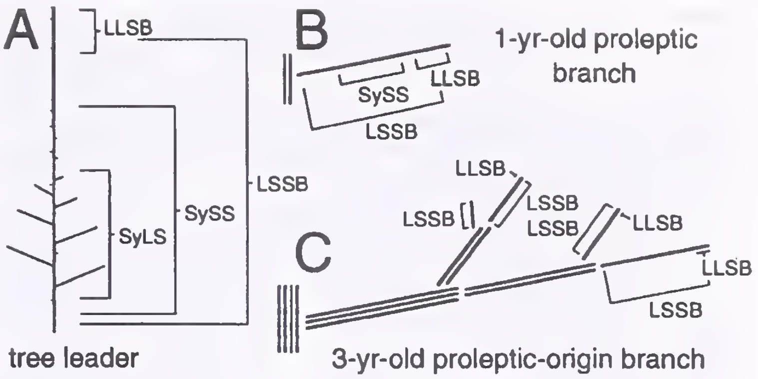

Figure 2—Zones of occurrence of lateral buds and sylleptic shoots on (A) a tree leader, (B) a 1-year-old proleptic branch, and (C) the current-year long shoots of a 3-year-old branch of proleptic origin: lateral long-shoot bud, (LLSB), lateral short-shoot bud (LSSB), sylleptic long shoot (SyLS), sylleptic short shoot (SySS). Sylleptic branches are shown joined to the main stem, proleptic branches and extensions to branches are shown separated from their parent shoot (indicating where a resting bud had occurred). Age of shoot is indicated by the number of parallel lines shown. Shoot order increases each time the angles of shoots change in reference to the vertical main stem. Based on Remphrey and Powell (1987) and Powell (1987).

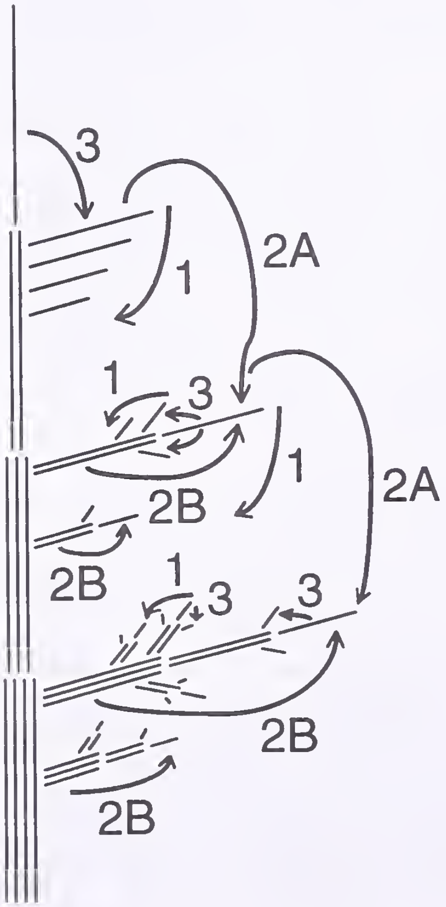

Figure 3—Kinds of patterns of decreasing shoot length on proleptic-origin branches in the upper 4 years of a crown: (1) among contemporary shoots of similar order on a given parent long shoot; (2A) among contemporary shoots in equivalent positions from "whorl" to "whorl" down the crown, and (2B) acropetally from shoot to shoot in a given axis; (3) among contemporary shoots from one order to the next higher order. Shoot and branch details as in figure 2.

shoots. Lateral buds occur along all leaders, but proportions of these lessen when syllepsis occurs. Lateral buds situated proximally are short-shoot buds, and those situated distally are long-shoot buds (fig. 2; Powell 1987). The proportions of the former tend to increase with decrease in length of the parent shoot.

Distributions of lateral axes on first-, second-, or third-order long shoots parallel those on the main stem (zero-order shoots), but their occurrence depends on the relative length or vigor of the parent axes, as described in the next section. Sylleptic long shoots occur only occasionally on first-order long shoots and seldom on extensions of those axes. They generally do not occur on second- or third-order long shoots. Sylleptic short shoots occur frequently on first-order long shoots, occasionally on subsequent-year extensions of those axes and on some second-order long shoots, and seldom on third-order long shoots. The great majority of long shoots therefore bear only lateral buds (and terminal buds), and of these, most are short-shoot buds. Long-shoot buds occur only near the terminal bud (except on the main axis—Remphrey and Powell 1984a), but they tend not to develop on many third-order long shoots. Thus, fourth-order long shoots are rare (Remphrey and Powell 1987). Later in a tree's life, long shoots may be induced to form on older short-shoot axes in response to perturbation (G. R. Powell, personal observations).

PATTERNS OF SHOOT SIZE

Three distinct patterns of lengths occur in proleptic long shoots (lateral shoots arising from rested long-shoot buds) and partly preformed/partly neoformed extensions of axes that initiated proleptically (fig. 3). First, proleptic shoots along the main stem (along the leader of the previous year) show a basipetal decrease in length (Remphrey and Powell 1984a). The same kind of decrease occurs among contemporary shoots along any axis (fig. 3). Second, successive extensions of lateral axes show decreases in length. This translates into basipetal decreases in lengths of comparably positioned shoots from "whorl" to "whorl" down the crown (fig. 3; Remphrey and Powell 1984a). Third, contemporary shoots of successively higher branching order show decreases in length (fig. 3; Remphrey and Powell 1987). As proleptic long-shoot length decreases, so the number of shoots and leaves borne and the lengths of those leaves decrease (Remphrey and Powell 1987, 1988).

Contemporary sylleptic long shoots generally decrease in length acropetally, except that the most proximal ones tend to be shorter than somewhat later-formed ones (fig. 2; Powell 1987; Remphrey and Powell 1985). When long-shoot extensions of sylleptic long shoots occur in subsequent years, they tend to follow the pattern of proleptic long shoots, increasing in length acropetally. This means that the early length advantage of a proximal sylleptic shoot is not maintained as subsequent annual extensions diminish in length rapidly, whereas those of distal sylleptic shoots may increase initially and then diminish less rapidly (fig. 4; Remphrey and Powell 1985).

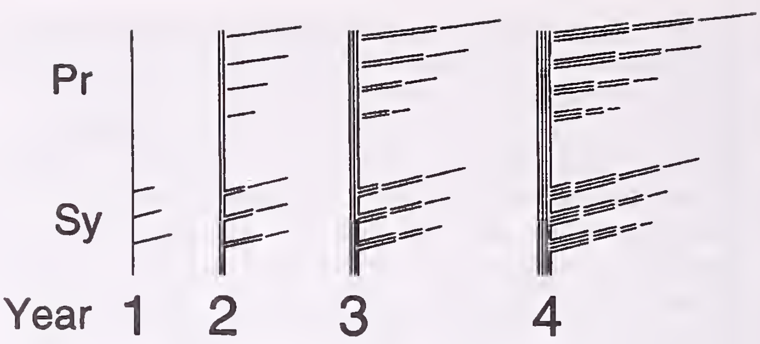

Figure 4—Relative annual extensions over 4 years of branch axes originating sylleptically (Sy) and proleptically (Pr) at different levels on a single extension of the main stem. Shoot and branch details as in figure 2. For simplicity, only first-order axes are shown and in only one plane.

Contemporary sylleptic short shoots bear more leaves when situated toward the lower middle section of their occurrence along the parent shoot (Powell 1987). However, numbers of axial-leaf primordia in terminal buds of sylleptic short shoots increase acropetally indicating that shoots developed from buds on sylleptic short shoots show acropetal increases in length (Powell 1987).

Successive short shoots in any one short-shoot axis (annual extensions of an axis) tend to bear fewer and shorter leaves and therefore to have less leaf surface area. This translates into decreasing basipetal trends in contemporary short-shoot size along axes made up of successive long-shoot extensions and among long-shoots in equivalent "whorl" positions, but of increasing age (Remphrey and Powell 1988). The patterns of decreasing long-shoot lengths and short-shoot size correspond with patterns of decreasing lengths of periods of expansion (Powell 1988a).

TYPES OF CONES

Both seed cones and pollen cones of tamarack are borne in two distinct ways: laterally along long shoots (lateral cones) and terminally on short shoots (terminal cones) (Powell and others 1984). Lateral seed and pollen cones respectively constitute about 90 and 20 percent of the crop at first bearing (Tosh and Powell 1991). Proportions of lateral cones decrease in subsequent years, but numbers per tree may still be substantial. Bisporangiate cones with a variety of amount and placement of female and male components, and sometimes leaves, occur fairly frequently (Tosh and Powell 1986) but will not be considered in this paper.

DISTRIBUTION OF CONES

In general, seed and pollen cones occur in similar levels in the crown, but pollen cones tend not to occur on the more vigorous shoots within any one level (fig. 5). Branches of sylleptic origin bear large proportions of seed-cone crops and substantial numbers of pollen cones (Tosh and Powell 1991). On young trees, among contemporary branches of either proleptic or sylleptic origin, seed cones are more concentrated on the upper branches and pollen

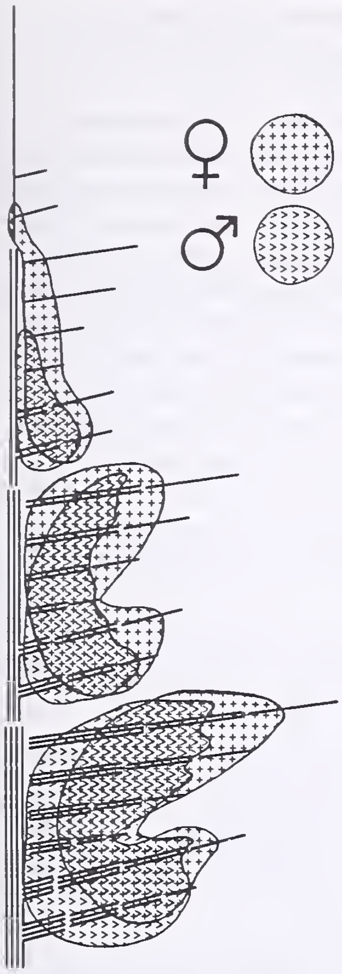

Figure 5—Zones of seed-cone and pollen-cone bud occurrence in the upper crown of a 7-year-old tree. Shoot and branch details as in figure 2. For simplicity, only first-order axes are shown and in only one plane. From data of Tosh and Powell (1991).

cones on the lower branches. Subsequently, pollen-cone bearing gradually extends to the higher order long shoots of the upper branches (and lower branches tend to demise). Greater insight into the patterns of cone distribution are revealed when one considers shoot categories in more detail, and positions of cones along and around individual long shoots (using the position of the terminal-cone-bearing short-shoot axis as comparable to the direct position of a lateral cone, and terming the long shoot the parent long shoot).

Distribution of Cones Among Shoot Orders

In the first year of cone bearing, seed cones occur predominantly on first-order long shoots: only a few occur on second-order long shoots (Tosh and Powell 1991). In subsequent years, first-order long shoots remain as heavy bearers, but second-order long shoots bear more of the crop, and some cones occur on third-order long shoots (fig. 6A). From early bearing, pollen cones occur predominantly on second-order long shoots but also occur on first- and third-order long shoots (fig. 6B) and to some extent on fourth-order long shoots (Tosh and Powell 1991). This, coupled with the pattern of distribution down different branch levels in the crown, corresponds, generally, with occurrence of pollen cones in relatively weaker situations.

Distribution of Cones Along Long Shoots

Distributions of lateral and terminal cones along parent long shoots differ (Tosh and Powell 1991). Most lateral seed cones occur proximally, some medially, and few distally (fig. 7A, 1-year-old shoots). Lateral pollen cones are at first concentrated proximally, but later some are borne medially and distally (fig. 7B). At first, few of the terminal seed cones are borne proximally, most occur medially or distally. Later, there is an acropetal shift, and the majority occur distally and relatively few proximally (fig. 7A). Terminal pollen cones are more evenly distributed with many medially situated (fig. 7B). Of the rest, more are at first borne proximally, but later more are borne distally (compare 2-year-old first- and second-order shoots

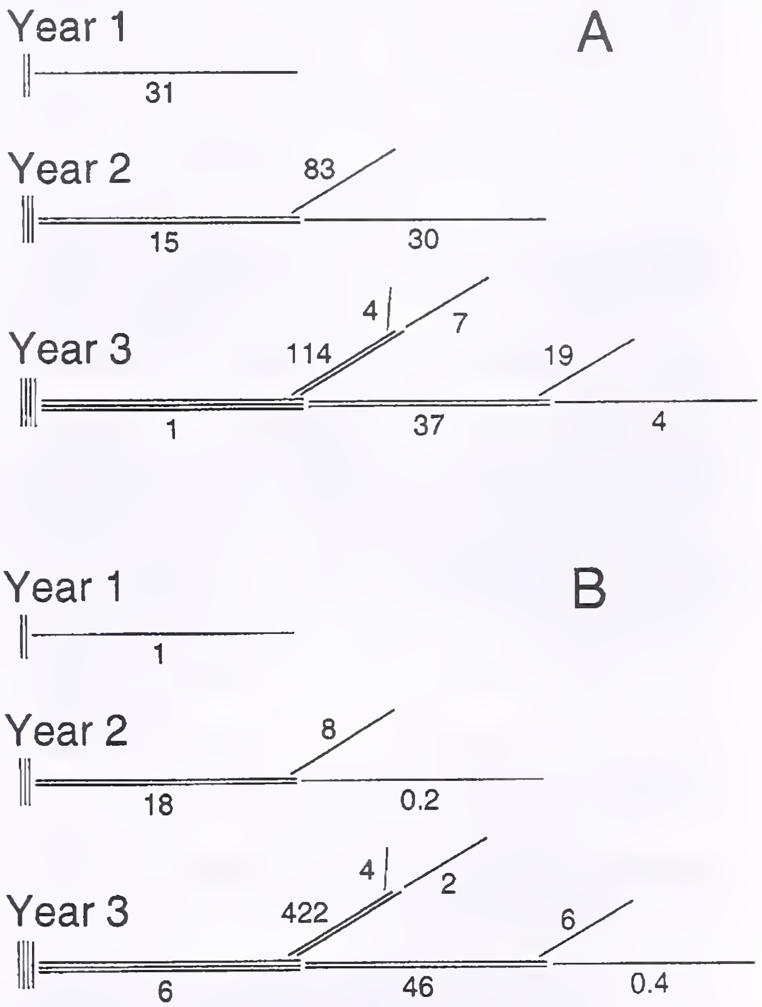

Figure 6—Numbers of seed cones (A) and pollen cones (B) borne per tree in each of 3 successive years on all long shoots of each age (number of lines) and order on branches that originated proleptically in year 1 (when the trees were 5 years old). Cones on 2- and 3-year-old long shoots are borne terminally on short shoots borne on those long shoots. Shoot and branch details as in figure 2. From data of Tosh and Powell (1991).

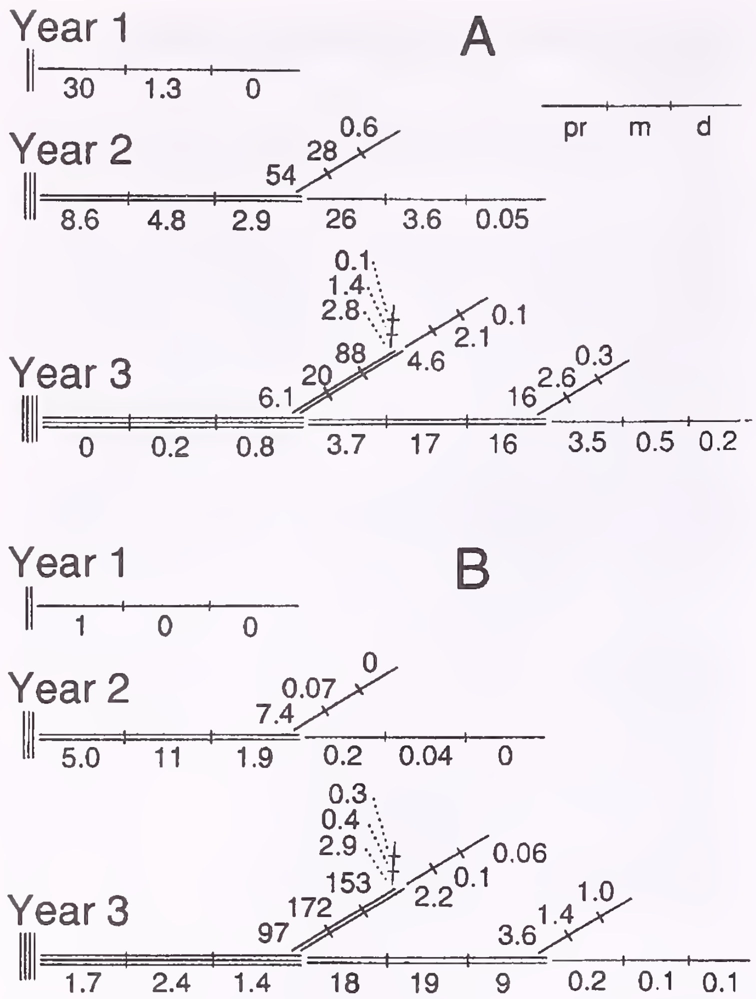

Figure 7—Numbers of seed cones (A) and pollen cones (B) borne per tree in each of 3 successive years in proximal (pr), medial (m), and distal (d) positions on long shoots of each age (number of lines) and order on branches that originated proleptically in year 1 (when the trees were 5 years old). Shoot and branch details as in figure 2; source as in figure 6.

of fig. 7B). Cones are distributed similarly on branches of sylleptic or proleptic origin (fig. 8).

Distribution of Cones Around Individual Long Shoots

Most long shoots of young tamarack have an obliquely upward to more or less horizontal orientation: relatively few have a downward orientation (Remphrey and Powell 1984a, 1987). This makes data on distribution of cones around individual long shoots reasonably compatible with respect to gravity (compare Longman and Wareing 1958). Nearly half of the seed cone crop is borne on the lower surfaces of their parent long shoots and about half along the side surfaces (Tosh and Powell 1991). Few occur on upper surfaces. Pollen cones are even more concentrated on lower surfaces. Side surfaces carry about one-fourth of the pollen-cone crop, and upper surfaces scarcely any.

Distribution of Cones on Individual Long Shoots Over Time

Because lateral cones occur on 1-year-old long shoots and those same long shoots bear short-shoot axes that can subsequently bear cones terminally, cones can occur along the same parent long shoot in at least three successive years (fig. 7). In the first year, lateral cones occupy many of the available lower-surface, and some side-surface lateral-axis positions in the proximal part of a 1-year-old long shoot. In the second year (assuming more or less equivalent cone bearing), many of the available lower-surface and some side-surface 1-year-old short shoots in the medial part of the now 2-year-old parent long shoot bear cones. Some proximal (mostly side-surface) and distal (lower surface) short shoots may also bear cones. In the third year, available unused sites for cone bearing are mostly distal lower- and side-surface 2-year-old short shoots. Thus, over time, cone bearing on an individual long shoot migrates acropetally (fig. 7) and to some extent from lower to side surfaces (Tosh and Powell 1991).

The relative length of the shoot also affects where on the parent long shoot cones are borne. Change in positioning of successive cones along shoots occurs more quickly on shorter shoots. This is especially so for pollen cones as they typically first form on shorter shoots, which have fewer possible cone sites available.

PATTERNS OF SEED-CONE SIZE IN RELATION TO DISTRIBUTION

Cone size can be expressed dimensionally or by numbers of component parts. The former is influenced more by conditions of the two seasons of cone growth (in the

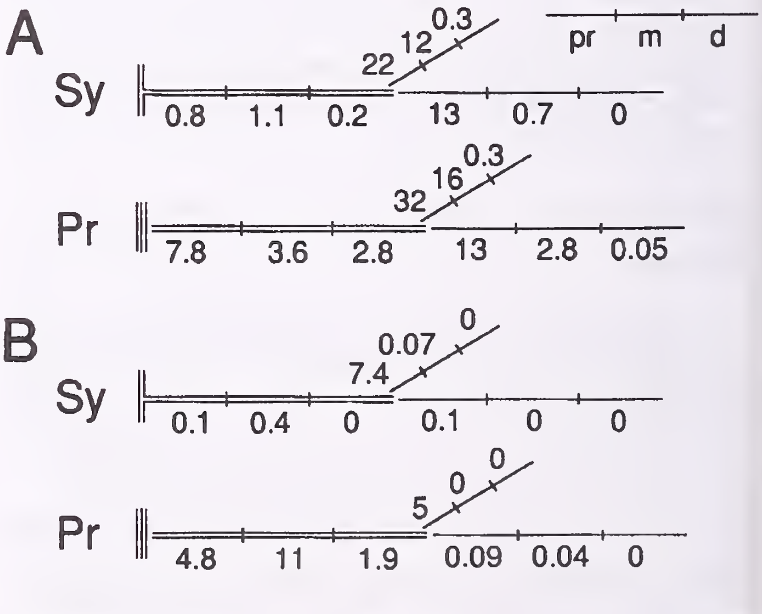

Figure 8—Numbers of seed cones (A) and pollen cones (B) borne per tree in 1 year in proximal (pr), medial (m), and distal (d) positions on 2-year-old branches of sylleptic and proleptic origin. Shoot and branch details as in figure 2; source as in figure 6.

bud and postbud) than is the latter (Powell 1979). Thus, numbers of component parts provide a sounder measure of positional response than do cone dimensions. In terms of numbers of all scales and of productive (seed-bearing, central) scales per cone, lateral seed cones are smaller than terminal seed cones, but, overall, cone size decreases down the crown and with increasing shoot order (Tosh 1986). This translates into seed cones in the upper parts of the cone-bearing portion of the crown being potentially more productive than other cones. The actual production of seeds, however, depends on the amount and success of pollination (Powell and Tosh 1991) and then fertilization, and presence or absence of agents that adversely affect seed development.

SOME IMPLICATIONS OF THESE FINDINGS

The shoot system of tamarack is far more complex than merely the production of long and short shoots. To the most common proleptic shoots, sylleptic long and short shoots must be added. In total, the shoot-system development follows distinct patterns of decreasing vigor. These patterns are related to leaf production and to where in the crown, and along and around shoots, cones occur. On young trees, lateral seed cones constitute the bulk of the early crops. Lateral pollen cones also occur but are relatively less numerous. In successive years, cones occur in different positions along the parent long shoots as first proximal, and then medial, positions are used up. Because most cones occur on lower and side surfaces of the parent long shoot, foliage continues to be borne on short shoots on the upper surfaces where, in the increasing shade of the expanding crown, light is least reduced. Cone bearing reduces the contemporary and subsequent foliage production, but quantification of this (compare Remphrey and Powell 1988) and implications with respect to resource allocation remain to be investigated.

Knowledge of where along and around any given parent long shoot cones are likely to be differentiated should be of value in determining the physiological basis for such differentiation. Relative vigor of growth appears to be involved—and involved also in sex determination—as distinctive patterns of cone occurrence exist.

Understanding the patterns of shoot and cone development is vital for any investigation of functioning in the crown and for any use of parts of the crown to determine functional status of trees. In tamarack, and any larch, the patterns are perhaps harder to discern and use than in other genera of Pinaceae. However, in relation to determining functional status, larches have the advantage that foliage is all of the same year, although within any year, leaf ages differ considerably because of the different modes of their production. Knowledge of the patterns also helps in understanding of the morphogenetic plasticity and opportunism of the species and its dendrological diversity.

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Flower Induction and Pollen Viability for Western Larch

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Abstract—A 14- to 20-year-old natural stand of *Larix occidentalis* Nutt. near Invermere, British Columbia, was selected for $GA_{4/7}$ and girdling treatments applied at vegetative bud flush of long shoots. Treatments significantly enhanced seed cone production but had no effect on pollen cone production. In a second study, 5-year-old root pruned potted grafts were treated with foliar sprays of $GA_{4/7}$ and compared to two adjunct heat treatments to two adjunct treatments applied at the beginning of short and long shoot vegetative bud flush. Seed and pollen cone response for the root pruned controls was 12.3 and 51.3, respectively. $GA_{4/7}$ treatments did not have a significant effect on seed cone production but significantly reduced the number of pollen cones. Heat treatments resulted in a significant reduction in the number of seed and pollen cones. Pollen quality was not a barrier to seed production in this test but rather other factors (pollination technique, ovule/embryo abortion) may be the cause of inconsistent seed production.

Western larch (*Larix occidentalis* Nutt.) is highly valued for its rapid growth, wood quality, and resistance to root diseases (Schmidt and others 1983). However, in its natural range of the western slopes of the Rocky Mountains, attempts to regenerate this species have been severely restricted by a lack of seed (Shearer and Schmidt 1987). In British Columbia and the United States, breeding and seed orchard programs have begun (Jaquish 1987) but natural collections will remain as the prime source of seed for several more years. However, natural stands flower infrequently before the age of 25 years (Owens and Molder 1979b). Thereafter, a good cone crop can occur, on average, every 5 years depending on site and stand conditions.

While western larch generally produces some cones every year, its seed production is about two-thirds that of similar size Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.]) growing in the same stands in western Montana (Shearer 1986). Typically, western larch averages about 5 to 10 filled seeds per cone (FSPC) from a potential of about 100 to 120 seeds per cone (Shearer 1984) whereas Douglas-fir averages about 35 to 40 FSPC from a potential of 75 to 70 seeds per cone (Owens and others 1991).

If reliable seed production is to occur from both seed orchards and natural stands, more consistent flowering and improvement in the FSPC values will be required. Shearer and Schmidt (1987) reported on the beneficial effects of spacing in developing good crown structures (more available flowering sites) and exposure to full sunlight. Seed production from 30-year-old trees thinned to 6x6 m spacing at 8 years was ten-fold greater than for trees thinned to 2x2 m. Pollen production was also greater in the wider spaced stand.

A number of other larch species have also responded to various cone induction techniques. Girdling is an effective treatment for enhancing both pollen and seed cone production in European (*Larix decidua* Mill.) and Japanese (*Larix leptolepis* Gord.) larches (Bonnet-Masimbert 1982; Katsuta and others 1981). Exogenously applied gibberellins (GA_3 and $GA_{4/7}$) have also enhanced flowering in Japanese and European larches (Bonnet-Masimbert 1982; Hashizume 1973) and tamarack (*Larix laricina*) (Eysteinsson and Greenwood 1990). In general, the response to gibberellin treatments is enhanced by adjunct treatments such as girdling (Bonnet-Masimbert 1982) and root pruning. In tamarack, Eysteinsson and Greenwood (1990) were able to induce both pollen- and seed-cone buds in potted and field grown stock with foliar applications of $GA_{4/7}$; an effect which was synergistically enhanced by root pruning.

For western larch, Graham (1986) tested ammonium nitrate fertilizer, alone and in combination with stem girdling, on a 70-year-old stand in Idaho. Girdling alone had a significant effect on the mean seed cone production per tree (77 versus 832). Ammonium fertilizer had no effect when applied by itself (86 seed cones per tree) but when

IN MEMORY OF STEPHEN DOUGLAS ROSS

Steve Ross died suddenly in November 1991. In passing, Steve left a legacy of research that will not be soon forgotten. Steve was a Senior Research Scientist with the Ministry of Forests and acted as project leader for the Seed Supply Research group. His career included many milestones. Most notable was his contribution to the physiology of flowering in conifers, including his pioneer work with the role of gibberellins in flowering and the development of the container approach and alternate orchard designs for seed production. He authored or co-authored over 100 scientific publications and served as Associate Editor for the *Canadian Journal of Forest Research* and Adjunct Professor in the Forest Biology program at the University of Victoria. Steve will be sadly missed by friends and colleagues.

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applied in combination with girdling, the fertilizer treatment negated the girdling effect (16 seed cones per tree).

In British Columbia, Prill (1990) compared similar treatments on a 90-year-old stand of western larch near Grand Forks. A significant increase in seed cone production was observed for girdling alone. Unlike the Graham (1986) study, ammonium nitrate promoted cone production and this response was enhanced when applied in combination with girdling. The form of applied fertilizer was important. If nitrogen was applied as urea, cone production was inhibited.

Poor cone production is not the only cause of poor seed production in larch. Perhaps the single most important factor affecting seed production in western larch are killing frosts (Lewandowski and Kosinski 1987; Shearer 1984). Within the seed cone, embryo abortion (30 percent), lack of pollen (17 percent), and poor pollen germination (17 percent) are the principal causes of poor seed production in European larch (Kosinski 1987). The lack of adequate pollen has also been cited as a major cause of poor seed production in western larch (Prill 1990; Shearer 1984).

This paper reports on two cone induction studies completed in 1991: one applied to a young natural stand ($GA_{4/7}$/girdling) and the other to root pruned, potted grafts using ($GA_{4/7}$/heat). Pollen viability procedures followed those used for Douglas-fir with the exception of germination. Selected media were tested to determine a medium type that maximized germination response for western larch pollen. The selected medium was used in conjunction with respiration and conductivity viability assays to determine the quality of a limited number of western larch pollen lots. These lots were also used under controlled pollination conditions to determine their actual fertility. An attempt was made to develop a relationship between in vitro response and actual fertility.

MATERIALS AND METHODS

Cone Induction in a Young Western Larch Stand

A young western larch stand (14 to 20 years old), at 1,200 m elevation on a moderate east-facing slope in the Invermere Forest District of British Columbia, was selected for treatment. Because the initial stocking of this site was low, these ±5 m trees had well developed crowns that extended nearly to the ground. Tree diameter ranged from 6 to 15 cm. Treatment trees were selected on the following basis:

- Diameter in the upper 30 percentile
- Crowns uniformly well developed
- No competing trees on at least three sides
- No mechanical or animal damage to the stem or crown
- Aspect, slope and topography were similar

Sixty trees were selected that met these criteria and matched to have a similar distribution of diameter ranges in both treatment and control trees.

Gibberellin ($GA_{4/7}$) and girdling were applied at vegetative bud flush of long shoots (VBFl). $GA_{4/7}$ was applied as a single stem injection (40 mg per 0.5 mL 95 percent ethanol) and the dosage was regulated by the number of holes treated. The number of holes receiving $GA_{4/7}$ was determined by the tree's diameter: 7 to 8 cm DBH, 2 holes (80 mg $GA_{4/7}$); 8.1 to 10 cm DBH, 3 holes (120 mg $GA_{4/7}$); 10.1 to 12.0 cm DBH, 4 holes (160 mg $GA_{4/7}$); and >12.0 cm DBH, 5 holes (200 mg $GA_{4/7}$). Double, overlapping stem girdles were applied at breast height with a pruning saw as long shoots began to flush. In the following spring, seed and pollen cones were counted by binocular assessment from the ground. In the fall, seed cones were recounted to determine abortion rates and samples of cones collected to determine seed yields.

Cone Induction in Potted Stock

Scions of 40- to 60-year-old unselected wild stand trees from east of Vernon were grafted onto seedling rootstock in the spring of 1986. Grafts were maintained in 11-L pots using a bark mulch media and kept in an open-sided polyhouse. Crowns were pruned in the summer of 1988 and again in February 1989 to keep excessive leader and lateral shoot growth under control.

All stock was root pruned in 1989 just prior to vegetative bud swell. About 2 to 3 cm of the outer rootball was removed with a reciprocating saw, and repotted in 20-L containers with the same hog fuel media type. All grafts were maintained under a fertilizer regime of 20-20-20 nutrient solution applied at a rate of 200 mg $L^{-1}N$.

Between one and four ramets from each of 10 clones (25 grafts per treatment) were randomly assigned to each treatment. $GA_{4/7}$ and heat treatments were applied to selected grafts on the basis of phenological bud flush of vegetative short shoots (VBFs) and long shoots (VBFl). Flushing of short and long shoots was defined as the date when 5 to 10 percent of the new needles emerged through the bud scales of unpruned shoots in the middle crown. $GA_{4/7}$ was applied as a foliar spray at 200 mg L^{-1} in 0.05 percent Aromox C-12W surfactant. Three days later, the trees were rinsed. Spraying commenced at bud flush (of either VBFs or VBFl) and continued weekly for 4 weeks. Heat treatment was applied in a closed polyhouse with temperatures maintained at 25 °C during the day (0800 to 2000 h) and 15 °C at night.

$GA_{4/7}$ was tested alone (stock maintained under ambient heat of an open-sided polyhouse) and in combination with heat. The treatments were as follows:

- Controls (no $GA_{4/7}$, ambient heat)
- $GA_{4/7}$ alone beginning at VBFl (ambient heat)
- $GA_{4/7}$ beginning at VBFl + heat beginning at VBFs
- $GA_{4/7}$ beginning at VBFl + heat beginning at VBFl

The following spring, seed and pollen cones were counted by ramet for each clone and treatment.

Pollen Viability Assays

Collection of Pollen Lots—Western larch pollen was collected in 1991 from two sites: Montana (seven lots from Hungry Horse) and Washington (one lot from Trout Lake). About 2.5 L of pollen-cone buds were collected from each source (single tree collections). The buds were kept cool and returned to Victoria for drying and extraction.

Each pollen lot was dried separately in a pollen dryer using an internal forced air system at 30 °C (Painter and Webber 1991). Drying times varied by pollen bud moisture content but average times ranged from 24 to 30 h. Dried pollen buds were sieved through a coarse (80) and fine (100) mesh screen.

For each pollen lot (defined as a family of pollen grains arising from a single clone or tree), the volumes of extracted pollen and its corresponding moisture content were measured. Moisture content was determined gravimetrically using 0.5 mg of pollen and drying for 4 h at 85 °C. Percent moisture content was expressed on a dry weight basis. Samples of pollen were then taken for viability assays (see below) and stored in heat-sealed foil pouches at –25 °C. The following spring, pollen lots were removed from storage and their viability determined. All pollen lots were hydrated at 100 percent RH for 16 h prior to testing. Selected lots were used to test fertility of the induced seed cone crop from the potted stock described above (see section on "In Vivo Fertility" later in this paper).

Germination—The effect of polyethylene glycol (PEG with a molecular weight of 4,000), sucrose, and Brewbaker and Kwack (1963) solution on western larch germination were tested for various levels and combinations. Four concentrations of PEG (10 percent, 20 percent, 30 percent, and 40 percent; 10P to 40P) were compared alone and in combination with 10 percent sucrose (10S) and Brewbaker and Kwack's solution (10B). The inorganic components of the Brewbaker and Kwack's solution included H_3BO_3 (0.1 mg/mL), $Ca(NO_3)_2{\cdot}4H_2O$ (0.3 mg/mL), $MgSO_4{\cdot}7H_2O$ (0.2 mg/mL) and KNO_3 (0.1 mg/mL). The actual germination solution was a 10 percent dilution of these components.

The germination procedures for western larch pollen used 3 mL of the medium added to 35 mm Petri dishes. About 10 mg of previously hydrated pollen (16h at 100 percent RH) was sprinkled over the surface and the Petri dish lid was replaced. The Petri dishes were placed in a larger Petri dish (90 mm) containing absorbent paper saturated with water. The lid of the larger Petri dish was secured and germination allowed to proceed at 25 °C for 48 h.

After 48 h, germination was scored based on the percent pollen grains in each of four classes. Class 1 germination was defined as those pollen grains elongating greater than twice the original, hydrated diameter of the pollen grain. Class 2 germination showed signs of pollen grains elongating but the length of elongation was still less than twice their hydrated diameter. Class 3 germination showed no signs of pollen grain elongation and remained at their hydrated diameter. Class 4 germination was those pollen grains showing signs of plasmolysis or other types of damage. The actual number of pollen grains counted followed the procedures of Stanley and Linskens (1974) for determining significant response differences at the 95 percent confidence level. All results were expressed as percent germination of either Class 1 or Class 1 + 2 grains.

Conductivity—Leaching of pollen lots followed the procedures of Webber and Bonnet-Masimbert (1993) in which 100 mg of pollen was soaked in 30 mL de-ionized water (specific conductance <2 µS/cm) at 25 °C for 60 min with constant shaking. After shaking, suspended pollen was allowed to settle (5 min) and then the conductance of the leachate determined using a standard conductivity meter (Orion Model 101) with an immersion cell (platinum electrodes). All measurements were made at 25 °C.

After determining the cold leachate conductivity, the solution was boiled for 60 min, cooled to 25 °C, de-ionized water added as required to make the total volume to 30 mL and the conductivity value recorded. Conductivity of each pollen lot was then expressed as either cold conductivity (COND) per gram dry weight (µS/cm/gdw) or as the ratio of cold to hot conductivity (percent COND).

Respiration—Measurement of oxygen uptake in an aqueous solution followed the procedures of Webber and Bonnet-Masimbert (1993). The depletion of dissolved oxygen in 3 mL of de-ionized water was recorded by a YSI oxygen probe (Model 5331 Clark type polarographic electrode) using a YSI standard bath assembly (Model 5301) and oxygen monitor (Model 5300).

About 100 mg of pollen was added to 3 mL de-ionized water contained in the cuvette of the water bath assembly and allowed to equilibrate at 30 °C for 3 min with constant stirring. After equilibration, stirring was stopped, the electrode inserted into the cuvette (making certain all air bubbles were removed), and stirring resumed. Oxygen depletion was recorded on a strip chart recorder using 1 volt as full range (100 percent) and a chart speed of 1 cm/min. The rate of oxygen consumption was calculated using the percent change in the volume of dissolved oxygen (5.48 µL O_2/mL at 30 °C) for a 5 min period. Results for oxygen consumption (RESP) were expressed as µL O_2/min/gdw where gdw was the dry weight of pollen used.

In Vivo Fertility

Sufficient pollen from four pollen lots, collected in 1991 were available for both in vitro assay response and in vivo fertility tests. Hydrated pollen lots were assayed using respiration, conductivity, and germination. Each lot was then used under controlled pollination conditions to determine actual fertility, expressed as filled seed per cone (FSPC).

Two ramets from each of three previously induced clones (see induction of potted stock) were used as seed-cone parent trees. Since most of the seed cones were located on main stem branches, the use of isolation bags was not possible. It was not necessary to protect seed-cone buds, however, because all pollen-cone buds were removed before shedding.

Seed-cone buds were pollinated about 5 to 6 days beyond bud burst at the estimated time of maximum receptivity (Owens per. comm.). Seed-cone buds to be pollinated were isolated from other buds (paper bag) during pollinations only and about 0.1 mL of pollen was applied to each seed-cone bud using a compressed gas-driven pollination devise operating at about 8 psi. Only one pollination was used.

After pollination, the paper bag was removed and the seed-cone buds tagged. For cone maturation, the seed-cone parent trees were kept in an open polyhouse and fertilized and watered as necessary. In the fall, mature seed cones were collected, kept separate by pollen lot and clone, and dried in paper bags at ambient temperature. All seeds per cone were hand extracted and the resultant seed expressed as total seed per cone (TSPC), potential seed per cone (PSPC) and filled seed per cone (FSPC).

PSPC is defined as those seed (filled and empty) arising from a mature ovule and having a fully developed seed coat. This includes seed with (FSPC) and without developed embryos as determined by X-ray analyses (see Webber and Bonnet-Masimbert 1993).

Statistical Analyses

All statistical analyses were completed using SAS PC (SAS Institute Inc. 1988). For estimating significant response to cone induction treatments within potted stock, a randomized block design was used in which clone was considered a random factor and treatments were considered fixed effects. Significant differences between specific paired treatments were tested with contrasts. For hydration and media effects, a one way ANOVA was used with Duncans multiple range test ($\alpha = 0.05$) to determine significant differences between germination response by class for selected media types.

RESULTS

Cone Induction in a Young Western Larch Stand

Table 1 shows the results of the spring 1992 assessment of flowering response at Invermere. Of the 30 control trees, only one produced three seed cones and none produced pollen. In the treated group, 63 percent of the trees produced seed cones but only one tree produced pollen cones. The number of seed cones ranged from 0 to 120 per tree. Average seed cone production per tree was 13.9 ± 5.12 (standard error).

In the fall, the trees were again assessed. Over 95 percent of the cones had aborted. Of the few cones left, seed yields averaged 2.6 filled seed per cone (FSPC).

Cone Induction in Potted Stock

There was no significant effect on seed cone production using GA$_{4/7}$ spray application at vegetative long shoot flush but pollen cone production was significantly reduced (table 2). However, day/night heat treatment (25/15 °C) applied for 4 weeks at either short shoot or long shoot vegetative bud flush caused a significant reduction in both seed- and pollen-cone buds. Average flowering response of control grafts was 12.3 (±3.1) and 51.2 (±14.1) for seed- and pollen-cone buds, respectively. GA$_{4/7}$ spray treatment resulted in fewer seed- and pollen-cone buds: 8.3 (±3.6) and 4.0 (±3.2), respectively. These differences were not significant for seed cone response but were significant for pollen cone response.

Table 1—Seed and pollen cone response to GA$_{4/7}$ and girdling in a 14- to 20-year-old western larch stand in Invermere, British Columbia. (N = 30).

	Controls	Treated
Seed cones	3	415
Pollen cones[1]	0	800
Percent trees with ♀	3	63
Range (♀/tree)	0-1	0-120
Means (♀/tree)	0.1	13.9

[1]Pollen cones were found on only one treated tree.

Table 2—Mean (± standard error) seed and pollen cone response to GA$_{4/7}$ and heat treatments applied to potted stock 5 years after grafting. (N = 25).

Treatment	Seed cones		Pollen cones	
Control	12.3	(3.1)	51.3	(14.1)
GA$_{4/7}$ @ VBFl	8.3	(3.6)^{ns}	4.0	(3.2)**
GA$_{4/7}$ + Heat @ VBFl	1.8	(0.8)*	0.0	(0.0)**
GA$_{4/7}$ + Heat @ VBFs	1.8	(0.8)*	0.0	(0.0)**

VBFl: vegetative bud flush of long shoots
VBFs: vegetative bud flush of short shoots

Significance values (ns=nonsignificant, *=significant at α=0.05 and **= significant at α=0.01) were determined using ANOVA procedures and specific contrasts to test control values against GA$_{4/7}$ alone and in combination with heat applied early and late. Actual probability values are 0.396, 0.017, and 0.019, respectively for seed cone response and 0.001, 0.001 and 0.001, respectively for pollen cone response.

Using ANOVA procedures and specific contrasts, probability values for control versus GA$_{4/7}$, control versus GA$_{4/7}$ + heat early and control versus GA$_{4/7}$ + heat late were 0.396, 0.017, and 0.019, respectively for seed cone response and 0.0001, 0.0001 and 0.0001, respectively for pollen cone response. Applying day/night temperatures of 25/15 °C for a thermoperiod of 14/10 h during shoot elongation of either short or long shoots was detrimental to production of both seed- and pollen-cone buds (table 2).

Pollen Viability Assays

Media Comparisons—Germination, conductivity, and respiration assays were all useful in determining the relative in vitro pollen viability of several pollen lots. Conductivity and respiration analyses used standard procedures previously defined for Douglas-fir pollen (Webber and Bonnet-Masimbert 1993). Because germination response is both species and media specific, we tested a number of solutions to select a medium that maximized the response of Class 1 and Class 1 + 2 germination.

Media constituents considered included sucrose, various concentrations of PEG (10P-40P), and Brewbaker and Kwack's (1963) solution. Each medium was tested alone and in combination with each other. Figure 1A compares five media types: H_2O, 10 percent sucrose (10S), 10 percent PEG (10P), 10 percent Brewbaker and Kwack's solution (10B), and a combined medium of 10B and 10P (10B10P). Sucrose alone (10S) yielded the lowest values for germination Class 1 (5.6 percent) and Class 1 + 2 (7.9 percent) and resulted in the highest proportion of damaged, Class 4, pollen grains (92 percent). The best medium type from this comparison was 10B which yielded significantly higher germination values for Class 1

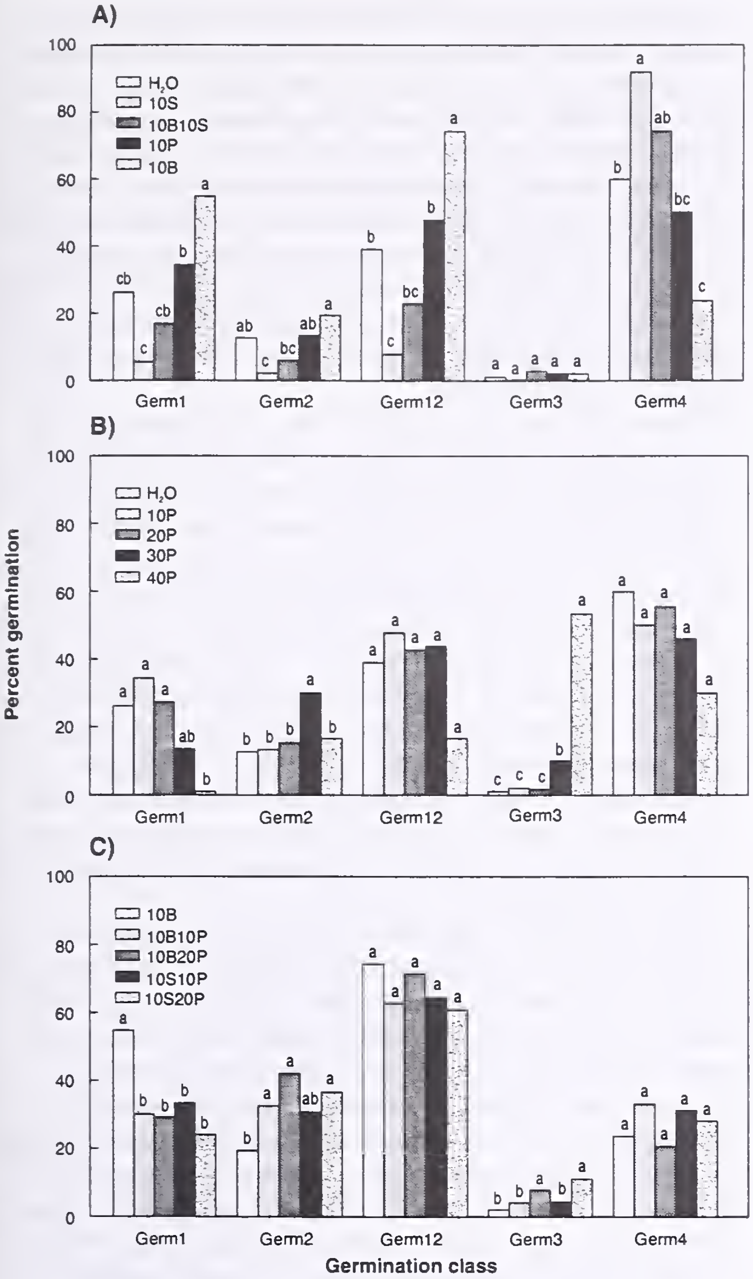

Figure 1—Average response of four western larch pollen lots to 10 percent Brewbaker and Kwack's solution (10B), 10 percent sucrose (10S), and 10 percent polyethylene glycol (10P) used alone or in combination. Average assay response by germination class noted with a different letter are significantly different at a confidence level of 0.05 percent.

(54.8 percent) and Class 1 + 2 (74.2 percent) and significantly lower values for Class 4 (23.7 percent).

The effect of four dilutions (10 percent to 40 percent) of PEG-4000 on germination of western larch pollen was compared to water alone (fig. 1B). There were few differences among the four dilutions of PEG and only at the highest concentration (40 percent) was Class 1 germination significantly reduced. There were no significant differences in germination response for Class 1 + 2 or Class 4 germination.

In the final media type comparison, combinations of 10P and 20P with 10B and 10S were compared to 10B alone (fig. 1C). Adding either 10 percent or 20 percent PEG or 10 percent or 20 percent sucrose to 10B had no significant effect on the proportions of Classes 1, Class 1 + 2, or Class 4 germination. This is in contrast to Douglas-fir pollen germination in which the presence of PEG either enhanced (low PEG concentration) or retarded (high PEG concentration) Class 1 and Class 1 + 2 germination (Webber and Bonnet-Masimbert 1993).

Based on these results, either 10B, 10B10P or 10B20P could all be used for germination of western larch pollen. We prefer not to use sucrose in our germination media because it facilitates the growth of contaminants and makes counting of the four germination classes more difficult. Some species (i.e., white spruce) actually germinate better when sucrose is included in the medium (Webber 1991). This is not the case for western larch pollen.

The Importance of Hydration on Viability Response—The importance of hydrating previously stored pollen on in vitro viability response and the effect on correlations to field fertility has been amply demonstrated in other species (see Webber and Masimbert 1993) including other larch species (Mellerowicz and Bonnet-Masimbert 1983). Table 3 shows the assay response for respiration, conductivity, percent conductivity, and germination by Class for each hydrated and unhydrated pollen lot. All assays showed a significant improvement in response due to hydration. Only germination of Class 3 pollen grains was unaffected by hydration.

In Vivo Fertility—The in vitro assay response of four western larch pollen lots is shown in table 4. Respiration values for each pollen lot was close to 20 µL O_2/min/gdw or better. These values correspond to good viability for Douglas-fir pollen (Webber and Bonnet-Masimbert 1993) where an average seed potential (FSPC/PSPC) of about 70 percent was obtained. For percent conductivity, the values for pollen lots 3 and 4 were relatively high. Corresponding values for Douglas-fir pollen were of lower viability and resulting seed potentials were less than 30 percent (Webber and Bonnet-Masimbert 1993). Percent germination for the four western larch pollen lots tested were 79.0, 94.2, 38.2, and 80.6 percent, respectively.

The actual fertility of the four pollen lots was expressed as filled seed per cone (FSPC) or as seed potential (FSPC/PSPC) and are shown in table 4. For the four pollen lots,

Table 3—Mean assay response for four hydrated and unhydrated western larch pollen lots using respiration (RESP), conductivity (COND), percent conductivity (PerCOND), and four classes of percent germination. All paired comparisons were significantly different ($\alpha = 0.05$) except germination Class 3 pollen grains. (N = 8).

	Response	
Assay	Hydrated	Unhydrated
RESP	26.0	16.0
COND	735.0	1261.0
PerCOND	44.4	64.5
Class 1	56.2	20.8
Class 2	16.7	9.2
Class 1 + 2	73.0	30.0
Class 3	2.3	0.1
Class 4	24.7	69.9

Table 4—Response of four hydrated western larch pollen lots to respiration (RESP), percent conductivity (PerCOND), and percent Class 1+2 germination (GERM1+2). Shown also is the actual seed yields (FSPC and percent FSPC) averaged over two ramets from each of three clones. (N = 6).

	Assay response			Seed yields	
Pollen lot	RESP	Percent COND	Percent GERM 1 + 2	FSPC	Percent FSPC
1	22.7	38.8	79.0	15.2	12.6
2	19.9	20.7	94.2	13.2	9.1
3	20.1	50.6	38.2	8.5	6.0
4	19.6	67.4	80.6	9.2	6.8

mean FSPC averaged over two ramets from each of three clones (N = 6) were 15.2, 13.2, 8.5, and 9.2, respectively. The extent of variability in FSPC response by clone (N = 2) is shown in table 5. Each pollen lot displayed both high and low yields suggesting, the source of variability in FSPC is not entirely attributed to pollen viability.

DISCUSSION

Western larch, like other larch species, does respond to cone induction treatments. While $GA_{4/7}$ has significantly enhanced cone production as a single treatment in other larch species, it is not an effective, single treatment in western larch. However, when $GA_{4/7}$ is applied as an adjunct treatment, coning response is generally better. Root pruning (Bonnet-Masimbert 1982) is a preferred treatment for younger material, especially potted stock (Eysteinsson and Greenwood 1990), while girdling is more often used under field conditions (Bonnet-Masimbert 1982; Graham 1986; Prill 1990).

For the young western larch stand, located in Invermere, British Columbia, only those trees treated with $GA_{4/7}$ and girdling flowered and the response was principally seed cones (table 1). Similar results were found for tamarack (Eysteinsson and Greenwood 1990) where induction of pollen cones was better on scion material collected from more mature ortets. Western larch may need a longer maturation period (i.e., greater than 20 years) for pollen production to begin under natural conditions. However, controlling shoot architecture and induction environment may facilitate better pollen production, especially in container stock.

Table 5—Seed yield response of four western larch pollen sources applied to two cones on two ramets from each of three clones. Seed yield values are expressed as filled seed per cone (N=2)

	Filled seed per cone					
	Clone 1		Clone 2		Clone 3	
Pollen lot	R1	R2	R1	R2	R1	R2
1	55.5	4.5	1.0	3.5	10.0	2.0
2	0.0	5.5	0.0	2.5	5.5	57.0
3	4.0	26.5	0.5	1.5	5.0	15.0
4	43.5	4.0	1.5	0.0	0.0	2.0

For 5-year-old potted grafts, $GA_{4/7}$ in combination with root pruning did not significantly enhance either seed or pollen cone production (table 2). While $GA_{4/7}$ spray treatment did result in lower seed and pollen cone production relative to root pruning alone, the differences were only significant for the number of pollen cones. Heat, as an adjunct treatment did not promote cone production in potted western larch grafts. Heat treatment has been successfully applied to interior spruce container stock (Ross 1985, 1988), but in this trial, heat as an adjunct treatment actually resulted in a significant reduction in both seed and pollen cone production.

We are not certain why $GA_{4/7}$ spray treatment did not enhance cone production in this material. Treatments were applied weekly for 4 weeks starting at vegetative bud flush of long shoots. According to Owens and Molder (1979a, b), differentiation of seed and pollen cones on vegetative short shoots coincides with the end of vegetative long shoot elongation. Eysteinsson and Greenwood (1990) were able to enhance cone production in tamarack with foliar spray applications of $GA_{4/7}$ beginning at long shoot flush. In both studies, 200 mg L^{-1} $GA_{4/7}$ were used but in the tamarack study, applications were biweekly over a 3 week period. Work is continuing to evaluate the cone response of both field and container grown western larch to $GA_{4/7}$ (including injection treatments), girdling and root pruning treatments.

Cone production alone does not guarantee seed production. In the Invermere trial, about 400 seed cones induced (table 1) but over 95 percent of these cones aborted. For those cones that survived, seed production was not more than 2 to 3 filled seeds per cone. Cone abortion due to frost and poor pollen production has been reported as two important causes of poor seed production in western larch (Shearer 1984). For the potted stock under controlled environment conditions, abortion losses were minimized and pollen supply controlled. Although average seed production was higher in the potted stock, variability within clones was also high.

Pollen quality was considered as a possible source of this variability. Viability assays developed for Douglas-fir pollen (Webber and Bonnet-Masimbert 1993) appeared to work equally well for western larch pollen. Although the best germination medium for western larch was slightly different from that used for Douglas-fir pollen, the differences were not significant. Furthermore, the importance of hydrating pollen before in vitro assay was confirmed for western larch pollen as well (table 3).

In all cases, assay response improved with hydration. Conductivity values decreased, indicating membrane leakage was less, and respiration and germination values increased, indicating both increased metabolic and membrane activity, respectively. Results from the media tests suggest that western larch pollen is less sensitive to osmotic stabilization than is Douglas-fir pollen. The components of Brewbaker and Kwack's (1963) solution (probably boron and calcium) are essential, however.

A simple sucrose solution (both alone and in combination with other constituents) has been used extensively for germinating other species (Stanley and Linskens 1974, pp. 67-76). Sucrose has been reported as an essential component in the in vitro germination of *Pinus roxburghii* pollen (Dhawan and Malik 1981) whereas Nygaard (1977) suggests that sucrose is not essential as a carbon source but rather it is acting as an osmoticum. For western larch pollen, however, sucrose was even a poorer germination medium than water alone suggesting that it was not even acting as an osmoticum. For Douglas-fir pollen (Webber and Bonnet-Masimbert 1993), sucrose did appear to act as an osmoticum but it was polyethylene glycol (10P or 20P) that was preferred. When combined with Brewbaker and Kwack's (10B) solution, the medium 10P10B gave the best germination response of all media types.

For western larch pollen, PEG (10P or 20P) did produce better germination response than sucrose alone but neither were as good as the 10B solution. Even the combination of the two solutions, 10P or 20P with 10B, did not significantly improve germination response over that of 10B alone. We will need to continue testing these media types on more western larch pollen lots. In the meantime, we will continue using the combined solution of 10P10B for germinating western larch pollen.

We were not able to develop a meaningful relationship between in vitro response of western larch pollen and actual seed yields (table 4). We will continue testing more pollen lots with a wider distribution of viabilities in an effort to develop correlations similar to those developed for Douglas-fir pollen viability and fertility (Webber and Bonnet-Masimbert 1993). We must also consider the cause of variability in filled seeds per cone. Table 5 shows the seed yield response for each of the four western larch pollen lots on two ramets from each of three clones. In all cases, each pollen lot produced both good and poor yields.

Whether pollen supply to cones producing poor yields was also low is not known. Owens (this proceedings) has reported on several causes for poor seed production in western larch, including poor pollination, inviable pollen and late abortion of both ovules and embryos. How these causes of poor seed production manifest themselves on cones even adjacent to each other on the same branch is not known. However, the challenge to improve controlled seed production in western larch probably lies in handling and application of pollen rather than in cone induction alone.

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Flowering Characteristics of Elite Trees in a Seed Orchard of Larch *Principis-Rupprechtii* Mayr.

Fu Yuhua

Abstract—The flowering characteristics of grafts of elite trees in a seed orchard of *Larix principis-rupprechtii* Mayr. were as follows: female cones of 10-year-old grafts decrease upward; the lowest layer of branches has the most cones; the most efficient area of cone differentiation is the middle and upper parts of the crown; flowering area changes upward and outward as the tree grows bigger. Male cones distribute wider than female cones and are three times more productive; the most efficient area of cone differentiation is the middle and lower parts of the crown; flowering area changes upward and outward as a tree grows bigger. The overlapped area of two cone differentiation areas is the highly efficient area of male and female cone differentiation.

A seed orchard is the population of grafts from many plus-trees. Its major function is to produce genetically improved seeds for commercial plantation. To raise genetic quality and yield of seeds in seed orchards, it is important to study the flowering characteristics of grafts and subsequently promote flowering through management.

By measuring 10-year-old grafts of *Larix principis-rupprechtii* Mayr. in the seed orchard at Changchen Mountain in Shanxi Province, China, this research studied the flowering characteristics of larch.

STUDY SITE

Changchen Mountain seed orchard is located at 113°25' east longitude, 40°15' north latitude, and 1,200 meters above sea level. Length of frost-free days of the site is 100 days. Annual rainfall is 384 mm, annual evapotranspiration is 1,940 mm, and relative humidity is 53 percent.

METHODS AND MATERIALS

Data were chiefly collected by field investigation. Forty-one individuals of 18 clones were investigated. The grafts were 10 years old, with 3 x 4 m spacing of the trees. Correlation analysis and analysis of variance were done.

FLOWERING CHARACTERISTICS

In the second year after grafting, a few grafts began to produce female cones. More trees began to produce female cones in the third year. Male cones appeared 1 to 2 years later. There were only a few cones at the beginning. Male cones began to increase in the fifth year. In the 10th year, a tree could have several hundred to several thousand female cones and as many as 15,000 male cones.

Distribution of Cones

The numbers of vegetative buds and reproductive buds decrease from the top to the bottom of a graft. Correlations of branch layer and number of vegetative buds, female cones, and male cones have significant coefficients of –0.748, –0.834, and –0.807, respectively. Correlations of branch number and vegetative buds, female cones, and male cones have significant coefficients of 0.721, 0.996, and 0.976, respectively.

Male cones on the first layer branches were 51 percent of all the male cones of a tree, and female cones, 40 percent. The lower five layers bear 91.6 percent of the female cones and 95 percent of the male cones.

First-year branches are mainly vegetative buds, while 2- to 4-year-old branches bear most of the female cones. The 3-year-old branches bear 43 percent of the female cones, 2- to 4-year-old branches bear 88.2 percent of the female cones, but the 5-year-old and older branches bear much fewer female cones. Male cones locate mainly on the 2- to 7-year-old branches.

F-test shows that number of male and female cones do not differ significantly in the four different directions.

The crown of *Larix principis-rupprechtii* is obviously composed of three layers: declined flowering area, flowering area, and vegetative growth area (Fu 1989). Female cones exist mainly in the flowering area. There are no female cones in the vegetative area. On the other hand, male cones exist in both the flowering area and the declined flowering area, but there are no male cones in the vegetative growth area.

Ratio of Cones

Female cone ratio, which refers to the percent of female cones in the total number of buds, is between 0.0 to 0.11. Female cones exist in the 2-year to 7-year-old branches. The 2-year, 6-year, and 7-year-old branches usually have fewer cones than 3-year to 5-year-old branches. Branches in the middle and upper parts of the crown have more cones than those in the lower part of the crown. The area with the highest cone ratio moves upward and outward.

Male cone ratio is between 0.0 and 0.42. Male cones exist in the 2-year to 9-year-old branches. The 4-year to 8-year-old branches have higher cone ratios. Branches in the middle and lower parts of the crown have more cones

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than those in the upper part of the crown. The area with the highest cone ratio moves upward and outward as the tree grows older.

Cone Differentiation

A branch has one to 11 female cones, and 95 percent of the branches have only one cone; one branch has one to 14 cones, and 65 percent of the branches have only one cone.

Female cone ratios are between 0.0 to 5.4 percent. The ratio for the middle part of the crown is higher than those for the lower and upper parts of the crown. On the other hand, male cone ratio decreases upward.

The ratio of female cone to male cone is 0.0 to 1.27. The ratio increases as branch layer increases. The ratio is positively related to the order of branch layers. The correlation coefficients of 0.757 for the 2-year-old branch segments and 0.774 for the 3-year-old branch segments are significant. The ratio of female and male cones decreases as branch segments become older.

The ratio of male cone bearing branches, which refers to the quotient of male cone bearing branches and total branches, ranges from 0.0 to 100 percent. The ratio does not differ significantly with directions and layers, but differs significantly with branch ages. The ratio increases with branch age, and the correlation coefficients of the ratio of cone bearing branches to branch age are 0.25 to 0.517.

The ratio of female cone bearing branches ranges from 0.0 to 64 percent. The ratio differs significantly with direction, branch layer, and branch age. Ratios of female cone bearing branches for middle and upper parts are higher than that for lower part, and the ratio for younger segments is higher than that for older branches.

Branch length for a male cone does not differ significantly with direction, branch age, and branch layer. The average length for a male cone is 2.19 cm.

Branch length for a female cone does not differ significantly with direction and layer, but differs significantly with branch age. As branches become older, branch length for every cone also increases. The average length for a female cone is 6.5 cm.

Flowering of Grafts from Different Plus-Trees

Number of female cones differs significantly among various clones. Some clones have only 20 to 30 cones, while some others have thousands of cones. There is no significant difference among ramets from the same ortet.

Plus-Tree Types and Flowering

Larix principis-rupprechtii can be classified into four types: narrow crown with dense branches; broad crown with dense branches; broad crown with thin branches; and narrow crown with thin branches (Fu and others 1989).

There are significant differences in number of female cones among the four different types just described and among clones within the same type. The number of female cones of narrow crown with thin branches type is greater than that of broad crown with thin branches type, which is greater than that of broad crown with dense branches type, which is greater than that of narrow crown with dense branches type.

For all four types, there are significant differences in number of female cones among different ages. The 3-year-old segments have the most cones, while 5-year-old segments have the fewest cones.

Female cone ratios do not differ significantly among the four different types, but they do differ significantly with branch ages. Female cone ratios are greatest for the 3-year-old branches, moderate for the 2- and 4-year-old branches, and least for the 5-year-old branches.

CONCLUSIONS AND DISCUSSION

Number of female cones on 10-year-old grafts from plus-trees of *Larix principis-rupprechtii* is greatest on the lowest layer of branches and decreases upward. The 2- and 4-year-old branches in the middle and upper parts of a crown have the greatest ability to produce cones. Areas for female cone differentiation move upward and outward but some cone production is maintained in the young branches as trees grow bigger because branches lose their ability to produce cones gradually.

Male cones distribute in every part of a crown except vegetative growth areas. Number of male cones is generally four times greater than that of female cones. The 2- to 7-year-old branches in the middle and lower part of the crown have the greatest ability to produce cones. Number of male cones decreases as branch layer grows higher.

Areas with high efficiency of male and female cone differentiation move upward and outward. Areas with high efficiency of female cone differentiation are higher and nearer to the upper parts than that of male cone differentiation.

Number of female cones differs significantly in number of female cones, but not in branch age and ratio of cone bearing branches. Number of cones of narrow crown with thin branches type is the greatest, and that of narrow crown with dense branches type is the fewest. Thin branch types have fewer cones than dense branch types.

Branch growth is positively related to the number of cones in the coming year. About 16 to 40 percent of the branches produce female cones. The 2-year-old and first-layer branches have fewer female cones. Those branches are thin and weak. Therefore, to promote flowering, it is necessary to intensify water and fertilizer management and to cut newly produced weak branches and the branches that are weak and in the inner part of the crown.

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Transfer and Expression of Foreign Genes in Larix: Opportunities for Genetic Improvement

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Abstract—A system for regenerating genetically transformed *Larix decidua* plants uses *Agrobacterium rhizogenes* as a vector. Multiple adventitious shoot buds are obtained on inoculated, sterile seedlings. Excised shoot buds are screened repeatedly for kanamycin resistance as they are elongated and rooted. The transfer and expression of the aroA and BT-toxin genes through southern, northern, and western blots of needle tissue from transgenic plants are documented, and work to improve expression of these genes continues.

Larch species and hybrids have excellent growth potential for the Northern United States and Southern Canada (Chiang and others 1988; Einspahr and others 1984; Palmer 1991). Traditional tree improvement studies have documented the large amounts of genetic variation in larch (Boyle and others 1989; Cheliak and others 1988; Lee and Schabel 1989; Magnussen and Park 1991; Maier 1992; Park and Fowler 1983; Riemenschneider and Nienstaedt 1983).

While considerable potential exists for using larches on a wider scale in many locations in the United States and Canada, some practical problems remain. For example, larches are notoriously poor and sporadic seed producers (Karnosky 1992). Seed crops vary greatly from year to year, and even in the best years poor seed quality often limits seed production (Campbell 1983; Hall and Brown 1976, 1977; Shin and Karnosky, this proceedings). Thus, for larch improvement, vegetative propagation is seen as an integral part of genetic improvement (Farmer and others 1986; Fowler 1986).

In the northern Lake States region, we have two additional limitations to the use of larch. First, larches are highly sensitive to herbicides used to release recently established conifer plantations from competing weedy vegetation (Netzer 1984). Second, cold winter temperatures and late spring and early summer frosts can have severe negative impacts on some of the exotic larches and larch hybrids (Robbins 1985) that are less cold hardy than the native tamaracks.

Since the early 1980's, our laboratory has had an active larch improvement program focused on developing the potential of larches as a pulp and paper fiber source for the northern Lake States region. This program has included traditional tree improvement activities such as species trials, provenance tests, genotype x environment studies, and interspecific hybridization. We have also examined methods for greenhouse seed orchard establishment and vegetative propagation via rooting of cuttings or micropropagation or both (Diner and others 1986; Karnosky and Diner 1984; Karnosky and Mulcahey 1988; Mulcahey and Karnosky 1986). Our goals in this research have been to develop (1) larch hybrids that combine the rapid growth characteristics of the exotic larches with the cold hardiness of the native tamarack and (2) vegetative propagation methods to enable us to mass propagate superior hybrids.

More recently, we have turned our attention to the potential for genetic engineering of herbicide and insect resistance in larch (Diner and Karnosky 1986). We have shown that larches are susceptible to infection with the genetic vectors *Agrobacterium rhizogenes* and *A. tumefaciens,* that we can recover adventitious shoots from inoculations with certain strains of these *Agrobacterium* species, and that these adventitious shoots express genes transferred to them from the *Agrobacterium* (Diner and Karnosky 1987). Recently, we documented the first case of a regenerated, genetically engineered conifer when we transformed *Larix decidua* with *A. rhizogenes* (Huang and others 1991a,b).

Currently, we are studying the possibility of increasing the tolerance to the herbicide glyphosate through the transfer of the aroA gene to larch. We are also working with several different BT-toxin genes to improve the resistance of larch to lepidopteran insects.

This paper outlines the progress we have made with the aroA and BT-toxin gene transfer, expression, and recovery of transgenic larch plants.

GENES OF INTEREST

Many insects attack larch, but the two most common and with the greatest potential to cause growth loss and mortality are the larch sawfly and the larch casebearer (Robbins 1985; Ryan and others 1987). An additional threat in the Lake States is the gypsy moth, which is currently establishing itself in the region. Improvement in the resistance of larch to the casebearer and to gypsy moth is possible through the introduction of BT-toxin genes. These genes, isolated from the bacteria, *Bacillus thuringiensis*, cause

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plants to produce compounds that are toxic to lepidopteran insects such as the larch casebearer and the gypsy moth.

Larch is extremely intolerant to shade, so that competition with other plants can seriously reduce seedling survival and vigor of established trees (Robbins 1985). In the northern Lake States, exotic larch and larch hybrids are generally planted on highly productive sites. These sites also tend to have rapid growth of competitive vegetation. Because larches are extremely susceptible to herbicides (Netzer 1984), there is a need to improve larch herbicide tolerance. We are working with the aroA gene, which conveys tolerance to glyphosate. "Roundup" and "Accord," two herbicides with glyphosate as their principal ingredient, kill plants by blocking aromatic amino acid biosynthesis by inhibiting EPSP (5-enolpyruvylshikimate-3-phosphate) synthase.

The aroA gene is a mutant gene that produces glyphosate-tolerant EPSP synthase. Improved levels of glyphosate tolerance has been found in several agricultural plants (Comai and others 1985; Fillati and others 1987; Thompson and others 1987) and in hybrid poplar (Riemenschneider and others 1988). Generally, the levels of improved glyphosate tolerance are measurable but are not yet sufficient to be useful on a commercial basis. Research on improved levels of aroA expression are continuing. In our laboratory, we are examining the effects of various promoters and of duplication of promoters on aroA expression in larch.

Our larch studies to date have all been conducted in the laboratory and greenhouse. Before we begin to release transgenic larch trees for commercial use, it will be desirable to minimize the potential interaction of these trees with native ones (Charest and Michel 1991). Thus, we are also interested in developing male-sterile larch trees to prevent the spread of these introduced genes into wild populations via pollen drift. We are currently exploring options (Peacock 1990) for developing male sterility in larch.

RECOVERY OF TRANSGENIC LARCH

We have developed a simple and effective system for genetic transformation and plant regeneration in European larch (Huang and others 1991a,b). Aseptically germinated young (7 to 10 day-old) seedlings are wound-inoculated high on the hypocotyl with *Agrobacterium rhizogenes* strain 11325, containing pRi11325 as a helper plasmid and either PCGN1133 with NPTII-aroA or PWB139 with NPTII-b.t gene as a vector plasmid. Multiple adventitious buds develop from the inoculated sites *in vitro* in 3 to 5 weeks. These buds are excised and placed on harmone-free shoot-elongation media for shoot development over 4 to 8 weeks. We supplement the shoot elongation medium for the first 2 weeks with 40 mg/L kanamycin to screen out untransformed buds. Elongated shoots were rooted in a root-induction medium supplemented with 40 mg/L kanamycin to facilitate a second kanamycin screening. Rooted shoots were transferred to the greenhouse where they were kept under a foglike mist in a plastic enclosure for about 2 weeks before they were placed on normal greenhouse benches.

Needle tissues from transgenic plants were then examined for stable integration of the DNA via southern blots, messenger RNA production via northern blots, and protein formation for transferred genes via western blots (table 1). For the BT-toxin gene, we also conducted feeding trials in the laboratory. First instar larvae were reared on 1.5 g of needle tissue for 7 days in sealed plastic petri dishes. Larval weights at the beginning and the end of each feeding trial were determined. Nontransformed control plants were used as comparisons both for the molecular biological studies and the insect-feeding trials.

We recovered seven regenerated plants from inoculations involving the BT-toxin genes. Six of the seven showed positive southern blots indicating the foreign DNA had been stably integrated into larch. Five of seven showed mRNA production, and three of seven showed the *Bacillus thuringiensis* toxin protein production. However, only one plant showed a significantly reduced feeding of gypsy moth larvae as compared to untransformed controls. We are running additional longer term feeding trials now to see if any of the other transformants have significant effects over time on the growth, development, and survival of gypsy moth larvae.

For the aroA gene, we have recovered three putative transformants. Two of these look promising as they have shown positive southern, northern, and western blots. We have not yet conducted glyphosate spray trials with these plants.

The process of recovery of transgenic larch plants in not yet efficient. We estimate that we currently get one BT-toxin transformant with the BT-toxin produced per approximately 1,000 larch seedlings inoculated. Thus, we are examining alternative methods for improving efficiency including the biolistics gene gun approach that Duchesne and Charest (1992) are currently studying for larch.

CONCLUSIONS

Our opinion is that the newly developing biotechnological methods can be used to supplement but not substitute for traditional larch improvement methods.

Table 1—Summary of evidence for successful gene transfer and foreign expression in larch

Gene	Plants regenerated	Gene integration (southern)	mRNA production (northern)	Protein formed (western)	Positive greenhouse trials
BT-toxin	7	6/7	5/7	3/7	1/7
aroA	3	2/3	2/3	2/3	NA[1]

[1] NA = not available as yet as studies are under way.

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Germination, Growth, and Mortality of Alpine Larch, Western Larch, and Their Reciprocal Hybrids: Preliminary Observations

Clinton E. Carlson
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Abstract—Reciprocal cross-pollinations were made in 1990 between western larch (*Larix occidentalis* Nutt.) and alpine larch (*L. lyallii* Parl.). A method was developed to successfully germinate alpine larch. Reciprocal first-generation hybrids were viable. Germination rates, height and basal diameter growth, and mortality were measured. Western larch and hybrids grown on western larch showed greatest growth and least mortality. This study confirms the crossability of western and alpine larch and supports other work dealing with natural hybridization between the species.

Interspecific hybridization in the genus *Larix* is common (Avrov 1982). Most species will interbreed, and hybrids often exhibit morphological characteristics intermediate to the parents. One exception is *L. eurolepis*, a hybrid of European larch (*L. decidua*) and Japanese larch (*L. leptolepis*). This heterotic hybrid significantly exceeds its parents in biomass growth (Kiellander 1974; Machanicek and Prudic 1978; Riemenschneider and Nienstaedt 1983), suggesting similar possibilities for other crosses in the genus. Yang and others (1985) confirmed this with their studies on hybrids of *L. kaempferi* and *L. gmelini* and other larch crosses. Western larch (*L. occidentalis*) and alpine larch (*L. lyallii*) coexist in the Northern Rocky Mountains of the U.S.A. and Canada, but seldom occur sympatrically; usually they are separated by 300 to 600 m elevation (Arno and Habeck 1972). Where the species are sympatric, putative hybrid swarms occur (Carlson and Blake 1969; Carlson and others 1990, 1991). Analysis of morphology and terpene chemistry suggested significant introgression; two of the putative hybrids at one site (Carlton Ridge) had outstanding volume growth compared to parental types (Carlson and others 1991).

The degree of introgression in the putative hybrid swarms confounds growth studies; one has more control when dealing with hybrids from known parentage. The purpose of the work reported here was to determine growth and development of first-generation (F_1) hybrids from controlled reciprocal crosses in comparison to open pollinated western and alpine larch seedlings. This study was exploratory and provided the basis for more intensive work done from 1991 through 1992 (Carlson, in review).

METHODS

Western larch pollen cones were collected during April 1990 from eight trees in the Blackfoot valley about 32 km east of Missoula, MT. Pollen cones from all trees were combined and air-dried for 48 hours at 30 °C. Pollen was cleaned and stored at –5 °C until late June, when alpine larch seed cones were receptive to pollen. Alpine larch pollen cones were collected in June 1989. Pollen was collected in the same manner used for western larch, but was stored in sealed vials at –5 °C for about 10 months until April 1990, when western larch seed cones were receptive to pollen.

Three western larch trees located about 35 km east of Missoula, MT, were selected for cross-pollination with alpine larch pollen. Trees selected had good growth form and abundant female conelets. Six alpine larch were chosen on Carlton Ridge, about 30 km southwest of Missoula; alpine larch also had good form and abundant female conelets. Developing seed cones were isolated from natural pollination by enclosing them in breatheable plastic bags. Immature western larch seed cones were bagged in mid-April 1990; alpine larch were bagged in early June 1990. All pollen cones were removed before placing the bags over the seed cones to prevent intraspecies pollination.

Cross-pollination was done when scales of the juvenile seed cones were nearly completely reflexed. At this stage the conelets were judged to be receptive to pollen (Owens and Moulder 1979). Pollen was injected into the isolation bags using a syringe fitted with a double-orificed bulb and a needle. Two to three squeezes of the bulb dusted the conelets with a thin, but visible, coat of yellow pollen. Isolation bags were left over the conelets until the scales closed. Then the plastic bags were replaced with lightweight nylon mesh bags to protect the cones from depradation by insects, and to catch any seed that might have cast before we could collect the mature cones. Mature cross-pollinated seed cones on alpine and western larch were collected in early September 1990 along with open-pollinated cones from the same trees. Seed was extracted,

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cleaned, and stored at 2 °C. Simple estimates of viability were made by cutting samples of seeds transversely to determine whether an embryo had formed. A sample of filled seeds was tested with tetrazolium chloride (Moore 1976) to determine whether embryos were living.

During January 1991, cross-pollinated and open-pollinated seeds were prepared for germination. Seeds were soaked for 5 minutes in 10 percent Clorox to reduce seed-borne fungal pathogens, then rinsed for 15 minutes in cold tap water. Seedling leach tubes 12 cm long by 2.5 cm diameter were filled to within 1 cm of the top with a peat-based soil. Soil pH was about 5.5. Soil in the tubes was then saturated with tap water. About 40 seeds were placed in each tube because we wanted to have at least one germinant per tube. Seed dissections indicated that no more than 4 percent of the hybrid seed contained embryos. About 33 percent of the alpine larch seed was filled, but earlier literature indicated alpine larch seed was difficult to germinate (Richards 1981; Shearer 1961). Therefore, we also sowed about 40 alpine larch seed in each tube. Western larch seed was about 20 percent filled, so we reasoned that 40 seeds per tube also would result in at least one seedling per tube. Seeds were covered with about 0.3 cm soil (packed); a thin layer of fine gravel was added to prevent seeds from washing away during irrigation. All tubes were then covered with polyethylene to prevent desiccation, and placed in a cold room at 2 °C for 30 days. We believed that this method of stratification would more closely emulate natural stratification under a snowpack, except for the length of time, which would be 7-8 months under natural conditions.

Following stratification, tubes were placed in an indoor greenhouse. Trays of tubes, representing various seedlots, were assigned at random to locations within the greenhouse. Temperature was maintained at 30 to 35 °C; fluorescent lighting was used with photoperiod set at 16 hours. Tubes were watered as needed, and fertilized with a balanced 20/20/20 mixture once monthly. Numbers of germinants were recorded weekly, and excess seedlings were removed so that each tube with germinated seeds ended up with only one seedling.

Alpine larch, western larch, and the reciprocal hybrid seedlings were outplanted in July 1991, in a 20- by 30-m garden plot adjacent to our laboratory in Missoula. The experimental design was completely random. Initial spacing was 0.3- by 0.3-m; seedlings were assigned at random to planting location.

RESULTS AND DISCUSSION

Fourteen months following planting we measured the germination, survival, height growth (cm), and basal diameter (mm) of reciprocal hybrids, alpine larch, and western larch.

Germination

About 40 percent of the alpine larch seeds had intact embryos/endosperm; of these, 99 percent stained positive with tetrazolium chloride for viability. About 30 percent of the western larch seeds were filled; filled seeds were 96 percent viable. The hybrid seeds, regardless of parentage, developed few embryos/endosperm; percentage filled seed ranged only from 0 to 5. However, 99 percent of the embryos stained positive for viability.

Based on total seeds planted, germination in the leach tubes paralleled the cutting tests. Germination of western larch seed varied from 16 to 24 percent, alpine larch varied between 6 to 37 percent, and hybrid seed ranged from 0 to 4 percent (table 1). Values for open-pollinated western larch concur with observations by Shearer (1989). The generally high percentage germination for alpine larch was unexpected. Richards (1981) was able to germinate only two of 5,000 alpine larch seeds; Shearer (1961) experienced a similar situation. Stratifying seed in situ in a peat mix, with acid pH, apparently overcomes inherent barriers to germination.

The poor seed set/germination of the cross pollinations was not expected. During cross-pollination trials in spring of 1989, we achieved over 40 percent filled seed when pollinating alpine larch females with western larch pollen. We did not do the reciprocal cross that year so we have no comparison for the 1990 cross of alpine larch pollen to western larch females. We suspect that weather may have contributed to the poor success of the 1990 cross to alpine larch females. We placed the isolation bags over seed cones just as they were flushing, just after about 2 weeks of warm, dry weather. A few days later a cold air mass moved in, staying for about 2½ weeks; during this period it snowed several times. Conelet development inside the bags proceeded at a faster rate than outside, but the conelets did not open properly; we delayed pollination but may have waited too long. This cross was repeated in the spring of 1991 with outstanding success—80 percent

Table 1—Percentage germination of alpine larch, western larch, and their reciprocal hybrids

		Germination	
Species[1]	Female	No. planted	Percent germination
AL	AL-1	2,000	37
AL	AL-2	1,500	35
AL	AL-3	1,500	17
AL	AL-4	1,500	37
AL	AL-5	2,000	20
AL	AL-6	1,500	6
WL	WL-1	2,500	16
WL	WL-2	350	22
WL	WL-3	2,500	24
HYB	AL-1	1,200	1
HYB	AL-2	2,000	1
HYB	AL-3	1,000	2
HYB	AL-4	600	0
HYB	AL-5	2,000	0
HYB	AL-6	2,000	4
HYB	WL-1	2,500	1
HYB	WL-2	2,500	1
HYB	WL-3	2,500	2

[1] AL = alpine larch; WL = western larch; HYB = hybrid.

filled seed in some cases (Carlson, in press). It seems probable that our decision to delay pollination within the bags due to the unusually cold weather of spring 1990 contributed to the poor pollination and fertilization success. Timing of pollination appears to be critically important.

The cross of alpine larch pollen to western larch in 1990 was barely successful; we had the same results in 1991 (Carlson, in press). Because pollen production of alpine larch occurs about 3 weeks after western larch conelet production, it is necessary to collect alpine larch pollen a year in advance and store it frozen. It is possible that pollen viability decreased during storage, leading to poor seed set. We did not test pollen for viability; more information is needed on the effects of storage on viability of alpine larch pollen.

Seedling Survival and Growth

Survival of seedlings 1 year after outplanting varied among taxa: 64 percent of the western larch and 57 percent of the hybrids with western larch as the female parent survived; 31 percent of the hybrids with alpine larch as female parent and 25 percent of the alpine larch survived (table 2). The garden site is located near our laboratory at 975 m mean sea level; western larch is well-adapted to mesic, relatively warm environmental conditions at this elevation. In contrast, alpine larch is best adapted to cool, moist conditions at elevations above 2,100 m. Survival appears to be related to female parentage. Hybrids with western larch as the female parent did almost as well as the western larch open-pollinated seedlings. Hybrids with alpine larch as the female parent closely approximated survival of alpine larch seedlings (fig. 1).

Height and basal diameter growth were significantly different among all taxa and followed the same pattern as survival. Western larch had the best height and diameter growth, about seven times better than alpine larch and at least three times better than either of the hybrids (table 3). The hybrids were decidedly intermediate, and those with western larch as the female parent grew significantly better than those with alpine larch as female parent (table 3). Alpine larch is known to grow slowly. Richards (1981) found that alpine larch grew about 1.5 cm per year in its natural environment. Our alpine larch grew an average 3.7 cm in two growing seasons, nearly matching Richard's (1981) findings, even though they were far outside their natural environment. Growth rates for western larch appeared normal (Carlson and others 1988; Schmidt and others 1976). It appears that the differences in growth seen in our garden plantation are under strong genetic control.

Table 2—Frequency and percentage mortality among alpine larch, western larch, and their reciprocal hybrids 1 year after planting

Species	Total seedlings	Percent living	Percent dead
Western larch	220	64.1	35.9
Hybrid, WL female	70	57.1	42.9
Hybrid, AL female	141	30.5	69.5
Alpine larch	224	24.6	75.4
Totals	655	42.6	57.4

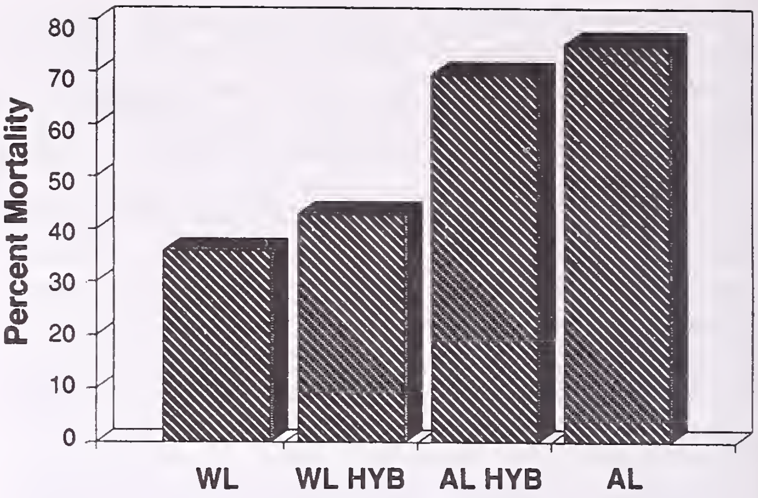

Figure 1—Percentage mortality of western larch, alpine larch, and their hybrids 1 year after planting.

Table 3—Means, and standard errors, and number of observations for height and diameter among western larch, alpine larch, and the reciprocal hybrids 1 year after planting

	Height (cm)		Diameter (mm)		
Species	Mean[1]	SE	Mean	SE	*N*
Western larch	26.1_A	1.19	6.6_A	0.20	141
Hybrid, WL female	8.2_B	.74	3.6_B	.20	40
Hybrid, AL female	6.3_C	.49	3.0_C	.22	43
Alpine larch	3.7_D	.20	1.7_D	.10	55

[1] Means not followed by the same letter are significantly different at $p \leq 0.05$.

CONCLUSIONS

This exploratory study demonstrated that first-generation reciprocal hybrids of western and alpine larch are viable. This knowledge strengthens our interpretations of natural hybridization observed at sympatric sites in the Bitterroot Range. We also developed a method to germinate and grow alpine larch; this represents a breakthrough because past attempts were mediocre at best. Future work will involve outplanting alpine larch, western larch, and the reciprocal hybrids at field locations with varying environmental conditions. Hybrids may have more tolerance to cold than western larch and may be suitable for planting in cold, moist habitats.

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In Vitro Embryogenesis in Larch

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Abstract—Larch species (*Larix decidua, L. leptolepis, L.x eurolepis*, and *L. occidentalis*) have been induced *in vitro* to form embryos from somatic and gametophytic explants. Embryogenic tissues were induced from zygotic embryos dissected from immature and mature seeds and from young seedlings. Complete development of somatic embryos was achieved on different maturation media. Haploid embryogenesis has been achieved from cultured megagametophyte tissue of *Larix decidua, L. leptolepis,* and their hybrids. The method applied to produce haploid plantlets was similar to the one used for somatic embryogenesis. Successful regeneration of trees was achieved.

Larix species have been the attention of numerous improvement programs in different parts of the Northern Hemisphere. The general attention of breeding programs is to discover heritability of various characteristics and then to selectively incorporate these aspects into material produced by silviculture. Improved trees may be used in seed orchards and breeding orchards, but if seed set is limited, the question arises how to improve production of a given family or even a particular genotype.

In vitro systems offer a variety of possibilities, of which only a few have been attempted in the genus *Larix*. In the case of limiting seed set, it would be ideal if somatic tissue of the mother tree could be induced to form embryos directly from cultured pieces of needle, shoot, apex, cambium, nucellus or any one of a host somatic tissues and organs. However, this has proven elusive. Somatic embryogenesis is therefore only possible with seeds from crosses of improved families. However, crosses themselves provide a limited mix of genetic material (Owens and Ross 1991).

Inheritance of cytoplasmic organelles is entirely paternal for chloroplasts and generally maternal for mitochondria. To put together novel combinations, cells can be joined together by employing *in vitro* cell fusion techniques. General breeding *via* pollination also suffers from the disadvantage of being unworkable with species which have barriers to breeding, such as phenological, ontological, sexual, or physiological ones. To get inbred, homozygous lines is not a practical goal in conifer breeding programs because of their long duration. Again, *in vitro* techniques may provide an option.

Haploid cells may be cultured, induced to form embryos, and doubled to form homozygous diploid cells. The resulting plants may very well be suited to breeding programs for gene transfer (Bonga and others 1988). Gene transfer itself may be possible by direct means such as biolistic transformation using DNA-coated gold particles shot into suitable plant material (Duchesne and others 1992). However, the ability to do much silviculture with such material may still depend on the number of propagules such transformed plants may produce. Genetic engineering is itself very dependent on using aseptic plant material, and is thus thrust into a dependence on tissue culture methodologies.

Readers interested in conifer genetic engineering are directed to other recent reviews (Charest and others 1992; Rogers and Cheliak 1990).

In vitro embryogenesis provides a number of possible methods, which include:

1. Somatic embryogenesis
2. *In vitro* fertilization and embryogenesis
3. Cell fusion and embryogenesis
4. Haploid embryogenesis

In larch only two of these four have been accomplished (1 and 4). To our knowledge, the other two have not been attempted. We will discuss the successful methods, somatic embryogenesis, and haploid embryogenesis.

SOMATIC EMBRYOGENESIS OF LARCH

Induction

In larch as well as in other conifer species, the induction of somatic embryogenesis is under the control of various factors. One of the most important is the development stage of the zygotic embryo. Thus, somatic embryogenesis can be achieved from immature and mature seeds, as well as from young seedlings.

In immature embryos, the induction of diploid embryogenic calli was achieved in *L. decidua* (Cornu and Geoffrion 1990), in hybrid larches (*L. decidua* Mill. x *L. leptolepis* Gord. and reciprocal cross), (Klimaszewska 1989; von Aderkas and others 1991) and in western larch (*L. occidentalis* Nutt.), (Thompson and von Aderkas 1992) from immature zygotic embryos at precotyledonary stage. After sterilization, seeds were excised and embryos were placed on MSG (Murashige and Skoog 1962) or 1/2 LM (Litvay and others 1985) media solidified with 0.4percent Gelrite gellan gum. Two plant growth regulators were added to the basal medium: 2,4-dichlorophenoxyacetic acid (2,4-D) and 6-benzylaminopurine (BA) at concentrations of 9.0 µM and 4.5 µM, respectively. Excised embryos of western larch placed directly on the induction medium produced more embryonic tissue than co-cultured with megagametophytes. In hybrid larches, embryonic structures were

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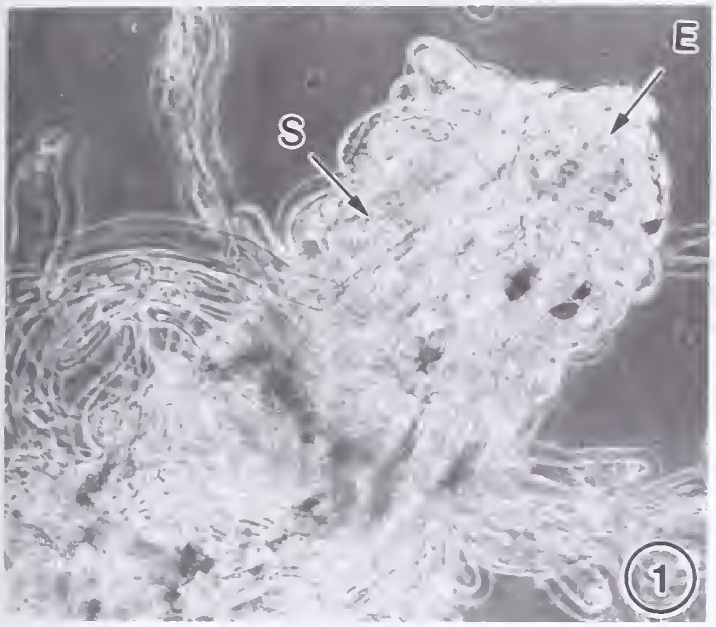

Figure 1—Embryogenic suspension cells of western larch cultured on 1.2 LM medium containing 2,4-D (0.9 µM). E = embryogenic cells, S = suspensor-like cells. (X 60)

induced only by zygotic embryos surrounded by the archegonial part of the megagametophyte. For all these larch species, only 3 to 25 percent of explants formed sustainable embryonic lines.

For mature embryos, utilization of stored mature seeds offers the advantage of experimentation during the whole year. After 4 weeks of culture in the induction medium (1/2 LM with 9.0 µM 2,4-D and 2.2 µM BA), excised zygotic embryos of western larch developed as either: brown calli, non-embryogenic white calli which turned green in the light and white embryogenic tissues. The induction percentage for somatic embryogenesis was quite low (between 5 to 33 percent depending on the lines). After a further 2months of subculture only 1 to 3 percent of the explants exhibited characteristic clusters of long suspensor-like-cells associated with small meri-stematic cells (fig.1). The other potential lines browned and degenerated, or exhibited a very slow growth rate. In white spruce, 4hours imbibition of seeds prior to dissection improved significantly the induction frequency (Tremblay 1990). But in western larch, no embryogenic tissues has been obtained from imbibed seeds. The effect of 2 weeks of stratification treatment at 5 °C, in the dark, applied to seeds or to isolated embryos was also tested; but no significant increases of induction was detected (Benkrima, unpublished).

For young seedlings, embryogenic tissue has also been induced from excised explants of 1-week-old western larch seedlings germinated from 1-year-old stored seeds. Induction frequency level was still very low (1 to 3percent) and only slow growing cultures were established. These proved difficult to maintain. Like in black spruce and white spruce (Attree and others 1990), no significant differences in induction rate had been detected between cytokinin (BA at 4,5 µM) pretreated explants and controls (Benkrima, unpublished).

Maintenance

Tissues induced from immature or mature embryos or from seedlings can be maintained in this embryogenic condition for years when regularly subcultured in a maintenance medium of 1/2 LM supplemented with 2,4-D and kinetin. Some lines grew very well and kept their embryogenic capacity at a low level of 2,4-D (0.9 µM) but other lines, in particular these obtained from mature seeds, needed higher levels of auxin (9.0 µM) and kinetin (4.5 µM) (Benkrima, unpublished).

Embryogenic cultures of western larch have been kept for 3 years at 21 °C in the light on maintenance medium containing low levels of 2,4-D and kinetin. Some embryogenic tissues of larch (*L.* x *eurolepis*) have also been cryopreserved (Klimaszewska and others 1992). They were still able to produce plantlets after a period of time spent in liquid nitrogen.

Somatic embryos do not mature when cultured on maintenance medium. For further development, they require to be transferred into a medium which will induce their maturation.

Suspension Culture

Suspension culture offers the advantage of growing cells quickly as well as furthering a more synchronous development of somatic embryos. Eventual mass-production of somatic embryos will require a large number of uniform embryos all at the same stage of development before the maturation process has begun.

For initiation, 1 to 3 g of callus was put in 125 ml Erlenmeyer flask containing 30 ml of liquid medium. Suspensions were rotated at 100 rpm and were subcultured every 2 weeks. When cultures were established (10^5 cells/ml) after three to four subcultures, 50 ml of suspension was transferred into 250 ml Erlenmeyer baffle-flasks to increase the production of cells. Differences in clones were observed in both cell density and in mitotic index (Benkrima and von Aderkas, unpublished). These may be due to genetic differences in growth capacity among the suspension lines. Microscopic observation showed a pattern of clustered small cells associated with suspensor-like cells, typical of early embryogenesis (fig. 1).

Eight lines of cell suspension cultures were derived from 2-year-old embryogenic tissues from immature embryos of western larch. After eight to ten subcultures, the suspensions were filtered and cell masses were transferred onto maturation media. Complete development of somatic embryos were achieved (Benkrima, unpublished).

Maturation

The most critical step of larch regeneration from somatic embryogenesis is maturation. Several reports suggested that abscisic acid (ABA) has an essential function in somatic embryo maturation (Durzan and Gupta 1987; von Arnold and Hakman 1988; Roberts and others 1990).

For western larch, the optimal concentration of ABA is highly variable (from 0.025 to 40 µM) and is strongly influenced by different factors including: genotype, stage of somatic embryos and possible differences in levels of endogenous ABA, length of the treatment, composition of the basal medium (in particular water potential, presence of other growth regulators), and environmental factors (Thompson and von Aderkas 1992).

High concentrations of ABA have been tested in different lines of western larch but just one line produced mature embryos after 4 weeks of exposure to 40 μM of ABA. But optimum results were obtained with 0.025 μM ABA for 1 to 2 weeks. Low concentration of ABA (0.38 μM) applied for 3 weeks also promoted maturation of hybrid larch (Klimaszewska 1989; Roberts and others 1990).

When embryogenic tissues or suspension cells were transferred to medium lacking ABA, all the embryos produced were called "precocious germinants." "Precociously germinating" embryos are characterized by elongating green hypocotyl and cotyledons, which are the result of a continuous development from the late embryogeny stage to the "germination" stage. Very little information is available on the morphology of these precocious germinants. In larches, these embryos don't always have radicles, and then cannot be defined like germinants but more like "precociously elongated embryos" (fig. 2).

A number of studies have indicated that seed water relations may be even more important than ABA in regulating embryo development and maturation and in preventing precocious germinations (Finkelstein and Crouch 1986; Xu and others 1990). ABA and highly negative osmotic potentials both induce desiccation and may promote the accumulation of storage proteins as well as inhibit precocious germination and other anomalies often observed *in vitro* when the somatic embryos do not mature properly.

ABA and osmoticum had additive effects on maturation of certain lines of western larch. Of all the treatments tested in order to improve the maturation, 1.2 LM medium containing 2percent sucrose 8percent PEG 1450 (polyethylene glycol) and 20 μM ABA gave the best results in term of quantity and quality of somatic embryos produced (144 embryos per g of callus for the line 2159) (fig. 3) (von Aderkas and Benkrima, unpubl.). PEG 1450 is a high molecular weight neutral osmoticum which induces a non-plasmolysing osmotic stress. The period of maturation was 2months, similar to those commonly reported in the literature. This long maturation process reduced the germination rate of the mature embryos which were only able to differentiate a small radicle. Further development of the root system was inhibited.

Germination and Soil Establishment

The success of germination and soil establishment depend essentially on the physiological state of the somatic embryos at the end of the maturation treatment. This physiological stage is influenced by the concentration and the type of osmoticum, the concentration of ABA, and the length of the maturation. Lengthy maintenance of somatic embryos on high concentrations of ABA affected root emergence, even though the embryos were very well-formed. Isolated somatic embryos of western larch which had been matured on 8percent PEG and 20 μM ABA showed the best germination rate (42.8percent), but the conversion rate into plantlets was low because of the long term effect of ABA. In general, "precociously elongated" embryos had poor root development but some of them were able to grow normally into viable plantlets. Cytogenetic analysis of some of these plantlets showed diploid count chromosomes (2N = 24) (fig. 4).

HAPLOID EMBRYOGENESIS

Haploid embryogenesis has been achieved from cultured megagametophyte tissue of larch species, *L. decidua*

Figure 2—Somatic embryo of western larch after 2 months of maturation on 1/2 LM, 2 percent sucrose, 8 percent PEG and 20 μM ABA. (X 10)

Figure 3—Elongated or "precociously germinated" western larch somatic embryos on 1/2 LM, 2 percent sucrose and 8 percent PEG, no ABA. (X 6)

Figure 4—Chromosomes of western larch somatic plantlet (2N = 24). Giemsa staining. (x 1300)

(Nagmani and Bonga 1985), *L. leptoleptis* and their hybrids *L.* x *eurolepis* and *L.* x *leptoeuropae* (von Aderkas and others 1990). The methods for achieving this are similar to those used in producing somatic embryos: plant material is induced to form embryogenic tissue which is maintained *in vitro.* Maturation and germination follow (Rohr and others 1987; von Aderkas and Bonga 1988a). The resulting trees are transplanted into soil. It differs from the somatic embryogenesis in the particular of some of these steps.

Induction

Induction is dependent on a number of factors: genotype, state of plant material, and seasonal influences. Much less important are media and the growth regulating substances. In various papers published on haploid embryogenesis, success was only achieved in a few genotypes (von Aderkas and others 1987). Genotype is known to be of importance in the regenerative response to haploid tissue culture of Douglas-fir (Glock and others 1988). The relationship of the material and its ability to respond has been called "phenocritical period of response" (von Aderkas and Bonga 1988b). It refers to the narrow window of opportunity for induction: the few weeks during which the megagametophyte characteristically initiates a corrosion cavity. This occurs 2weeks after eggs normally would be fertilized (Nagmani and Bonga 1985; von Aderkas and Bonga 1988b).

The inductive response is the regeneration of tissues from the megagametophyte leading, eventually, to embryogenesis. It is relatively easy to induce haploid tissues to divide, but much more difficult to achieve embryogenic development.

Induction can be difficult to achieve because of seasonal factors which influence cone development of the larch. The female cone is initiated in the year previous to meiosis and its development is strongly influenced by temperature fluctuations. We have had widely variable responses from the same tree in different years. Induction itself has been achieved on media such as Murashige and Skoog's (1962) and Litvay's (1985). Neither the strength (one half or full strength) nor the combination of inductive plant growth regulating substances (2,4-dichlorophenoxyacetic acid with or without benzylaminopurine or kinetin) made a significant difference. In a few cases, even the control (possessing no growth regulators) produced embryogenic tissue (Nagmani and Bonga 1985; von Aderkas and others 1987).

Maintenance

Growth regulators were omitted at this stage, as the culture did quite well without them. We have found that maintenance is best on 1/2 LM medium supplemented with 500 mg/1 glutamine, 100 mg/1 inositol and 1.0 g/1 casein hydrolysate. The frequency of subculture is not as critical as in other somatic embryogenic systems. We have maintained some lines for almost 8years and many of these are still producing mature embryos. Generally, cultures are subcultured every 4 to 6weeks. They are kept in low light at 20 °C or 25 °C. Long-term subculture has not led to change in the cultures at an obvious level. Some cultures have lost their embryogenic capacity, but one line, after not having produced a green embryo in 5years, regained its embryogenicity, though no changes had been made in any of the growing condition. Changes in ploidy level have been found in at least one line (von Aderkas and Anderson, in press), but generally lines seem to be stable.

Maturation

Clones of *Larix* spp. mature spontaneously without any treatment. As they are not maintained using growth regulating substances, maturation cannot be brought about by staging different plant growth regulators as was done for a number of conifers. Various levels of abscisic acid were tested but did not improve the responses of our lines. Maturation differed from line to line with only two lines ever having produced any plantlets (von Aderkas and Bonga, in press).

Germination

Trees were developed from cultures of haploid megagametophytes germinated *in situ* on 1/2 LM medium without growth regulators and were potted in vermiculite potting mixture, placed in a greenhouse and acclimatized. Rooted cuttings were struck from the ortet and have successfully established themselves. These will be the source of breeding stock for future experiments.

CONCLUSIONS

In vitro cultures of larch trees is well established. Somatic embryogenesis has been successfully carried out in a number of species. Haploid embryogenesis has also been accomplished. This tissue culture system provides the vehicle for a number of novel breeding strategies which incorporate either artificial seed or specially selected genotypes. More importantly, novel breeding technologies may be brought into play, such as cell fusion to produce novel genotypes and developing gene transfer methodologies. Larch species will provide interesting opportunities in the future.

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Genetic Differences in Physiology and Morphology Among Western Larch Families

Jianwei Zhang
Lauren Fins
John D. Marshall

Abstract—Rapid height growth has often been associated with susceptibility to frost damage or water stress. In a study with western larch from the Inland Empire, height growth, shoot growth components, and water-use efficiency as measured by stable carbon isotope discrimination showed that mean height for a family was positively correlated with mean number of stem units, predetermined growth, and water-use efficiency. Stem unit production and water-use efficiency appear to be under genetic control and both are strongly associated with height growth in western larch.

Plants growing in natural environments may not be able to express their full genetic potential for productivity (Boyer 1982), and forest trees native to northwestern North America often grow where environmental resources limit tree growth. Nonetheless, evidence from other native plant species suggests that relatively high productivity can occur in these environments (Abul-Fatih and others 1979). Since genotypic selection for adaptation to such environments will play an important role in future forest production, an understanding of tree growth, genetic control over growth traits and the mechanisms by which trees cope with adverse environments is fundamental to the practice of sound forest management.

Rapid height growth in western larch (*Larix occidentalis* Nutt.) has been associated with relative high susceptibilities to water stress (Zhang and Marshall 1994) and to frost damage (Rehfeldt 1982, 1992). Thus, trees from the fastest growing populations may be poorly adapted to colder and drier habitats than those from which they came. Most current breeding programs of western larch and other tree species concentrate primarily on selection for growth traits, while ignoring the physiological mechanisms that link environmental conditions to genetic processes and growth. We argue that these relationships must be understood for long-term success in breeding programs because physiological traits are important determinants of both growth and adaptation. This paper reviews the relationships between growth and some physiological and morphological traits that we have studied with western larch. The underlying physiological mechanisms are also discussed.

PHOTOSYNTHETIC GAS EXCHANGE AND GROWTH

Photosynthesis is one of the most obvious factors determining the rate of plant growth. Yet plants have to lose water by transpiration in order to fix carbon dioxide. Most plants adjust their carbon gain and water loss in response to the environments in which they grow. The range within which these adjustments can occur is genetically determined and furthermore can be transmitted genetically to the progeny populations (Boyer 1982).

Genetic variation in photosynthetic rate has been found in various tree species, provenances, families, and clones, with demonstrated differences in response as a function of temperature or elevation of the seed source (Ledig 1976). However, recent studies failed to detect variation in photosynthetic rate when the studies were based on small subsamples of leaves (Matyssek and Schulze 1987; Samuelson and others 1992). In our studies with western larch we did not detect significant differences in photosynthetic rate among either populations (Zhang and Marshall 1994) or families (Zhang and others 1994), although the differences among groups in height and diameter were pronounced in both studies. Furthermore, height and diameter do not appear to be well-correlated with photosynthetic rate as measured. However, the photosynthetic rate of a small subsample of leaves measured for a short period of time may not be representative of either the whole tree at that time or that tree over its whole life. Besides photosynthetic rate, plant growth also depends on the amount of photosynthetically active tissue constructed by the plant and many other aspects of carbon use, such as respiration and carbon allocation. Under conditions where resources are limited, differences in plant growth may be associated more with efficient use of these resources than with high rates of photosynthesis.

Bidlake and Black (1989) developed a generalized regression equation to describe the relationship between sapwood and leaf area for western larch. Because the trees in our study were too young to have produced much heartwood (Zhang and others 1994), we used tree diameter in their equation to predict the projected leaf area of our trees. These predicted values were significantly correlated with growth traits (height and diameter) for the five western larch families in our study (fig. 1). Thus differences in the amount of photosynthetic tissue on a larch tree appear to be more important for carbon gain than differences in rate of photosynthesis. But this relationship may hold true only within a limited range of leaf areas,

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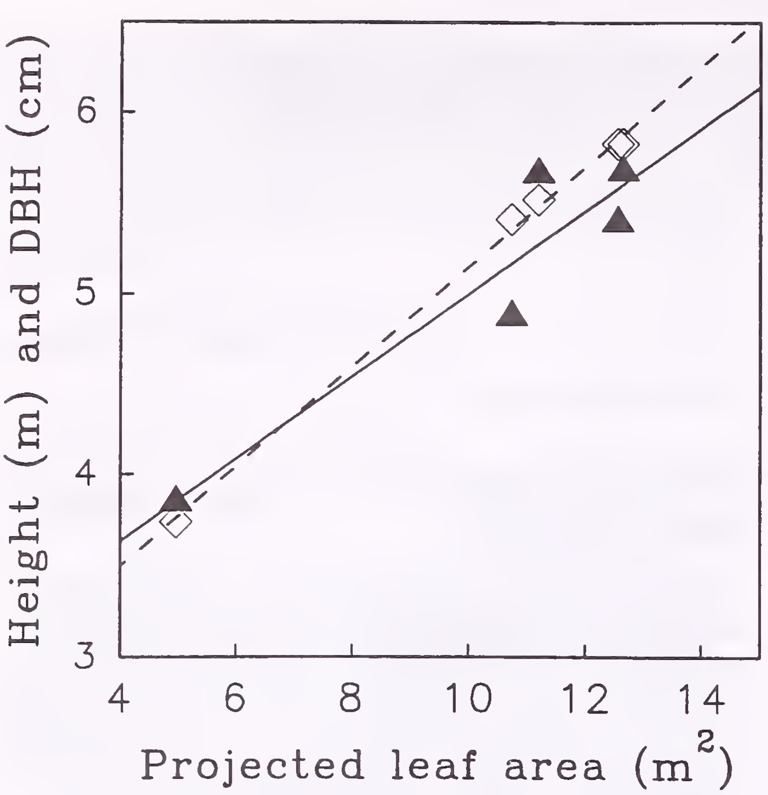

Figure 1—Relationship between total projected leaf area (m²) and height (▲) ($r = 0.94$, $P = 0.01$) and diameter at breast height (d.b.h.) (◊) ($r = 0.999$, $P = 0.0001$) of western larch families.

because beyond a certain point, the additional benefit of more leaf area would be minimized by mutual shading.

Water-use efficiency was also assessed in the western larch family study using the carbon isotope discrimination (Δ) technique (Zhang and others 1994). Stable carbon isotope discrimination (Δ) has several advantages over other measures of water-use efficiency. First, because it is relatively quick and easy to measure, many trees can be sampled over a short time period. Second, this technique integrates the accumulated carbon isotope ratio ($^{13}C/^{12}C$) for a whole growing season (if samples are leaves), so that it represents an overall response of plants to their environments. Third, the theory, which predicts a negative relationship between carbon isotope discrimination and water-use efficiency, has been well tested (Farquhar and others 1989), including a study involving western larch. Figure 2 shows the relationship between carbon isotope discrimination and water-use efficiency in a study of 2-year-old western larch seedlings grown under two water conditions (Zhang and Marshall 1994). This study sampled 14 populations across the range of the species.

We also found significant variation in carbon isotope discrimination among families and strong negative correlations between Δ and height and diameter in 12-year-old trees (fig. 3). Similar relationships have been reported in *Pseudotsuga menziesii* (Mirb.) Franco (Zhang and others 1993). Water-use efficiency was positively correlated with height growth (fig. 4). Thus, it appears that western larch trees with high water-use efficiency are either able to conduct photosynthesis (as measured by gas exchange) for a relatively longer time with a given amount of water or are more efficient in their conversion of photosynthate to biomass.

Western larch, which has been described as "a deciduous conifer in an evergreen world" (Gower and Richards 1990) has lower water-use efficiency and higher nitrogen use efficiency compared to its sympatric evergreen species (Gower and Richards 1990) and even quaking aspen (Marshall and Zhang 1994). In terms of its carbon budget, larch has several disadvantages compared to evergreen trees. First, it has to construct a full complement of foliage compared to the annual single age-class of foliage produced by evergreen conifers, and second, larch has a much shorter growing season than evergreen trees, which have been reported to conduct photosynthesis even during winter months (Waring and Schlesinger 1985).

Furthermore, during the growth season, larch endures environments of low precipitation and high evaporation (Schmidt and Shearer 1990). Under these conditions, we might expect natural selection to favor physiological and morphological adaptations that allow the efficient use of resources, such as higher photosynthetic rates or greater leaf area compared to competing neighbor species. The evidence has shown that western larch's photosynthetic rates are similar to those of its sympatric evergreen conifers on a leaf area basis, but its specific leaf area (a

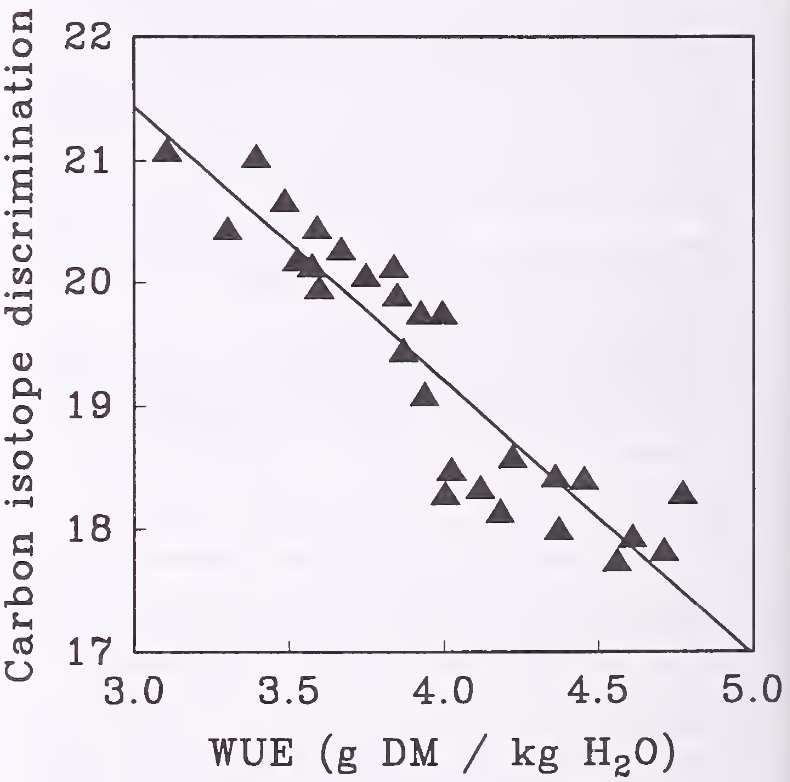

Figure 2—Relationship between carbon isotope discrimination (Δ) and water-use efficiency (amount of dry matter accumulated per unit water transpired) ($r = -0.91$, $P = 0.0001$) in 2-year-old seedlings growing under two water conditions in University of Idaho nursery in 1991. The study included samples from 14 populations of western larch from British Columbia, Idaho, Montana, Washington.

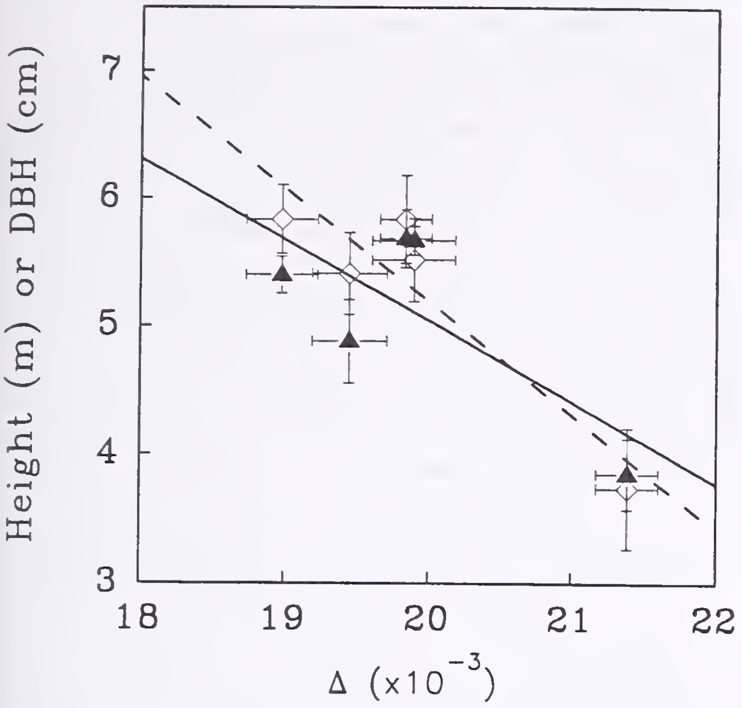

Figure 3—Relationship between carbon isotope discrimination (Δ) and height (▲) (*r* = –0.75, P = 0.15) and diameter at breast height (d.b.h.) (◇) (*r* = –0.92, P = 0.03) of western larch families at age 12.

measure of the amount of leaf area per unit of leaf mass) is much higher than those same species. In fact, on a leaf weight basis, larch's photosynthetic rates are often twofold greater than evergreen conifers (Higgins and others 1987). As a consequence, larch can fix the same amount of carbon during its short growing season as do evergreen conifers during a whole year.

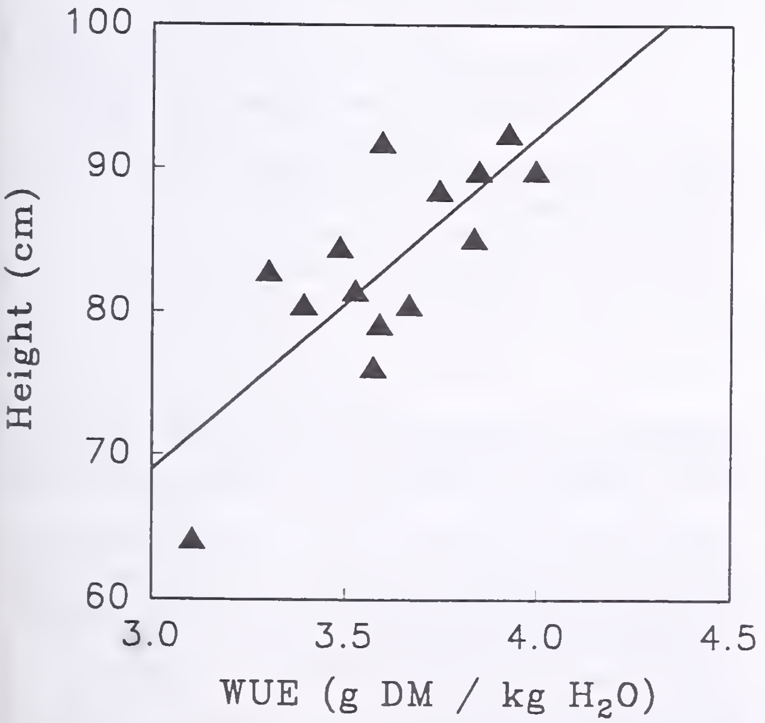

Figure 4—Relationship between water-use efficiency and height in 2-year-old seedlings growing under well-watered conditions (*r* = 0.77, P = 0.001).

As for water-use efficiency, it is, as yet, not clear whether plants with high water-use efficiency are more competitive than their counterparts in terms of growth. Some research suggests low water-use efficiency is a more competitive strategy but these conclusions are based primarily on community studies that show a negative correlation between water-use efficiency and total leaf area. Our studies, however, show that within a single species, families with higher water-use efficiency are most likely to gain more carbon, and consequently, produce more growth under common garden conditions. Clearly additional studies are needed to fully understand how these different competitive strategies function within and between species.

SHOOT GROWTH COMPONENTS AND GROWTH

Shoot growth patterns in forest trees have been studied extensively for the last two decades, and quantification of the components of shoot growth has been suggested as a potential basis for early selection (Cannell and others 1976; Kremer and Larson 1983).

Shoot growth in western larch comprises both predetermined growth and free growth. Predetermined growth consists of the portion of an expanding or expanded shoot for which the stem units were initiated in the previous growing season and enclosed in the over-wintering bud (Cannell and others 1976; Lanner 1976; Steeves and Sussex 1989). Free growth is that portion of the shoot that is initiated and expanded during the same season (Jablanczy 1971; Pollard and Logan 1976; Cannell and Johnstone 1978). While in many coniferous species free growth is a juvenile trait, western larch continues to produce both types of growth considerably beyond the juvenile growth phase (Owens and Molder 1979; Joyce 1987; Zhang and Fins 1993). Each of the components of shoot growth can be further evaluated in terms of the number and length of stem units it contributes to a growing stem.

We found significant variation among 14 families in total number of stem units, predetermined growth stem units, and tree height at age 9 (Zhang and Fins 1993). Although the proportion of free growth stem units in this study represented 20 percent of the number of stem units, the differences among families were not significant for this trait. In a small study of five western larch families, variation in both number of stem units and predetermined growth stem units at age 9 accounted for about 40 percent of the variation in 9-year height (data not shown), whereas they accounted for 86 and 77 percent, respectively, of the variation in 12-year height (fig. 5). The correlations between free growth stem units and mean stem unit length with height were also weak in this study (fig. 6). This pattern is different from those reported for some other species. Genetic variation between provenances of Douglas-fir and blue spruce (*Picea pungens* Engelm.) (Bongarten 1986) and jack pine (*Pinus banksiana* Lamb.) (Kremer and Larson 1983) has been largely explained by differences in number of stem units, while

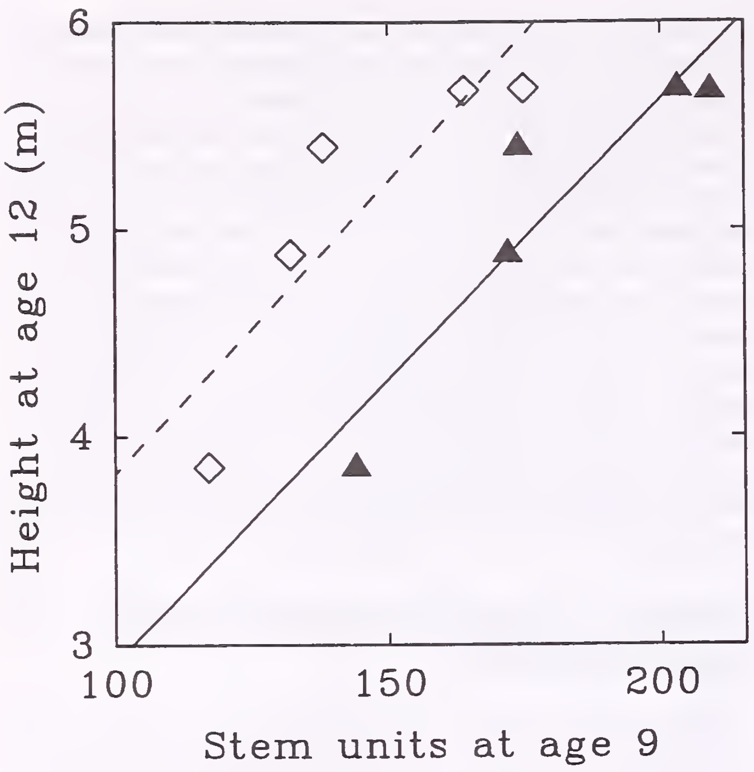

Figure 5—Correlation between total number of stem units (▲) ($r = -0.93$, P = 0.02) and predetermined growth stem units (◇) ($r = 0.88$, P = 0.05) at age 9 and height at age 12.

genetic variation among families within a provenance has been largely explained by differences in mean stem unit length.

Zhang and Fins (manuscript in review) compared a series of alternative selection regimes for western larch and found that none of the components of shoot growth served better than direct selection for total height at age nine. However, the lack of data for very young trees limited the calculation of age-age correlations and early direct selection. But working with loblolly pine (*Pinus taeda* L.), Bridgwater (1990) found that total annual height increment produced during the second year was a better predictor of tree size after eight years in a field study than any of the components of shoot growth. If this same pattern holds true for western larch, height increments, which are easily measured, can be used for early selection. Additional work is clearly needed for the development of an efficient selection strategy for western larch.

To fully understand plant growth, Körner (1991) suggested that a multitude of variables that influence growth be studied simultaneously. But because it is very difficult and costly to conduct a comprehensive growth analysis, the alternative chosen by most researchers is to detect the dominant variables in small scale trials and then to use the important variables to improve selection efficiency. However, some traits may be negatively correlated with each other, which would make improvement more difficult. Thus a full understanding of the relationships between the selected and target traits will be critical to a program's success. With this knowledge, it will be possible to base selection programs on the appropriate combination of the dominant variables that strongly influence the target trait.

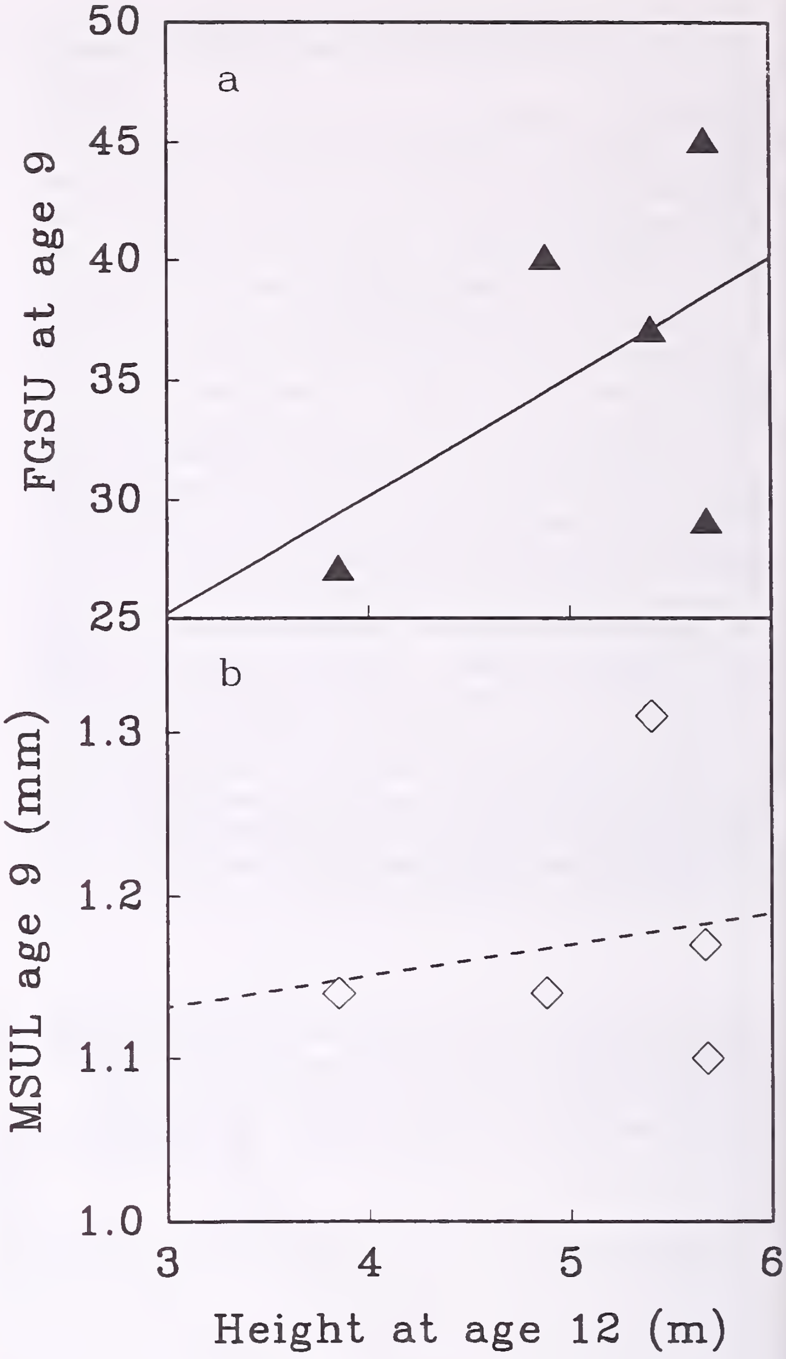

Figure 6—Correlation between height at age 12 and (a) free growth stem units ($r = 0.51$, P = 0.38) and (b) mean stem unit length ($r = 0.18$, P = 0.77) at age 9 for 5 families of western larch.

PHOTOSYNTHETIC GAS EXCHANGE AND SHOOT GROWTH COMPONENTS

From the discussion above, it is clear that both photosynthetic gas exchange and shoot growth components are related to tree growth in western larch. What is not yet clear are the relationships among these variables. Perhaps because we made the measurements in different years, it was not surprising to find only weak relationships between photosynthetic gas exchange and shoot growth components. In terms of their contributions to growth, we expected stronger correlations because in the early stages of growth the quantity of tissue available to fix carbon dioxide is determined by the number of predetermined growth stem units which were formed during the previous growing season and the length of stem units, which is controlled by the amount of photosynthate available during the current growing season. However, a plant with many short stem units may have less net carbon gain than a plant with many long stem units because of mutual shading by the tightly packed leaves.

In summary, tree breeders may find indirect selection for physiological and shoot growth traits to be useful alternatives and/or additional refinements for selecting suitably adapted genotypes that are able to exploit the available growing season between damaging frosts or droughts, which can conduct photosynthesis under conditions of potentially limiting resources, and which can form more stem units (more leaves) and/or longer stem units for intercepting more PAR. If it is possible to identify several dominant traits that are related to growth and expressed in juvenile trees, a selection index can be used to make early selections, and therefore the length of the breeding cycle may be reduced. Several such adaptive traits show promise, including frost tolerance (Rehfeldt 1982), water-use efficiency and total projected leaf area.

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Comparison of Cone Production by Rooted Cuttings, Grafts, and Seedling-Origin Trees of Western Larch

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Abstract—Rooted cuttings from juvenile trees, grafts from mature scions, and seedling-origin trees planted in a common garden in Plains, MT, U.S.A., were compared for cone production for two consecutive years. The differences between stock types were statistically significant for the mean number of cones per producing tree for the second year but were not significant for the percent of trees producing cones in either year. A projection of cone production per 1,000 live trees showed that the grafted trees would produce nearly twice the number of cones as the seedling-origin trees and more than five times the number of cones as trees from rooted cuttings under the same conditions.

Despite its relatively limited natural distribution, western larch (*Larix occidentalis* Nutt.) is one of the most desirable forest tree species in the Inland Northwest, U.S.A. It produces high-quality, high-value wood that is used interchangeably with Douglas-fir for construction lumber, plywood, and other industrial uses (Schmidt and others 1976). Genetic studies of growth and phenological characteristics of western larch seedlings have shown similarities among sources across much of its range. This finding suggests that relatively long-distance seed transfer is feasible with moderate restrictions on elevational transfer (Rehfeldt 1982). Additionally, relatively high genetic gains have been predicted for juvenile height growth in this species (Fins and Rust 1989).

All of these factors contribute to increased interest in planting western larch, but efforts at artificial regeneration have been hampered by a shortage of seed due to repeated cone crop failures. Although cone crops have been irregular for many years (Schmidt and others 1976), only recently have spring frosts been implicated in the frequent failures. In studies conducted over a widespread area from 1985 through 1990, nearly all sample trees produced male and female strobili each year. However, spring frosts subsequently killed most of the strobili in all but the lowest elevation sites and insects often killed or damaged the few remaining cones (Shearer 1990).

Assuming that spring frosts will continue to decimate western larch cone crops, the development of practices that would increase the reliability of cone production would be highly valuable. One alternative is to establish seed orchards in areas that are not subject to spring frosts and that can be protected from other damaging agents. Such orchards are often established using grafted trees, which preserves the integrity of the scion's genotype and in general maintains the physiological stage of sexual maturity of the scion's donor (Olesen 1978; Zobel and Talbert 1984). Thus, for western larch, a late-maturing species which does not produce abundant cone crops until 40-50 years of age (Schmidt and Shearer 1990), grafts made with scions from mature donors would be expected to produce seed considerably sooner than sexually immature seedlings. Grafting, however, is relatively costly and some coniferous species are subject to problems of graft incompatibility. As a result, seedling seed orchards or rooted cutting orchards have gained in popularity in recent years, but little is known about the onset and relative rates of cone production by these stock types compared to grafts in the same environments. Without long-term comparisons, the full impact of the use of seedlings and rooted cuttings is difficult to assess, but we suspected that early cone-production from these stock types would be low compared with grafted orchards.

Our work began in the early 1980's as a project to develop and refine techniques for vegetatively propagating western larch (Staubach 1983). This work resulted in recommendations for using the top cleft graft for establishing seed orchard stock (Staubach and Fins 1988). Through later research we refined our methods and developed recommendations for rooting juvenile cuttings (Edson and others 1991).

At the completion of the earlier vegetative propagation studies, we planted our grafted trees and successfully rooted cuttings from juvenile donors in a comparison test with seedlings at Champion Timberlands' Nursery in Plains, MT. Our two major objectives in establishing the plantation were first, to compare the timing and quantity of cone production among the three stock types, and second, to establish a visual demonstration of the results of the study.

MATERIALS AND METHODS

In fall 1981, rooted cuttings, grafts, and seedlings of western larch were planted in 10-tree row plots at 6 ft x 6 ft spacing at the Champion Timberlands Nursery at Plains, MT. Cutting donors (34 2-year-old seedlings) and scion donors (20 50-year-old trees) were obtained from the same stand at Pryne's Reservoir in western Montana. Grafting and rooting took place during spring 1981 (Staubach 1983).

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The rootstock used for the grafts were 2-0 bareroot seedlings. Comparison seedlings were operational planting stock grown by three private nurseries in Montana. Thirty-eight percent of the seedlings were containerized stock that had been germinated in the spring of 1981, while the remainder were 2-0 bareroot stock. A total of 80 grafts, 50 rooted cuttings, and 130 seedlings were planted. Prior to planting, black plastic was laid on the ground for weed control. Overall survival by the fall of 1991 was 69 percent.

A second block of this experiment was planted adjacent to the first in the fall of 1983. Scion donors for grafting were the same 20 trees as were used in the first block and cutting donors (55 2-year-old seedlings) were from the same stand as those planted two years earlier. Scions were grafted onto rootstock in March 1982 and cuttings were collected and set in the rooting house in July 1982 (Staubach 1983). Comparison seedlings were all 6-month-old container-grown stock. A total of 100 grafts, 90 rooted cuttings, and 200 seedlings were planted at 6 ft x 6 ft spacing. Weeds were not controlled in this block, and survival by fall 1991 was only 30 percent.

In 1987, 10 trees in the experiment produced their first cones. Of the 10, seven trees were grafts and three were seedlings. Cone production slowly increased until 1990 and 1991 when a sufficient number of cones was produced to make reasonable comparisons between the three stock types. At the time these comparisons were made, 297 trees were alive in the plantation: 94 rooted cuttings, 78 grafts, and 125 seedlings. Overall survival was about 46 percent and was considerably higher in the 1981 planting than in the 1983 planting. Rooted cuttings had the highest survival at 67 percent, with the grafts and seedlings at 43 and 38 percent, respectively.

In addition to cone counts for all producing trees, heights and diameters breast height were measured on a small sample of trees of each stock type. Stock types were compared for the percent of trees producing cones, the mean number of cones per producing tree and the projected number of cones per 1,000 live trees of each type. Cone production data were analyzed by two-way analysis of variance for each year. Male strobilus production was not assessed.

RESULTS AND DISCUSSION

In 1990, the differences among stock types or blocks were not statistically significant for the percent of trees with cones, the average number of cones per producing tree, and the projected number of cones per 1,000 trees. Cone production data for 1990 are summarized in table 1. By 1991, however, the differences among stock types in average number of cones per producing tree were significant ($P = 0.03$), and differences in percent of trees with cones were near statistical significance ($P = 0.11$). Differences in the projected number of cones per 1,000 live trees were not statistically significant ($P = 0.28$). Block effects for 1991 data were significant for number of cones per tree ($P = 0.01$) and percent of trees producing cones ($P = 0.03$), and were near significant for cones per 1,000 live trees ($P = 0.13$). Cone production data for 1991 are summarized in table 2.

Perhaps the most telling figures in tables 1 and 2 are those for projected cone production per 1,000 live trees. Despite the lack of statistical significance, these figures, which combine the effects of the percent of trees producing cones and the number of cones per tree, show that in these early years, 1,000 live grafts would produce nearly twice the number of cones as would the same number of seedlings and approximately 5-8 times the number of cones as would rooted cuttings.

We suspected that some of the differences in cone production may have been a function of tree size. However, the differences in heights and diameters breast height of the samples (table 3) were not statistically significant for either trait ($P = 0.14$ and $P = 0.33$, respectively), although the probability value for height was suspiciously close to statistical significance. Correlation analysis between tree size with percent of trees producing cones and mean cones per tree were not statistically significant. Thus, differences in cone production among tree types do not appear to be confounded by differences in tree size.

Although our study was conducted on a single site only and should be repeated under other environmental conditions, our results suggest that, like other coniferous, late-flowering species, western larch grafts maintain their mature physiological state and produce female strobili sooner

Table 1—Cone production by rooted cuttings, grafts, and seedlings of western larch in 1990 at Plains, MT

	Alive (N)	Trees with cones (N)	Trees with cones (%)	Total cones	Mean cones/ producing tree	Cones/1,000 trees
Block I[1]						
Rooted cuttings	42	6	14.3	32	5.3	762
Grafts	36	20	55.6	615	30.8	17,083
Seedlings	101	30	29.7	612	20.4	6,059
Block II						
Rooted cuttings	52	4	7.7	23	5.8	442
Grafts	42	6	14.3	110	18.3	2,619
Seedlings	24	0	0.0	0	0.0	0
Totals						
Rooted cuttings	94	10	10.6	55	5.5	585
Grafts	78	26	33.3	725	27.9	9,295
Seedlings	125	30	24.0	612	20.4	4,896

[1] Blocks I and II were field-planted in 1981 and 1983, respectively.

Table 2—Cone production of rooted cuttings, grafts, and seedlings of western larch in 1991 at Plains, MT

	Alive (N)	Trees with cones (N)	Trees with cones (%)	Total cones	Mean cones/ producing tree	Cones/1,000 trees
Block I[1]						
Rooted cuttings	42	12	29	263	22	6,262
Grafts	36	23	64	1,010	44	28,056
Seedlings	101	42	42	1,022	24	10,119
Block II						
Rooted cuttings	52	2	4	12	6	231
Grafts	42	9	21	202	22	4,810
Seedlings	24	0	0	0	0	0
Totals						
Rooted cuttings	94	14	15	275	20	2,926
Grafts	78	32	41	1,212	38	15,538
Seedlings	125	42	34	1,022	24	8,176

[1] Blocks I and II were field-planted in 1981 and 1983, respectively.

Table 3—Mean heights and diameters breast height (d.b.h.) of rooted cuttings, grafts, and seedlings of western larch in 1991 at Plains, MT

	Block I[1]			Block II		
	Height (ft)	D.b.h. (inches)	N[2]	Height (ft)	D.b.h. (inches)	N[2]
Rooted cuttings	19.32	0.88	25	13.83	0.59	13
Grafts	14.92	0.61	21	8.83	0.24	4
Seedlings	18.26	0.95	21	9.15	0.28	4

[1] Blocks I and II were field-planted in 1981 and 1983, respectively.
[2] Number of sample trees measured.

and in greater abundance than the physiologically less mature rooted cuttings or seedings. And, because the economic value of a seed orchard often depends on early and abundant seed production (Fins and Moore 1984), we recommend the use of grafts with mature scions for establishing western larch seed orchards in the Inland Northwest. We also recommend that this study and others like it be followed over successive years to determine the long-term trends in cone production for the three stock types.

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Accelerated Breeding of Three Larch Species

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Abstract—In 1987, an accelerated breeding program was initiated using select clones of tamarack, European, and Japanese larch. Gibberellin ($GA_{4/7}$) promoted flowering by all three species when applied shortly after the start of long shoot extension. Treatments led to sufficient flowering for breeding starting 3 years after the parental population was grafted. Over 120 crosses were made with seed viability averaging around 50 percent. Fifty full-sib families were planted in a field trial in 1992.

In addition to traditional land-use pressures such as agriculture and development, there is increasing pressure to set aside large areas of forest for wildlife habitat, water resource protection, and recreation. At the same time, demand for forest products has increased. One response to this situation is to grow more wood on less land, practicing intensive forestry for wood production in some areas and not harvesting trees in others. Intensive forestry often includes plantations, where using genetically improved trees can further increase productivity per unit of land (Zobel and Talbert 1984).

Trees can be genetically improved in much the same way as agricultural crop plants. Individuals with desirable characteristics are selected and crossed with one another, followed by field tests of their offspring, some of which should exhibit further improvement of selected traits. Additional breeding, testing, and selection over several generations can increase genetic gain even further. However, unlike annual crop plants, trees often have a juvenile period of 5 to 20 years prior to the onset of flowering, and reselection of their progeny for genetic gain in important traits such as wood production may only be possible at rotation age, which may be 25 years or more.

To accelerate the process of tree breeding, techniques have been under development to accelerate growth, stimulate early flowering, and accelerate progeny testing (Bonnet-Masimbert 1987; Hanover 1980; Lambeth 1980; Lambeth and Greenwood 1987; Paques 1989).

Interest in planting larches (*Larix* Mill.) has been increasing. Larch wood is comparable in fiber length and superior in specific gravity to that of spruces (*Picea* L.) as well as being decay resistant. The trait that evokes the greatest interest in larches as plantation species, however, is their rapid early growth rate. In northern forests (with the possible exception of Northwestern North America), larches will outgrow all other conifers over rotations of 30 years, in some cases reaching a height of 14 m in 16 years (Mroz and others 1988). Because there is considerable variability in growth and form within larch species, prospects for genetic gain through tree improvement efforts are good.

AN ACCELERATED BREEDING PROGRAM FOR LARCH

The limited amount of work on improving larch has largely taken place in arboreta or seed orchards, mostly focusing on European larch (*Larix decidua* Mill.), Japanese larch (*L. leptolepis* Gord.), and their hybrid (*L.* x *eurolepis* Henry). More recently, programs to improve tamarack (*L. laricina* [DuRoi] K. Koch) and western larch (*L. occidentalis* Nutt.) have been instigated (Ross 1990; Simpson 1983).

Drs. Michael S. Greenwood and Katherine K. Carter began an accelerated breeding and testing program for larch at the University of Maine in 1987. The objective was to set up a program for demonstration and research in accelerated tree breeding, and in the process, to create families of tamarack, exotic larches, and hybrids with improved volume growth and stem straightness.

Selection of the Parental Population

A parental population of six clones each of tamarack, Japanese larch, and European larch were selected in 1986. The tamaracks were plus-trees identified in forest stands in central Maine. The European and Japanese larch selections were based on measurements in provenance tests in Maine (Carter and others 1981), New Hampshire, and Iowa. The European larch selections were all Polish in origin. Selections were made on the basis of superior height and straightness. Scions from the select trees were grafted onto tamarack and Japanese larch rootstock in early 1987.

Accelerated Growth

The grafts were initially grown in peat-vermiculite-sand (2:1:1) in 12-L plastic pots, then transferred to 60-L pots in January 1989. Time-release fertilizer (9 month Osmocote 18-7-10 at 8 g/L) was incorporated into the potting medium in 1988, 1989, and 1990 at the beginning of each growing season. In 1990 and 1991, liquid fertilizer (Peters 20-20-20 at 100 ppm N) was applied weekly during the summer. Foliar samples were taken on a regular basis, two to three times per growing season, and analyzed for mineral nutrient

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content. Fertilization schedules were adjusted and trace elements (Peters Professional soluble trace element mix at 0.6 g/L) applied if needed. Watering was done as needed using a drip-irrigation system, usually every 2 to 4 days during the summer.

The greenhouse in which the grafts were grown was constructed of corrugated fiber glass, 29 m long, 10 m wide, and 5 m high in the center. The greenhouse was kept above freezing during the winters of 1987 through 1990, but not heated during the winters of 1990 and 1991, 1991 and 1992. This change had no apparent effect on tree survival, pollen viability, timing of bud-break, or growth of the larch. However, the greenhouse was kept from freezing once buds started to swell, around the middle of February each year. Thus, the greenhouse growing season lasted from bud burst in early March to the end of October when the larches set bud and shed their foliage. Summer temperatures were quite high, with mean daily maxima at crown-top level averaging 27, 30, 32, and 30 °C, May through August, and occasional peaks of over 40 °C.

The larch grafts responded to the plentiful water and fertilizer and the long, warm growing season with terminal growth of up to 2 m per year, so that by the end of their second growing season, many had to be top pruned at a height of 3.5 m because of height constraints in the greenhouse. Top pruning is recommended at least once each year to increase branchiness for flowering.

Flower Induction

From 1989 to 1992, six flower stimulation experiments were carried out in the indoor larch breeding orchard, including foliar spraying and stem injection of the plant growth regulator gibberellin ($GA_{4/7}$), root pruning, drought, and girdling. The objectives were to (1) compare responses of the three species to treatments intended to stimulate flowering, (2) optimize treatments, and (3) induce flowering for breeding purposes.

Flowering response to $GA_{4/7}$ foliar spray treatments of various timing and duration was tested. Starting time of treatments ranged from just after short shoot bud burst (early March in the greenhouse) to 1 month after the start of long shoot extension (mid-May). Duration ranged from one to 10 weekly applications, and as many as nine biweekly applications lasting from May to September. The $GA_{4/7}$ solution used for foliar spraying was constant; 200 mg/L $GA_{4/7}$, 88 percent active ingredient, in 5 percent ethanol with 0.2 mL/L Aromox C/12 w added as a surfactant. The control solution was the same minus $GA_{4/7}$. Single stem injections of 50 or 100 mg $GA_{4/7}$ per tree in 5 or 10 mL of 95 percent ethanol were also tested.

The results of experiments in flower stimulation were analyzed using analysis of variance (ANOVA). The ANOVA's are not presented here, but can be found in the primary author's Ph.D. degree dissertation (Eysteinsson 1992).

Drought, root pruning, and branch girdling were applied as adjunct treatments along with the $GA_{4/7}$ in some of the experiments. Periodic severe drought stress during early summer did not increase flowering by any of the three species. Branch girdling appeared to enhance flowering in both European and Japanese larch, but the effect was not statistically significant. The effect of root pruning on flowering was inconsistent; sometimes increasing flowering overall, sometimes increasing flowering only on GA-treated branches, sometimes having no effect.

Tamarack—The most obvious outcome of these experiments was the consistently good flowering response by tamarack to $GA_{4/7}$ foliar sprays. Also, few applications were clearly sufficient to obtain the maximum flowering response, while long-duration treatments did not improve flowering. The optimum time for $GA_{4/7}$ application was during the month immediately following the start of long shoot extension; applications prior to the start of long shoot extension were less effective, as were applications starting 4 weeks after the start of extension (Eysteinsson and Greenwood 1990).

Root pruning enhanced male flowering and root pruning plus drought retarded female flowering slightly on $GA_{4/7}$-treated branches of tamarack. On the whole, grafts, root pruning, and drought led to reduced flowering of both sexes. Thus, $GA_{4/7}$ stimulates flowering by tamarack, and the near optimum growth conditions and occasional temperature stress in the greenhouse probably enhance flowering, but additional stress treatments are not required.

Although there were clonal differences in fecundity, all six tamarack clones included in these studies responded to $GA_{4/7}$ with increased flowering.

Japanese Larch—Japanese larch responded to $GA_{4/7}$ foliar sprays with increased pollen, but not seed cone production, and to stem injection with increased flowering of both sexes. Girdling seemed to enhance flowering, but there was no evidence that root pruning or drought, as applied here, affected flowering by Japanese larch. These results are consistent with other studies on flower promotion in Japanese larch (Bonnet-Masimbert 1982; Katsuta and others 1981; Mikami and others 1979).

Fecundity among the six Japanese larch clones varied greatly. In 1990 and 1991, the more fecund clones responded to $GA_{4/7}$ foliar sprays with increased male flowering while the less fecund clones showed little or no response. In 1992, flowering of both sexes was increased by $GA_{4/7}$ stem injection in five of the six clones.

European Larch—European larch never responded significantly to $GA_{4/7}$ foliar sprays, but stem injection, on the other hand, resulted in increased cone production by all four clones treated. Root pruning also significantly promoted female flowering.

The variation in fecundity among European larch clones was greater than for the other two species, ranging from 59 pollen cones and 13 seed cones (total on five ramets of clone LD-4-80) to over 19,200 pollen cones and 400 seed cones (clone LD-1-80) in 1991.

There is no obvious explanation for why tamarack responded better to $GA_{4/7}$ foliar sprays than the other two species. There may be differences in the thickness or structure of needle cuticles, which could affect uptake. In any case, a single stem injection applied around the start of long shoot extension is effective and easier to apply than foliar sprays and is recommended for seed cone induction in all three species.

The greenhouse conditions (heat, long summer, plentiful fertilizer) were themselves flower stimulation treatments, and they resulted in sufficient pollen production by all three species, although the $GA_{4/7}$-induced increase in pollen cone production made a considerable difference in breeding in 1990.

In conclusion, the greenhouse environment plus flower stimulation treatments led to sufficient flowering to make over 120 crosses between 16 clones in 1990 and 1991. However, more research is needed on methods to stimulate female flowering by European and Japanese larch, especially on mature, less fecund clones, which may nevertheless be of interest for breeding and seed production.

Controlled Mating and Seed Production

The reproductive process in *Larix* has been thoroughly described (Barner and Christiansen 1960; Kosinski 1986; Owens and Molder 1979; Said and others 1991; Villar and others 1984), and we found no major departures from these descriptions in our indoor-grown trees.

Because we wished to stress production of hybrids, paired matings were used to generate full-sib families. The limited number of clones and differences in fecundity and in sex expression made it impossible to perform full diallels. Therefore, the strategy was to make as many crosses as possible with emphasis on (1) making complete half-diallels within species (as far as was possible), (2) making as many hybrid crosses as possible, (3) making reciprocal hybrid crosses, and (4) creating families large enough for progeny testing.

Seed viability after open pollination or controlled crossing in larch is notoriously poor in established seed orchards and natural stands alike, typically ranging from 10 to 40 percent (Greenwood and Eysteinsson 1989; Hall 1985; Kosinski 1987). The ability to identify the cone's peak of receptivity and one-time application of pollen directly to the cone are probably most important in obtaining reasonable seed viability while conserving limited supplies of pollen (Bramlett and O'Gwynn 1981).

Pollen must also be sufficiently viable to ensure good seed set. Kosinski (1987) identified four factors that lead to decreased seed viability in larch: (1) female gametophyte degeneration, (2) embryo abortion, (3) lack of pollination due to insufficient quantities of pollen being present at the time of receptivity, and (4) failure of fertilization due mostly to nonviable pollen. To maximize seed viability, we placed emphasis on the success of pollination using fresh, viable pollen because we had limited control over gametophyte degeneration and embryo abortion.

Flowering occurred over 1 month from late February to late March, ending approximately 1 month prior to the onset of flowering on larch outdoors. Some European and Japanese larch clones produced copious quantities of pollen cones but relatively few seed cones. Tamarack produced many more seed cones (largely the result of $GA_{4/7}$ treatments), but pollen was always in short supply due to the low number and small size of tamarack pollen cones. The orchard produced a total of 3,317 seed cones and 53,545 pollen cones on 70 grafts in 1991.

Pollen was collected daily as it shed into folded paper "boats" suspended directly under pollen cone-bearing branches. Pollination was accomplished using a #2 camel's-hair brush when each seed cone was deemed to be at peak receptivity based on the number of days from bud burst and on visual observation. In the greenhouse, this turned out to be about 10 days, or roughly 850 degree hours based on a threshold of 5 °C for all three species, and did not vary much between years.

Only fresh pollen was used in these studies. Pollen viability was tested in vitro by rehydration for 24 hours (on a microscope slide in a closed Petri dish with wet filter paper) followed by 4 to 6 hours in a hanging drop of distilled water. This treatment resulted in swelling, elongation, and the appearance of clearly visible cellular structures (nuclei) in live pollen grains. Larch pollen does not form pollen tubes in vitro (Ho and Rouse 1970; Said and others 1991).

Pollen viability tests revealed that fresh pollen allowed to shed naturally in the greenhouse was generally highly viable, although it varied from 60 to 98 percent. However, one Japanese larch clone was apparently sterile, producing pollen cones but not shedding pollen, and one European larch clone shed little pollen, and of low viability, from each pollen cone. Pollen maintained its viability over at least 1 month of dry storage at room temperature and at least 1 year when stored dry in a refrigerator at 4 °C.

Ovule dissection revealed that pollination was consistently effective, with more than 93 percent of ovules in pollinated cones receiving pollen. As noted during dissection after fertilization, when seeds had reached their final size, seeds in which the female gametophyte failed to develop were small, flat, and easily detectable (see Barner and Christiansen 1960). Female gametophyte failure averaged 7, 11, and 29 percent for European larch, Japanese larch, and tamarack, respectively. Full-size seeds that failed to germinate contained a shriveled gametophyte or embryo and were the result of either pollination/fertilization failure or embryo abortion.

In all, 121 crosses were made in the breeding orchard in 1990 and 1991, with viability averaging from 41 to 57 percent for intraspecies and European x Japanese larch hybrid crosses. A tamarack cross yielded the highest viability—82 percent. Tamarack (female) x European larch (male) hybrid crosses yielded 18 percent seed viability, but their reciprocals (that is, using tamarack as the pollen donor) largely failed. Tamarack and Japanese larch are almost incompatible, yielding less than 1 percent seed viability.

The difficulty of interspecific hybridization between tamarack on the one hand and European and Japanese larch on the other has been reported previously (Paques 1992). This incompatibility is genetic and not mechanical in nature because, in the present study, pollen was engulfed into the ovule and fertilization took place in the same manner for all crosses. However, it is interesting that using tamarack as the seed parent results in better seed viability, especially for the tamarack x European larch cross.

Seed viability from the greenhouse crosses compared favorably with published results of outdoor larch breeding where average viability was usually less than 30 percent (Hall 1985; Kosinski 1987; Villar and others 1984). Considering these results, the plausibility of indoor seed production orchards of larch should be investigated, especially for the production of European x Japanese larch hybrid seed, which is in great demand and expensive.

ACCELERATED PROGENY TESTING

Research into accelerated growth, early flower induction, and seed production deals with only part of accelerating the tree breeding process. Research into acceleration of progeny testing is equally important in maximizing gains from tree improvement efforts. Establishing progeny test plantations, including eight larch species and hybrids, will result in opportunities for research in early selection and accelerated progeny testing while providing information on genetic, physiological, and phenological differences between and within the species and hybrids. Traditional field progeny tests are the necessary controls against which attempts at accelerated progeny testing will be measured.

A progeny test consisting of 50 families from the indoor breeding orchard was planted in a clearcut in Johnson Mountain Township, ME, in May 1992. The test is a traditional progeny test in the sense that it was set up for long-term testing of families, was planted on a site typical of where larch plantations might be established, and can, therefore, provide information directly applicable to plantation forestry. It differs from other progeny tests in that it includes three species and five hybrids (including reciprocals).

Finally, because the parental population was made up of select individuals, there is every reason to expect that at least some families will exhibit improved growth and form traits. Therefore, the progeny test could be used to identify individuals for inclusion in seed orchards and advance generation breeding.

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Provenance Selection and Stem Volume Production of Tamarack (*Larix laricina* [DuRoi] R. Koch) in Sweden

Owe Martinsson

Abstract—Six field trials of *Larix laricina* including 5 to 55 provenances on each locality were evaluated 17 to 21 years after establishment. For optimal production in southern Sweden, provenances should be transferred 6 to 7 degrees of latitude north of their origin. Seed sources to be used in northern Sweden should originate from high elevation. In suitable sites the stem volume production of *L. laricina* may reach 90 to 100 m³/ha during the first 20 years.

Tamarack was originally the common name for all three species of the genus *Larix* growing on the North American continent. The European immigrants have exclusively used the name tamarack for *Larix laricina* (DuRoi) R. Koch. This tree species has a natural distribution within the boreal forests all over the North American continent. However, large areas in British Columbia and the Yukon have no tamarack. The natural habitats of tamarack are bogs or other wet lands or land covered with a peat layer. It usually does not form pure stands but grows in mixture with black spruce, willows, and poplars. In the eastern parts of its area of distribution, tamarack can also associate with white cedar, red maple, eastern white pine, and black ash.

Traditionally tamarack was used for fence material in farms. In large-scale forestry tamarack was for a long time regarded as a noncommercial species in North America. Not until the middle of this century was it discovered that tamarack is among the most fast-growing boreal conifers (Johnstone 1973; MacGillivray 1968; Mead 1978). Research on breeding of tamarack was initiated by Park and Fowler (1982) and Simpson (1983).

Tamarack was introduced into Sweden already at the end of the 1800's (Schotte 1917). This species attracted attention because of its fast juvenile growth and the great tolerance to wet, swampy soils where it is difficult to grow any other tree species. The first provenance trial in Sweden was established in 1958 (Ahlberg and Johansson 1984). In 1968 the Royal Swedish College of Forestry started a breeding program for tamarack (Simak 1979). From 1968 to 1974, field trials were established in 10 localities throughout Sweden (Simak and Jeansson 1987). This report is based on data collected in six of these trials.

The objectives of this study are to determine rate of survival, height growth, stem volume production, and stem quality. Based on this information, recommendations for optimal choice of provenances are given.

MATERIALS AND METHODS

Basic data of tree height, diameter at breast height, survival, and stem quality were collected from six field trials listed in table 1.

The experiments 1904 Jonstorpsmossen and 1907 Storänget are both at Remningstorp, east of Skara in Västergötland. 1886 Skallsjön and 1887 Hedmark are in central Norrland, and 1888 Kärleksallen and 1889 Svevekull are in the most southern part of Sweden.

Experimental design, number of provenances, date of establishment and revision are given in tables 2 and 3. Provenances used in the six experiments are listed in tables 4 and 5. The origins of provenances used in experiments 1904 and 1907 are also shown in figure 1.

Table 1—Name, locality, and soil type of experimental sites

Experiment number and local name	Latitude north	Longitude east	Altitude	Soil
			m	
1904 Jonstorpsmossen	58 28	13 36	115	Poor peat
1907 Storänget	58 28	13 37	125	Rich peat
1886 Skallsjön	63 29	15 47	465	Silt
1887 Hedmark	64 46	17 53	470	Morain
1888 Kärleksallen	55 35	14 12	70	Morain
1889 Svevekull	55 35	14 10	55	Rich peat

Table 2—Experimental design and total area of experiments

Experiment number	Plot size	Number of provenances	Number of replications	Spacing	Total
				m	*ha*
1904	1-tree	55	40	1.5x2	0.90
1907	1-tree	45	30	1.5x2	0.45
1886	4x4-tree	16	6	2x2	0.61
1887	4x4-tree	23	6	2x2	0.88
1888	5x6-tree	17	6(12)	1.5x1.5	0.50
1889	6x6-tree	5	6(12)	1.5x1.5	0.40

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Table 3—Date of establishment and revision

Experiment number	Established	Revision
1904	1974, spring	1990, autumn
1907	1974, spring	1991, autumn
1886	1967, spring	1987, autumn
1887	1967, spring	1987, autumn
1888	1968, spring	1988, spring
1889	1968, spring	1988, autumn

Tree height and diameter at breast height were recorded from all surviving trees in five of the six experiments. In 1987 Hedmark only the two most vigorous provenances were recorded. In experiments 1907 and 1886 the stem straightness was also classified according to a 4-degree scale: 1 = completely straight, 2 = some small stem crooks, 3 = very windy stem, 4 = long sweep of stem. In these trials as well as in 1889 Svevekull a first thinning was also done. In experiments 1907 Storänget and 1889 Svevekull the total stem volume and the dominant height were calculated before and after the thinning. The function used for stem volume was developed for *Larix decidua* by Carbonnier (1954):

$$V = 0.04801d^2{*}h + 0.08886d^2 - 0.01012d^3 - 0.08406d{*}h + 0.1972h$$

where:

V = Stem volume in dm³ above stump including bark
h = Tree height above ground, m
d = Diameter at breast height including bark, cm.

Each provenance's rate of survival and productivity were calculated. Productivity was defined as:

(Number of surviving trees/Number of planted trees) * mean tree height.

For the two experiments, 1904 and 1907, a multiple regression analysis was carried out using mean height or productivity as dependent variables and latitude, longitude, and elevation as explaining variables.

RESULTS AND DISCUSSION

The mean tree height of provenances is illustrated in figure 2A-E for all trials except 1887 Hedmark. The same figure also indicates the productivity.

Provenance Selection

1904 Jonstorpsmossen and 1907 Storänget—The provenances listed in table 4 were planted in two trials, 1904 and 1907, close to each other in south-central Sweden. The growth habitats of the two sites are different. Plot 1904 is a poor sphagnum bog, while 1907 is a rich fen, formerly used for agriculture.

The mean height and productivity of provenances tested in trial plots 1904 and 1907 are illustrated in figure 2A,B. A great variation among seed sources in these characteristics can be observed, also among provenances originating from the same area. In the regression analysis of experiments 1904 and 1907 using latitude, longitude, and elevation as explaining variables for mean tree height and productivity, I found that these variables have a significant influence. The strongest influence on mean tree height and productivity of provenances was $(La)^2$. The regression functions achieved for mean tree height and productivity are:

$$H4 = -193.3154 + 10.44074(La) - 0.02603(Lo) + 0.01306(E) - 0.1082193(L)^2;$$
$$r = 0.65, F = 7.24$$

$$H7 = -123.4832 + 9.93708(La) + 0.13189(Lo) + 0.00170(E) - 0.1099069(La)^2;$$
$$r = 0.51, F = 2.24$$

$$P4 = -377.0236 + 15.94651(La) - 0.15757(Lo) + 0.01084(E) - 0.1486001(La)^2;$$
$$r = 0.39, F = 6.36$$

$$P7 = -865.4722 + 34.69354(La) + 0.11599(Lo) - 0.01389(E) - 0.3318159(La)^2;$$
$$r = 0.38, F = 1.08$$

where:

$H4$ = mean tree height of provenances in experiment 1904, dm
$H7$ = mean tree height of provenances in experiment 1907, dm
$P4$ = mean productivity of provenances in experiment 1904, dm*%
$P7$ = mean productivity of provenances in experiment 1907, dm*%
La = Latitude of origin, degree N.
Lo = Longitude of origin, degree W.
E = Elevation of origin, m above see level.

Figure 3 shows the mean tree height and the productivity of provenances in relation to latitude of origin (La). In this figure the seed sources' longitude and elevation of origin are not considered. Best choices of provenances for maximum productivity in Remningstorp, that is, 1904 Jonstorpsmossen and 1907 Storänget, are those provenances originating from latitude north 53-54, which means a maximum transfer of 6 to 7 degrees to the north. Compared to Simak and Jeansson (1987), who recommended a transfer of 7 to 8 degrees north of the origin of seed source, this result indicates a shorter distance of transfer. The regression analysis indicates that the productivity of experiment site 1904 is favored by high-elevation seed sources, while the experimental site 1907 is favored by low-elevation seed sources.

1888 Kärleksallen and 1889 Svevekull—Mean tree height and productivity of the two trials 1889 and 1888 are shown in figures 2C,D. These two trials are in the southernmost part of Sweden only 2 km apart. However, the local habitats of the two trials are different. Experiment 1889 is in a fen and former farm land with a 0.5-m-thick peat layer and 1888 in a dry slope with mineral soil at the surface. In experiment 1889 the mean tree height

Table 4—Seed sources used in experiments 1904 Jonstorpsmossen and 1907 Storänget

Provenance number	State or Province	County	Latitude north	Longitude west	Altitude
					m
1	Alaska	Tanana River	65 00	147 30	150
2	Northwest Territory	—	58 58	111 40	229
3	Alberta	Waterways	56 39	111 14	335
4	British Columbia	Fort S.t John	56 38	120 35	732
5	Saskatchewan	Buffalo Narrows	56 05	108 55	427
6	Manitoba	The Pas	53 55	101 15	260
7	Saskatchewan	Meadow Lake	53 50	108 40	640
8	Alberta	—	51 00	101 00	740
9	Manitoba	Winnipeg	50 05	95 25	229
10	Ontario	Gurney Twp	49 30	82 14	213
11	Quebec	Chagel	48 55	79 03	290
12	Quebec	Preissac	40 30	78 15	—
13	Quebec	Roberval	48 26	72 16	336
14	Quebec	Roberval	48 26	72 16	—
15	Michigan	Isle Royale	48 05	88 42	186 **
16	Minnesota	St. Louis	48 02	91 37	397 **
17	Quebec	Preissac	48 01	78 17	321
18	Quebec	Guerin	47 45	79 20	—
19	Quebec	Lake Lortie	47 40	74 15	—
20	Quebec	Seign Malbaie	47 40	70 20	244
21	Quebec	Cabano	47 39	68 57	
22	Quebec	Cabano	47 39	68 57	244
23	Minnesota	Itasca	47 31	94 05	396
24	Quebec	La Malbaie	47 20	70 20	—
26	Michigan	Houghton	47 01	88 25	201
27	Minnesota	St. Louis	47 00	93 00	387 *
28	Quebec	Radnor	46 45	72 50	—
29	Minnesota	Carlton	46 42	92 31	335 **
30	Nova Scotia	Chignecto	46 35	64 25	80
31	Quebec	Langevin	46 21	70 22	—
32	Michigan	Alger	46 21	86 20	244 **
33	Michigan	Alger	46 20	86 20	244 **
34	Michigan	Alger	46 20	86 20	244
35	Michigan	Chippewa	46 19	84 14	183 *
36	Michigan	Cogebic	46 15	89 10	488
37	Quebec	Berthier Parta	46 15	73 15	—
38	Quebec	Lake Chertsey	46 11	73 52	—
39	Nova Scotia	Beddec	46 07	59 45	30
40	New Brunswick	Acadia Forest	46 00	66 29	98
41	Ontario	—	46 00	77 26	146 **
43	Wisconsin	Oneida	45 46	89 12	366
44	Maine	Somerset	45 38	70 16	362
45	Minnesota	Anoka	45 10	93 05	244
46	Vermont	Franklin	44 57	73 05	70
47	Nova Scotia	Annapolis	44 48	65 03	229
49	Vermont	Lamoille	44 30	72 37	229
50	Maine	Mt. Desart Island	44 30	68 00	30 **
51	Michigan	Wexford	44 15	85 31	393
55	Wisconsin	Lacrosse	43 51	91 08	206
56	Ontario	Oxford	43 13	80 35	297
57	Michigan	Livingstone	42 30	83 30	274 **
59	Michigan	Livingstone	42 29	84 20	244 **
64	Michigan	Kalamazoo	42 23	85 22	256 **
66	Pennsylvania	Lackawanna	41 15	75 39	598 **
67	Maryland	Garrett	39 42	78 56	820 **
68	Maryland	Garrett	39 42	78 56	820 **
69	British Columbia	—	—	—	—

* Not planted in 1904 Jonstorpsmossen.
** Not planted in 1907 Storänget.

Table 5—Provenances included in the field trials 1886 Skallsjön, 1887 Hedmark, 1888 Kärleksallen, and 1889 Svevekull

Provenance number	Local name	Latitude north	Longitude	Altitude	
				m	
	Larix laricina				
1	Barry Bay	45 30	77 45		* #
2	Bancraft, ON	45 00	78 00	—	* #
3	Douglas	45 30	77 00		*
6	Powassan	46 00	79 15		*
7	Soundridge	45 45	79 15		* #
8	Watt Lake	49 10	81 04	360	* + #
9	Port Arthur	48 27	89 18	420	* #
10	Dog River	48 58	89 55	400	* + # =
11	Clute Twp	49 10	81 04	800	* + # =
12	Sutton Lake	53 38	84 40	1,500	* + #
14	Ely, MN	47 53	91 51	400	* + # =
16	Site reg, ON	46 30	84 20	—	* + # =
17	SCA (local Swedish seed source unknown origin)				+ =
	Larix decidua				
5	Stilfser Tal	47 00	10 00	800-1,200	* + #
17	Pragelato			1,700	*
44	Krnov	50 05	17 40	650	* + #
55	Blizyn	51 06	20 45	360	*
58	Nödebo	56 00	12 00	40	* + #
61	Schlitz	50 40	9 35	350	* + #
84	Ipoltica	49 00	20 00	800	* + #
85	Brezovicka	49 07	20 50	830	* + #
87	Strbske Pleso	49 07	20 05	1,370	* + #
115	Krvavec	46 18	14 30	—	* + #
	Larix gmelinii				
1	Shansi Pr				*
2	Unknown seed source				* + #
4	Ugkgorsk	50 44	142 42	270	* #
6	Unknown seed source				+
	Larix sibirica				
61	Verchkatunskoje			1,900	* #
	Larix sukaczewii				
29	Shenkursk	62	43	45	* #
62	Utjaly Basjkirija-		—		* #
63	Onega	63 57	38 11		* #
	Larix occidentalis				
4	Cranbrook	49 35	115 50	900	*

* Provenance present in 1886 Skallsjön.
+ Provenance present in 1888 Kärleksallen.
# Provenance present in 1887 Hedmark.
= Provenance present in 1889 Svevekull.

varies among provenances before thinning between 10.1 m (provenance 11) and 9.5 m (provenance 17). After thinning, the mean tree heights of the same provenances are 10.6 and 9.9 m. If only mean tree height and productivity are considered provenance 11, Clute Twp from western Ontario, is the best provenance in experiment 1889. The difference compared to the other four provenances is small but significant ($P = 0.01$). In experiment 1888, the mean tree height of provenances varied between 9.4 m (provenance 17) and 4.7 m (provenance 12). Provenance 8, Watt Lake (from the same area as 11), is the most productive, while provenance 11 has a lower rank in this dry site. Unfortunately, I have no information about the local habitat of these two seed sources other than geographic positions.

1886 Skallsjön and 1887 Hedmark—In the two northern experimental sites, 1886 and 1887, provenance 12, Sutton Lake at latitude north 53°38', longitude west 84°40', is the most productive. This is the northernmost seed source and it also originates from a high altitude (table 2).

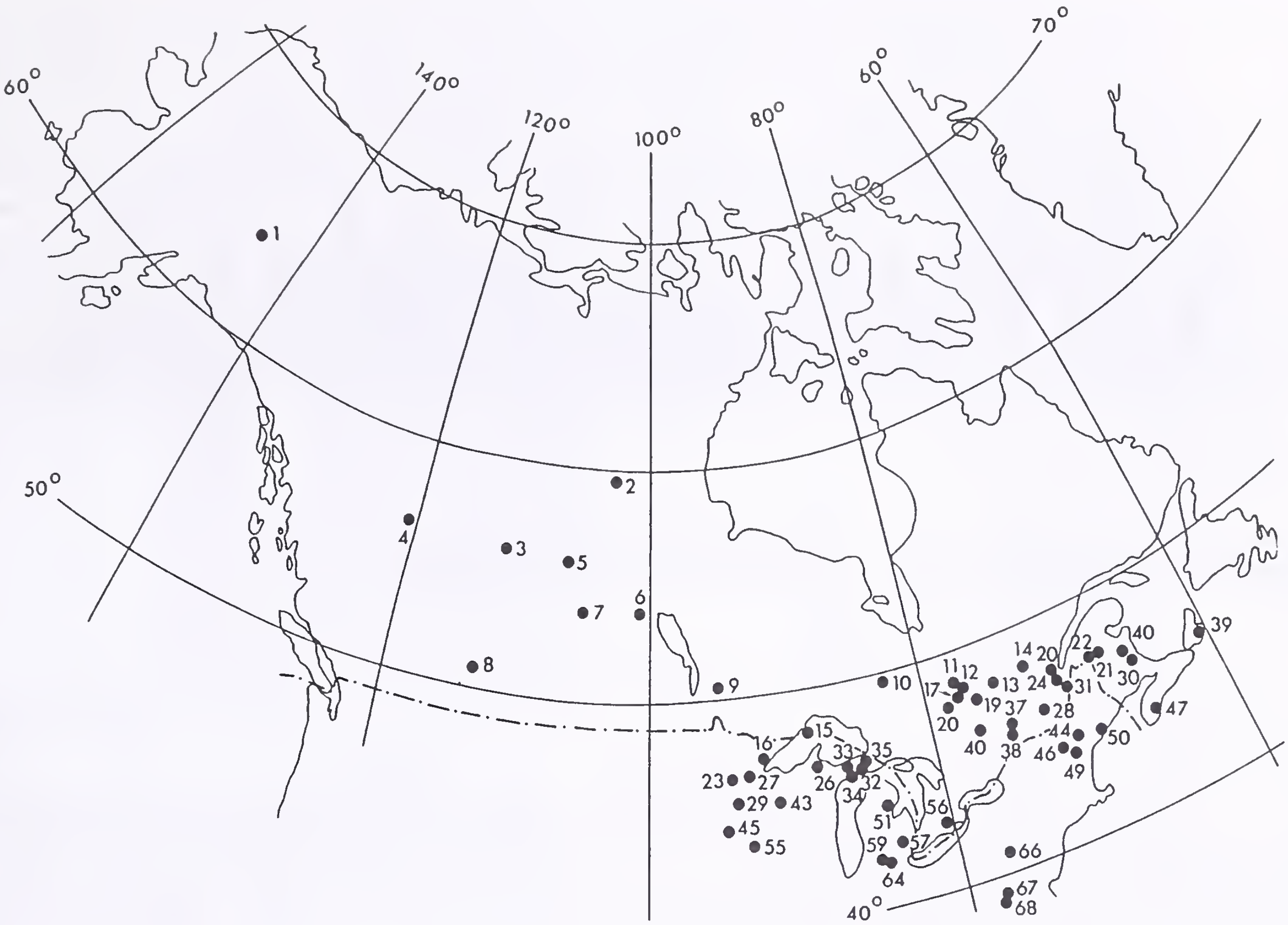


Figure 1—Origins of provenances used in experiments 1904 Jonstorpsmossen and 1907 Storänget, both in Remningstorp.

In experiment 1886 Skallsjön the highest productivity is to be found in provenances 11, 12, and 6, originating north of the Great Lakes in Ontario. The tallest provenance in 1886 Skallsjön, 12, reached the mean height of 5.73 m in 21 years, while the shortest mean tree height, 4.6 m, was to be found in provenance 16. The site index determined from Scots pine planted at the same occasion as the larch is H100 = T21, which corresponds to a dominant height of approximately 8 m at this age. Simak (1979) evaluated this experiment 6 years after establishment. The ranking of provenances was similar at that time.

Six of the provenances used in 1886 Skallsjön were also used in 1888 Kärleksallen (fig. 2C). However, the ranking order is different in the two localities. In the southern locality, 1888 Kärleksallen, provenance 12 is the most slow growing (mean tree height 4.65 m), while provenances 8, 14, 16, and 17 are better. Provenance 17 has the highest mean height, 9.45 m, and a dominant height of more than 13 m in experiment 1888 Kärleksallen. In 1889 Svevekull the mean tree heights and the productivities of these provenances are still higher.

In experiment 1887 Hedmark, only the two most productive provenances were measured: 1 and 12. The mean tree height of these two was 3.9 and 3.6 m 20 years after planting, while the local Scots pine was 3.7 m. The mortality of these two larch provenaces was 13 percent (provenance 1) and 23 percent (provenance 12), which is a good result. The mortality of the local Scots pine in Hedmark was 8 percent. However, provenance 12 suffers from bad stem form (minor stem crooks), and provenance 6 or 11 may be a better choice. It is remarkable that any provenance of tamarack that has moved more than 14 to 17 degrees of latitude to the north shows this growth and vigor.

Unfortunately, the small number of provenances planted on the northern sites does not make a regression analysis meaningful, using latitude, longitude, and elevation as variables. Among the 12 provenances of tamarack used in 1886 Skallsjön, some of the best producing, such as 6 and 11, were transferred 14 to 17 degrees to the north. The elevation of seed source seems to have a greater influence on growth and survival, moving the provenance into a harsh climate.

Stem Volume Production

Only two of the trials have an acceptable design and average size of tree for a calculation of stem volume production per hectare: experiments 1889 and 1907.

1889 Svevekull—Basic data of the material in experiment 1889 Svevekull before and after the thinning are given in table 6. Before the thinning the total stem number was 2,400 per hectare corresponding to an average mortality of 45 percent for the 20 years. There were no

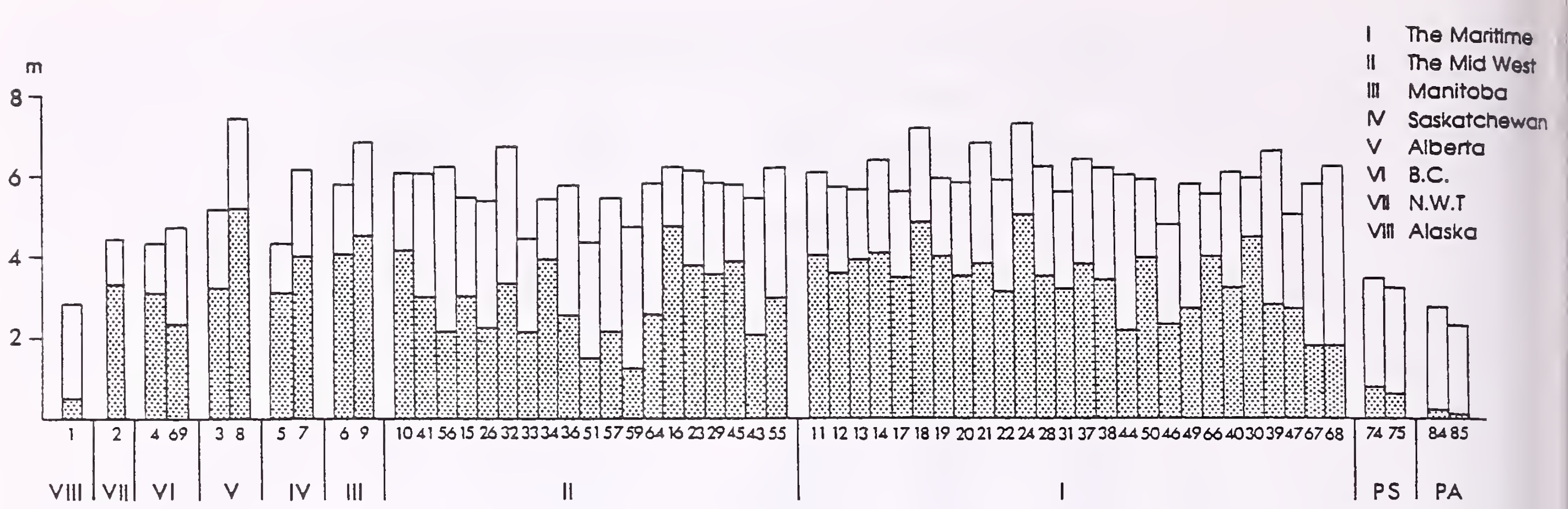


Figure 2A—Mean tree height and productivity (hatched part) of provenances in experiment 1904 Jonstorpsmossen 17 years after planting. PS = *Pinus sylvestris*, PA = *Picea abies*, local provenances.

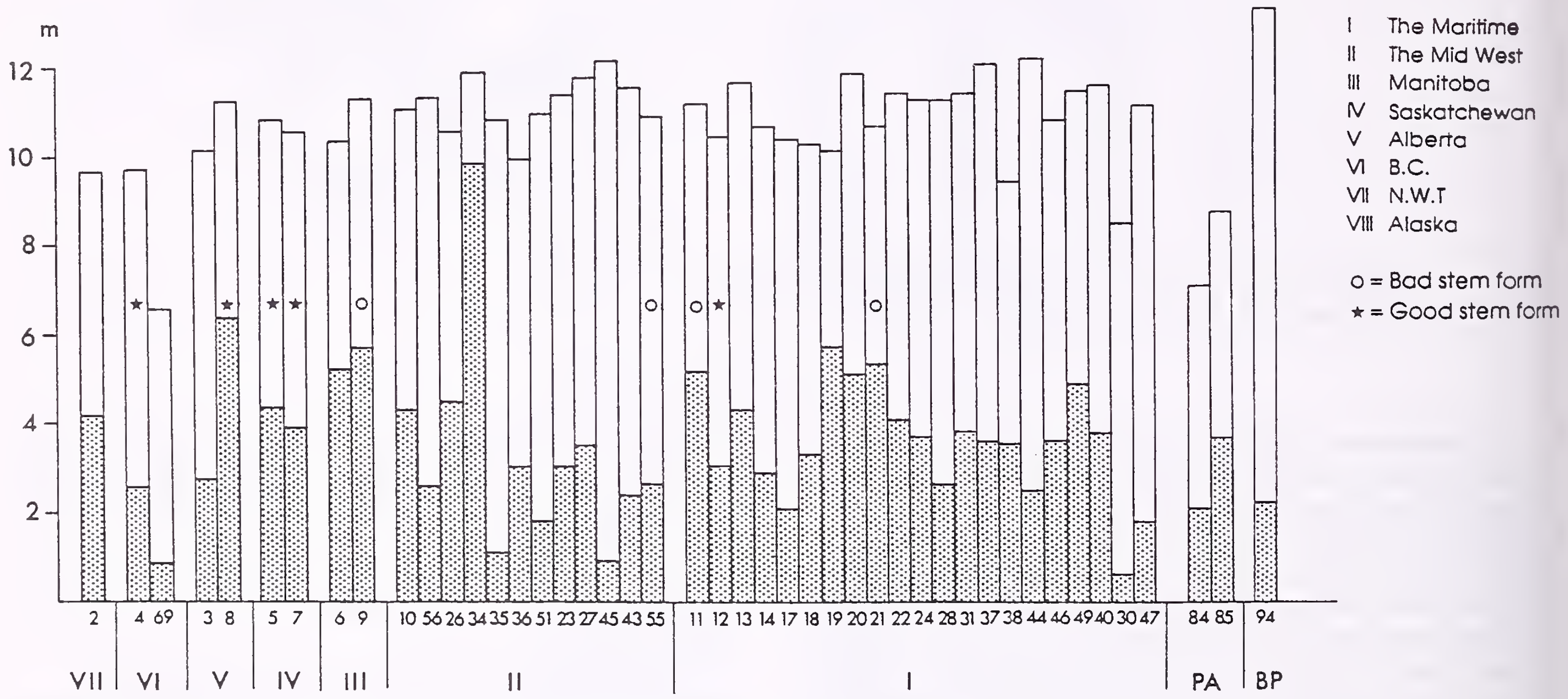


Figure 2B—Mean tree height, productivity (hatched part), and stem quality of provenances in experiment 1907 Storänget 18 years after planting. PA = *Picea abies*, BP = *Betula pendula*, local provenances.

significant differences in mortality between the provenances. After the thinning, 1,550 stems per hectare remained on the experimental area.

Before the thinning the total stem volume of the experimental area was 37.6 m^3, corresponding to a production of 96 m^3/ha. After thinning 29.5 m^3 was left corresponding to 76 m^3/ha. The four tallest trees of the experimental area had a mean of 13.1 m. Two of these four trees belonged to provenance 11, while the remaining two trees belonged to provenances 10 and 14.

1907 Storänget—The total number of stems in Storänget at the first thinning was 855, corresponding to 1,900 stems per hectare. The originally planted individuals were reduced by 43 percent during 18 years. Most of this mortality was caused by roe-deers and competition from vegetation. The total stem wood production 18 years after planting was 91 m^3 /ha. The mean height of the five tallest trees of the total trial was 13.9 m. The mean tree height of the tallest provenance, 44, Somerset, Main, was 12.3 m ± 1.6 m. However, seven other provenances had a mean tree height above 11.5 m, i.e. provenances no. 13, 20, 27, 37, 40, 43, and 45.

After thinning, the remaining number of stems was 1,000 per hectare. The total stem volume was reduced to 67 m^3/ha. The mean tree height of the total experiment

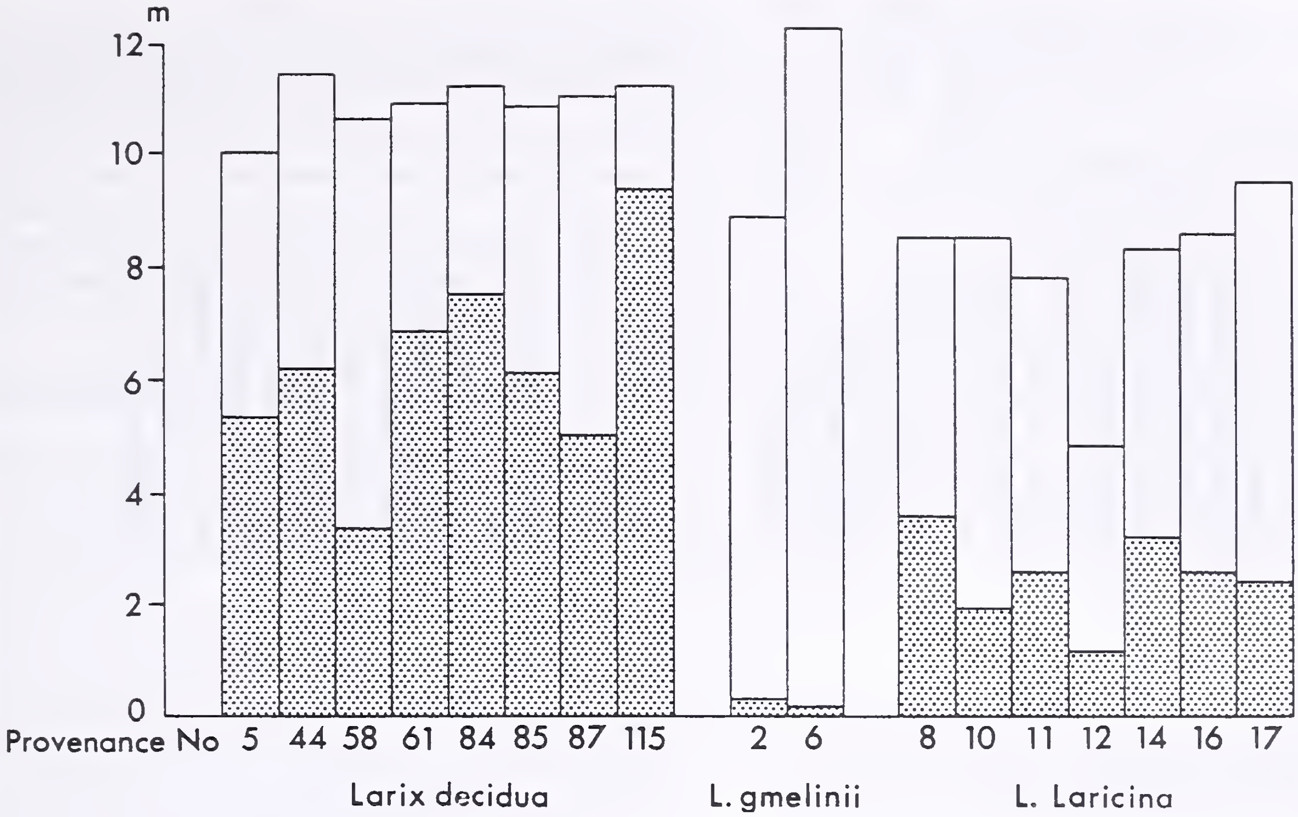


Figure 2C—Mean tree height and productivity (hatched part) of provenances in experiment 1888 Kärleksallen 20 years after planting.

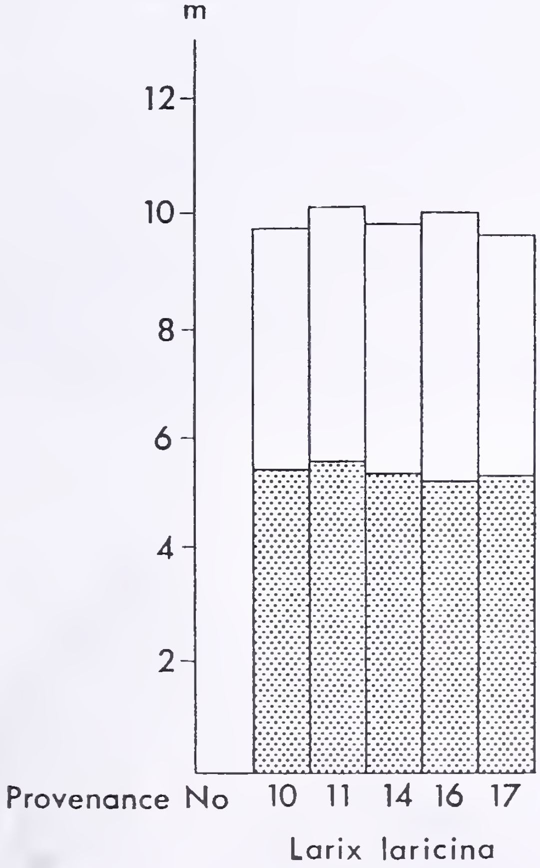


Figure 2D—Mean tree height and productivity (hatched part) of provenances in experiment 1889 Svevekull 20 years after planting.

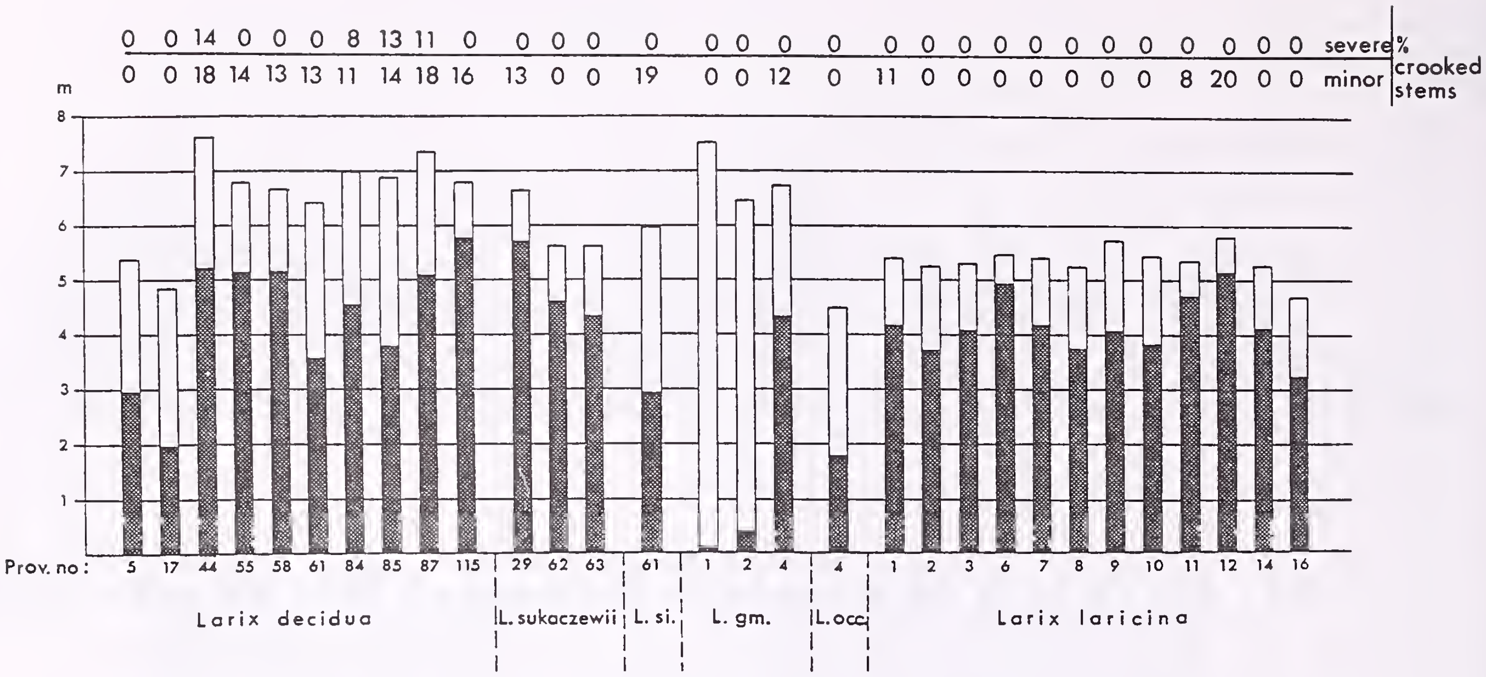
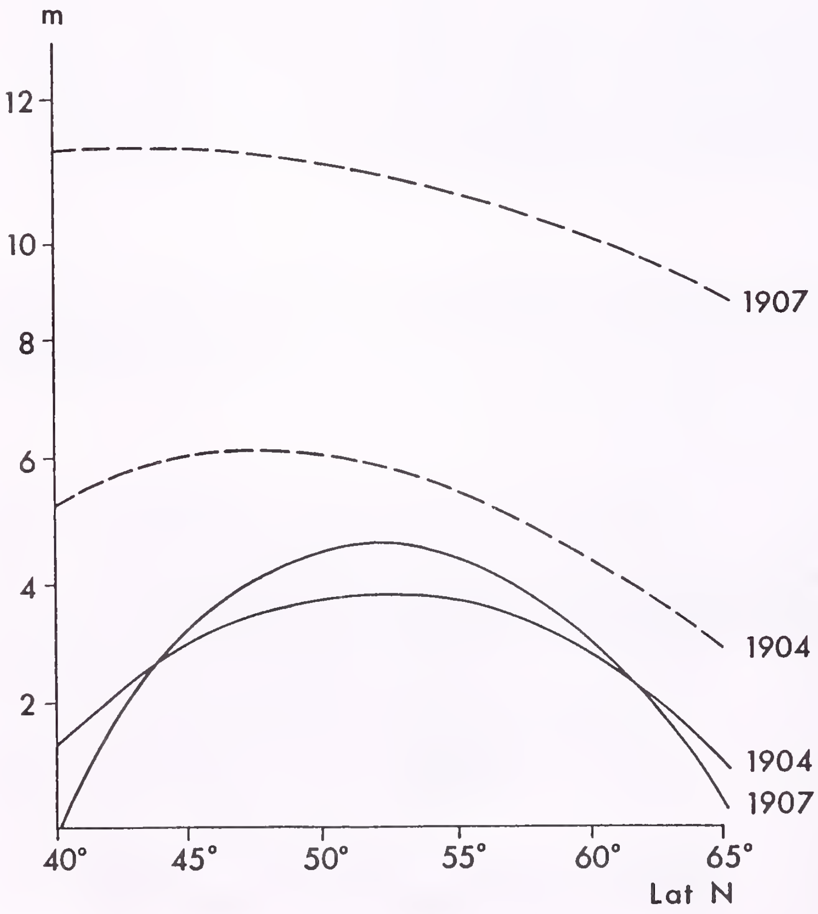


Figure 2E—Mean tree height, productivity (hatched part), and stem quality of provenances in experiment 1886 Skallsjön 21 years after planting.

increased from 5.6 to 10.6 m, and the mean diameter at breast height from 10.0 to 12.1 cm.

Figure 4 shows a picture of a cross section of a tree grown in experiment 1907 Storänget. The mean annual increment of stem diameter was 14 mm during the 10 last years, and the annual rings were even.



CONCLUSIONS

From this investigation I conclude that tamarack is a highly productive tree species on wet and fertile lands in Sweden.

To achieve optimal production in the southern part of Sweden the seed sources should not be transferred more

Figure 3—Mean tree height and productivity of provenances used in experiments 1904 and 1907 as a function of latitude of origin.

than 6 to 7 degrees of latitude to the north. In the northern part of the country and on sites with a harsh climate, provenances originating from a high elevation and northern latitudes should be preferred.

On suitable sites in southern Sweden tamarack can produce 90 to 100 m^3 of stem wood during the first 20 years and reach a dominant height of 14 m.

On wet sites with a good supply of nutrients, probably no other tree species growing in Sweden can demonstrate a higher capacity of wood production than tamarack.

Table 6—Basic data of the trees in experiment 1889 Svevekull, before (B) and after (A) thinning 20 years after establishment

Provenance number	Total trees B	Total trees A	Height B	Height A	Diameter at breast height B	Diameter at breast height A	Volume per tree B	Volume per tree A
			- - - *m* - - -		- - *mm* - - -		- - *dm³* - -	
10	122	75	9.7	10.4	95.7	111.2	39.7	51.9
11	238	159	10.1	10.7	98.5	109.4	42.6	52.0
14	232	148	9.8	10.4	99.7	109.8	42.2	51.0
16	229	142	9.9	10.5	97.9	108.8	40.7	49.6
17	121	78	9.5	9.9	84.4	94.3	28.8	35.1
Total	942	602						
Mean			9.9	10.4	96.5	107.6	39.9	49.0

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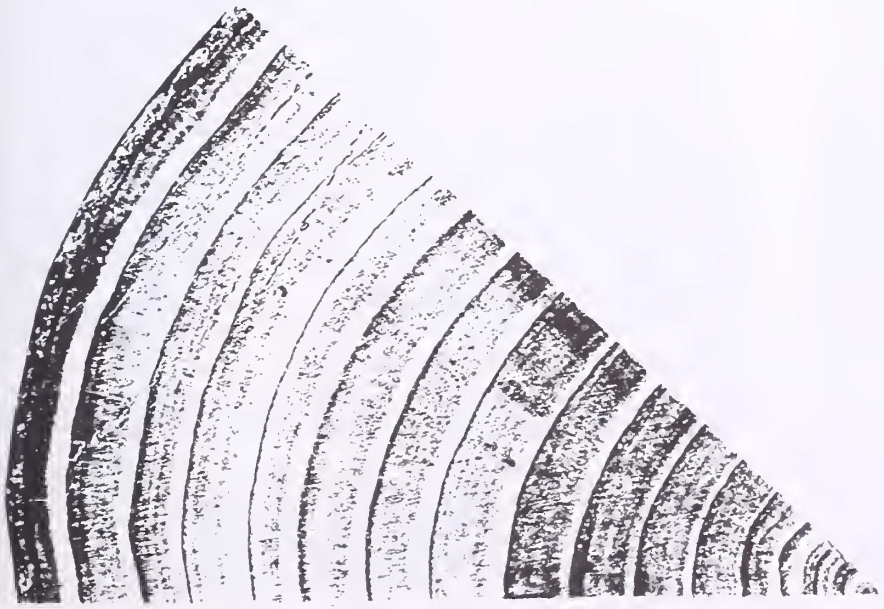

Figure 4—Cross section of a tamarack cut down in experiment 1907 Storänget.

Larch (*Larix decidua* Mill.) of Polish Provenances on Experimental Areas in Poland

Zenon Rzeźnik

Abstract—Larch grows in the mountains and lowlands of Poland in two subspecies: European larch, subsp. *decidua*, and Polish larch, subsp. *Polonica*/Racib./Domin. Due to their rapid growth rate, both species have great cultivational and economic importance. They have biological differences, and the origin of larch seeds influences the success and development of the cultivations. It is not advisable to collect seeds from some larch stands in Poland. The establishment of pure larch cultivations has proven economically justified in Poland. Within 35 years, one can obtain 400 m^3 per hectare.

Europe extends from the Atlantic Ocean as far as Ural Mountains. On this area, larch has its natural range of distribution. It occurs in the form of enclaves on several separate comparatively small areas. The greatest natural area of larch occurrence is the region in the north-eastern part of Europe being connected with the area of the natural occurrence of the Siberian larch (*Larix siberica* Ldb.) in Asia. This localization is comparatively far away from the European larch (*Larix decidua* Mill.) area occurring in Middle Europe. There exist several territories of larch occurrence in Middle Europe, they are: the Alps, Carpathian Mountains and Sudeten. The isolation of the particular ranges of distribution has lead to the creation of local varieties, sometimes described as independent taxons, even in the classification of species.

In Middle Europe, larch occurs as a mountain subalpine species, and in the north-eastern region of its occurrence, it is also found on the foreland of mountains and in the lowland. Poland lies in Middle Europe to the north of the Tatra Mountains. Poland extends 689 km from the West to the East, and 649 km is the length of the country from the North to the South. The total area of Poland covers 311,730 km^2.

In Poland, 50 percent of the land lies lower than 150 m elevation. The areas lying at the altitude from 150 to 300 m cover 41 percent, therefore 9 percent lie above 300 m elevation. From this number 6 percent lie at the altitude of 300 to 500 m, and only 3 percent are situated higher than 500 m elevation. In spite of the supremacy of low-land, the Polish landscape cannot be called lowland. It is not the absolute altitude but the relative altitude that is important. Altitude differences encountered on given areas sometimes exceed 100 m and even 200 m.

In Europe, there are two contrasting climatic types: the oceanic climate in the West, and the continental type in the East. The area of Poland lies in the contact zone of these two climates. The Polish climate is closely related to the geography and local relief of the terrain. A third climatic type is sometimes distinguished. It is the transitional climate which differs from the Atlantic zone by having snowy and frosty winters, and from the continental zone by its inclination to thaw which often destroys the whole snow cover.

Larch is considered a very variable species. In Poland, we distinguish two subspecies: *L. decidua*-subsp. *decidua* - the European larch (*L. decidua sensu stricto*), and *L. decidua*-subsp. *polonica* (Racib.) Domin - the Polish larch (*L. polonica* Racib.). The first of the mentioned subspecies is divided into separate varieties: The Sudeten population var. *sudetica* (Domin.) Svoboda, and the population from Tatra var. *adenocarpa* Borb. (=subsp. or var. *carpatica* Domin.). From the commercial point of view, the larches var. *sudetica* and subsp. *polonica L. decidua* subsp. *decidua* are important. Var. *sudetica* occurs mainly in the southwestern and western part of Poland. It includes the following regions: Kotlina Klodzka, Sudeten and Wyżyna Sląska. *L. decidua* subsp. *polonica* occurs in southeastern and eastern regions of Poland. The center of Polish larch occurrence is in Wyżyna Malopolska, in the Swiętokrzyskie mountains, in Wyżyna Lubelska and in Lower Beskids. It also occurs in Wyżyna Lódzka, Roztocze, in West Beskids and on Pogórze Karpackie.

The present geographical distribution of the majority of the larch subspecies is rather well known, but it is more difficult to define the natural distribution range of these subspecies. In Poland, already in the 18th and 19th centuries, the seeds of Polish larch and the Sudeten larch were distributed in order to introduce them into cultivation on a wider scale. Actually, on separated areas, there exist old and very frequently magnificent stands of both larch taxons. Most of them seem to be of natural origin. As a result, the borderline of the natural occurrence of these larches has been blurred (Boratyński 1986).

It is very difficult to distinguish not only the varieties or families of larches, but also their subspecies and species. A good example of this situation are the taxonomic attempts to classify one of the most beautiful stands in Poland growing in the reservation "Lenki" near Paslęk. An outstanding botanist, Gross (1932), described this larch as the Siberian larch, while Rubner (1939) believed that it was a Polish larch or a Sudeten larch. Krzysztofik (1957)

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tended to agree with Gross that it was a Siberian larch, but Polakowski (1966), after a biometric analysis of the flowers and cones, stated that it was a European larch (Mejnartowicz, Kosiński 1986).

The oldest specimens of larch in Poland reach 45 m of height, and 1.2 m of diameter at breast height (d.b.h.). It is estimated that stands of all larch taxons, both the indigenous and the artificially planted ones, which exceeded the III age class, occupy 127,800 ha; i.e., 1.8 percent of the area of state-owned forests in Poland. The growing stock is estimated at about 1.5 million m^3 (Boratyński 1986). The established experimental areas of provenances provide one of the best methods to compare the extent of features variability, the breeding value of the different ecotypes of larches, and their productivity. Representatives of different populations grow on this area in the same climatic and environmental conditions.

THE EXPERIMENTAL AREA

In the spring of 1967, the author established an experimental area with indigenous larch provenances in the experimental forest station in Siemianice belonging to the University of Agriculture, Poland. The station is situated at 18° 19' of eastern longitude and at 51° 11' of northern latitude. Romer (1949) relates this area to the climate of the Great Valleys in the north-western part of Kraina Warszawska. The mean annual temperature in this region is 7.7 °C, and the sum of annual rainfall is 651 mm. This area is situated in the V Kraina Sląska, Wroclaw region and mesoregion of Oleśnicka Plane (Trampler 1990). The research area is localized on even land, in the habitat of a mixed fresh coniferous forest with the quality class I for pine and the commercial type of oak-fir-pine stands.

This study was established in a random block system with 5 replications (blocks) in 21 variants of origin in each block. Totally, there are 105 plots. The soil for the larch plantation on the experimental area was prepared with big planting scalps. Two-year-old larches, after one transplantation were planted on the scalps into 40 cm deep pits at a spacing of 2 x 2 m. On one plot, 96 larches were planted. The area of each plot is 384 m^2. Plots were separated from each other by a free row. The total experimental area covers 49,140 m^2; i.e., almost 5 ha.

Larches growing on the experimental area originated from 21 stands from the whole country of Poland without any division into the controversial European and Polish larches (table 1, fig. 1). During 25 years of the trees' life on the experimental area, increment measurements, phenological and morphological observations were carried out (Rzeźnik 1980). The nutritive components in the needles were investigated (Nebe and Rzeźnik 1982), technical properties of wood were studied (Miler and Rzeźnik 1982), and the overgrowing of knots was observed (Miler and Rzeźnik 1989).

PURPOSE AND METHOD OF STUDIES

The objective of the studies was to compare the progenies that originated from the seeds of different larch stands from the area of Poland in order to determine the growth dynamics of tree height and diameter, the production of wood mass, morphological evaluation of the stems of trees and the biological characteristic of the stands. The studies were remeasured in 5 year intervals and they covered the tree height from the 5th year of age, and the diameter at breast height (d.b.h.) from the 10th year of tree life to the 25th year of age. Stand volume was calculated for the 20- and 25-year-old trees. The morphological evaluation of the stems and the biological characteristics of the stands were made in 25-year-old trees. The morphological evaluation of stems was made in a 5-degree scale: 1 - a completely straight stem, 2 - stem with one or two slight curvatures, 3 - stem with up to five slight curvatures, 4 - stem with many slight and one bigger curvature, 5 - stem with many big curvatures. The vitality of the trees was determined on the basis of the color of needles. The following colors were distinguished: 1 - dark green, 2 - green, 3 - light green, 4 - with a yellow shade. For the biological division of trees in the stand, the following categories were distinguished: 1 - predominant trees, 2 - dominant trees, 3 - codominant trees, 4 - suppressed trees, 5 - withering trees. The fructification of trees was determined on the basis of the number of cones on the tree: 1 - no cones, 2 - up to 50 cones, 3 - from 50 to 100 cones, 4 - 100 to 500 cones, and 5 - more than 500 cones on the tree.

The percentage participation of trees in the degrees of vitality and fructification in the biological classes of trees precisely characterize the stands. However, the comparison of these numbers among the investigated provenances of larches was very difficult and toilsome. In order to facilitate the interpretation of these numbers, the score method was applied. Each scale of the investigated features obtained an agreed number of scores.

The vitality of the trees was scored in the following way: 1st degree = 15 scores, 2nd degree = 10 scores, 3rd degree = 5 scores, 4th degree = 1 score. In the biological division of trees in the stand, the quality classes received the following scores: class 1 - 3 scores, class 2 - 2 scores, class 3 -1 score, class 4 - 0.5 scores and class 5 - 0 scores. In the fructifications of trees the particular degrees were scored in the following way: 1st degree - 0 scores, 2nd degree - 1 score, 3rd degree - 2 scores, 4th degree - 10 scores and 5th degree - 15 scores.

The results of the measurement of the d.b.h. and the stand volume were subject to individual analysis of variance in order to investigate whether the differences in these features in the larch provenances were statistically significant (Elandt 1964). In cases where significant statistical differences were found, the larch provenances were grouped into homogeneous groups using the Duncan test (Oktaba 1971).

RESULTS

Height of Trees

The greatest increment in the height was by larches between 5 and 15 years of life (fig. 2). Extreme differences in tree height among the larch provenances increased with tree age. Differences were: 5 years - 0.66 m, 10 years - 1.10 m, 15 years - 3.10 m, 20 years - 3.10 m, and 25 years - 5.38 m. Larches in Konstancjewo-Plonne dominated in tree height from the very beginning until 25 years of age.

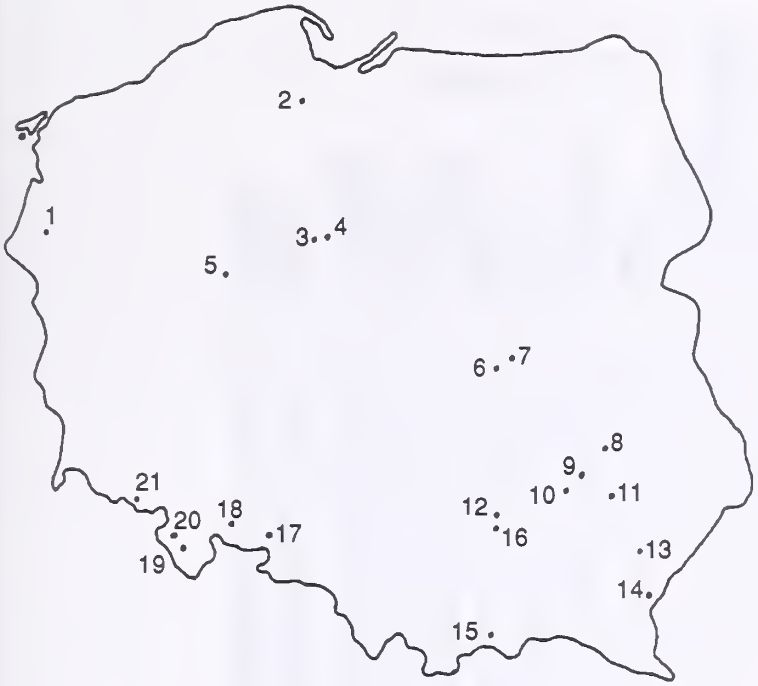
Table 1—Origin of larch seeds in the experiment in 1967.

Provenance	Forest inspectorate	Forest district	Division	Type of habitat	Quality class	Species composition of stand	Afforestation	Stand density	Date about trees which supplied cones			
									Trees	Age	Height	Dbh
									(pcs)	*(years)*	*(m)*	*(cm)*
1	Myślibórz	Zieleniec	391,40b	LM	I	7Md 2Sw 1So	0.7	przeryw.	20	115	34	43
2	Pelplin	Opalenie	64a	LM	I	7Md 1So 1Db 1Lp	0.7	przeryw	5	120	38	52
			87c	LM	I	7Md 3Sw 1So 1Db	0.8	przeryw.	15	110	37	45
3	Konstancjewo	Rez. Plonne	706g	BMsw	I	Md	1.0	pelne	10	35	15	18
4	Konstancjewo	Rez. Tomkowo		BMsw	I	Md,Js,Sw,Lp,Wz	0.6		20	120-160	24	50
5	Czerniejewo	Rez. Bielawy	76j	Lsw	I	4Md 2Gb 2Wz2Brz	0.9	pelne	12	90	33	58
6	Rawa Mazow.	Rez. Trebaczew	90ce	LM	I	5Db 3Brz 2Md	0.6	nierówn.	20	90	26	35
7	Grójec	Mala Wieś	158c	Lsw	I	9Md 1So	0.8	przeryw.	20	120	31	40
8	Marcule	Rez. Piotrowe	135c	LM	II	6Md 3So 1Db	0.8	przeryw	3	135	27	52
		Pole	157a			8Md 2So	0.5		17		28	58
9	Skarżysko	Ciechostowice	129a	LM	III	7Db 3Jd	0.4-0.8		4	200	30	58
			130a		II	4So 4Jd 2Md			2	140	30	61
			128a		III	4Jd 2Md 2So 2Brz			1	250	30	58
			86a		II	8So 2Jd			1	60	18	
			107a		II	8So 2Jd			1	65	17	
			87a		III	8Jd 2So			6	50	16	
			88c		I	6Jd 3So 1Db			2	130	38	
			89a		II	7Jd 3So			3	80	20	
10	Bliżyn	Jastrzębia	217b	BM	I	7So 1Jd 1Md 1Db	0.6-1.0		1	120	31-45	37-70
			216b			4Jd 3Bk 3Md			3			
			242c			5Jd 2Md 2Db 1Bk			2			
			192a			6So1Jd1Md1Db1Brz			8			
			194a			3Md2Brz2Jd1Db1Sw1Gb			3			
			190d			3Md3Db2So1Jd1Brz			1			
			187a			6So 2Db 1Md 1Brz			2			
11	Swięt.P.Nar.	Rez. Góra Ch.	A1						20			
12	Moskorzew	Feliksowka	35l	BMsw	I	Md	0.7	umiark.	18	140	30	50
13	Dąbrówki	Wydrze	35f,45b	Lsw	Ia	9Md 1Bk	0.9	umiark.	20	100	36	45
14	Holubla	Lętownia	46b,49i	Lsw	Ia	8Md 2So	0.4-0.7	luźne	20	90	35	55
15	Krościenko	Rez.Księży Las	62i	LG	III	Md	0.4	luźne	20	45	16	17
16	Pilica	Rez. Smoleń	170g	Lsw	II	8So 1Md 1Js	0.7	przeryw.	6	80	25	28
17	Prószków	Jaskowice	120f	LM	I	5Md 3So 2Sw	0.7	przeryw.	20	145	35	52
18	Henryków	Muszkowice	282a	Lsw	I	7Md 3So	0.6	przeryw.	20	95	33	56
19	Klodzko	Oldrzychowice	202a	LM	II	6So 4Md	0.9	umiark.	20	110	30	38
20	Szczytna Sl.	Borowina	322b	BMG	II	Md	0.8	umiark.	20	105	27	47
21	Kowary	Jedlniki	299a	LMG	III	8Md 2Sw	0.7	umiark.	20	115	27	30

Legend: LM - mixed forest, BMsw - mixed fresh coniferous forest, Lsw - fresh forest, BM - mixed coniferous forest, LG - commercial forest, BMG - mixed commercial coniferous forest, LMB - mixed commercial forest

Md - larch, Sw - spruce, So - pine, Db - oak, Lp - lime, Js - ash, Wz - elm, Gb - hornbeam, Brz - birch, Jd - fir, Bk - beech

przeryw. - interrupted, pelne - complete, nierówn. - unequal, umiark. - moderate, luźne - loose



1 - Myślibórz
2 - Pelplin
3 - Konstancjewo-Plonne
4 - Konstancjewo-Tomkowo
5 - Czerniejewo
6 - Rawa Mazowiecka
7 - Grójec-Mala Wieś
8 - Marcule
9 - Skarżysko
10 - Bliżyn
11 - Góra Chelmowa
12 - Moskorzew
13 - Dąbrówki
14 - Holubla
15 - Krościenko
16 - Pilica
17 - Prószków
18 - Henryków
19 - Klodzko
20 - Szczytna Sląska
21 - Kowary

Figure 1—Localities of larch seeds collection.

At age 25 years, the tallest trees were those from Konstancjewo-Plonne, Rawa Mazowiecka and Moskorzew. Also the larches from Bliżyn, Klodzko, Grójec, Góra Chelmowa, Skarżysko, Prószków and Krościenko were satisfactory in reference to the height increment. The larches of these provenances, due to their height, should be widely utilized for the establishment of plantations in Poland. The larch from Góra Chelmowa that grew slowly until the age of 20 years averaged much greater from age 20 to 25 years. A number of the very low and curved trees without any hope for proper development were removed during the improvement felling. On the other hand, a very poor increment in height was shown by the larches from Holubla, Pilica, Pelplin, Henryków, Konstancjewo-Tomkowo and Dąbrówki. No cultivations should be established from these provenances in the V Kraina of natural forest in Poland.

DIAMETER AT BREAST HEIGHT OF TREES

The provenances which at 10 years of age were larger in diameter than the average on the whole experimental area generally maintained the supremacy of tree diameter until age 25 (fig. 3). Larches which were small in diameter at age 10, were also small at age 25. An exception was the larch from Góra Chelmowa. In age of 10, 15 and 20 years, these trees had smaller diameters than the average on the whole area, but at age 25, these same trees had the largest diameter of all larch provenances. This was the result of

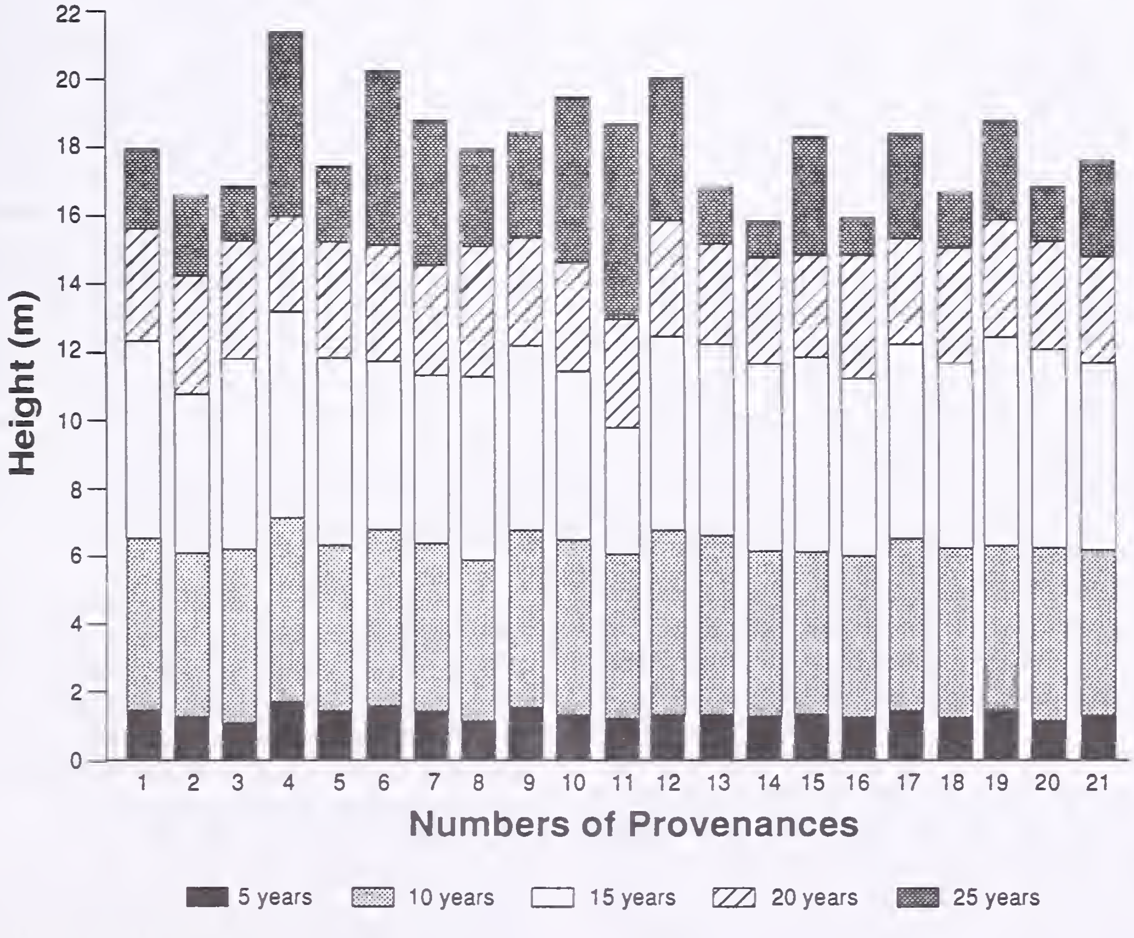


Figure 2—Height of larch.

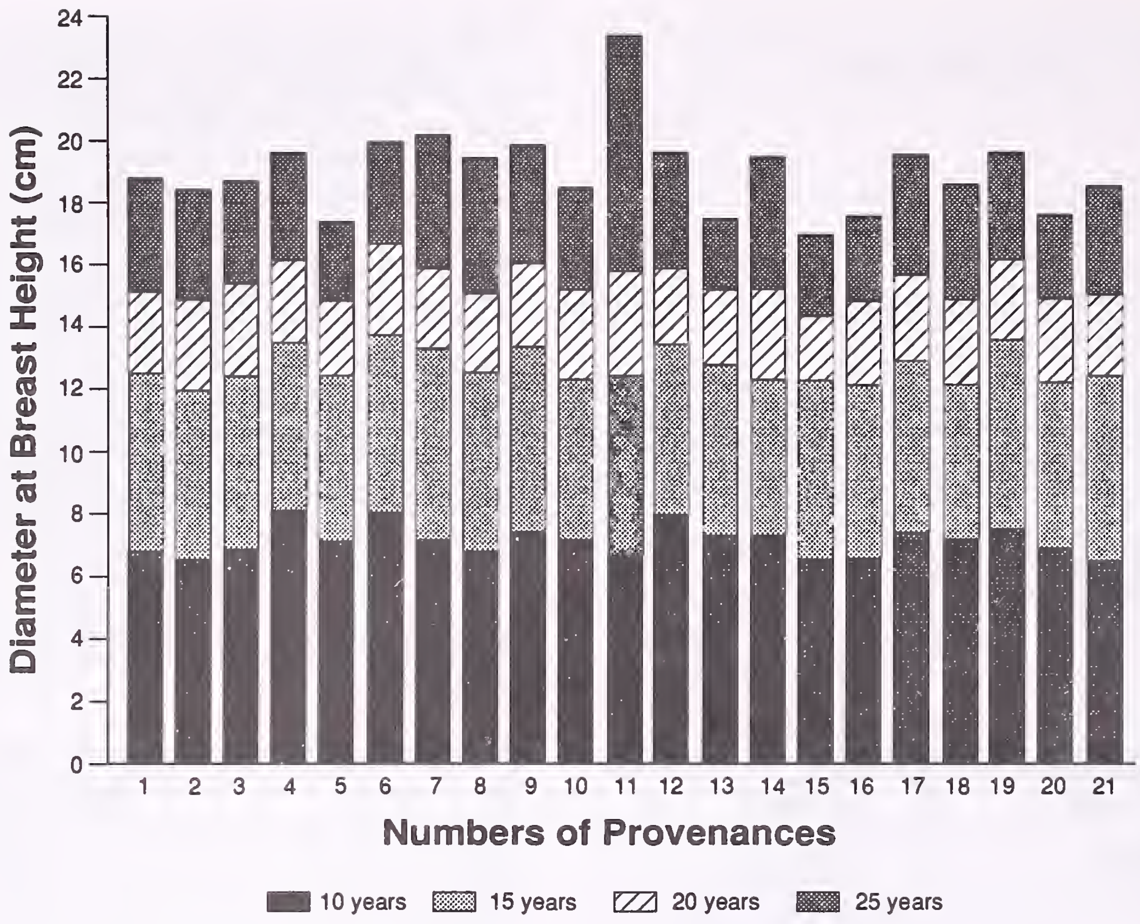


Figure 3—Diameter at breast height of larch.

the removal from this larch provenance of very small trees during the improvement fellings. The number of trees per hectare in this provenance was also the smallest.

The extreme differences among the larch provenances in the thickness increased with each vegetation season. At the age of 10 years the difference was 1.45 cm, 15 years - 1.7 cm, 20 years - 2.2 cm, and 25 years - 3.5 cm. The differences of d.b.h. among the larch provenances at the age of 25 years were statistically significant at the level of $F = 0.01$. Regarding the d.b.h. at age 25, the larch of Góra Chelmowa were the largest. Satisfactory results of diameter increment were also shown by the larches from Grójec, Rawa Mazowiecka, Skarżysko, Klodzko, Moskorzew, Marcule, Konstancjewo-Plonne, Prószków and Holubla. The smallest trees were the larches from Krościenko (table 2).

STAND VOLUME

At age 20, the greatest stand volume was shown by the larches from Moskorzew (154 m^3/ha), Skarżysko (149 m^3/ha), Konstancjewo-Tomkowo (146 m^3/ha), Rawa Mazowiecka (145 m^3/ha), Dąbrówki (143 m^3/ha) and Konstancjewo-Plonne (141 m^3/ha). The smallest volume was demonstrated by larches from Góra Chelmowa (75 m^3/ha), Kowary (96 m^3/ha) and from Prószków (102 m^3/ha). The greatest stand volume was reached at age 25 by larches from Rawa Mazowiecka (383 m^3/ha), Skarżysko (361 m^3/ha), Moskorzew (360 m^3/ha), Konstancjewo-Plonne (324 m^3/ha), Bliżyn (322 m^3/ha) and Grójec (320 m^3/ha). The larches of these provenances should be utilized as extensively as possible for the establishment of plantations, particularly in short production cycles.

The smallest volume was reached by larches from Kowary (190 m^3/ha), Pelplin (217 m^3/ha), Prószków (221 m^3/ha), Dąbrówki (222 m^3/ha), Pilica (226 m^3/ha), Czerniejewo (234 m^3/ha), Marcule (243 m^3/ha), Henryków (251 m^3/ha), Szczytna Slązka (259 m^3/ha) and Góra Chelmowa (260 m^3/ha). The larches of these provenances should not be used for the establishing of cultivations with short production cycles.

Differences in stand volume of the larch provenances from age 20 to 25 were great, exceeding 100 percent (fig. 4). These differences in the stand volume among larch provenances at age 25 were statistically significant at the level of $F = 0.01$ (table 3). The stand volume for the total experimental area at age 20 was 124 m^3/ha and at age 25 it was 276 m^3/ha. These are high stand volumes for this age.

MORPHOLOGICAL EVALUATION OF TREE STEMS

The degree of tree curvature varied in the different provenances of larch (table 4). The greatest number of trees with curvature was noted in the two first degrees of curvature, then in the 3rd, 4th and 5th degrees. The only exception was Góra Chelmowa where the greatest number of trees was in the 4th degree; i.e., they were curved the least and involved only 638 trees per hectare. The proportion of trees in the degrees of tree curvature in all larch provenances is presented in table 4. Accepting that the best trees with a straight stem developing regularly are in the first two degrees of evaluation, the best quality from the technical and productional point of view was shown by the

Table 2—Diameter at breast height at age 25.

No.	Provenances	D.b.h.	Groups							
		(cm)								
11	Góra Chelmowa	23.4	X							
7	Grójec - Mala Wieś	20.2		X						
6	Rawa Mazowiecka	20.0		X						
9	Skarżysko	19.8		X	X					
19	Klodzko	19.7		X	X	X				
12	Moskorzew	19.6		X	X	X				
8	Marcule	19.5		X	X	X	X			
3	Konstancjewo - Plonne	19.5		X	X	X	X	X		
17	Prószków	19.5		X	X	X	X	X	X	
14	Holubla	19.4		X	X	X	X	X	X	X
1	Myślibórz	18.7		X	X	X	X	X	X	X
21	Kowary	18.6		X	X	X	X	X	X	X
18	Henryków	18.6		X	X	X	X	X	X	X
4	Konstancjewo - Tomkowo	18.6		X	X	X	X	X	X	X
2	Pelplin	18.4		X	X	X	X	X	X	X
10	Bliżyn	18.4		X	X	X	X	X	X	X
20	Szczytna Sląska	17.9			X	X	X	X	X	X
16	Pilica	17.6			X	X	X	X	X	X
5	Czerniejewo	17.4			X	X	X	X	X	X
13	Dąbrówki	17.4			X	X	X	X	X	X
15	Krościenko	17.0					X	X	X	X

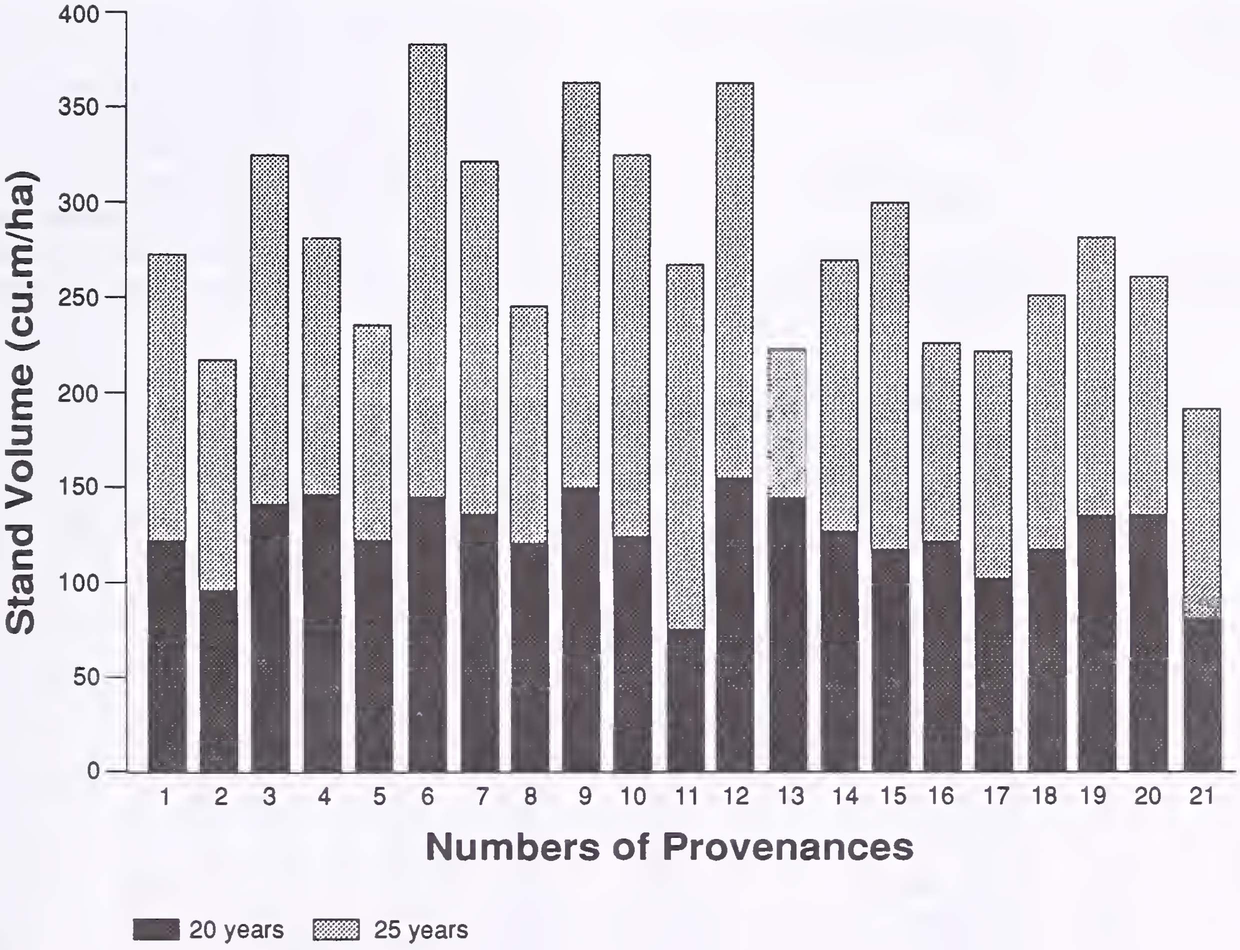


Figure 4—Stand volume.

Table 3—Stand volume of larches at age 25.

No.	Provenances	Stand volume	Groups							
		(m³/ha)								
6	Rawa Mazowiecka	383	X							
9	Skarżysko	361	X	X						
12	Moskorzew	360	X	X						
3	Konstancjewo - Plonne	324	X	X	X					
10	Bliżyn	322	X	X	X					
7	Grójec - Mala Wieś	320	X	X	X					
15	Krościenko	299		X	X	X				
4	Konstancjewo - Tomkowo	281			X	X	X			
19	Klodzko	279			X	X	X			
1	Myślibórz	272			X	X	X	X		
14	Holubla	268			X	X	X	X	X	
11	Góra Chelmowa	266			X	X	X	X	X	X
20	Szczytna Sląska	259			X	X	X	X	X	X
18	Henryków	251			X	X	X	X	X	X
8	Marcule	243				X	X	X	X	X
5	Czerniejewo	234				X	X	X	X	X
16	Pilica	226				X	X	X	X	X
13	Dąbrówki	222				X	X	X	X	X
17	Prószków	221				X	X	X	X	X
2	Pelplin	217					X	X	X	X
21	Kowary	190						X	X	X

larches from Dąbrówki, Bliżyn, Kowary, Myślibórz, Marcule, Prószków, Holubla, Konstancjewo-Plonne and Krościenko. They had over 90 percent of trees in the first and in the second quality class of tree stems.

THE VITALITY OF LARCHES

The experimental area showed very few trees with a dark green color indicating the highest vitality of trees. They occurred only in six larch provenances, and in a comparatively small percentage ranging from 2.9 to 0.6 percent. The greatest number of trees with a dark green color were seen in the provenance from Holubla (2.9 percent), Krościenko (1.6 percent), Czerniejewo (1.3 percent) and Konstancjewo-Plonne, Henryków and Klodzko (0.6 percent each). In the remaining 15 larch provenances, there were no trees with a dark green color. The participation of trees with a green color of needles varied between 4.8 and 22.7

Table 4—Morphological evaluation of larch tree stems (in percent).

Provenances		Tree classification degrees of curvature				
No.	Name	1	2	3	4	5
1	Myślibórz	64.0	31.5	3.5	1.0	—
2	Pelplin	38.7	44.3	12.7	3.5	0.8
3	Konstancjewo-Plonne	61.4	32.9	3.6	2.1	—
4	Konstancjewo-Tomkowo	45.4	44.2	9.4	1.0	—
5	Czerniejewo	45.6	39.9	13.5	1.0	—
6	Rawa Mazowiecka	15.1	48.0	32.8	4.1	—
7	Grójec-Mala Wieś	25.3	51.6	20.6	2.5	—
8	Marcule	59.5	35.5	4.0	1.0	—
9	Skarżysko	27.4	50.3	18.7	3.6	—
10	Bliżyn	58.6	37.5	3.9	—	—
11	Góra Chelmowa	12.4	24.7	26.3	32.6	4.0
12	Moskorzew	32.9	44.3	19.2	3.0	0.6
13	Dąbrówki	52.3	41.1	5.6	—	1.0
14	Holubla	49.4	44.5	4.4	1.7	—
15	Krościenko	52.4	39.9	4.8	2.9	—
16	Pilica	26.7	42.7	25.6	3.4	1.6
17	Prószków	42.9	52.6	3.9	—	0.6
18	Henryków	39.5	48.4	9.8	1.8	0.5
19	Klodzko	37.2	50.0	11.9	—	0.9
20	Szczytna Sląska	41.8	41.1	16.2	0.9	—
21	Kowary	49.4	47.5	3.1	—	—

Table 5—Biological characteristics of larch stands (in percent).

Provenances		Tree vitality					Biological division of trees						Tree fructification					
		Vitality degrees					Kraft's classes						Fructification abundance					
No.	Name	1	2	3	4	Scores	1	2	3	4	5	Scores	1	2	3	4	5	Scores
1	Myślibórz	—	5.6	53.6	40.8	364	15.5	52.3	21.0	9.3	1.9	177	33.3	45.0	10.3	9.4	2.0	191
2	Pelplin	—	11.2	61.4	27.4	446	15.8	44.4	21.2	14.5	4.1	165	34.1	36.8	16.1	10.5	2.5	213
3	Konstancjewo-Plonne	0.6	11.8	55.6	32.0	451	12.0	53.1	22.5	10.5	1.9	180	15.2	41.2	22.1	17.0	4.5	324
4	Konstancjewo-Tomkowo	—	10.0	57.2	32.8	425	15.6	55.2	19.2	7.7	2.3	171	40.2	41.8	14.1	3.0	0.9	113
5	Czerniejewo	1.2	7.2	59.4	32.2	421	10.0	54.8	22.9	10.5	1.8	168	29.4	46.5	18.1	6.0	—	143
6	Rawa Mazowiecka	—	12.1	62.9	25.0	480	9.9	54.9	25.8	8.5	0.9	170	32.7	43.6	10.9	11.1	1.7	202
7	Grójec-Mala Wieś	—	10.1	68.9	21.0	462	13.5	54.2	24.5	5.0	2.8	176	64.6	26.5	6.1	2.0	0.6	87
8	Marcule	—	15.0	72.6	12.4	525	12.5	52.9	17.7	14.5	2.4	168	40.2	42.0	10.6	6.7	0.5	138
9	Skarżysko	—	11.5	69.2	19.3	480	12.3	56.6	21.0	8.1	2.0	175	28.6	59.4	5.5	5.5	1.0	142
10	Bliżyn	—	10.4	75.2	14.4	495	14.2	50.7	23.3	9.1	2.7	172	35.1	46.8	10.3	7.8	—	145
11	Góra Chelmowa	—	8.3	41.3	50.4	340	14.4	55.1	20.3	6.1	4.1	177	42.7	30.8	10.1	14.4	2.0	225
12	Moskorzew	—	7.4	58.5	34.1	401	6.8	65.0	22.7	3.7	1.8	175	34.9	41.5	16.7	6.4	0.5	148
13	Dąbrówki	—	4.8	66.1	29.1	408	14.2	46.6	31.5	4.7	3.0	170	47.9	46.0	5.0	1.1	—	67
14	Holubla	2.9	10.5	72.3	14.3	527	14.5	44.7	24.8	12.4	3.6	174	35.8	45.7	10.2	7.3	1.0	154
15	Krościenko	1.6	12.0	63.1	23.3	472	8.4	53.4	24.7	12.4	1.1	158	37.7	46.0	9.6	6.7	—	153
16	Pilica	—	7.2	59.3	33.5	291	12.7	48.7	26.6	11.4	0.6	168	36.2	36.8	15.6	9.1	2.3	194
17	Prószków	—	4.2	74.5	21.3	454	8.8	58.3	20.4	10.4	2.1	180	29.4	40.5	22.5	7.6	—	162
18	Henryków	0.6	8.2	68.3	22.9	455	19.3	38.1	25.3	16.8	0.5	168	30.1	34.5	19.3	15.5	0.6	237
19	Klodzko	0.6	20.2	61.1	18.1	537	14.4	58.9	20.2	5.0	1.5	184	18.7	31.9	27.8	18.8	2.8	319
20	Szczytna Sląska	—	6.4	59.3	34.3	426	9.7	55.9	21.3	12.3	0.8	168	17.1	53.1	14.5	13.6	1.7	244
21	Kowary	—	22.1	72.7	5.2	595	6.9	54.2	27.8	11.1	—	162	25.4	52.7	11.8	8.3	1.8	220

percent depending on the larch provenance. The greatest participation of green color trees was shown by larches from Kowary, Klodzko, Marcule and Rawa Mazowiecka (from 22.6 to 12.6 percent), and the smallest number was found in the provenances from Szczytna Sląska, Dąbrówki, Prószków and Myślibórz (from 9.5 to 5.6 percent).

The proportion of trees with a light green color of needles varied between 75.9 and 57.2 percent, depending on the provenance. The greatest proportion in this category had larches from: Prószków, Bliżyn, Kowary and Marcule (over 72 percent). The greatest number of trees with a yellow color were larches from Góra Chelmowa (50 percent), Myślibórz (41 percent), Pilica (36 percent). The smallest numbers were found in larches from Kowary (5 percent), Marcule (12 percent), Holubla and Bliżyn (14 percent each). The proportion of trees in the scale of colors varied in each larch provenance (table 5).

The greatest tree vitality was shown by larches from Kowary, Klodzko, Holubla and Marcule, and the least vitality was revealed by the trees from Pilica, Góra Chelmowa and Myślibórz (table 5). No variability of needle color was found that could have been associated with sub-species or the geographical origin of the larch seeds.

BIOLOGICAL DIVISIONS

The proportion of trees in the biological classes of the stand varied, depending on the provenance of larch. Trees in the predominant class varied between 6.8 and 19.3 percent. Trees in the dominant class ranged from 38.1 to 65 percent, and those in the codominant class ranged from 17.7 to 31.5 percent. Trees in the dominated tree class ranged from 3.7 to 16.8 percent, and in the suppressed tree class from 0 to 4.1 percent (table 5).

In spite of big differences in the biological classes, the percent differences of larch among the particular provenances in the group of trees constituting the main stand (tree classes: predominant, dominant, codominant) were comparatively small. The total proportion of trees in this group ranged from 81.4 to 95.5 percent. The highest score number was reached by larches from Klodzko (184 scores), Prószków (180 scores) and Konstancjewo-Plonne (180 scores), and the lowest evaluation was received by larches from Krościenko (158 scores), Kowary (165 scores) and Czerniejewo, Marcule, Pilica, Henryków and Szczytna Sląska (168 scores each). No relationship of larch subspecies or geographical localization of stands from which the seeds originated was found.

Fructification of Trees

The proportion of trees in the different levels of cone fructification illustrates fully the fructification of cones at age 25 in the investigated provenances of larch (table 5). However, these numbers are difficult to interpret. In order to facilitate the interpretation of larch fructification in the investigated provenances, the score method was applied. This approach has shown the problem in the following way. The most abundant fructifying larches included the trees from: Konstancjewo-Plonne (324 scores), Klodzko (319 scores), Szczytna Sląska (244 scores), Henryków (237 scores), Rawa Mazowiecka (202 scores). The least fructifying larches included the trees from: Dąbrówki (67 scores) and Grójec (87 scores).

For the total experimental area the mean value of fructification was 182 scores. Differences in the fructification of trees among the various provenances proved to be high. However, it is difficult to decide whether abundant fructification in the age of 25 years should be regarded as a positive or a negative feature. Abundant fructification in this age can indicate an early and good development of trees, but also the beginning of the degenerating processes (growing old) of the larch provenances.

CONCLUSIONS

1. These studies have shown that at age 25, the investigated features of particular progenies of larch stands in Poland were different. It was shown that the diameter and stand volume were significantly different. These results confirm the differentiation of some biological and technical features of the wood in the progenies of larch at younger ages.
2. The larch of Gora Chelmowa, due to genetic reasons and because of the technical value of the wood should not be introduced into the forest cultivations. Both the progenies and the maternal stands were characterized by numerous and big curvatures in the tree stems.
3. The production of wood mass from larch stands at age 25 years can reach over 300 m^3/ha.
4. These studies should be continued. The results obtained during the first 25 years of tree life should be regarded as preliminary. With the lapse of time they can show some changes. Larch in Poland reach ages significantly exceeding 100 years.

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Siberian and Western Larch: Comparisons to Other Species in Central British Columbia

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Abstract—Siberian larch (*Larix siberica*) and western larch (*Larix occidentalis*) may have potential for extension into central British Columbia, Canada. These larch species were grown with three native and one introduced species on four ecosystems. The 5-year results indicate that Siberian and western larch perform as well as, and in some cases better than, the native and other introduced species. On three of the four ecosystems, the performance of Siberian larch is slightly better than western larch.

The number of commercial tree species that are acceptable for reforestation is limited in the Cariboo Forest Region, central British Columbia, Canada (fig. 1). If larch performs well in this area it would provide another choice of species that could be beneficial, especially on the drier ecosystems where lodgepole pine (*Pinus contorta* var. *latifolia*) is often the only viable species. Larch may even become a preferred species when all of its attributes are considered. On productive sites, larch is generally a fast-growing species. Occasionally the growth of western larch (*Larix occidentalis*) exceeds that of lodgepole pine (Fowells 1965).

Western larch also appears to be more resistant over time than other native conifers to *Armillaria* root disease (*Armillaria ostoyae*) (Morrison and others 1988), which is becoming a serious problem in the Cariboo Forest Region. Western larch trees produce high-quality wood that is similar to that of Douglas-fir. The uses for larch wood range from building materials to decorative products to pulpwood (Panshin and de Zeeuw 1970).

Natural stands of western larch are found just south of the Cariboo Region, and extension of this species into the Region may be possible, especially into subzones of the Interior Cedar Hemlock Zone (Klinka and others 1990). In 1988, West Fraser Mills Limited, in Quesnel British Columbia, obtained Siberian larch (*Larix siberica*) seed from a Finnish sister company Enso-Gutzeit. Siberian larch grows over a large range in Eurasia extending from below the 50th parallel and into the Arctic Circle (Gower and Richards 1990). It has performed well in a trial established in Alberta, Canada (McLeod and Rapp 1978). Therefore, this species may be adapted to the short growing seasons and cold winters of the central interior of British Columbia.

A species trial, begun in 1987, tested the potential of these two larch species in this region. The objective was to assess the suitability of western and Siberian larch for reforestation across four biogeoclimatic subzones in the Cariboo Forest Region. We compared seedling performance of larch to the performance of three native species—interior spruce (*Picea glauca* x *engelmannii*), lodgepole pine, and Douglas-fir (*Pseudotsuga menziesii* var. *glauca*)—and one introduced species, ponderosa pine (*Pinus ponderosa*). Ponderosa pine has a limited range in the southern portion of the Cariboo Region but does not naturally occur where the species trial was established.

METHODS

The trial is in the Cariboo Forest Region, which encompasses a number of ecosystems over a range of climatic conditions. In British Columbia, the forest and range

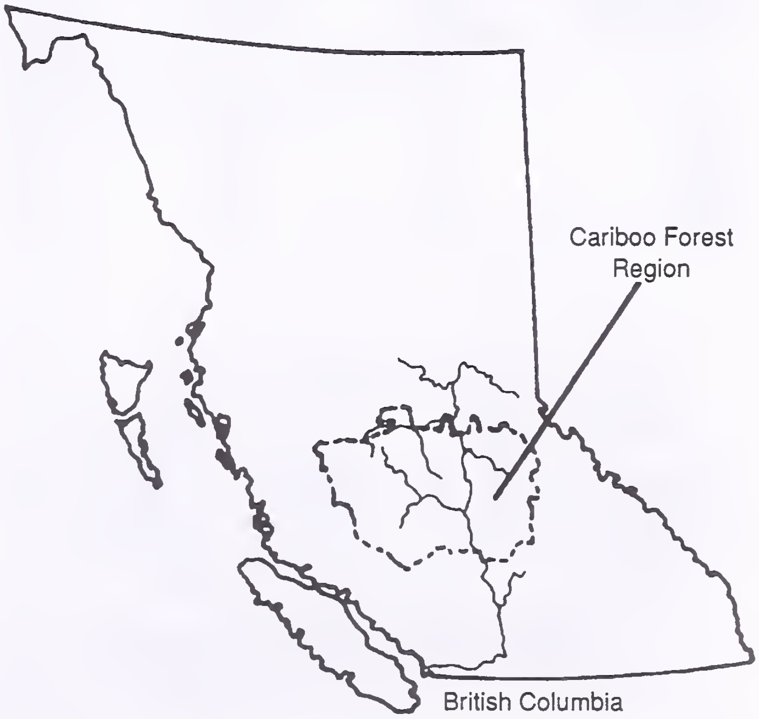

Figure 1—British Columbia and the Cariboo Forest Region.

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land has been ecologically mapped using a biogeoclimatic classification system. The land base is divided into broad climatic zones and further divided into subzones according to climate, vegetation, and soils (Meidinger and Pojar 1991). The Cariboo Forest Region is divided into 30 subzones. From these, four major subzones were chosen for this larch species trial. The subzones chosen ranged from a cold, wet, high-elevation site (ESSFwk1) to mild, moist, mid-elevation sites (SBSmw and ICHwk2) to a cool, dry site characterized by large diurnal temperature fluctuations (IDFdk4). General climatic data of these subzones are given in table 1 (B.C. Ministry of Forests 1987).

Six species were used for this trial but not all were planted in each subzone (table 2). Spruce was not appropriate on the dry IDFdk4 site, while Douglas-fir and ponderosa pine were not suitable on the high-elevation ESSFwk1 sites.

The seed for the Siberian larch was second-generation seed produced by Enso-Gutzeit in its seed orchard in Imatra, Finland. The original seed was from Russia, Raivola provenance, with a location of latitude 61°12' N., longitude 28°48' E., and an elevation of 70 m. Seed for the other species came from native British Columbia seedlots appropriate for the specific site and elevation. One-year-old seedlings of each species were planted in the spring of 1987. Most of the seedlings were grown in styroblock containers with a cavity volume of 65 mL (PSB 313). The exceptions were the lodgepole pine seedlings and the western larch seedlings planted on the ESSFwk1 site, which were grown in slightly smaller styroblock containers with a volume of 39 mL (PSB 211). Both these stocktypes are commonly used for operational planting in British Columbia.

Table 1—Description of biogeoclimatic subzones

Biogeoclimatic subzone	Annual temperature	Annual precipitation	Mean elevation
	°C	*mm*	*m*
ESSFwk1	1.4	1,123	1,450
ICHwk2	3.9	844	975
SBSmw	3.5	650	850
IDFdk4	3.7	357	1,150

Table 2—Species planted on each subzone

Subzone	Tree species[1]
ESSFwk1	SL, WL, LP, SX
ICHwk2	SL, WL, LP, SX, DF, PP
SBSmw	SL, WL, LP, SX, DF, PP
IDFdk4	SL, WL, LP, DF, PP

[1] SL = Siberian larch, WL = western larch, LP = lodgepole pine, SX = interior spruce, DF = Douglas-fir, PP = ponderosa pine.

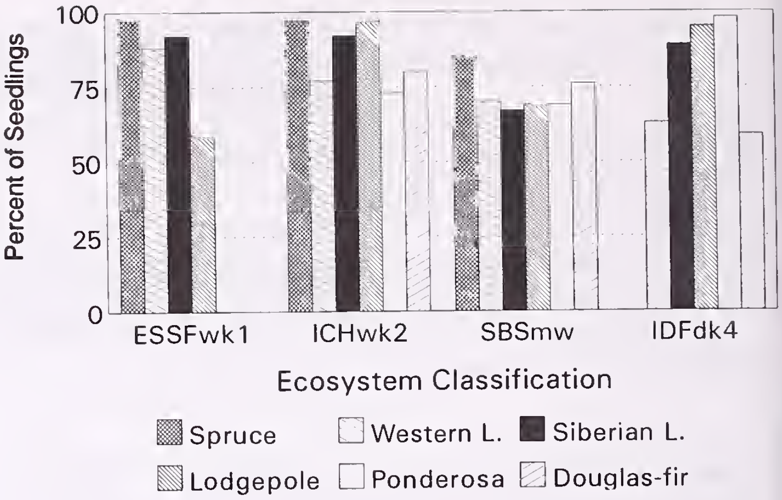

Figure 2—Seedling survival after 5 years.

The trial was laid out in a randomized block design with three replications of each species on each site. One site was established per subzone. The seedlings were planted on a 12- by 12-m tree grid at 2-m spacing and assessed periodically for seedling height, leader growth, diameter, condition, and damage. We analyzed the data using ANOVA and Duncan's Multiple Range Test.

RESULTS

We assessed survival, condition, and seedling growth.

Fifth-Year Seedling Survival and Condition

Seedling survival was adequate on all sites and for most species. The exceptions were lodgepole pine on the ESSFwk1 site and western larch and Douglas-fir on the IDFdk4 site (fig. 2). The poor pine survival is unusual. Most of the mortality occurred in the first year after planting and was probably due to problems with stock quality or handling at the time of planting. Conversely, low survival of Douglas-fir is common in the IDFdk4 subzone due to dry conditions and frequent frosts during the growing season (Newsome and others 1990). The survival of western larch also appeared to be adversely affected by the climate on the IDFdk4 site. However, the survival of Siberian larch was good and comparable to pine on all sites.

We estimated seedling condition in terms of the number of seedlings that have the potential of becoming crop trees. Seedlings with poor vigor and any major damage were eliminated. In all subzones, except the IDFdk4, the majority of surviving seedlings were considered potential crop trees (fig. 3). On the IDFdk4 site Douglas-fir and western larch performed poorly, with only 7 and 10 percent of the seedlings, respectively, expected to become crop trees. Also, the performance of Siberian larch on this site was marginal with only 43 percent of the seedlings assessed as potential crop trees.

Fifth-Year Seedling Growth

Lodgepole pine had significantly larger mean diameters than western and Siberian larch on all four sites (fig. 4). However, the larch diameters were either larger, or not significantly different, from all other native species. A comparison of the two larch species shows that Siberian larch had significantly larger mean diameters than western larch on all the subzones except the ICHwk2 where there was no significant difference.

The 5-year total height growth data show the same general trends as the diameter measurements (fig. 5). Lodgepole pine was significantly taller than the larch on all sites except the ICHwk2 where height of western larch was not significantly different than that of lodgepole pine. On all other sites the heights of Siberian and western larch seedlings were not significantly different, and they are equal to, or larger than, the heights of the other native species.

The 5-year leader growth did not always follow the same trends as total height growth, especially for western larch. Its leader growth was significantly smaller than that of lodgepole pine on the ICHwk2 site and Siberian larch on the SBSmw and IDFdk4 sites (fig. 6). Seedling heights over the first 5 years on the SBSmw (fig. 7) and ICHwk2 (fig. 8) sites indicate that although the larch were as tall or taller than the lodgepole pine in the third year, by the fifth year the pine equaled or exceeded the larch. Also, the growth rate of larch appeared to be slowing down while the growth of lodgepole pine was continuing at a high rate.

To help explain this reduction in growth, we examined the number of seedling leaders damaged in the fifth year (fig. 9). Most of the leader damage was from dead, missing, or damaged terminal buds. Although the cause of damage can be difficult to identify, the majority was probably due to frost during the growing season. The highest incidence of leader damage was on the IDFdk4 site where frosts can occur throughout the growing season (Steen and others 1990). Annual frost damage would help to explain the poor growth and vigor of Douglas-fir and larch seedlings in this subzone.

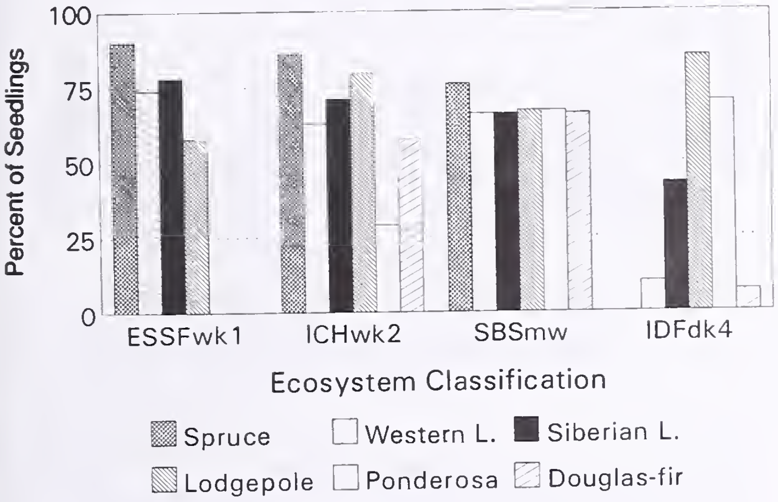

Figure 3—Seedlings determined to be potential crop seedlings in the fifth-year assessment.

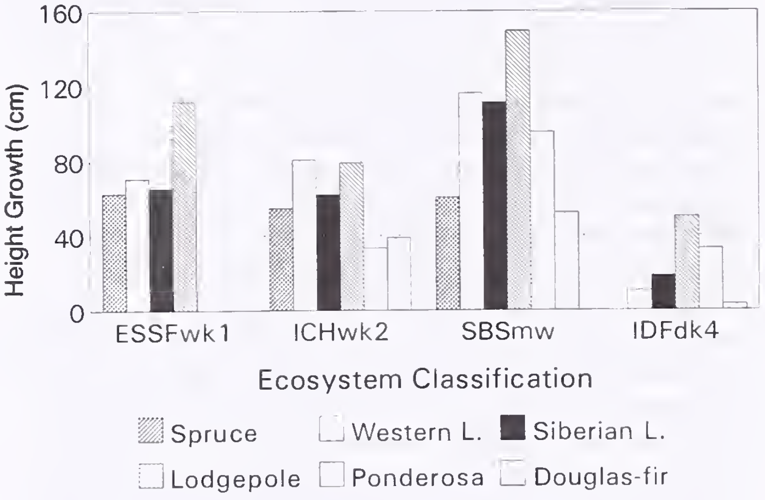

Figure 5—Seedling total height growth after five growing seasons (total height growth = total height – planting height).

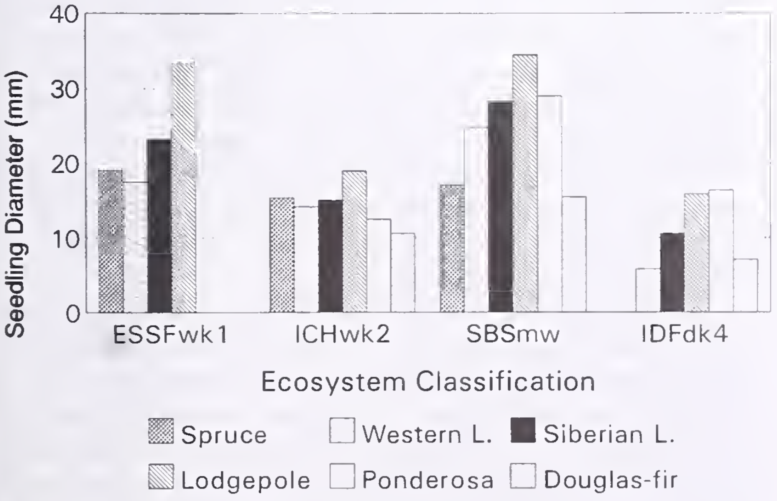

Figure 4—Seedling diameter after five growing seasons.

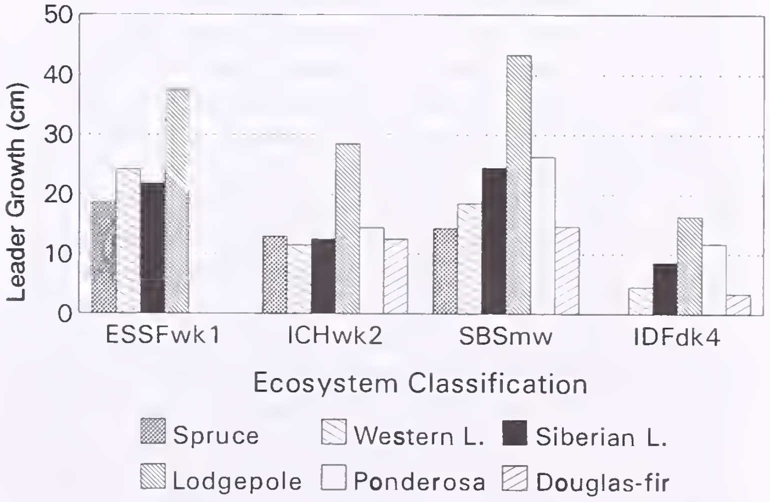

Figure 6—Fifth-year leader growth.

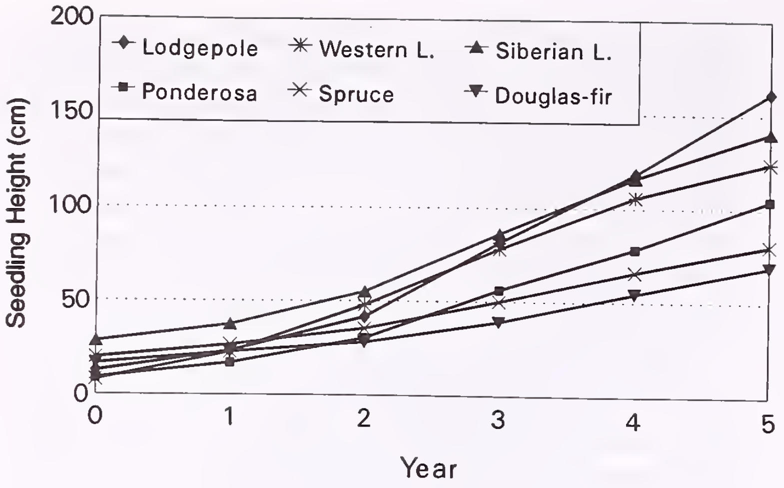

Figure 7—Seedling height versus time on the SBSmw subzone.

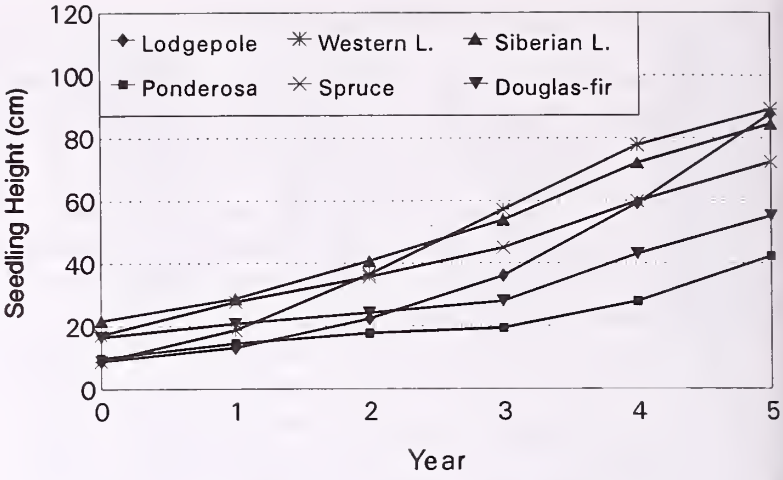

Figure 8—Seedling height versus time on the ICHwk2 subzone.

DISCUSSION

A comparison of western and Siberian larch shows that Siberian larch performance is superior on three subzones: the IDFdk4, SBSmw, and ESSFwk1. Although the total height growth of the two species on these three sites was equal, the diameter of Siberian larch was larger. This larger diameter increases the ability of the tree to withstand mechanical damage from snow or vegetation press, which can be a problem on the wetter sites. In the future, Siberian larch may also exceed western larch in height growth on two subzones, the IDFdk4 and the SBSmw, if the leader growth of Siberian larch continues to exceed that of western larch. On the ICHwk2 site, western larch did show better total height growth than Siberian larch. However, similar leader growth for both species in the fifth year indicates that western larch may not maintain the superior growth. The poorest performance of both larch species was in the IDFdk4 subzone, although Siberian larch performed much better than the western larch on the IDFdk4 site. The location is in a toe slope position making it vulnerable to frost (Steen and others 1990). Siberian larch may exhibit improved growth and condition on a site with a lower frost hazard.

In all subzones lodgepole pine performance was superior to both larch species. Although the total height of western larch was equal to lodgepole pine in the ICHwk2 subzone, the pine height will exceed the larch height if the present growth rates continue. However, compared to other native species the larch was growing as well if not better. On the IDFdk4 site the performance of western larch and Douglas-fir were similar, but neither is acceptable. In the IDF zone, Douglas-fir is shade tolerant and can be successfully regenerated under a canopy that protects the seedlings from environmental extremes such as frost. Poor performance is common in a clearcut situation (Newsome and others 1990). Conversely, western larch is shade intolerant and cannot perform well under an overstory that would help to protect the seedlings from frost. Therefore, western larch may not be a suitable species for this subzone.

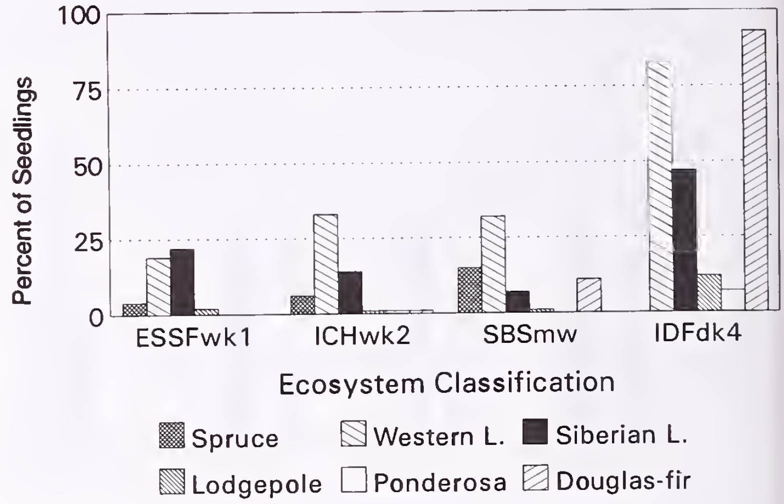

Figure 9—Seedling terminal damage occurring in the fifth growing season.

On the other three subzones, the 5-year growth performance suggests that larch may be a suitable species for regeneration. However, both larch species appear susceptible to terminal damage probably due to frost. Siberian larch seedlings showed moderate to high frost damage on the ESSFwk1 and IDFdk4 sites, and western larch seedlings had moderate to extremely high frost damage on all sites. Although this damage had not seriously affected overall seedling performance on any site other than the IDFdk4, it may produce slower growth rates and poor seedling form in the future.

Both species appear to have potential for extension into the Cariboo Forest Region. The data suggest Siberian larch is well suited to the milder moist ecosystems, the ICHwk2 and the SBSmw. It may also have potential in the ESSFwk1 and the IDFdk4. However, its performance in the IDFdk4 was marginal, and further trials may be required to determine its acceptability. According to our results, western larch does not perform well on the IDFdk4 subzone primarily due to high terminal damage. Early seedling growth and condition are acceptable on the other three subzones. However, we need further monitoring of seedling performance and terminal damage before recommendations can be made concerning the use of either species for regeneration in the Cariboo Forest Region.

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Western Larch Tree Improvement Programs in the Inland Empire and British Columbia

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George Howe
Lauren Fins
Marc Rust

Abstract—Western larch tree improvement programs in the Inland Northwest are coordinated by the Inland Empire Tree Improvement Cooperative, the U.S. Department of Agriculture Forest Service's Northern Region, and the British Columbia Ministry of Forests. The objectives are to develop seed that has been selectively bred to produce trees with improved volume growth and quality, while maintaining acceptable levels of adaptation and genetic diversity. Program breeding strategies, progress to date, results from long-term genetic tests, and ongoing western larch tree improvement research are discussed.

While commercial harvest of western larch (*Larix occidentalis* Nutt.) began in the early 1900's and increased substantially in the mid-1940's (Schmidt and others 1976), western larch genetics research and tree improvement only began in the U.S. Inland Northwest in the mid 1970's and in British Columbia in 1987. These programs of genetics research have focused on describing the genetic structure of natural populations (Rehfeldt 1982; Fins and Seeb 1986); elucidating relationships between growth and adaptive traits and environmental gradients (Rehfeldt 1982); and estimating additive genetic variances, covariances and response to selection for traits relating to early growth, components of growth, growth rhythm and disease resistance (Joyce 1985; Rehfeldt 1992; Zhang 1990; Zhang and Fins 1993). Results derived from this body of research have been used to delineate seed zones and establish seed transfer guidelines; to facilitate tree improvement investment decisions; and to guide the development and implementation of breeding plans for tree improvement programs (Fins and Franc 1984; Howe and Franc 1988; Jaquish 1987), which have grown rapidly and are now beginning to produce improved seed for planting.

This paper (1) outlines several silvical, genetic, and wood property attributes of western larch that make investment in western larch tree improvement attractive; (2) identifies and describes the structure, goals, and strategies of agencies involved in western larch tree improvement in the Inland Northwest and British Columbia; (3) describes the progress and presents early results from these programs; and (4) describes ongoing research and identifies areas where further research is needed to ensure the efficient long-term delivery of well-adapted, genetically diverse, and genetically improved seed.

SILVICAL CHARACTERISTICS

Like all species of larch, western larch is a very shade intolerant pioneer species that thrives in open-grown, full sunlight conditions. It demonstrates very rapid early growth and often outgrows its associates for about 90 years, after which it is overtopped by more shade tolerant, slower growing sympatric species (Schmidt and others 1976). On many sites, growth rates of 1 meter per year are not uncommon and on productive sites maximum tree height can easily reach over 55 meters. Western larch has exceptionally good form. Trees readily self-prune and, consequently, have clear, straight boles. The species' crown architecture is characterized by a large tree height/crown width ratio, which enables individuals to capture high levels of solar radiation (Gower and Richards 1990). Branches are short and small in diameter, and much of a tree's photosynthate is allocated to bolewood.

Western larch is relatively free of serious insect pests and disease, and since it is only somewhat susceptible to root diseases such as *Armillaria* (Sutherland and Hunt 1990), silviculturists are increasingly interested in planting western larch on sites infected with root rots. It performs well in plantations and readily responds to stand cultural treatments such as precommercial thinning (Seidel 1982) and fertilization (IFTNC 1988).

Unfortunately, across much of western larch's natural range flower crops are infrequent and sporadic, particularly in overly dense young stands (Owens and Molder 1979; Shearer and Schmidt 1987). Male and female reproductive structures are often damaged by spring frost, and developing seeds are prone to insect predation (Shearer 1989). Consequently, seed yields are typically low, and in many areas, attempts to regenerate western larch naturally have been hampered by chronic shortages of high quality seed (Shearer and Schmidt 1987). Similarly, the procurement of large quantities of high-quality seed for planting has always been a challenge, particularly in

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northern Idaho (Graham 1986) and the West Kootenay/Shuswap regions of British Columbia.

GENETIC CHARACTERISTICS

The gene pools of forest tree species are shaped by the forces of natural selection, mutation, migration, and random genetic drift; by factors such as life history characteristics, mating systems and interspecific hybridization; and by human actions such as urban and rural development, industrial activity, agriculture, timber harvesting, and, in some instances, programs of domestication through selective breeding. Given the relatively short time that western larch forests in North America have been exploited for timber, the reliance on natural regeneration as the primary mode of regenerating the species, and the general lack of large-scale urban, rural and industrial development throughout its natural range, the contemporary gene pool of western larch remains largely intact. Also, since introductions of exotic species of *Larix* into the region for timber or horticultural use have been minimal, and because there are no sympatric species with which to form hybrids, this gene pool remains relatively unadulterated with genes of exotic or sympatric species. Carlson and Blake (1969) and Carlson and others (1990) have recognized putative natural hybrids of western larch and subalpine larch (*Larix lyallii* Parl.) in a small number of local areas where the species meet. However, because the two species are typically separated elevationally, they are seldom sympatric and hybrid swarms are rare (Arno and Habeck 1972).

Electrophoretic surveys of isozyme variation in natural populations distributed throughout the Inland Empire indicated that stands of western larch were generally less variable than other western conifers (Fins and Seeb 1986). The proportion of total diversity (Gst) among 19 populations was only 9 percent, with the remaining 91 percent of the observed genetic variation residing within populations (tree-to-tree). Observed heterozygosity (0.06) was less than expected heterozygosity (0.08), a result contrary to experience with most other western conifers.

In common garden studies of natural populations from the Inland Northwest, Rehfeldt (1982, 1992) detected genetic differences among populations for an array of growth and adaptive traits, but these differences occurred across relatively flat geographic and elevational clines. Abundant genetic variation has been detected within populations for growth and adaptive traits (Rehfeldt 1992) and for free and predetermined components of growth (Joyce 1985; Zhang 1990; Zhang and Fins 1993).

Quantitative genetic studies in western larch have shown abundant additive genetic variance for growth traits and disease resistance (Fins and Rust 1989; Rehfeldt 1992). These results are encouraging and suggest that for most commercially important traits large gains are possible through selective breeding, even with relatively modest selection intensities. However, strong genetic correlations link these traits (Rehfeldt 1992). For some traits, such as total tree height and resistance to *Meria* needle cast, genetic correlations are positive and seem almost serendipitous—strong selection for tree height will result in greater resistance to needle cast. For other traits, such as total tree height and duration (number of days) of shoot elongation, genetic correlations are also positive. Consequently, strong selection for tree height will result in an extended growing period and concomitant losses in adaptation (Rehfeldt 1992). In all of these reported studies, genotype by environment interactions for growth traits have been minimal.

WOOD CHARACTERISTICS

Western larch wood is straight-grained, durable, moderately resistant to decay, and has high relative density and modulus of elasticity (Mullins and McKnight 1981). These characteristics make western larch a preferred structural product in the Douglas-fir/larch species group. Value-added western larch products such as glue-laminated beams also command premium prices. Unfortunately, western larch wood is difficult to dry and is susceptible to greater shrinkage than most other softwoods. However, these problems can be easily overcome through continuous long-term experience and training of processing staff (Kinghorn, this publication).

Jozsa and Sen (1992) established baseline values for wood relative density from old-growth forests in British Columbia, and presented pith-to-bark profiles of average ring density as determined by x-ray densitometry for wood from second-growth forests. Their results demonstrated that western larch had high relative density (.45) as old-growth, had no elevated relative density near the pith, and had approximately a 15-year period of juvenile wood production, after which mature wood was produced at a constant relative density that approached the value of old-growth wood (fig. 1). These results suggest that unlike most other western conifers (Kellogg 1982), second-growth or managed western larch forests will produce a relatively high proportion of mature wood with relative density levels similar to old-growth forests. These wood characteristics will become increasingly important as industrial users move away from old-growth forests as a source of raw material and towards second-growth and, ultimately, to managed forests, where log size will be reduced, the proportion of juvenile wood will be increased and changes to important wood characteristics are expected (Jozsa and Sen 1992).

Collectively, these silvical, genetic, and wood characteristics suggest that western larch is a high value species that is ideal for high-yield, intensive management on a relatively short-rotation basis. It is genetically diverse and will respond to selective breeding. Economic analysis has indicated that investment in western larch tree improvement can be profitable providing seed production from seed orchards is kept high and planting programs are large enough to use all of the seed (Fins and Moore 1984).

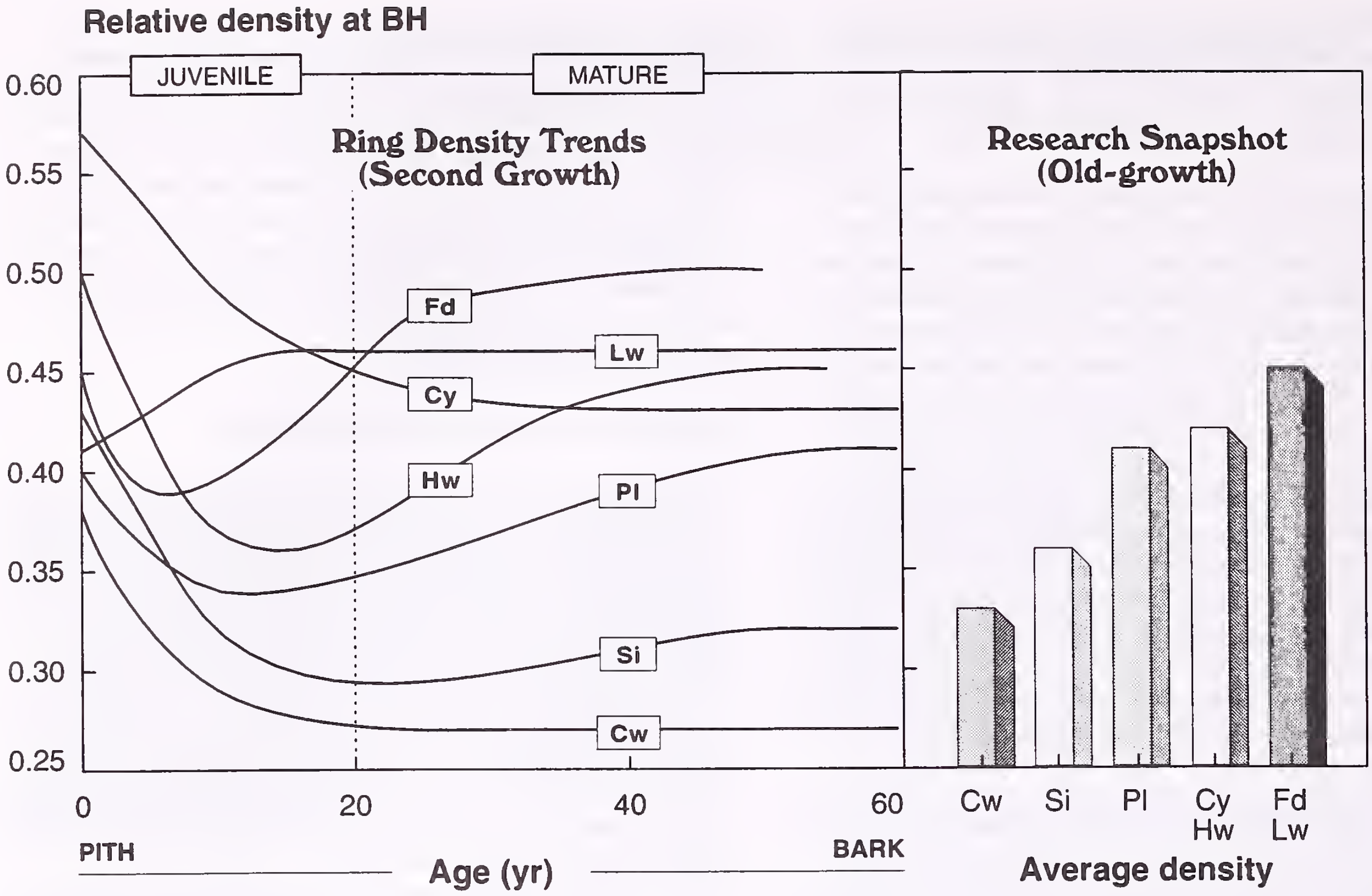

Figure 1—Average wood relative density for British Columbia species from old-growth forests, and pith-to-bark profiles of average ring wood density at breast height as determined by x-ray densitometry for species from second-growth forests. Species symbols are as follows: Cw = western redcedar; Si = interior spruce; Pl = lodgepole pine; Hw = western hemlock; Cy = yellow-cypress; Lw = western larch; Fd = Douglas-fir. (Source: Jozsa and Sen 1992; figure used with permission of senior author).

AGENCIES ENGAGED IN WESTERN LARCH TREE IMPROVEMENT

In Montana, Idaho, and British Columbia, three agencies are presently engaged in operational western larch tree improvement: the Inland Empire Tree Improvement Cooperative (IETIC); the United States Department of Agriculture, Forest Service, Northern Region; and the British Columbia Ministry of Forests.

Members of the Inland Empire Tree Improvement Cooperative have landholdings throughout the Inland Northwestern United States and Southeastern British Columbia and include forest companies, state and federal agencies, tribal councils, and universities. The general objective of the cooperative is to exchange information, ideas and scientific data. More specifically the IETIC was established to identify improved seed and trees for use in reforestation on landholdings of its cooperators and to develop and demonstrate methods and procedures for producing genetically improved forest trees, seed, and other plant material. The administration center for the IETIC is the College of Forestry, Wildlife and Range Sciences, University of Idaho.

The USDA Forest Service, Northern Region is a member agency of the IETIC; however, it maintains a separate western larch program whose goal is to produce genetically improved seed for planting on federal lands within the Inland Northwest. All of the Northern Region's tree improvement activities are coordinated through the western larch working group of the IETIC and, whenever possible, program activities are performed cooperatively. The administration center for the Northern Region's program is located in Missoula, MT.

The British Columbia Ministry of Forest's western larch tree improvement program targets low to mid elevation western larch sites on crown lands administered by the Ministry of Forests. Given the natural distribution of western larch in British Columbia, this encompasses the eastern extent of the Kamloops Forest Region and much of the Nelson Forest Region. Research Branch and Silviculture Branch share responsibility for various aspects of the program. Research Branch is responsible for the development of breeding plans, all genetic testing and breeding activities, supportive flowering physiology research, and the establishment and maintenance of gene archives of all selected materials. Silviculture Branch is responsible for the establishment and management of all seed orchards, and seed extraction, storage, and deployment. Both branches cooperate in parent tree selection activities. Program activities for all tree improvement programs in British Columbia are coordinated through tree improvement councils comprised of provincial, federal, industrial, and university cooperators. The administration center for the BC western larch program is the Kalamalka Forestry Centre, Vernon, BC.

PROGRAM OBJECTIVES AND STRATEGIES

While the stated objectives of all three programs vary somewhat, the general objectives are consistent across programs; that is, to develop seed that has been selectively bred to produce trees with improved volume growth and quality, while maintaining acceptable levels of adaptation and genetic diversity. Similarly, all three share common breeding strategies and program components: recurrent selection for general combining ability for traits related to tree size and quality; wind-pollinated genetic testing in various combinations of long-term, short-term, and clonal testing on high-quality sites; and soil-based and potted-indoor seed orchards.

The current goal of these programs is to produce sufficient quantities of seed to meet the species' projected annual planting demand, which by year 2000 will be approximately nine million seedlings (table 1). Figures 2 and 3 outline the current western larch breeding strategies for the Northern Region and the BC Ministry of Forests, respectively. Since the Northern Region is a key member of the western larch working group of the IETIC, their breeding plans are very similar. The major differences between the two breeding plans relate to breeding zones (figs. 4 and 5), and the Northern Region's initiative to employ rooted cutting performance tests of individuals selected in early selection tests.

Table 1—Projected year 2000 annual seedling requirements (millions of seedlings) in the Inland Northwest and British Columbia by species.

Species	Inland Empire	British Columbia
Spruce	2.05	81.93
Lodgepole pine	3.84	65.16
Interior Douglas-fir	9.13	8.25
Western larch	6.75	1.71
Western white pine	4.26	0.27
Ponderosa pine	5.65	0.03

BREEDING ZONE DELINEATION

Both the IETIC and the Northern Region's breeding zones (figs. 4 and 5) were delineated according to Rehfeldt's (1982) recommendations for seed transfer and breeding zone delineation. The Northern Region has delineated two relatively large breeding zones (Montana and Idaho) and recognized a transition zone where the northern Idaho and Montana zones meet (fig. 4). Seed produced from either the Idaho or Montana seed orchards will be used in this transition zone. To account for genetic differences associated with elevation, the Northern Region further subdivided its breeding zones into two discrete elevational units. Alternatively, the IETIC delineated four smaller breeding zones with some elevational divisions (fig. 5) and, relies on seed transfer guidelines to adjust for genetic differences associated with elevation. The disparity between the IETIC and Northern Region's breeding zones largely reflects the different target land base for management.

The BC Ministry of Forests delineated two breeding zones (East Kootenay and West Kootenay/Shuswap Adams) primarily on the basis of their biogeoclimatic system of ecological classification (Meidinger and Pojar (editors) 1991), and on administrative units (figs. 4 and 5). Since the ecological amplitude of lands targeted for planting

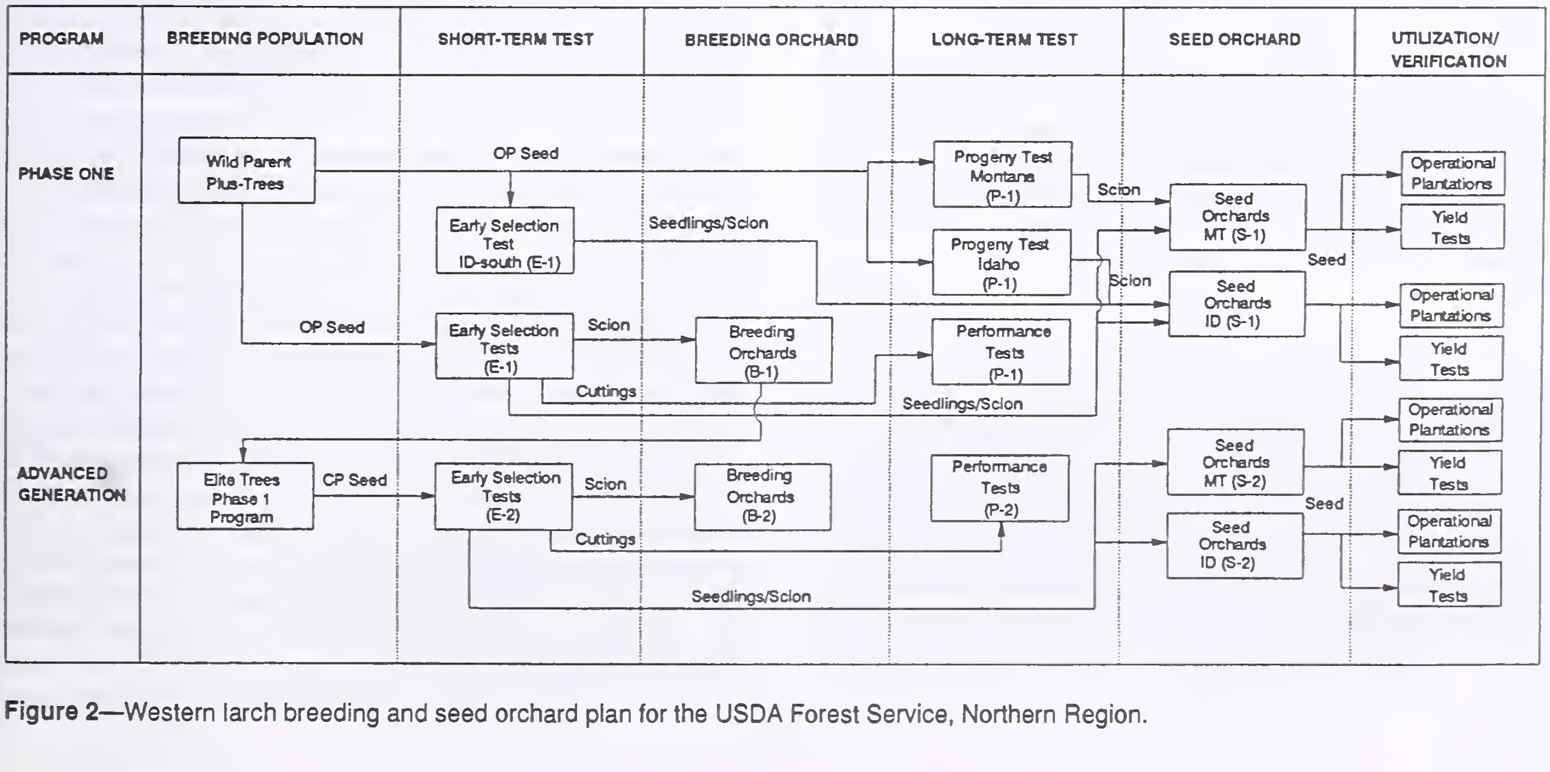

Figure 2—Western larch breeding and seed orchard plan for the USDA Forest Service, Northern Region.

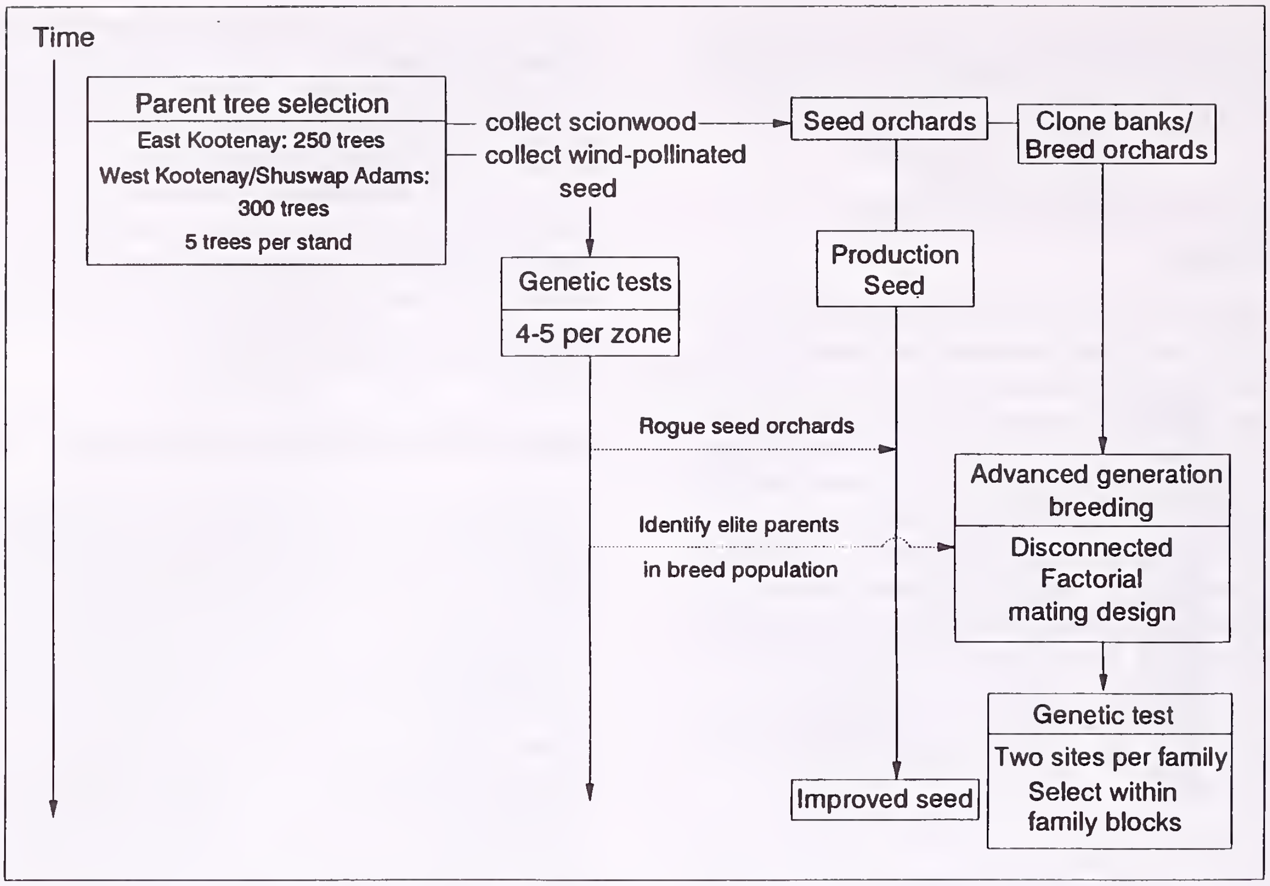

Figure 3—Western larch breeding and seed orchard plan for the British Columbia Ministry of Forests.

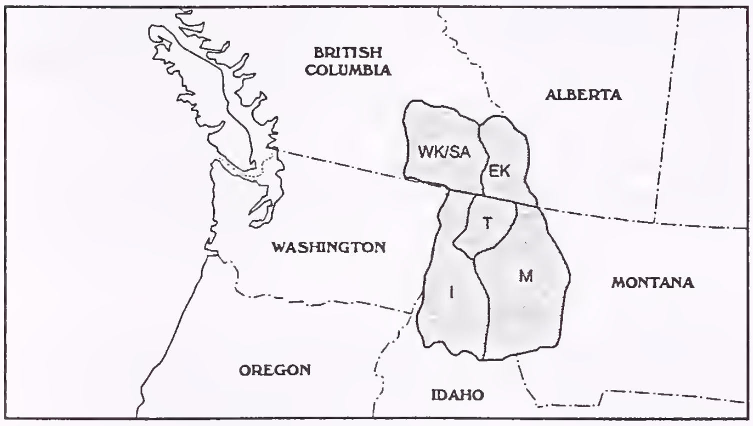

Figure 4—USDA Forest Service, Northern Region, and British Columbia Forest Service western larch breeding zones. Zone identification is as follows: M = Montana; I = Idaho; T = Transition; EK = East Kootenay; WK/SA = West Kootenay/Shuswap Adams.

was relatively narrow and because of western larch's broad adaptability (Rehfeldt 1982, 1992), western larch breeding zones in British Columbia were not subdivided into elevational units. Despite the different method used for delineation, breeding zones in British Columbia are generally consistent with those delineated by the IETIC and Northern Region in terms of size, species composition, and environmental conditions.

PROGRESS TO DATE

Parent Tree Selection

In the IETIC and Northern Region programs, parent trees for the first generation of breeding were selected in natural stands that spanned the geographic distribution and ecological amplitude for which intensive management of western larch was anticipated. In Montana, 10 phenotypically superior parents per stand were selected from the upper fifty percent of the best phenotypes. In Idaho/Washington, between three to five trees were selected per stand. Sufficient wind-pollinated seed was collected for genetic testing from approximately 75 percent of the selected trees. In this phase of selection, wood quality characteristics were given minimal consideration. Parent tree selection in these programs culminated in the early 1980's with the selection of 1,730 parent trees.

In British Columbia, parent tree selection is ongoing. The target number of trees for selection is 550 (East Kootenay zone—250 trees; West Kootenay/Shuswap Adams zone—300 trees). The selection strategy is based on five phenotypically superior trees per stand, the collection of wind-pollinated seed for genetic testing, and the collection of scionwood for the establishment of first-generation seed orchards and gene archives. Two wood core samples are collected from each selected tree for wood relative density determination by Forintek Canada (Gonzalez 1992). To date, 383 parent trees have been selected and propagated by field grafting.

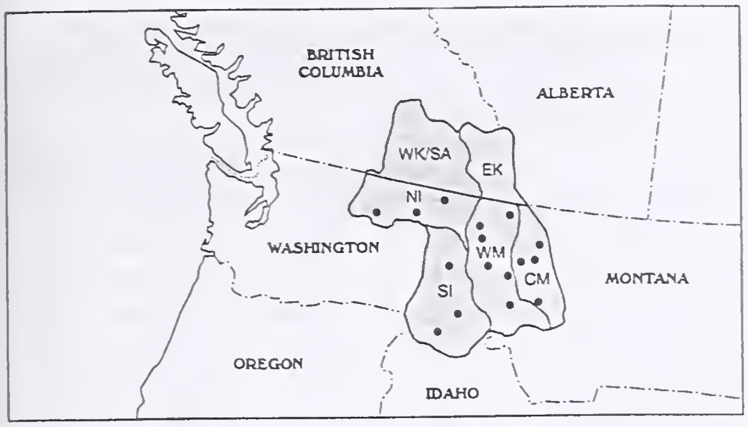

Figure 5—Inland Empire Tree Improvement Cooperative (IETIC) and British Columbia Ministry of Forests western larch breeding zones. Filled circles indicate the location of IETIC long-term genetic tests. Zone identification is as follows: CM = Central Montana; WM = Western Montana; SI = South Idaho; NI = North Idaho; EK = East Kootenay; WK/SA = West Kootenay/Shuswap Adams.

Genetic Testing

The cooperative IETIC/Northern Region genetic testing program combines long-term, short-term, and clonal testing. The goals of the long-term wind-pollinated tests are to evaluate family growth performance and adaptedness across sites within breeding zones, and to provide material for cooperators' seed orchards. Two series of long-term tests (Montana and Idaho/Washington) were planted in 1981 and 1983, respectively. Although formal breeding units had not been delineated at the time of planting, the Montana series was subdivided into three testing zones: central Montana, western Montana low elevation, and western Montana high elevation. This series consisted of 10 test sites (fig. 5) with approximately 450 families included in each test. Genetic entries for each test consisted of all families within the zone (table 2), plus a common set of 100 families from all zones that were planted on all ten sites. These common families serve as standards against which to measure relative performance in all of the tests. The field tests were established in a randomized complete-block design with five replicate blocks of eight seedlings per family per block planted at 1.8 x 1.8 m spacing in non-contiguous plots.

Similarly, the Idaho/Washington series was subdivided into northern and southern zones along latitude 48 degrees. However, in order to reduce the cost of testing and to account for the lack of sufficiently large, uniform sites available for testing, only three field tests were used for each zone (fig. 5). Between 170 to 220 families from within the zone were included on each site and no common families were planted across zones. This series was established in a randomized complete-block design with three replicate blocks of nine seedlings per family per block planted at 2.1 x 2.1 m spacing in non-contiguous plots. In total, the IETIC/Northern Region long-term field test program includes 1,223 wind-pollinated families.

In 1985 and 1988, the Northern Region established early selection tests for the IETIC Idaho North and South breeding units (fig. 5) and the Northern Region's Idaho and Montana breeding units (fig. 4), respectively. The objectives of these tests were to provide data on early growth performance and adaptedness of the wind-pollinated families, and to provide material for cooperators' seed orchards. These early selection tests were established on highly uniform, well prepared test sites that were irrigated and kept free of competing vegetation. A total of 1,060 wind-pollinated families were included in the early selection testing program. The experimental design for these tests consisted of three randomized complete-blocks of 24 seedlings per family per block planted at 1 x 1 m spacing in 3 x 8 tree rectangular plots. Baseline seedling height measurements were recorded after one growing season, and shoot growth and total tree height measurements were recorded during the fourth growing season. The best individuals within the best families were selected on the basis of rate of growth and incidence of *Meria* needle cast for inclusion in advanced generation breeding orchards and production seed orchards.

In order to evaluate the long-term growth performance, response to damaging agents, and adaptedness of forward selections from these early selection tests, the Northern Region adopted a clonal testing program whereby selected trees were cloned by rooting cuttings, and stecklings were outplanted in long-term field tests. Clones of the material included in these long-term tests were held as the breeding population, and subsets of this collection were included in seed orchards.

The British Columbia wind-pollinated genetic testing program began in 1991 with the planting of 140 East Kootenay families, 31 West Kootenay/Shuswap Adams families, and 5 local operational check seedlots on four high-quality sites in the East Kootenay breeding zone. Also, in order to evaluate the long-term effects of extensive seed displacement in western larch, seedlings from 31 wild-stand seed source collections from northern and southern Idaho were planted on all four sites. These field-tests were established in a randomized complete-block design with ten blocks per site. Experimental units consisted of four-tree row plots planted at 2 x 2 m spacing. The second series of genetic tests, which consists of 192 West Kootenay/Shuswap Adams families, 24 East Kootenay families and seven local operational controls, were planted on five West Kootenay/Shuswap Adams sites in spring 1993.

Genetic Test Results

Analyses of 7-year height data from the IETIC/Northern Region long-term genetic tests indicated that stand effects were statistically significant only in the western Montana zones, and family effects were significant in all zones (table 2). Stand x site interactions were significant in western Montana high, and northern Idaho low and mid zones; family x site interactions were nonsignificant across all zones. In the western Montana zones, stand heights were positively correlated with latitude, and negatively correlated with elevation (Fins and Rust 1989).

Average family and individual heritabilities varied considerably across zones, but were highest in the western Montana-low zone (table 3). Average family and individual heritabilities for all zones were .55 and .18, respectively. Estimates of genetic gain from seed orchards based on parental breeding values for 7-year height and 10 percent selection intensity suggested that the largest gains (35 percent) would accrue in the western Montana low zone and the smallest gains (11 percent) would accrue in the North Idaho low zone (table 3). These estimates of gain in early growth are generally consistent with other published estimates of genetic gain for western larch (Rehfeldt 1992) and are very encouraging. They suggest that high economic returns can be made in western larch through selection and breeding.

While these estimates of genetic gain are impressive, enthusiasm should be tempered somewhat as research has shown that genetic gains in early height growth of western larch accrue through small increases in rate of growth and relatively large increases in length of the growing season (Rehfeldt 1992). Consequently, strong selection for early height over just a few generations could inadvertently degenerate traits related to adaptedness and jeopardize genetic gains in future generations. Therefore, it is incumbent upon western larch breeders to continue exploring relationships among traits in breeding and seed production populations; to monitor the effects of selection on genetically linked traits from generation-to-generation; and, if necessary, to develop or refine selection methods that minimize the adverse effects of strong selection for early growth on traits related to adaptedness.

Also, in these data, the relative contributions of predetermined shoot growth and free-growth to genetic variances and the ranking of parents are unknown. As tests mature and the relative contribution of free-growth diminishes, changes in genetic variances, above those normally associated with scale, could occur and rank changes among families might be expected (Joyce 1985; Zhang 1990). Therefore, it is important that these genetic tests be measured over time in order to establish temporal estimates of genetic variances and gain, and to adjust the parental composition of breeding and production populations.

Table 3—Average within zone individual and family heritabilities, estimated genetic gain (cm) and percent gain from ten percent parental selection in 7-year height from western larch long-term genetic tests.

Breeding zone	Heritability Individual	Heritability Family	Estimated gain (cm)	Percent gain
North Idaho low	.21	.50	19	11
North Idaho mid	.24	.60	34	19
North Idaho high	.18	.60	34	19
South Idaho low	.11	.32	37	22
South Idaho mid	.17	.48	27	15
South Idaho high	.19	.53	31	18
Central Montana	.20	.67	26	20
Western Montana low	.27	.73	45	35
Western Montana high	.09	.56	15	16

Seed Orchards

For now and quite likely for the foreseeable future, seed orchards will constitute the primary system for producing genetically improved western larch seed. Since natural stands of western larch typically flower sporadically, frequently lose emerging conelets to spring frosts, and have very low seed yields, existing first-phase seed orchards are located either on sites that are conducive to flowering and are relatively free of spring frosts, or in greenhouses.

Various members of the IETIC western larch working group, including the Northern Region, are in the process of developing seed orchards. Champion Timberlands has established grafted soil-based seed orchards at Plains, MT, for three breeding zones: western Montana high, western Montana low, and central Montana; the Montana Department of State Lands has established a grafted potted-indoor seed orchard at Missoula, MT; Potlatch Corporation has established a small grafted orchard at Cherry Lanes, ID, for their northern Idaho lands; and the Northern Region has established grafted soil-based seed orchards for their Idaho and Montana: high and low breeding zones at tree improvement centers in Sandpoint, ID, and Big Fork, MT, respectively.

Each of the Northern Region seed orchards contains grafts of selected trees from the top 50 families from the respective breeding zone. Expected production date from these orchards is about year 2000. The Northern Region has also established potted-indoor seed orchards for their Idaho low and high, and Montana low breeding zones at Coeur d'Alene, ID. These orchards each contain grafts of two selected individuals from the top 54 families from early selection tests. Expected production date from these orchards is 1996.

Table 2—Analysis of variance significance levels for seven-year height in IETIC western larch long-term genetic tests.

	Breeding zones								
	Central	Western Montana		Southern Idaho			Northern Idaho		
Source of variation	Montana	Low	High	Low	Mid	High	Low	Mid	High
Stand	0.07	0.00	0.00	0.71	0.40	0.07	0.29	0.15	0.39
Family (stand)	0.00	0.00	0.00	0.05	0.00	0.01	0.00	0.00	0.00
Stand x site	0.12	0.56	0.01	0.71	0.40	0.38	0.00	0.01	0.83
Family (stand) x site	0.89	0.47	1.00	0.19	0.32	0.63	0.69	0.66	0.64
Number of families	50	140	185	21	75	75	54	87	45
Number of stands	11	32	44	7	25	25	18	29	15

In British Columbia, two soil-based first-generation seed orchards were established at Vernon in spring, 1990 by field-grafting scionwood collected from wild-stand parent trees. The East Kootenay orchard contains 176 clones, and the West Kootenay/Shuswap Adams orchard contains 147 clones. Both orchards were established in a completely randomized design with between 10 and 20 ramets per clone planted at 2.5 x 5 m spacing. The anticipated date of seed production is about year 1997. As genetic tests mature, both orchards will be rogued to improve their genetic quality. By 1993, virtually all of the clones contained in these first-generation orchards were included in wind-pollinated genetic tests. Separate breeding orchards/gene archives have also been established at Vernon.

ONGOING AND FUTURE RESEARCH ACTIVITIES

In order to ensure the efficient long-term delivery of well adapted, genetically improved and genetically diverse seed for planting, supportive research is critical to these programs. Since seed procurement and reproductive physiology are major areas of concern for western larch tree breeders, seed orchard managers, and silviculturists, several western larch flowering research projects are presently underway. These projects, which are described in detail in Webber and Ross (this proceedings), aim at the following: (1) improving flower production in seed orchards and natural stands through various combinations of GA4/7 application, heat treatment and girdling; (2) improving pollen collection and storage techniques; (3) defining optimal timing of pollen application for controlled breeding and supplemental mass pollination; and (4) exploring the utility and efficiencies of potted-indoor western larch seed/breeding orchards.

Additional ongoing western larch research that is supported either directly or through in-kind contributions include a cooperative USDA Forest Service/BC. Ministry of Forests range-wide provenance test, which consists of short-term and long-term testing of 128 provenances that sample the natural range of western larch; western larch somatic embryogenesis and other methods of vegetative propagation; a comparison of cone production in grafts, rooted cuttings and seedlings; and experiments that explore the genetic relationships between growth and physiological traits such as water-use efficiency as measured by stable carbon isotope discrimination.

Critical issues that are important to the advancement of these programs and have been targeted for future research include: (1) seed orchard technology and management, (2) age-age correlations for selected traits, (3) relationships between performance in long-term field tests and early selection trials, (4) the effects of inbreeding on select and non-select traits, (5) interspecific hybridization, (6) realized gain estimates from area-based yield plantings, and (7) integrating the products of biotechnology research.

CONCLUSIONS

As with all long-term forestry research investments, these western larch tree improvement programs are subject to periodic technical review by panels of invited outside experts. In 1992, the IETIC/USDA Forest Service, Northern Region subjected all of their tree improvement programs to technical review, and are presently in the process of incorporating recommendations into advanced generation breeding plans. Likewise, in 1988, all of the tree improvement programs in British Columbia were technically reviewed, and panel recommendations were incorporated into breeding/seed orchard plans.

In the interim, western larch seed orchards from the first-generation of breeding are beginning to produce seed for planting. As genetic tests mature and inferior clones are removed from these orchards, the genetic quality of seeds produced in the orchards will increase substantially. By year 2000, virtually all of the seed used for planting western larch in the Inland Northwest and British Columbia is expected to be derived from seed orchards. Indeed, the future looks "golden" for western larch.

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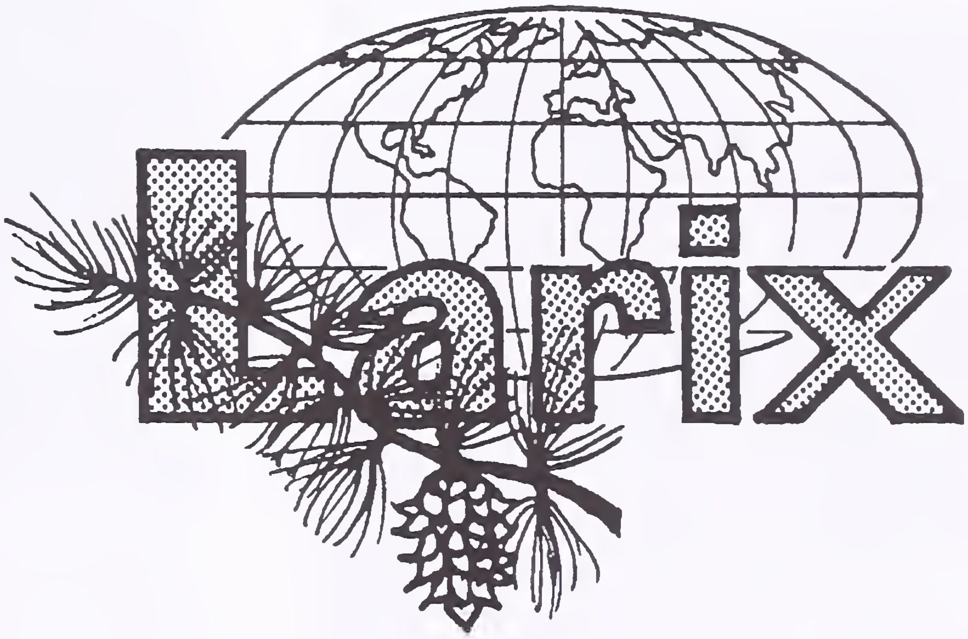
VI. A Look Ahead



Closing Address: Ecology, Environmentalism and Green Religion—Challenges and Opportunities and the Management of Larch Forests

J. P. (Hamish) Kimmins

Forestry around the world is facing unprecedented challenges. A public that was previously too uninformed, too preoccupied with providing the basic necessities for life, or simply too disinterested in environmental issues, has been awakened to the threats to the world environment in general, and to forests in particular. In many cases, the aroused public is challenging the way forests have been, and are being, managed, and in some cases mismanaged. In forestry, business can definitely <u>not</u> continue "as usual."

If this "environmental revolution" had not occurred, there is little question that much of the world's tropical forest would eventually have been lost due to land use changes or degraded by nonsustainable harvesting methods, and that large areas of temperate and northern/high elevation forest would have been subject to continued harvesting at rates and by methods that some people believe to be nonsustainable. Without the past decade of concern about how forests are managed, it is probable that much of the world's forest area would have been managed mainly to achieve timber production objectives, to the detriment of some of the other values of the forest.

One consequence of the "environmental movement" of the 1980's and early 1990's has been a reexamination of how we manage forests and of the values for which they are managed. There is no doubt that this reexamination will result in many improvements in forest management and forest conservation.

However, there are continuing threats to the world's forests. The combined pressures of population growth and poverty will result in a continuing loss of the forest resource in many countries, and continuing inadequate levels of management, especially in the tropical third world. In addition, well-intended efforts to conserve forests may fail, or even be counterproductive, if they are not adequately based in the science of forest ecology and if they do not recognize existing social and economic realities.

Credit for the recent change in public attitudes toward the world's forests lies largely with the environmental movement. Although many foresters have expressed concern about the way in which forests have been harvested and managed, their message went largely unheard by governments and forest companies. Few scientists and academics participated in these issues; most were too preoccupied with reductionist research and the demands of their careers that they do narrowly focused science; many were not interested in dealing with "real world" problems. It was rare for researchers to become involved in the broad social, environmental, and resource issues that beset society, and those who did were frequently ignored by the forest industry and government forestry agencies. It has been a relatively small group of dedicated environmentalists, working largely through the media, who have wrought the change in public awareness of environmental issues that others failed to do. Society owes them a debt of gratitude.

However, society will thank them less if the public consciousness-raising stage (the "political" phase of conservation) in which they have been so successful is not followed by the development and implementation of policies, regulations, and resource management strategies that are successful in solving environmental problems and achieving both sustainable resources and a sustainable environment (the "implementation" phase of conservation).

If the environmental movement is only able to participate in the political phase of conservation, they will have played a necessary but not a sufficient role in the overall conservation process. Unless environmentalists are able to make the transition, when the time is appropriate, from the strategies that are necessary for the political phase to the strategies that are effective in the implementation phase of conservation, the environmental movement will be much less successful in achieving its overall long-term objectives than it has been with its short-term objectives.

One of the threats to the success of the environmental movement is the current confusion between the roles of ecology, environmental belief systems ("green religion"), and what I interpret to be environmentalism: an activity that has as its objective sustaining both the multiple values of the environment and the supply of resources for people from the environment. My objective in this paper is to review the contributions that ecology, environmentalism, and green religion make to conservation and sustainable forest management, and to suggest that environmentalism, rather than ecology or green religion, provides the paradigm for sustainability.

The challenge to foresters today is to find methods of managing forests that will achieve both the social and environmental goals of society, and are consistent with the ecology of the species in the forest. They must also learn to communicate the scientific and social basis for their choice of sustainable systems of management to the

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concerned public. The opportunities posed to foresters by the present level of environmental concern is to use this public pressure to persuade both governments and forest companies to adopt forest policies, regulations and practices that are consistent with good stewardship of the forest and which constitute sustainable management for multiple values.

ECOLOGY

Ecology is a science. It provides no value judgments, though the understanding of ecosystems that ecology can provide may be a partial basis for them. Phrases such as "ecologically sound" forest harvesting or "ecologically destructive" forest management have no scientific basis and no information content outside of the context of society's prevailing value judgment system. Such terms imply that the science of ecology can tell us that one particular condition of a particular ecosystem is best: that it is better than all other possible conditions which that ecosystem might be in.

Implicit in such statements is the idea that ecology, like Father Christmas, knows which forest management has been good and which has been bad. However, ecology cannot tell you if a clearcut is better or worse than a shelterwood, if a young forest is better or worse than an old growth stand, or whether low species diversity is better or worse than high species diversity. These questions can only be answered in the context of forest management objectives or society's prevailing preferences and value systems. Once these preferences and values have been established and agreed upon, ecology can help in the evaluation of whether the present ecosystem condition satisfies society's environmental and resource objectives, whether the effects of management on the form and functioning of ecosystems is consistent with the declared preferences and value systems, and, if not, how management might be altered to satisfy them.

But it is society, not the science of ecology, that establishes the standards. Ecology merely describes, explains, provides a means of predicting future ecosystem conditions, and contributes to the development and implementation of sustainable management strategies.

Ecology had its origins in the middle of the last century. Beginning with the earlier concerns of Malthus about human populations growth, and moving through the developing ideas of evolution, species diversity and genetics (Darwin and Mendel), it became increasingly apparent that the disciplinary sciences of biology, chemistry, physics, and the earth sciences needed a complementary activity that could describe, explain, and predict conditions and events in entire natural or managed ecosystems or landscapes. The genesis of ecology was encouraged by the failure of traditional scientific disciplines to provide a basis for sustainable agriculture and forestry, and to provide the understanding needed to predict and manage outbreaks of pests and diseases. Forest science and agricultural science had the same origins as ecology.

Ecology has not yet served society as well as it might have done. Established as a science dealing with entire ecological systems, it rapidly evolved into subdisciplines dealing with the ecology of individual organisms, with the distribution, abundance, and change over time in groups of organisms of the same species (populations) and with complex mixtures of species (communities). A few ecologists maintained an interest in whole landscape units (ecosystems), but they tended to focus on individual functional processes of the entire system (such as energy dynamics and nutrient cycling) and not on the complex interactions of multispecies assemblages in ecosystems. Ecology began to lose sight of the central focus of the science: how ecosystems work and how they respond to disturbance.

In their attempts to become rigorous and scientifically respectable, ecologists increasingly adopted the reductionist research approach of the disciplinary sciences. Essential for the advance of our understanding of individual ecological processes, reductionism led many ecologists away from the natural complexity of ecosystems into the simplified, artificial realm of experimental science. The lack of appropriate methods and tools for studying whole, complex ecosystems, and the need to understand ecosystem processes in order to understand whole ecosystems, made this trend both inevitable and necessary. However, for a long time it prevented ecology from making major advances in our understanding of, and ability to predict, whole ecosystems, and greatly reduced the contributions of ecology to solving the emerging environmental and social problems associated with overuse, misuse, and abuse of forest ecosystems. Reductionism led many ecologists to focus on the individual pieces of the forest jigsaw puzzle rather than focusing on interpreting the assembled picture and how it changes over time in the face of periodic disturbance, whether natural or human caused.

It is not surprising, therefore, that the science of ecology failed to become the "knight in shining armor" that rescued the environment from its "attackers": us, the human species. Unless it is synthesized and integrated to the level of the ecosystem, much of the current body of ecological knowledge provides little basis for predicting whole ecosystem response to management or natural disturbance; the knowledge was created at the wrong temporal, spatial, and complexity scales for this purpose. But this is not the main problem. No matter how good our ecological knowledge, it cannot, on its own, provide a basis for deciding what is good and what is bad resource management. That must be decided by society.

ENVIRONMENTALISM

Environmentalism is a movement that had its origins in the writings of people such as Thoreau and Leopold: individuals who saw many values in natural, unmanaged ecosystems, and who believed in the need to respect nature. Environmentalists are people concerned about, and who actively work to solve, environmental problems. They are people who advocate the control of human population growth and who promote conservation and sustainable management of the environment and of renewable resources. Environmentalism reflects the desire to conserve and sustain specific values and conditions in the environment in the face of increasing pressures on, and demands from, that environment by people.

People who think of themselves as environmentalists form a remarkably heterogeneous group: from young school children to elderly seniors, from "alternative lifestylers" to "conservative" business people and professionals, and from scientists and academics to applied engineers. "Environmentalists" include concerned citizens who believe in harvesting the things people need from their environment and managing ecosystems to achieve particular ecosystem conditions or resource values, but who insist that this be done sustainably and in a way that respects many resource values. Such people generally base their opinions on the best available information, both scientific and social.

There are also people who call themselves environmentalists for whom environmentalism has become a belief system. Faith is unquestioning belief. It does not require evidence or facts. These people have embraced "green religion" and they have absolute faith in its teachings. Green religion is characterized by many profound beliefs about forest ecosystems, including such ideas as:

- Clearcutting always destroys forest ecosystems.
- Monoculture forests are unnatural and are inherently unstable.
- Plantation forestry always reduces genetic diversity.
- Forests established by planting seedlings (plantations) are not forest ecosystems.
- Natural disturbance (such as fire or windthrow) is the "rebirthing" of nature, whereas management-caused disturbance such as clearcutting is the "crucifixion" of nature.
- High biological diversity is good; low diversity is bad.
- Forests cannot be harvested and sustained.
- The only timber harvesting that should be permitted anywhere is individual tree selection.
- The present condition of a mature or old-growth forest is the correct condition for that forest ecosystem and it should not be changed.
- All forests should be grown on long rotations of at least several centuries.
- Old-growth forests should not be logged.
- Herbicides destroy forest ecosystems and poison wildlife and people.
- There are no forests that have been harvested sustainably more than two or three times. After this, there is progressive ecosystem breakdown.

These ideas are often held passionately, irrespective of whether they agree with our current scientific understanding of what ecosystems are and how they work (which is certainly incomplete and sometimes in error), or whether practical experience around the world suggests that these beliefs are only justified under certain circumstances, or only in particular forest ecosystems, or are entirely unjustified.

Green religion cannot be considered to be environmentalism, because any activity that systematically ignores available knowledge about the scientific and social dimensions of environmental problems poses a major risk of failing to arrive at solutions to these environmental problems. Belief systems that ignore our current understanding of environmental issues are not consistent with the aims and objectives of environmentalism. People who embrace green religion rather than environmentalism must be considered to be a separate and distinct group in society.

CONTRIBUTIONS TO CONSERVATION AND SUSTAINABLE DEVELOPMENT

Ecology

As the science that describes and seeks to understand and predict ecosystems and their components and processes, ecology has a vital role to play in the design of sustainable forest management systems and successful conservation strategies. All too often, conservation measures and resource management activities that ignore our current understanding of ecosystems fail to achieve their objectives. History is replete with examples of the failure of well-intentioned efforts to protect species and environments against mismanagement and exploitation because they were not based on an adequate understanding of ecology.

A sound understanding of ecology is one of the necessary foundations for conservation and sustainable development of resources. However, it is not a sufficient foundation on its own. Because ecology provides no understanding of the social values required from, and provided by forests, and because it provides no basis for value judgments, the science of ecology on its own cannot be a paradigm for conservation or sustainable development. We cannot design "ecologically sound management" or "ecologically wise conservation" based solely on this science. We can only design "environmentally sound" and "environmentally wise" activities based on prevailing social value systems.

Ecology is necessary for conservation and resource management, but it is not sufficient.

Green Religion

Belief systems about forest ecosystems are an essential part of how humans have, and should, conduct their relationships with forests. The concepts of respect for the forest environment, of the spiritual and aesthetic values of forested ecosystems, and of the ethical responsibility to pass on forest ecosystems to future generations without unacceptable loss of values at the landscape level are central to the design of sustainable forest management.

Green religion provides to society a set of ethical standards and moral responsibilities about our forests. This contribution parallels the contributions of the classical religions to human societies. Society would be impoverished without the ethical contributions of religions. However, there is ample evidence that belief systems, on their own, fail to provide a workable paradigm for the organization and conduct of modern society. Unfettered by secular considerations and scientifically based information, religion can become a rigid control system that, taken to extremes, can lead to totalitarian political control.

The intolerance and violence that frequently accompanies the adoption of fundamental religious belief systems as the operational paradigm for a society stands as a warning that belief systems are, like the science of ecology, a necessary but not a sufficient basis for successful conservation and resource management.

Environmentalism

Defined as a system that integrates the inputs from the sciences, both biophysical and social, and "green" belief systems with the needs and aspirations of human societies, environmentalism is surely the paradigm that we need for sustainable resource development and conservation.

Environmentalism and forestry have the same origins: the desire to sustain a defined set of conditions and values in our forested landscapes. There may be a conflict over what balance of conditions and values should be sustained, but there can be no question that sustainability is the cornerstone of both activities. Unfortunately, forestry has often become confused in the public's mind with unregulated exploitation of forests, with greed and wastefulness, and with environmental "damage," none of which should occur in a well managed, sustainable forestry endeavor.

Equally unfortunate, environmentalism has become confused with green belief systems and ecology, neither of which constitute the central concept of environmentalism. The green religion movement has become synonymous in the minds of many people with the environmental movement, and it is assumed by many that ecology provides the guidelines for environmentalism.

As a result of these confusions, foresters are often portrayed as being antienvironmentalist, and environmentalists as being antiforestry. The conflict between economic belief systems and "green" belief systems is used to imply that there is a fundamental conflict between forestry and environmentalism. This is incorrect because economics, though it is of fundamental importance in forestry, is not the sole consideration in forest management, and conversely economics is a vital part of successful environmentalism. Forestry should not be practiced solely according to green belief systems, but foresters should respect such systems and accept that they are one of many necessary inputs to their decisionmaking. Similarly, forestry should not be guided solely by economic belief systems, although economic inputs will always constitute one of the important contributions of planning how forests are managed.

FORESTERS AS ENVIRONMENTALISTS

It is time to sort out the confusion between ecology, environmentalism, and green religion and to recognize the unique contributions that each of these makes to conservation and sustainable management of forests. Failure to do so will render the resolution of our forestry-environmentalism conflicts akin to "bailing fog" (a New Brunswick expression): it is hard to see what you are achieving and little apparent progress is made.

It is time for foresters, environmentalists, and green religion people to establish where they share common goals, where the differences lie, and how they can use the science of ecology to help to design more sustainable forest management.

It is time for foresters to accept that they should be the leaders in the forestry-related environmental movement, and to accept the responsibilities that this implies. This does not mean leaving behind economic, biophysical, and social realities, and embracing uncritically all that green belief systems hold. Rather, it implies a respect for these belief systems and the adoption of values provided by these systems where these values will clearly assist in the achievement of sustainable forest management for a variety of different resource values.

None of this will be easy. But it could not be more difficult and unsatisfactory than continuing the status quo of confusion between the distinct and important contributions made to our quest for sustainability by ecology, environmentalism, and green religion.

CONCLUSIONS

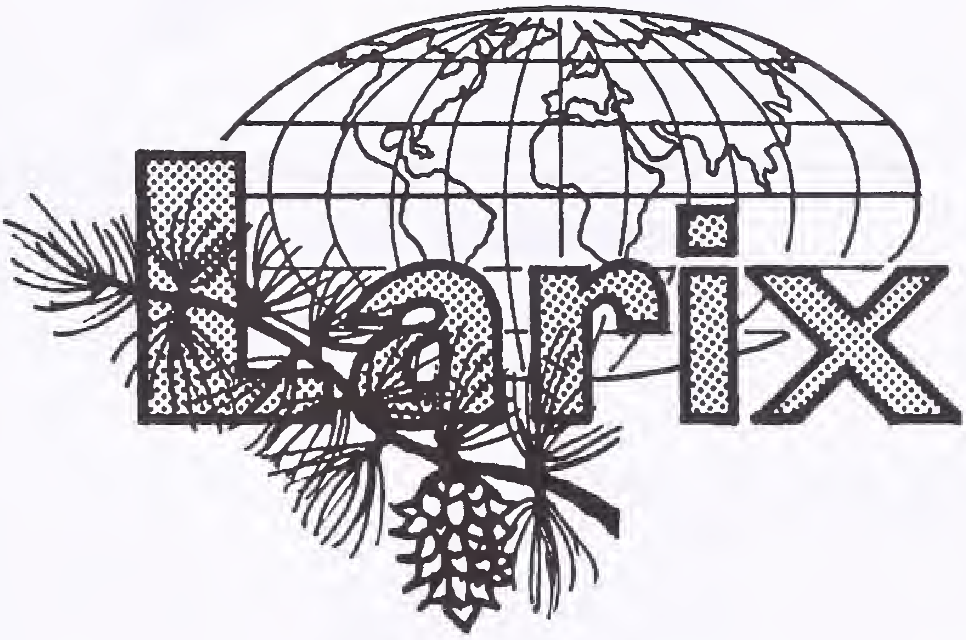
What does all this mean for the future management of larch forests.

Larch forests offer diverse values to society, including timber, aesthetics, wildlife, and biodiversity values. They must be managed to provide the balance of values at the landscape level that the prevailing society deems to be consistent with the basic concept of sustainable development: to satisfy the needs and aspirations of present generations of humans without compromising the ability of future generations to satisfy their needs and aspirations.

Management of larch forests to satisfy the requirements of sustainability will not be successful if based solely on the science of ecology, because this science cannot tell foresters what their goals should be. It will also fail if it is based solely on green religion, because this frequently ignores the ecological requirements of many of the living organisms in forest ecosystems, and the needs of the world's present 5.6billion people, let alone the 12 to 16billion that are expected within the next century.

Broadly defined environmentalism should be the basis for managing and conserving the world's larch forests. This management should be based on the ecology of these forests, should address the multiple values provided by larch forests, and should respect current ethical standards concerning the environment. The foresters performing this management should be dedicated environmentalists (in the broad sense). Unless the forestry profession becomes the leader in forest environmentalism, there is a significant risk that forestry will be based largely on green religion.

VII. Poster Papers



POSTER PAPERS

This section contains 25 poster papers presented at the Symposium on Ecology and Management of Larix Forests: A Look Ahead, Whitefish, MT, U.S.A., October 5-9, 1992.

The Distinctive Distribution of Alpine Larch: Clear Patterns and Enigmas

Stephen F. Arno

GEOGRAPHICAL LIMITS

Several northwestern evergreen conifers—grand fir (*Abies grandis*), white pine (*Pinus monticola*), western yew (*Taxus brevifolia*), western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), and mountain hemlock (*T. mertensiana*)—have natural distributions along the North Pacific coast with an extension inland into the Northern Rocky Mountains (Little 1971). In contrast, alpine larch (*Larix lyalli* Parl.) and western larch (*Larix occidentalis*) are unique in having distributions confined to the inland Northwest only, without an accompanying coastal distribution (Arno 1970) (figs. 1 and 2). Both larches are evidently intolerant to the wet, maritime climate west of the Cascade Crest. The inland Northwest, between the Cascade Crest and the Continental Divide in the Rockies, has a distinctive continental-maritime climate characterized by long, cool, humid winters (mid-October to May at high elevations) and short, relatively dry summers.

Alpine larch's distribution in the Cascades is unusual because it is the only tree occurring in Washington that does not extend south into Oregon. The northern Cascades, where alpine larch is abundant, is a broad band of high mountains with considerable timberline and alpine habitat in the inland, rainshadow zone. Both southward and northward of the species' present range, the suitable high-elevation zone of the Cascades is narrower and often discontinuous.

Like the North Pacific evergreen conifers previously mentioned, alpine larch and western larch appear to be intolerant of the subarctic macroclimate that predominates north of their range limits in the Canadian Rockies. Also like these Pacific conifers, both larches are excluded from the semi-arid continental climates characterizing mountain ranges in eastern and southern Idaho and southern Oregon. Nevertheless, alpine larch shows more tolerance of moderately humid continental climates than western larch or the North Pacific conifers because it alone extends east across the Continental Divide into Alberta and north-central Montana, where it occupies some of the adjacent east-side mountain ranges. In winter this area is subject to extreme temperatures and fluctuations when subarctic cold waves alternate with warm

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ALBERTA
CALGARY
LETHBRIDGE
Bow R.
Milk R.
Missouri R.
Sun R.
CONTINENTAL DIVIDE
MISSOULA
Flathead
Clark Fork R.
Kootenai R.
Big Hole R.
MT
ID
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OR
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NELSON
SPOKANE
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Oregon

Figure 1—Natural distribution of alpine larch (*Larix lyallii*), revised from Arno and Habeck (1972). Snowflake symbols represent isolated occurrences less than 5 km long. Because of fewer detailed observations, the distribution in the Canadian Rockies is illustrated more broadly than in the United States.

Numbers on the map correspond to areas of occurrence as follows (elevations indicate usual zone of occurrence): (1) Salmon Mt., Stripe-Waugh Mts., W. Swet Point; (2) Allan Mt.; (3) Piquett Mt.; (4) Saddle Mt.; (5) Sapphire Range; (5A) Mt. Emerine; (6) E. of Quigg Peak;
(7) Anaconda-Pintler Range (2,440-2,900 m); (8) NW Pioneer Range; (9) Granulated Mt.; (10) Flint Creek Range; (11) Bitterroot Range (2,200-2,900 m); (12) Grave Pk.-Walton Lakes; (13) Mineral Peak; (14) S. Mission Range (2,000-2,500 m); (15) Swan Range; (16) Red Mt.; (17) Chinese Wall and Sun River Mts.; (18) S. Glacier National Park; (19) Preston Park; (20) Logging Mt.; (21) E. of Waterton Lake; (22) Flathead Range; (23) Whitefish Range; (24) Galton Range;
(25) MacDonald Range; (26) S. Canadian Rockies (2,070-2,380 m); (27) Palliser and other ranges E. of Bow River; (28) N. Yoho National Park; (29) Cabinet Range (1,830-2,440 m); (30) Savage Mt.; (31) Roman Nose; (32) Northwest Peak-Rock Candy Mt.; (33) Purcell Mts.; (34) Nelson Range; (35) Slocan Range; (36) Stuart Range and Wenatchee Mts. (1,770-2,300 m); (37) Paddy-Go-Easy Pass; (38) Chiwaukum Mts.; (39) North Cascades (1,680-2,200 m); (40) Tiffany Mt.; (41) Okanogan Range (2,130-2,440 m); (42) Fourth Brother Mt. and Blackwall Peak; (43) Luna Peak.

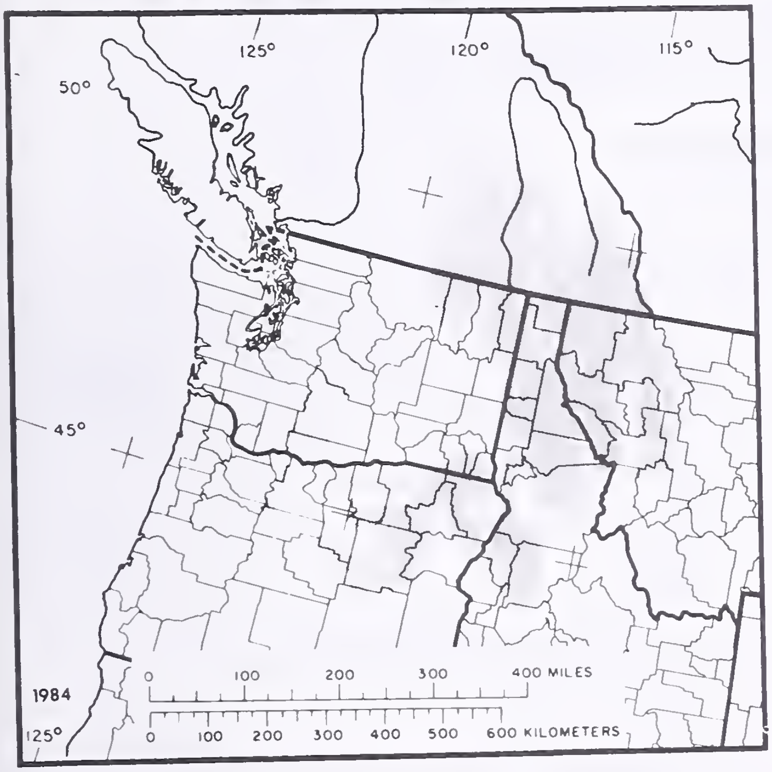

Figure 2—Natural distribution of western larch (*Larix occidentalis*), from Little (1971).

(1970) except for Mineral Peak in the Rattlesnake Mountains, which was discovered later. Perhaps only the outlier populations survived Pleistocene mountain glaciation or maybe they became established as a result of long-distance seed dispersal by Clark's nutcracker (*Nucifraga columbiana*) or some other bird (Vander Wall 1992).

Alpine larch's northern range limits in the Rockies are puzzling because alpine habitat extends continuously northward far beyond this point, which is near 51°35' N. on both the British Columbia and Alberta slopes of the Continental Divide and at 51°36' N. in the Bare Mountains 40 km (25 miles) east of the Divide (Arno 1970). At the species' northern limit on Mount Hector, north of Lake Louise, AB, the trees are thrifty, relatively young, and cone producing. This suggests an expanding distribution. However, Luckman (1986) identified the remains of an alpine larch tree that grew 90 km (56 miles) northwest of the current known distribution between 1000 and 1250 A.D., during the warm Vinland climatic period. Clearly more ecological investigation of the species' northern limits is needed.

The southern limits of alpine larch also exemplify both consistencies and enigmas. The species is abundant throughout the Bitterroot Range, a granitic fault block south of Missoula that maintains constant high elevations southward to 45°46' N. (fig. 1). South of this point lies an increasingly arid region with an undifferentiated mountain complex having only four mountain masses that approach the elevational limit of erect trees—about 2,740 m (9,000 ft). (Evergreen conifers reach their upper limits 200 to 300 m lower than this on steep, rocky north and east aspects, allowing larch to dominate.) All four of these isolated mountain masses—Piquett, Allan, Salmon, and Stripe-Waugh mountains (fig. 1)—support well-developed groves of alpine larch containing both ancient and young trees. Numerous other isolated mountains reaching about 2,620 m (8,600 ft) are without larch. Two small isolated groves occur on north slopes of 2,560 m (8,400 ft) peaks—on an exceptionally steep cirque headwall at Saddle Mountain and in coarse talus on the peak immediately west of Swet Point.

The southernmost groves occupy the north slope of 2,710 m (8,887 ft) Waugh Mountain at 45°30' N. on the north side of the immense, semi-arid Salmon River Canyon. This 1,830-m (6,000-ft) deep gorge slices east-west through the mountains, and although high peaks (2,740 to 3,050 m, 9,000 to 10,000 ft) occur as little as 20 km (12 miles) south of Waugh Mountain, alpine larch is absent. Standing on the summit of Waugh Mountain, one can see what appears to be the effect of a dry microclimate adjacent to the Salmon River Canyon. Looking northward, groves of old and young alpine larch occupy the open rocky cirques down to 2,440 m (8,000 ft) or lower. In contrast, on the high ridge (2,656 m, 8,712 ft) that extends southward 3 km before dropping off into the canyon, the rocky cirques support only a single, mature larch.

CONCLUSIONS

The range of alpine larch is still imperfectly known and presents a fascinating subject for phytogeographical sleuthing. Because of its open habitat and distinctive form, the species often can be identified from a distance using binoculars. From mid-October through May it is distinguished by a defoliated crown composed of long, often gnarled branches. In summer its light green deciduous foliage contrasts with the evergreen conifers, and in late September and early October its yellow and golden color is spectacular. I would appreciate learning of any new locations or other revisions needed in the range map (fig. 1).

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Provenance Testing Use of *Larix Sibirica* and *Larix Sukaczewii* in Iceland

Árni Bragason

More than 100 provenances of eight *Larix* species have been tested in Iceland. Because of good results, the work is concentrated on *Larix sukaczewii* and *L. sibirica,* of which more than 50 provenances have been tested. The best provenances are:

Larix sukaczewii	
Pinega (Archangelsk)	64°35'N
Schenkursk	62°08'N
Yarensk	61°10'N
Velsk	61°10'N
Raivola	60°50'N
Karpinsk	59°45'N
Sverdlovsk	56°51'N
Larix sibirica	
Bogradsk	54°13'N
Askiz	53°08'N
Irkutsk-Altai	52°10'N
Sebalino-Altai	51°17'N

The overall results of a comparison of these provenances show small differences at Hallormsstadur, East Iceland. All showed good growth.

The mean temperature in Iceland (latitude 65°6'N, longitude 14°43'W, altitude 60 m), Archangelsk (latitude 64°35'N, longitude 40°40'E, altitude 13 m), and Irkutsk (latitude 52°16'N, longitude 104°19'E, altitude 467 m) is shown in figure 1. This is a good example of the flexibility of the larch.

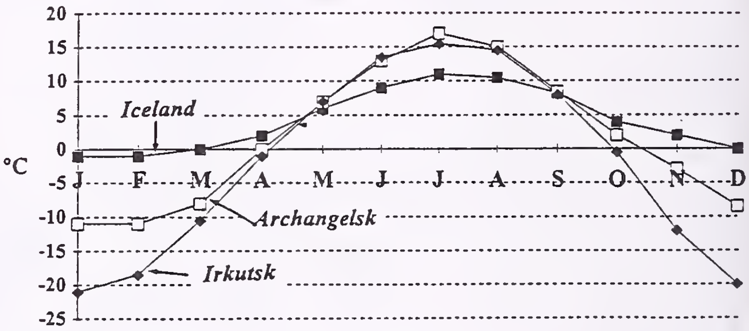

Figure 1—Year-long, mean temperatures in centigrade in three Northern Hemisphere locations.

Larix decidua, L. gmelini, L. kaempferi, L. laricina, L. lyalli. and *L. eurolepsis* have been tested on a smaller scale. The most promising older result is for *L. laricina,* from latitude 63°N, longitude 146°W in Alaska. It outgrows both Siberian and Russian larch at one locality in North Iceland. Most of the recent work has not given any clear lines yet.

Russian and Siberian larch has shown a unique ability to establish on eroded sites in Iceland without use of fertilizers.

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Natural Hybrids of Western and Alpine Larch

Clinton E. Carlson

Western larch (*Larix occidentalis* Nutt.) and alpine larch (*L. Lyallii* Parl.) are two deciduous conifers with overlapping geographical ranges in the Northern Rocky Mountains of Canada and the United States. Western larch thrives at the lower elevations between 760 to 2,300 m; alpine larch is best adapted to higher, more climatically rigorous habitats above 2,600 m. The two species rarely occur together (sympatric because they are usually separated by at least 300 m elevation. This intervening zone is usually occupied by dense forest composed largely of subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) and lodgepole pine (*Pinus contorta* v. *latifolia* Engelm.).

Occasionally, however, western larch and alpine larch occur sympatrically. To date, the only known locations are in the Bitterroot Range southwest of Missoula, MT, U.S.A., and in the Cabinet Range of northwestern Montana. We located these overlap sites by aerial reconnaissance in late September when the species are easily distinguishable due to earlier foliage senescence of alpine larch. Ten sympatric locations were found in the Bitterroot Range (fig. 1) and two in the Cabinet Range. We made on-the-ground visits to five of the sites in the Bitterroot Range and discovered hybrids at all five locations: Big Creek, Kootenai Creek, Bass Creek, Carlton Creek, and Carlton Ridge. The Cabinet sites have not yet been studied.

It is reasonably easy to determine in the field whether a larch tree is a hybrid. Current-year twigs of alpine larch are densely pubescent (hairy), bark of 3-year-old branchlets

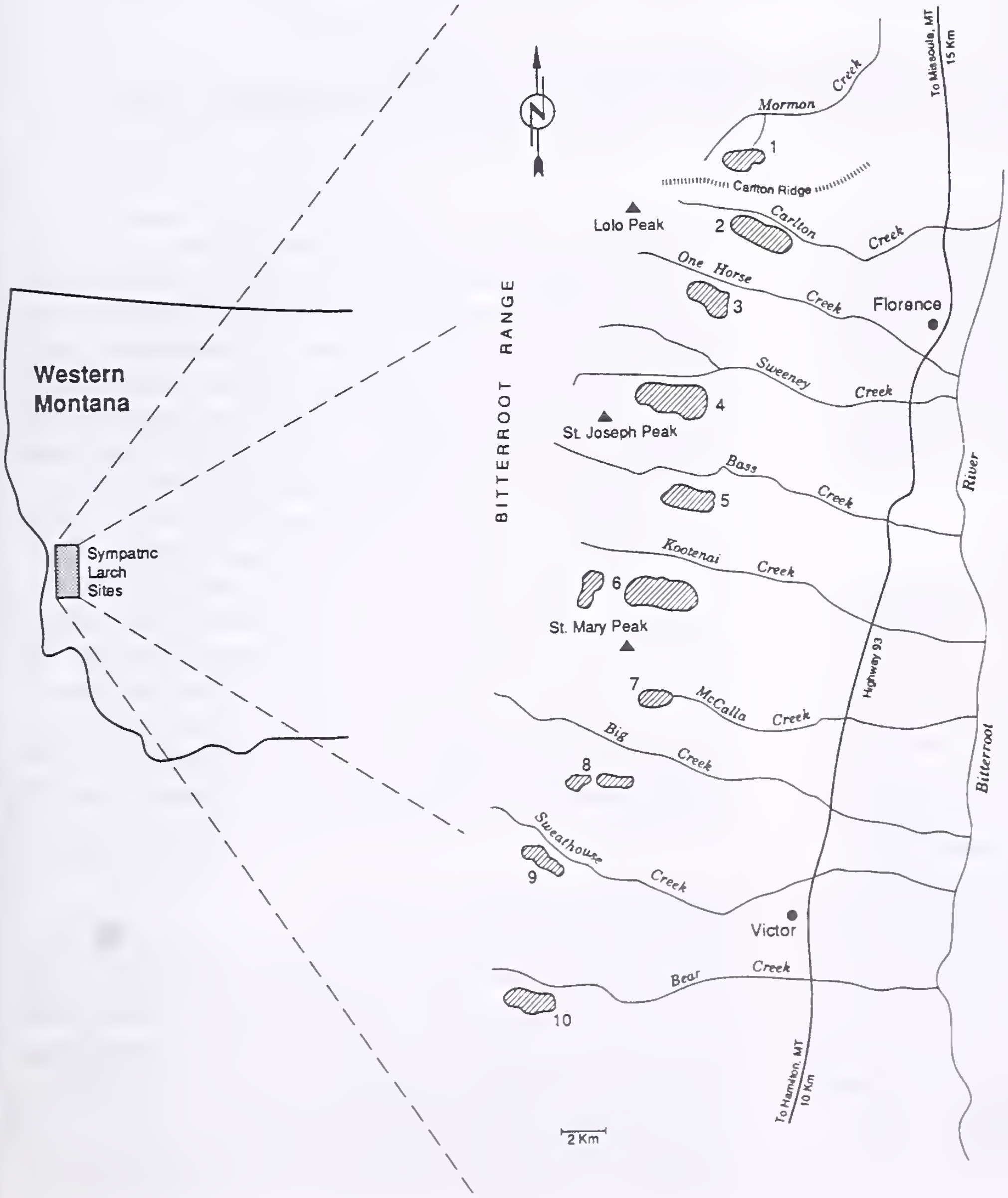

Figure 1—Locations where alpine larch and western larch are sympatric in the Bitterroot Range southwest of Missoula, MT, U.S.A.

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is black-gray and rough textured, color of summer foliage is blue-green, the needles have little luster (not shiny), and foliage by the third or fourth week of September turns a bright golden-yellow. In contrast, current-year twigs of western larch are usually glabrous (not hairy), bark of 3-year-old branchlets is tan and quite smooth, summer foliage is yellow-green and shiny, and foliage by the third or fourth week of September is usually still green, unchanged from summer color.

Hybrids have numerous combinations of the parental characteristics but are usually intermediate in pubescence. Some hybrids have intermediate values for bark and pubescence, have blue-green summer foliage like alpine larch, but have shiny needles like western larch. Others have smooth branchlets like western larch, intermediate pubescence, yellow-green summer foliage like western larch that, however, is not shiny (like alpine larch), and foliage that, like alpine larch, has begun to turn color by the third week of September when western larch are still entirely green. One should observe at least three characteristics before deciding whether the tree is a probable hybrid, but intermediate pubescence is a reliable indicator variable. The high degree of morphological variation observed in the hybrids likely is the result of extensive backcrossing and introgression over time, resulting in a heterogenous population.

During the spring months of 1990 and 1991 we successfully conducted controlled reciprocal crosses (alpine larch pollen to western larch female cones, and western larch pollen to alpine larch female cones). Seeds resulting from the cross pollination were viable, and seedlings are growing well. This work was necessary to determine positively that alpine larch and western larch are genetically compatible. Hybrid seedlings have been outplanted in a replicated experimental design to test growth and development in warm/moist (alpine larch site) environments. Our work on hybridization between these two larches should provide insight concerning the evolution of North American larch species. The first-generation hybrids may be more cold-hardy than western larch and could be suited for cold, wet habitats where neither western nor alpine larch grow.

Advanced Biotechnology in the Genus *Larix*: Potential Integration into Tree Improvement Programs

Pierre J. Charest, Linda L. DeVerno, Krystyna Klimaszewska, Marie-Anne Lelu, and Christine Ward

Several biotechnologies have recently been developed and applied to *Larix* species. Among the most important are somatic embryogenesis, cryopreservation, genetic transformation, and restriction fragment length polymorphism (RFLP). This review of recent progress in these areas includes a discussion on the potential integration of such technologies into conventional tree improvement programs.

SOMATIC EMBRYOGENESIS

Somatic embryogenesis is a tissue culture process that mimics zygotic embryogenesis (Lelu and others 1992). For larch species, it includes the following steps: (1) initiation of embryogenic callus from immature zygotic embryos, (2) maintenance of the embryogenic callus, (3) maturation of somatic embryos, (4) germination of the somatic embryos, and (5) transfer and acclimation of the somatic plantlets.

The process is work intensive and time consuming; a number of improvements are required if we want to use somatic embryogenesis in tree improvement. For instance, it was impossible to obtain embryogenic larch callus from tissues other than immature zygotic embryos. This limited the potential source of improved propagules to a certain period in the year and also limited the time when source material could be preserved. Preliminary results in our laboratories indicate that initiation of embryogenic callus is possible at a low frequency from mature seeds (2/32 for the same provenance of *L. decidua*) and from needles of plants derived from somatic embryos (6/265 explants). In addition, early publications (Klimaszewska 1989; von Aderkas and others 1990) have shown that the somatic embryos produced germinated precociously.

Improvements in the tissue culture sequence has allowed the production of normal somatic embryos in less time than was required initially (10 versus 21 weeks). Our next goal is to achieve the capability to manipulate and produce millions of propagules in a short time (2 to 3 months). We expect to use a bio-reactor to produce large amounts of somatic embryos and robotics to automate the transfer of these propagules efficiently.

CRYPRESERVATION

This process allows the conservation of plant tissues in an arrested state for an extended period. For embryogenic larch callus (Klimaszewska and others 1992), cryopreservation consists of (1) pre-treatment with DMSO and Sorbitol, (2) gradual freezing at a rate of –0.03 °C per minute down to –40 °C followed by immersion in liquid nitrogen, (3) storage in the vapor phase of liquid nitrogen

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(−140 °C), (4) fast thawing when the tissues are required, followed by (5) a posttreatment to eliminate cryoprotectants. The procedure is relatively efficient, and callus tissues grown on solid media can be used without problems.

Cryopreservation is required to properly integrate somatic embryogenesis into tree improvement. It will allow the safe storage of tissues while propagules are being tested for field performance and will reduce the risk of regular subculture such as contamination, somaclonal variation, and loss of embryogenic potential. On that last point, we have observed that in the larches the embryogenic potential decreased noticeably after only 1 year of regular subculturing.

GENETIC TRANSFORMATION

Genetic transformation is the transfer of exogenous genes into living organisms. Numerous methods are available for this, but not all are suitable for conifers. For larch, there is a report of transgenic tree recovery using *Agrobacterium rhizogenes* (Huang and others 1991) but the data presented are preliminary. We have used electroporation (Charest and others 1991) and microprojectile DNA-delivery (Charest and others 1991; Duchesne and Charest 1992; Duchesne and others 1992) to introduce chimeric genes, but no transgenic tissues have been recovered yet. However, microprojectile DNA-delivery appeared to be the most promising approach because of a recent report of transgenic white spruce recovery (Ellis and others 1991). In addition, because the method does not have host range restriction as with *Agrobacterium*, it would undoubtedly be more practical.

In our laboratories, the Biolistic™ method has been used for gene transfer. Optimum conditions were determined. The helium-driven device in combination with gold particles gave the best results. Our work has included haploid and diploid larch embryogenic calli of 21 lines. Differences in transient gene expression were observed, but no correlation was possible except for diploid calli where older cell lines yielded lower transient gene expression. Two gene promoters were identified as suitable for stable transformation work: the wheat ABA-inducible EM promoter and the double 35S promoter of CaMV (cauliflower mosaic virus) linked to the AMV (alfalfa mosaic virus) translational enhancer. This will provide the basis for future gene transfer.

Two avenues could be of potential interest for tree improvement: the introduction of single gene traits that cannot be manipulated through conventional breeding such as insect resistance and the introduction of markers allowing selection of somatic hybrids after cell fusion between larch species.

RESTRICTION FRAGMENT LENGTH POLYMORPHISMS (RFLP)

RFLP's are used as molecular markers to detect genetic variation and to map the position of major genes in the genome and the genetic loci affecting traits controlled by more than one gene. Restriction fragments of nuclear, chloroplast, and mitochondrial—DNA that vary in length depending on parental genotypes—are detected by restriction endonuclease digestion and Southern blot hybridization to specific cloned DNA sequences to compare homologous DNA fragments within and between species. The RFLP markers behave in a codominant manner and are free of epistatic effects; an almost limitless number can be monitored in a single population. Because of its high rate of rearrangement, mitochondrial DNA is useful for studies of interspecific and intraspecific variability.

We have used this technique to determine that the mitochondrial genome is maternally inherited in *Larix* hybrid crosses (DeVerno and others, submitted). Heterologous hybridization analysis of the mitochondrial genome of *Larix leptolepis* indicated that several mitochondrial genes are present in multiple copies. In addition, both qualitative and quantitative differences in mitochondrial restriction fragments were observed between somatic embryogenic callus tissues and the corresponding regenerated trees. The RFLP's in the orf25 gene were used to distinguish among several *Larix* species.

The RFLP technology can help breeders in choosing breeding crosses by identifying lines that have the desired traits and by developing linkage maps for phenotypic traits. The RFLP markers can be used to detect genetic diversity in tree populations for germplasm preservation and phylogenetic analysis and to identify questionable tree species or hybrids.

CONCLUSIONS

The work presented here comprises both manipulative and analytical biotechnologies that can help accelerate tree improvement. The manipulative tools are somatic embryogenesis, cryopreservation, and genetic transformation. They can shorten the time required to obtain improved propagules either by producing large quantities of propagules or by introducing traits of interest faster. The analytical tool presented is RFLP, and it can assist the breeder in selection work to identify specific characters or to determine lineage.

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Knowledge-Based Systems for Larix Forests

Jimmie D. Chew and Elizabeth D. Reinhardt

We have the information necessary to manage natural resources wisely, but it is often difficult to access and use. The information is often fragmented, unwieldy, and time consuming to use. Methods of sharing, distributing, and applying this knowledge are not well developed. But social demands have resulted in increasing complexity in resource management, and economic considerations demand that we look for more efficient ways to capture our knowledge and make it usable.

A combination of fundamental concepts from systems science and principles from artificial intelligence can be used to develop a broad category of decision support systems known as knowledge-based systems. For the Larix forests of the Northern Rockies, several knowledge-based systems exist in various stages of development to help make information accessible and to interpret it for application. These systems cover the range of scales from landscape analysis to individual stand prescriptions.

LANDSCAPE ANALYSIS SYSTEM

A knowledge-based system is currently being developed to provide a framework for the application of the Forest Service's Northern Region's ecosystem management effort. This system will use concepts associated with landscape structure, function, and change. Rule-based components will be used to identify structure and make inferences for function. Knowledge on ecosystem processes will be used to identify the probability of change in both structure and function. The interpretation of changes will be used to design desired landscapes. Differences between current and desired landscapes can identify where management activities are needed to achieve and maintain ecosystem functioning.

STAND DIAGNOSIS SYSTEM

Whether or not one has used a landscape-level analysis to identify large, contiguous areas of stands that need to be evaluated for treatment needs, the stand diagnosis expert system (Chew 1989) is available. This knowledge-based system is called an expert system because it captures the expertise of silviculturists in diagnosis in the silvicultural prescription process. This step compares the existing stand to a desired future condition, a target stand, and identifying possible treatment needs. Silviculturists' and other resource specialists' knowledge in identifying stand conditions that are necessary to meet specific resource objectives on specific types of sites, is captured within the target stands. Stocking level concepts in the Regional Silvicultural Practices Handbook are a fundamental part of the target stand. Limitations on harvest methods identified by Forest Plans or habitat type guidelines are used. Insect and disease information is incorporated as hazard ratings. The system captures local variables such as how suitable leave trees are defined and how one determines the feasibility of removing overstories. The system is available for National Forests within the Northern Region.

The treatment alternatives developed by the system are not prescriptions. Additional interdisciplinary work is necessary before a choice can be made from the possible

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treatments. For the chosen treatment, the silviculturist has to develop a sequence of detailed activities that compose the prescription.

STAND CULTURE SYSTEM

To help prepare the detailed prescriptions, another system is being developed to use the existing research knowledge that is available for stand culture. The results of research at Miller Creek and Coram Experimental Forest on thinning and regeneration of western larch will provide the initial basis for the system. Concepts in stand dynamics will be incorporated into the system. This knowledge will be combined with many tools that are currently available at the Forest and District level such as rating guides for thinning stands. The system will provide a vehicle for technology transfer and consistency in making sure knowledge is applied at the prescription level.

PRESCRIBED FIRE SYSTEM

Prescribed fire is used to manipulate forest ecosystems to accomplish a variety of resource management objectives. Managers use information from a variety of sources that include results of scientific research and of their own experience. A knowledge-based system (Reinhardt and others, in press) was developed to retrieve both technical and qualitative information and interpret it for application. Site data and the manager's objectives for treating the site with prescribed fire are user inputs to the expert system. The system develops a fire prescription: ranges of acceptable fire effects, a description of the desired fire treatment, and a range of conditions under which to burn to achieve the desired treatments and effects. The system's performance was validated using data from research burns in a variety of forest types throughout the Interior West of the United States. It performed well within the limited geographical domain of that area.

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Can Western Larch Plantations Survive and Grow on the East Slope of the Montana Rockies?

Dennis M. Cole and Jack A. Schmidt

With minor local exceptions, the range of western larch (*Larix occidentalis* Nutt.) is restricted to mountainous maritime-influenced areas west of the Continental Divide in the United States and Canada. Frost effects on the flowering and seed production phases are often factors limiting natural regeneration of western larch. However, it has long been known that planted western larch can survive and grow east of the Continental Divide in Montana.

For some years, we have heard of western larch being planted on different eastside Ranger Districts in National Forests, so we made a survey of them, and of personnel of other agencies, to find out more. We were informed of 15 western larch plantings east of the Divide and were able to locate nine of them (fig. 1), each representing a different forest habitat type (table 1). Elevations of the planting sites ranged from 1,340 to 2,164 m, and ages of the plantings ranged from 11 to 25 years.

General differences in survival, development, and condition of the planted western larch could be seen between the different plantations. Because few records exist on the plantations, neither percent survival nor the origin of planting stock could be determined in most cases. However, from visual examinations, we conclude that some of the larch in each plantation will likely persist—perhaps even to maturity.

The major factor limiting fully successful establishment at all sites was frost damage to terminal leaders. This

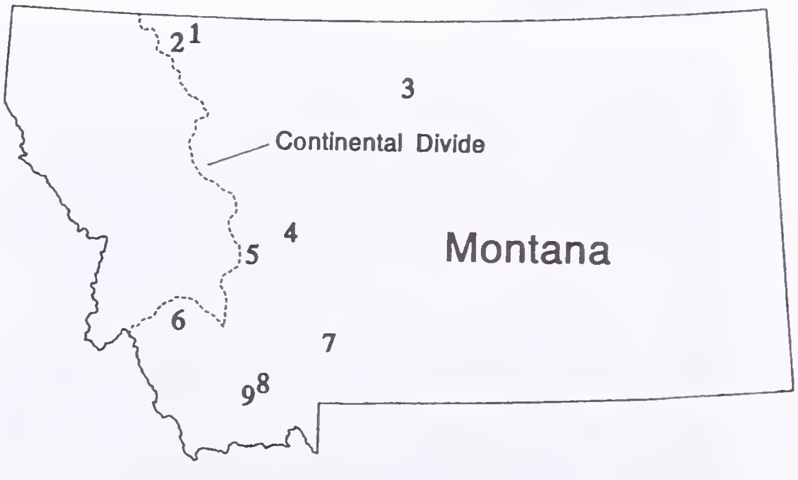

Figure 1—Locations of plantations.

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Table 1—Characteristics of western larch plantations located east of the Continental Divide in Montana

Plantation number[1]	Location	Latitude/longitude	Elevation	Forest habitat type	Plantation age	Range in total heights
			m			*m*
1	Livermore Creek	48°45'N/113°15'W	1,707	*Abies lasiocarpa/Vaccinium globulare*	22	4.6-7.0
2	St. Mary's Lake	48°42'N/113°24'W	1,737	Transition between *Abies Lasiocarpa/ Menziesii ferruginea* and *Abies lasiocarpa/Xerophylum tenax*	12	1.0-4.0
3	Bearpaw Mtns.	48°17'N/109°45'W	1,340	*Pseudotsuga menziesii/Festuca scabrella*	21	4.6-7.6
4	Magpie Ridge	46°46'N/111°32'W	2,000	*Abies lasiocarpa/Linnaea borealis-Linnaea borealis* phase	16	1.2-4.3
5	Lazyman Gulch	46°32'N/112°14'W	1,580	*Pseudotsuga menziesii/Vaccinum globulare-Vaccinum globulare* phase	17	4.6-6.7
6	Bryant Creek	45°48'N/113°10'W	2,134	*Abies lasiocarpa/Menziesii ferruginea*	25	3.7-6.9
7	Bear Canyon	45°36'N/110°55'W	1,646	*Picea/Physocarpus malvaceus*	11	1.5-5.1
8	Timber Creek	45°7'N/111°57'W	2,164	*Abies lasiocarpa/Calamagrostis rubescens*	25	2.1-6.1
9	Sawlog Creek	45°6'N/111°58'W	2,164	*Abies lasiocarpa/Galium triflorum*	25	2.6-7.6

[1] Plantation numbers are the same as shown on the map in figure 1.

effect was greatest in the juvenile years, with some indication that damage is lessening in later years in the older plantations.

The persistence of the planted western larch in some of these relatively severe eastside habitats suggests that, if well-chosen high elevation seed sources are used and the colder or drier sites avoided, western larch can be successfully grown on the east slope of the Montana Rockies. Even more encouraging is the possibility of planting hybrids of western larch and alpine larch (*Larix lyalli* Parl.). We encourage study of this possibility.

Western Larch Containerized Seed Orchards: Adapting a Concept to Meet the Production Seed Needs of the Pacific Northwest

Judith Danielson and Lee Riley

RATIONALE

Western larch (*Larix occidentalis*) presents a well-known seed production problem throughout its range. If its flowering phenology is not out of synchronicity with weather patterns, then either poor pollination or insect damage causes loss of a high proportion of the seed in most years. Larch seed extraction is also difficult and labor intensive, so its notoriously low natural seed set makes the seed costly.

At present, a promising solution appears to be the establishment of greenhouse containerized seed orchards (CSOs). This approach has been in progress since the mid 1970's in the Southeast and in Canada, with such species as loblolly pine, western hemlock, white spruce, Engelmann spruce, and Eastern, Japanese, and European larches. Results with some species have shown that flowering-induced indoor orchards produce ten times as much seed as an equivalent outdoor soil-based orchard, with the seed from both showing the same weight and germination percent, and with indoor-source seedlings outperforming outdoor-source seedlings at 1 year (Eastham and Ross 1988).

Since the initial groundwork on feasibility of CSOs as a seed production strategy has been done, much of the risk has already been allayed. There are, then, several ways in which CSOs can be superior to soil-based seed orchards.

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1. A combined indoor/outdoor environment in a mild climate such as that at Dorena Tree Improvement Center in Oregon, U.S.A., provides manageable control over environmental and insect problems. Freezing of flower buds, poor wind patterns for pollination, drought stress, and cone insect infestations are among the problems that can be controlled. Also, the fact that flower induction requires stress, while cone development and healthy seed production require nurturing conditions, can be used when planning and managing.

2. Experience has shown that, particularly with fast juvenile growth species such as larch, a CSO environment can produce more consistent seed crops, and at a younger age, than a soil-based orchard (Ross and others 1986).

3. CSOs provide more flexibility with the genetic makeup of a seed orchard than soil-based plantings. As progeny test and evaluation plantation results are received, the clonal makeup of the CSO can be modified, with seed production results in 4 to 5 rather than 15 to 20 years. Soil-based orchards seem always to be a generation behind the testing knowledge by the time they reach production capability (Nanson 1986).

4. Control of pollen parentage, controlled-cross pollination, and advanced generation breeding are all facilitated in a CSO environment. A more panmictic seed crop (with a broader genetic base) can also be produced by tailoring pollinations so that male and female clones which ripen at different times can be interbred.

5. Distinct breeding zones can be managed together in the same CSO environment by isolating them with polyethylene barriers or by physically moving pots during pollination. This is a particularly attractive option for minor-component species and species with several breeding zones because it negates the necessity of several distinct sites being maintained for production needs that may vary considerably from year to year.

PROJECT DESCRIPTION

Dorena Tree Improvement Center (DTIC) is located in the foothills of the far southern Willamette Valley of Oregon (lat. 43°45"N, long. 123°W, elevation 240 m). The DTIC is an operational studies station of the Forest Service, U.S. Department of Agriculture, and an administrative subunit of the Umpqua National Forest. In 1991, three National Forests in eastern Washington and Oregon requested Dorena's technical assistance in setting up a strategy for producing practical quantities of western larch seed for reforestation. A plan was developed for establishing containerized seed orchards sited at Dorena, with some paired field seed orchards (FSOs) on the participating forests. Cooperators in the project are DTIC, Colville National Forest, Umatilla National Forest, and Wallowa-Whitman National Forest. Much informational assistance has willingly been supplied by contacts in the British Columbia (Canada) Ministry of Forestry, the Montana (U.S.A.) Department of State Lands, the University of Maine (U.S.A.), and the Iceland Forest Research Station.

Dorena began culturing some rootstock in 1991, and grafting began in 1992, using young (P-1, 1-0, 1-1, and 2-0) rootstock transplanted to 3-5 L pots and select-tree scion from late winter collections on the three National Forests. Ages of ortet scion donors range from 40 to 150, with the majority between 80 and 125. The technique employed is top cleft bench grafting in a greenhouse, using budding strips but no sealant. We attempt a situation in which the rootstock is beginning to show root growth and the scion is still dormant at grafting. To accomplish this, rootstock are brought into the greenhouses 2 to 3 weeks before grafting; the scion are collected, maintained, and transported in a dormant state just above freezing until grafting. The polyhouse grafting has been done as early as possible, in the first 2 weeks of February. Seedling sowing began with 1,700 in 1992 and continued with 760 in 1994. Sowing is done in late March into Leach Supercells, with transplant to 3 L pots the following spring.

As of April 1994, we have now grafted 10,700 potted trees and sowed 2,460 seedlings for FSOs and CSOs in six breeding zones, with plans to graft about 3,000 more in 1995 and 1996. At present we are culturing 8,200 potted grafts and 2,300 potted seedlings at Dorena, with 60 percent in polyhouses and 40 percent outside on gravelled beds; 110 grafts were outplanted to an eastern Oregon FSO in October 1993, and 1,100 more grafts will be outplanted in similar FSOs in fall 1994. The current grafts represent 315 clones, and the current seedlings represent 123 half-sibling families; 19 select trees have both progeny and grafted ramets in the program. Each clone originally has from 20 to 60 ramets grafted, with most at 35. The intent is to produce 10 ramets for FSO outplanting, and 15 to 20 for CSO culture. For each seedling family, 20 progeny are sown. In 1994, 65 clones from two breeding zones were serially regrafted from 1992 grafts, to increase numbers of ramets.

Based on information gathered from past and on-going work in British Columbia (Ross 1991; Webber, J. pers. comm. 1993), we are predicting that we will begin flower induction treatments on half of the 1992 grafts in 1995, with managed pollination and first cone collections expected in 1996. The intervening time will include culturing for vegetative growth; staking, repotting, and moving some trees to an outdoor environment; and pruning to stimulate lateral long shoots and consequent short shoot bud sites in the years before induction treatments. Flower induction treatments will include stimulation with gibberellins and other possible stress treatments such as root pruning, heat, and managed drought.

CURRENT TRIALS

In an effort to develop and refine cultural regimes, flower induction techniques, and pest management plans for production containerized seed orchards, Dorena TIC has undertaken a variety of studies and trials over the past few years.

- Cultural trials were established to determine which combination of factors would yield the highest growth and survival rates in western larch grafts. The trials compared the effects of three fertilizer regimes, two media types, three different environments, and three rootstock types on phenology and morphology of newly grafted stock.

- Monitoring groups have been established for each breeding zone during each grafting year. These groups have been used to compare phenology and morphology under each year's standard cultural regimes.
- Preliminary flower induction trials have been done on four species—western larch (*L. occidentalis*), Port Orford cedar (*Chamaecyparis lawsoniana*), sugar pine (*Pinus lambertiana*), and western white pine (*P. monticola*). Three- to six-year-old seedlings of all species and 30-year-old sugar pine were injected with two different amounts of $GA_{4/7}$ in an effort to induce flowering.
- Preliminary pruning trials have been established to determine the effects of varying amounts of rootstock pruning on the survival and growth of the scion during the first year following grafting. In addition, top pruning at various times and various locations on the scion has been tested to determine the effects on branching and short shoot versus long shoot development in the following year.
- Needle blight, specifically *Meria laricis*, has recently become a problem at Dorena. Small pathology trials have been established to determine the best combination of chemical and cultural methodology for prevention and control.
- In an effort to determine the feasibility of utilizing juvenile material in containerized seed orchards, seedlings have been incorporated into the CSO for two breeding zones. Phenological and morphological traits of the seedling families have been compared with those of the grafted material over time. In addition, these families will be incorporated into future induction trials, as well as any production CSO induction, to identify differences in flowering potential between juvenile seedling material and mature scion material.
- The majority of scion utilized for grafting into the CSO has been collected from 80- to 125-year-old trees. In 1994, a small amount of serial grafting was done using scion collected from stock which was grafted in 1992. A trial was established to investigate the differences in growth rates, survival, and phenology between the two scion sources.

PRELIMINARY OBSERVATIONS AND RESULTS

Two years into this program, we note the following:

- Potted grafts and seedlings of larch (and probably most species) are highly sensitive to excess salinity and excess moisture content in the pot media. In our cultural trials designed to produce rapid graft healing and vegetative growth, our first overwintering experience was disastrous, with the loss of over 60 percent of our original established grafts. This was most certainly due to excess fertilizer salts and moisture retained in the media while the trees were dormant. Currently, we are approaching the puzzle of rapid growth fertilization with frequent monitoring of media conductivity and leaching as required, with as little other irrigation as possible. This is a problem more inherent in the polyhouse than in the outdoor environment in a rainy climate such as Dorena's, but in general we can attain better growth in the greenhouse.
- There are observable growth and vigor differences among clones regardless of culturing regime or rootstock or age of ortet.
- Given the above, there are greater observable differences among some culturing regimes than among the mean of clonal differences.
- We observe eccentric growth patterns of flushing, setting bud, and reflushing which appear to be controlled by a complex of nutrient availability, clonal differences, and possibly juvenile/mature hormonal anomalies between young rootstock and old scion, as well as possible relation to the scion's original position on the ortet.
- Our top-cleft pot grafting technique shows a consistent 86 percent success rate in the first year. This is based on results from 1992 and 1993, as well as what we can observe 90 days after the 1994 grafting. As noted above, survival in the second year for the initial grafts was low, due to a culturing problem. For the 1993 grafts, second year survival is currently at 80 percent, with current losses more related to culturing than to graft failure or demonstrated incompatibility.
- In initial trials with gibberellin ($GA_{4/7}$) on four species, we have observed flowering and seed production in young Port Orford cedar, increased lammas growth in sapling sugar pine, and a possible increased branching response in young potted larch.
- A small number of potted trees grafted in both 1992 and 1993, in two different breeding zones, are showing volunteer female cone flower production in 1994, 1 and 2 years before expected flower induction treatments for seed production.
- There are wide variations in responses to pruning treatments; some of these variations appear to be based on family/clonal differences, and some on season of treatment.
- We experience pathology problems with infestations of the needle cast fungus *Meria laricina*, originally imported on one lot of rootstock. Efforts to control this disease involve pruning, spacing, sanitation methods such as needle vacuuming, and chemical spray to control the spread of spores. However, we are not aware of a practical, IPM-based cure for the problem.
- There are possible differences in growth after serial grafting; the 1994 regrafts are growing faster than the original forest scion grafted in 1992. Whether this is due to grafting-induced phase change or to adaptation to the polyhouse environment after 2 years remains of interest.

PROJECTED TRIALS

Further studies and trials are planned for the near future. The purpose of these trials will be to investigate future aspects of CSO and FSO management, avoid potential production set-backs, as well as fine tune current culturing and induction methodology.

- Further flower induction trials will be established on both grafted and seedling western larch stock. To study the effects on timing and amount of flowering, the trials will include the following variables: different concentrations of $GA_{4/7}$, various times and methods of $GA_{4/7}$ application, root pruning at various times, and exposure to different environments.

- Cultural regimes for potted western larch which will yield optimum growth while remaining cost effective continue to require investigation. Future trials will test various combinations of fertilization and irrigation regimes, as well as environmental requirements, on morphology and phenology of CSO grafts and seedlings.
- Maximizing the numbers of potential flowering sites is one of the key objectives in CSO management. Top pruning during various seasons and at various sites on the scion will continue to be investigated as one of the primary methods to increase branching and short shoot production.
- The Nursery and CSO at Dorena TIC are operated under an Integrated Pest Management plan for prevention and control of pests and diseases. As larch is a relatively new species under culture at Dorena, new problems will continue to be encountered. Therefore, investigations into biological and chemical control methods will be an on-going part of CSO management.
- Unlike the majority of commercial tree species, many aspects of western larch phenology are not well understood. Investigations into budbreak/multiple flushing, growth patterns, dormancy/cold hardiness are scarce. Therefore, phenology trials will continue to be a portion of the objectives of the larch CSO.
- Pollen management, including production, collection, storage, and handling, will be of prime importance for CSO and FSO management in the near future. Consequently, Dorena is working with a variety of methods to determine the optimal management regimes for enhancing seed production.
- As with any movement and culturing of seed orchard stock outside its breeding zone, the possibility exists for effects (or "after-effects") on the seed and progeny produced in the non-native environment. These after-effects may be the result of temperature, nutrition, photoperiod, or hormonal treatment which vary considerably from the natural habitat (Johnsen 1988). In an effort to investigate this possibility, paired orchards—for example, both field and CSO—have been established in three breeding zones, with a fourth pair to be established in the near future. When available, seed from the paired orchards will be tested in germination and nursery studies to examine viability, phenology, and morphology of seed and seedlings from the two environments.
- The time course of maturation in *Larix* species has been examined through grafting of scion of different ages (Greenwood and others 1989). Phase change—for example, juvenile to mature or mature back to juvenile states—is also being studied at Dorena. Methods to produce mature flowering sites on juvenile material (seedlings) is under investigation. In addition, the effects of grafting scion from 80- to 100-year-old trees onto 1- to 2-year-old nursery stock will continue to be explored.

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Factors Affecting Seed Yields of *Larix* in Michigan's Upper Peninsula

Dongill Shin and David F. Karnosky

Low seed yield and poor seed quality in larch result from genetic and environmental factors that act at different stages in the reproductive cycle. These factors can be categorized into three stages according to their time of action:

1. Prepollination factors (pollen quality and strobili abortion).
2. Factors acting between pollination and fertilization (frequency of pollination, number of pollen grains in the ovule, degeneration of female gametophyte, and degeneration of female strobili after pollination).
3. Postfertilization factors (frequency of fertilization and embryo degeneration).

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We investigated these factors in four larch species (European larch—*Larix decidua*; Japanese larch—*L. leptolepis*; Siberian larch—*L. sibirica*; tamarack—*L. laricina*) growing in the Upper Peninsula of Michigan. Our study showed that some seed loss was caused by all of these factors. However, abortion of female strobili and embryo degeneration were most important factors affecting seed yield in our study.

MATERIALS AND METHODS

Meiotic Irregularities During Pollen Formation

Male strobili were collected at monthly intervals from October 20 until March 16 when 2-day interval collections were made until meiosis was completed. Strobili were fixed in FAA solution. For staining, microsporangia were squashed in acetocarmine and examined microscopically. Five hundred PMC's from five strobili for each species were analyzed and irregularities were identified.

Pollen Germination

Male strobili-bearing branches of four species were collected on April 15 and forced to dehisce pollen in 7-up solution at room temperature. Subsamples of the pollen were placed in sterile microplates containing 100 µl of medium in each well. After 5 days incubation at room temperature in the dark, germination rates were determined from five replications of 100 pollen grains from each well.

Pollination and Frequency of Pollination

Branches with abundant female strobili were bagged after removing all male strobili on April 10. When female strobili were fully receptive (April 25), pollen grains were applied on the strobili with a fine paint brush. Two weeks after pollination, three cones from each cross were collected and ovules were examined under a dissecting microscope to determine the presence of pollen on micropylar arms. To determine the number of pollen grains in the micropylar canal, ovules were taken from cones collected 5 weeks after pollination. Ovules were fixed in FAA solution, dehydrated in a alcohol-xylene series, and embedded in TissuePrep. Embedded specimens were serially sectioned longitudinally at 8 µm and stained with safranin and fast green for microscopic observation. Probability of successful pollination was calculated by multiplying pollen germination rate by the number of pollen in the ovule.

Degeneration of Female Strobili

Two weeks after pollination, the number of degenerated strobili in pollination bags were counted and the rate was determined.

Degeneration of Female Gametophyte

On May 20, three cones from each cross were collected and ovules were cut in half transversely. Ovules with shrivelled megagametophytes were counted from collected cones.

Fertilization

Frequency of fertilization was determined for ovules collected from late May to mid-June. Twenty ovules from three cones for each cross were fixed and longitudinal serial sections were made as described above. Ovules showing pollen tubes, egg cells with male gametes present, or vacuolated and granular-shaped egg cells were considered to have been fertilized.

Embryo Degeneration

To determine the rate of embryo degeneration, 20 ovules from three cones for each cross were collected at 8 and 12 weeks after pollination. They were fixed and sectioned as described above. Presence and number of early embryo (globular stage: 8 weeks after pollination) and late embryo (torpedo stage: 12 weeks after pollination) were analyzed for sample ovules of each cross and the rate of embryo degeneration was determined.

RESULTS

Table 1 shows estimated losses by factors investigated.

Meiotic Irregularities

The major abnormalities observed commonly in all four species were chromosomal stickiness, degeneration of pollen mother cells, acentric chromosome fragments, unequal distribution of chromosomes at anaphase, lagging chromosomes, and aberrant microspores. Among the four species, Siberian larch was observed to have the highest frequency

Table 1—Comparison of losses as expressed as percentages attributed to various factors and actual loss of seed determined by undeveloped and empty seeds at harvest time

Factors	Cross[1]			
	E x J	T x E	J x E	S x E
	Percent			
Pollen quality	2.0	14.8	6.8	6.2
Lack of pollination	7.3	25.0	4.5	2.3
Degeneration of female gametophyte tissue	5.8	4.0	6.8	4.6
Lack of fertilization	10.0	25.0	15.0	20.0
Embryo degeneration	20.0	40.0	35.0	30.0
Cumulative loss by above factors	45.1	108.8	68.1	63.1
Actual loss[2]	38.6	92.0	41.4	61.6

[1] E x J = *L. decidua* x *L. leptolepis*, T x E = *L. laricina* x *L. decidua*, J x E = *L. leptolepis* x *L. decidua*, S x E = *L. sibirica* x *L. decidua*.

[2] Loss determined by sorting seeds from 10 cones of each cross at harvest time.

of abnormal meiosis. Around 16 percent of its PMC's were degenerated, and 12.4 percent of cells formed aberrant microspores. We believe that high frequency of meiotic irregularity in Siberian larch was partly due to its earliness in meiosis.

Pollen Germination

Tamarack showed the highest germination rate (78.7 percent) while European larch was the lowest (46.5 percent). The germination tests revealed that there was little correlation between frequency of meiotic abnormality and pollen germination. For example, the pollen germination rate of Siberian larch was higher than that of Japanese larch, which had the lowest in frequency of meiotic abnormality. This result indicated that some meiotic irregularities could recover to form normal pollen, while pollens that seemed cytologically normal may have other deficiencies.

Pollination Frequency

Pollination frequencies were more than 90 percent except in tamarack, whose frequency was 75 percent. Furthermore, most of the ovules were pollinated with more than one pollen. This fact indicated that pollen quality was not the major factor reducing seed yield.

Abortion of Female Strobili

Strobili abortion soon after pollination was high in all four species. In Siberian larch, about 80 percent of strobili were aborted either by contact with pollination bags or by frost damage.

Degeneration of Female Gametophytes

Abortion of ovules before fertilization, which gave rise to flat seeds, was observed in 4 to 6.8 percent of ovules depending on the species.

Fertilization Frequency

Frequency of ovules in which fertilization had occurred ranged 75 to 90 percent depending on the cross. The cross between tamarack and European larch was the lowest, while the cross between European larch and Japanese larch was the highest. It seemed that there might be a certain degree of incompatibility between some larch species.

Embryo Degeneration

Embryo degeneration during early stages of development was common in all four species. Embryos degenerated in 20 to 40 percent of the fertilized ovules depending on the cross but were most common in the tamarack x European larch cross. The frequency of polyembryony at the early stage of embryo development influenced later stage embryo condition. It is possible that competition among embryos in a seed contributed to degeneration of embryos.

Larix Lyallii and Larix Occidentalis Within USDA Forest Service Research Natural Areas

Angela G. Evenden

The Forest Service, U.S. Department of Agriculture, participates in a federal program to develop a national network of Research Natural Areas. The major goal of this network is to preserve a representative array of all significant natural ecosystems and their inherent processes as ecological baseline areas. The Forest Service has established nearly 300 Research Natural Areas nationwide. These areas are important ecological reference sites and are used for scientific studies, education, and long-term ecological monitoring. The areas are managed to maintain natural conditions, with as little human intervention as possible. However, in some ecosystems, human activities have interrupted natural processes. In these cases, prescribed management actions may be required to restore the processes upon which the natural communities and species depend.

Habitat type and plant association classification systems are often employed to set targets for ecosystems to include within the Research Natural Areas network. *Larix lyallii* (alpine larch) and *L. occidentalis* (western larch) are represented in these areas within a variety of classified vegetation types. *Larix lyallii* is found at high elevations, often near treeline, in *Abies lasiocarpa* forest types of Idaho, Montana, and Washington. Table 1 lists the eight areas in the Northwestern United States containing *L. lyallii*. *Larix occidentalis* is a seral component of mid-elevation *Pseudotsuga menziesii* forest types. Old-growth and mature stands of *L. occidentalis* occur within 27 areas in Idaho, Montana, Oregon, and Washington (table 2). Common overstory dominants in these RNAs

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Table 1—List of Research Natural Areas (RNA) on National Forest System lands in Idaho and Montana representing subalpine forests dominated by *Larix lyallii* Parl. (alpine larch). National Forest, RNA size (hectares), elevation range (meters), and associated species are also presented

State and RNA	National Forest	RNA size	RNA elevation range	Associated tree species
		ha	*m*	
IDAHO				
Allan Mountain	Sawtooth	668	2,912 to 3,707	*Abies lasiocarpa*
Grave Peak	Clearwater	146	2,088 to 2,524	*Pinus albicaulis,* *Abies lasiocarpa*
Salmon Mountain	Bitterroot	778	1,939 to 2,682	*Pinus albicaulis,* *Picea engelmannii,* *Abies lasiocarpa*
MONTANA				
Bass Creek (proposed)	Bitterroot	803	1,244 to 2,564	*Pinus albicaulis*
Carlton Ridge	Lolo	372	1,700 to 2,500	*Pinus albicaulis* (overlaps with *Larix occidentalis* at lower limits in RNA)
Dexter Basin (proposed)	Deerlodge	448	2,347 to 3,899	*Abies lasiocarpa*
Sapphire Divide (proposed)	Bitterroot Deerlodge	546	2,316 to 2,708	*Pinus albicaulis,* *Picea engelmannii,* *Abies lasiocarpa*
Tuchuck	Flathead	835	1,585 to 2,220	*Pinus albicaulis,* *Abies lasiocarpa*

Table 2—List of Research Natural Areas (RNA) on National Forest System lands in Idaho, Montana, Oregon, and Washington representing subalpine forests dominated by *Larix occidentalis* Nutt. (western larch). National Forest, RNA size (hectares), elevation range (meters), and associated species are also presented

State and RNA	National Forest	RNA size	RNA elevation range	Associated tree species
		ha	*m*	
IDAHO				
Aquarius	Clearwater	1,579	488 to 1,218	*Thuja plicata,* *Pinus monticola,* *Abies grandis,* *Pseudotsuga menziesii*
Bear Creek	Payette	126	2,106 to 2,537	*Pseudotsuga menziesii*
Cuddy Mountain	Payette	425	1,474 to 2,754	*Pseudotsuga menziesii*
Hunt Girl Creek	Idaho Panhandle	609	1,200 to 1,900	*Thuja plicata,* *Tsuga heterophylla,* *Pinus monticola,* *Abies grandis*
Montford Creek	Idaho Panhandle	118	930 to 1,341	*Pseudotsuga menziesii,* *Abies grandis,* *Pinus monticola*
Upper Fishhook	Idaho Panhandle	130	1,823	*Thuja plicata,* *Abies grandis,* *Pinus monticola,* *Pseudotsuga menziesii*
Upper Shoshone Creek	Idaho Panhandle	534	1,090 to 1,954	*Pseudotsuga menziesii,* *Pinus contorta*

(con.)

Table 2 (Con.)

State and RNA	National Forest	RNA size	RNA elevation range	Associated tree species
		ha	*m*	
MONTANA				
Bass Creek (proposed)	Bitterroot	803	1,244 to 2,564	*Pseudotsuga menziesii, Abies grandis*
Barktable Ridge (proposed)	Lolo	341	1,646 to 1,905	*Pinus ponderosa, Pinus monticola, Pseudotsuga menziesii*
Big Creek	Kootenai	77	745 to 800	*Pinus ponderosa, Pseudotsuga menziesii*
Carlton Ridge	Lolo	372	1,700 to 2,500	*Abies lasiocarpa, Picea engelmannii, Pinus contorta* (overlaps with *Larix lyallii* at upper limits in RNA)
Coram	Flathead	340	1,060 to 1,440	*Pseudotsuga menziesii, Abies lasiocarpa*
Lower Ross Creek (proposed)	Kootenai	368	866 to 1,402	*Thuja plicata, Pinus contorta*
Petty Creek	Lolo	125	1,200 to 1,500	*Pseudotsuga menziesii, Pinus contorta, Abies grandis*
Plant Creek	Lolo	105	1,500	*Pseudotsuga menziesii, Pinus contorta*
Pyramid Creek	Lolo	210	1,600 to 2,460	*Pseudotsuga menziesii*
Swan River	Flathead	276	942 to 1,049	*Pinus contorta, Pinus monticola, Pseudotsuga menziesii*
Ulm Peak	Kootenai	279	1,273 to 1,953	*Pseudotsuga menziesii,*
Wolf-Weigel	Kootenai	101	1,082 to 1,311	*Pseudotsuga menziesii*
OREGON				
Canyon Creek	Malheur	284	1,433 to 1,798	*Pseudotsuga menziesii, Abies grandis*
Indian Creek	Wallowa Whitman	396	1,872 to 2,125	*Pseudotsuga menziesii, Pinus contorta, Abies lasiocarpa, Tsuga mertensiana*
Metolius	Deschutes	581	850 to 1,460	*Pseudotsuga menziesii, Pinus ponderosa, Arctostaphylos patula*
Mill Creek	Mt. Hood	330	790 to 1,040	*Abies grandis, Pinus ponderosa*
Ochoco Divide	Ochoco	777	1,250 to 1,650	*Pseudotsuga menziesii*
Rainbow Creek	Umatilla	170	1,100 to 1,440	*Abies grandis, Pseudotsuga menziesii*
WASHINGTON				
Meeks Table	Wenatchee	27	1,280 to 1,585	*Pseudotsuga menziesii, Calamagrostis rubescens*
Salmo	Colville	563	1,158 to 2,080	*Thuja plicata, Tsuga heterophylla*

are *Pseudotsuga menziesii, Abies grandis, Thuja plicata,* and *Pinus monticola.*

All Research Natural Areas are available to the scientific community for nonmanipulative research and ecological monitoring. Permission to utilize an area for research may be obtained through the National Forests and the Forest Service Research Stations.

Distribution and Sustainability of *Larix Gmelini* Seed in the Soil in Northern Da Xingan Ling Mountains, China

Huacheng Xu and Yong Ban

Old-growth larch (*Larix gmelini*) produce heavy seed crops that are naturally dispersed in the soil after a mast year. Seed dispersed in the different forest types varies from 190 to 320 seeds/m^2—the most in the vegetative association of *L. gmelini-Betula fruticosa*, followed by that in the *L. gmelini-Alnus mandshurica*, and *L. gmelini-Ledum palustre* associations. Seed dispersal does not vary greatly within each forest type.

Seeds are located mainly in the upper 2 to 4 cm of soil. Seeds distributed through all soil layers averaged 70 to 80 percent viability. Seeds germinate rapidly under optimal conditions, but seed viability, for the most part, lasts no more than a year. However, a few will germinate in the second year. The presence of soil pathogens may accelerate the loss in viability. A seed sowing experiment with this larch produced the same results as those observed in the natural forest. The *L. gmelini* seed bank quite evidently belongs to the interrupted type.

Authors were not able to attend the symposium but did submit this poster. Huacheng Xu is Professor of Forest Ecology, P.O. Box 120, College of Forest Resources and Environment, Beijing Forestry University, 100083, People's Republic of China; Yong Ban Ph.D., is Research Ecologist, P.O. Box 68, Chinese Academy of Forestry, Beijing, 100091, People's Republic of China.

Net Photosynthesis of Western Larch and Sympatric Evergreen Conifers Along a Precipitation Gradient in Western Montana

Brian D. Kloeppel, Stith T. Gower, and Peter B. Reich

Several studies have compared the productivity of larch and sympatric evergreen conifers at one location (Gower and others 1989; Matyssek 1986). However, we are not aware of any studies that have compared the productivity and carbon assimilation across an environmental gradient to elucidate how resource availability may influence the carbon balance, and hence, the competitiveness of larch and co-occurring evergreen conifers.

This study is part of a larger study to compare the productivity and resource use efficiency of western larch (*Larix occidentalis* Nutt.) and sympatric evergreen conifers along a large edaphic gradient within the natural distribution of western larch in Montana. The objective of this study is to compare the diurnal net photosynthetic rates for western larch and sympatric evergreen conifers during June and August when water stress is moderate and severe, respectively.

MATERIALS AND METHODS

Site Descriptions

Three sites were established in May 1992 along an edaphic gradient in western Montana. The sites were selected to include a broad range in edaphic conditions within the natural distribution of western larch (fig. 1). Selection criteria for all sites included (1) a closed canopy, (2) a lack of recent (10 years) stand disturbance, (3) a 50/50 mix (basal area basis) of western larch and a sympatric evergreen conifer, (4) an even-aged stand, and (5) adequate road access for whole tree sampling and equipment transportation.

Mean annual precipitation for the three sites—Bonner, Lost Creek, and Savage Lake—was 330, 450, and 640 mm, respectively (table 1). A seasonal drought in July and August is common at all sites. Despite considerable effort, all of the site selection criteria could not be achieved.

The Bonner site consists of an even-age stand of western larch and Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco) that originated after a fire in approximately 1894 (B. D. Kloeppel and S. T. Gower, unpublished data). The Lost Creek site consists of an even-age

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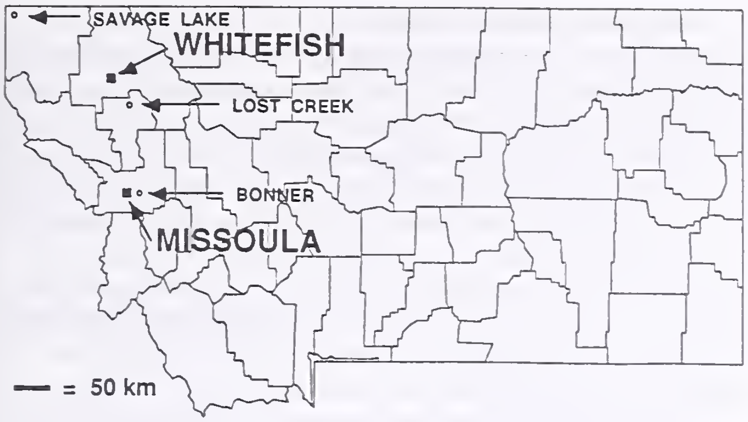

Figure 1—Location of western larch study sites in the Rocky Mountains of western Montana, U.S.A., in referece to the communities of Whitefish and Missoula.

stand of western larch and Douglas-fir with a small component (less than 4 percent basal area) of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.); this forest originated after the large Swan Lake slash fire of 1920 (J. Yates, personal communication). The Savage Lake site consists of an even-age stand of western larch and lodgepole pine with a small component of ponderosa pine (*Pinus ponderosa* Laws.); this forest originated after a clearcut in 1958 and was precommercially thinned in 1985 (R. Hudson, personal communication).

Field Measurements

Net photosynthesis was measured during moderate and severe water stress periods of the 1992 growing season. All photosynthetic measurements were restricted to days with full sunlight. Since the study sites were a considerable distance apart (375 km), only one site could be measured per day. Consequently, net photosynthesis was measured between June 19 and 23 and August 4 and 10; while at each site, net photosynthesis was measured five times diurnally during regularly spaced intervals from 0800 to 1800 hours (MDT).

Five to seven sunlit foliage samples of each species were obtained by cutting samples from a scaffold (Lost Creek) or by shooting branches with a shot gun (Bonner and Savage Lake). Gas exchange measurements were restricted to short shoots of larch foliage and 1991 new foliage for all sympatric conifers since 1992 new foliage was not fully developed until after the June sampling date. Gas exchange measurements were made with an ADC LCA-2 portable gas exchange system (Analytical Development, Ltd., Hoddesdon, UK). Calculations of net photosynthesis on a mass basis (A_{mass}) were made according to von Caemmerer and Farquhar (1981). One-sided leaf area of each fresh photosynthesis sample was measured with a Dias II image analysis system (Decagon Devices, Inc., Pullman, WA, U.S.A.) and oven dried to constant mass at 70 °C. Specific leaf area was calculated as the area square meter of fresh needles per kilogram of oven-dried tissue. Because A_{mass} can be significantly affected by variation in SLA when expressed on an area basis (Givnish 1988; Kloeppel and others 1993), all gas exchange data were expressed on a weight basis (nmol CO_2 g^{-1} s^{-1}), facilitating comparisons between species and sites. Bulk leaf water potential (Ψ) was measured with a pressure bomb (PMS Instrument Co., Corvallis, OR, U.S.A.); all samples were obtained from the same branch used to measure net photosynthesis.

RESULTS AND DISCUSSION

Specific leaf area was considerably higher for larch than either Douglas-fir or lodgepole pine at all three sites. Specific leaf area averaged (± standard error) 12.10 ± 0.23, 10.51 ± 0.17, and 11.49 ± 0.19 m^2/kg for western larch at Bonner, Lost Creek, and Savage Lake, respectively; 4.01 ± 0.12, and 4.17 ± 0.06 m^2/kg for Douglas-fir at Bonner and Lost Creek, respectively; and 5.30 ± 0.06 m^2/kg for lodgepole pine at Savage Lake. Foliage with a high specific leaf area enables plants to support a large leaf area with a relatively small carbon investment (Gower and others 1993, this proceedings; Matyssek 1986). This may possibly facilitate carbon assimilation due to higher utilization of light within the canopy (Kuuluvainen and Pukkala 1989; Oker-Blom and others 1989).

Table 1—Location and climatic conditions of the three western larch study sites in western Montana, U.S.A.

Site	Location	Elevation	Average annual precipitation	Average daily temperatures (°C) January	July	Weather data source[1]
		m	*mm*			
Bonner	N46°51'30" W113°53'45"	1,158	330	–2.0	20.5	1
Lost Creek	N47°55'10" W113°49'0"	1,012	450	–3.6	17.4	2
Savage Creek	N48°25'10" W115°48'30"	706	640	–3.8	17.1	3

[1] Weather Data Sources: 1 = Lackschewitz (1991), 2 = DeYoung and Roberts (1929), 3 = 32-year average (1960-1991), Fire Weather Station, Three Lakes District, Kootenai National Forest, Troy, MT, U.S.A.

Predawn water potentials (PDΨ), with more negative values indicating greater stress, reached their seasonal low at all sites during the August sampling period (B. D. Kloeppel, and S. T. Gower, unpublished data). This resulted in decreased net photosynthesis due to stomatal closure. However, the greater precipitation and deeper volcanic ash soils at Savage Lake than at the other sites provided a more dependable supply of water, thereby increasing rates of A_{mass} when temperatures became more favorable later in the season.

Net photosynthesis was greater for both western larch and Douglas-fir at the Bonner and Lost Creek sites during June compared to August. Because soil water was least limiting in the early growing season at Bonner and Lost Creek, A_{mass} peaked when temperatures were favorable but before water became limiting during the July and August drought. At the Savage Lake site, A_{mass} was greater in June than August for lodgepole pine but was greater in August than June for western larch. Because PDΨ for western larch was similar during both sampling periods, we speculate that the lower A_{mass} rates observed in June were due to cool night temperatures commonly occurring at the northern Savage Lake site during the early growing season (B. D. Kloeppel, unpublished data). Cold night temperatures have been shown to limit the enzymatic reactions controlling A_{mass} (Fahey 1979; Fitter and Hay 1987).

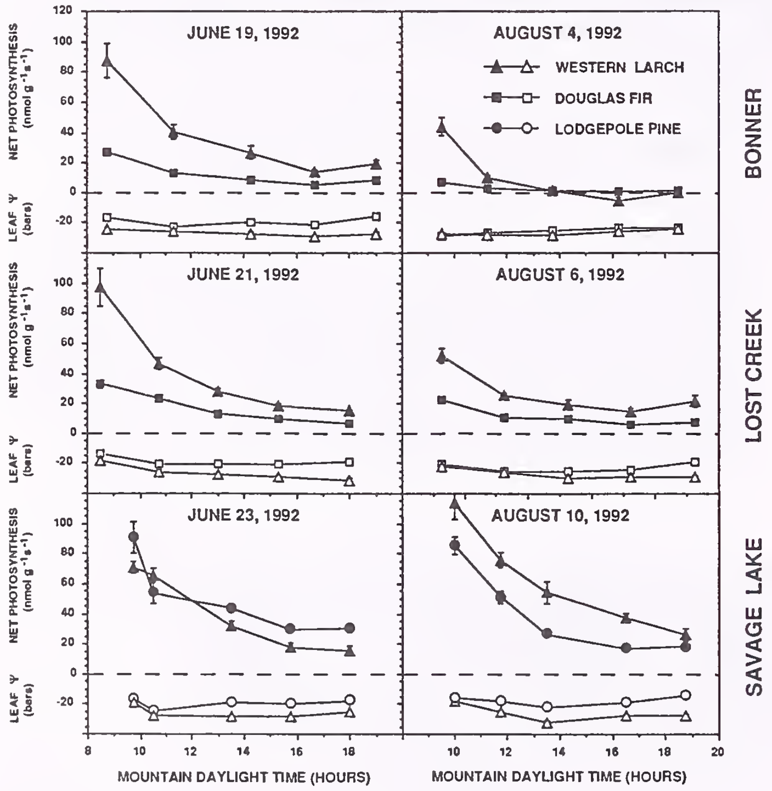

Figure 2—Weight-based net photosynthesis (closed symbols) and leaf water potentials (open symbols) of larch and sympatric evergreen conifers during June and August 1992 diurnal measurement periods. The three study sites are along a 375 km edaphic gradient from Bonner, MT, U.S.A. (most xeric) to Troy, MT (most mesic). Means ± standard errors are indicated, but in most cases SE bars are smaller than the symbols.

Net photosynthesis also differed between species. In general, A_{mass} was greater or equal for western larch than sympatric evergreen conifers (fig. 2). However, A_{mass} was significantly greater for lodgepole pine than western larch at Savage Lake on June 23, probably because the optimal temperature for photosynthesis is lower for the cold-tolerant lodgepole pine than for western larch. The higher A_{mass} rates by western larch than by the evergreen conifers were most pronounced at the drier Bonner and Lost Creek sites during June, whereas this difference became more pronounced at the end of the season at the more mesic Savage Lake site.

Because larches have lower water use efficiencies than evergreen conifers, both instantaneously (Matyssek 1986) and seasonally (Gower and Richards 1990), larches tend to dominate in locations and microsites where water is more available (Schmidt and others 1976; Whitford 1905). In this study western larch exhibited greater rates of A_{mass} during periods when soil water was most available. At Bonner and Lost Creek this occurred during the early growing season, whereas at Savage Lake the deep volcanic ash soil maintained a more favorable soil water balance for a greater length of the growing season. Consequently, western larch responded by increasing its values of A_{mass}, relative to sympatric conifers, during periods of high moisture availability. This same pattern is apparent when comparing the same species across sites. Western larch had similar A_{mass} values among the sites early in the season, but A_{mass} increased from the xeric Bonner site to the mesic Savage Lake site later in the season when water stress was more pronounced.

Based on this and other studies (Gower and Richards 1990; Matyssek 1986; Small 1972), larches have greater net photosynthetic rates than sympatric evergreen conifers. However, evergreen conifers often exhibit less negative xylem water potentials. This suggests that evergreen conifers display a more conservative water-use pattern. These relationships are true across all six sampling dates in figure 2 except for August 4 at Bonner when PDΨ's were less than –20 bars, causing both species to restrict stomatal conductance and photosynthesis. This conservative mechanism may in part explain why Douglas-fir and lodgepole pine occur on drier sites, while western larch appears to be restricted to more mesic microsites (Higgins and others 1987; Schmidt and others 1976). These data help to elucidate one mechanism by which the deciduous western larch is able to achieve a positive carbon balance and maintain its predominance among evergreen conifers in the Intermountain West.

ACKNOWLEDGMENTS

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Service, Flathead National Forest, Swan Lake District) for helping us to locate the Lost Creek site. Tom Steele and Dan Meyer assisted with plot establishment at each site, while Jason Vogel and Leslie Ross assisted with field data collection. This project was funded by a National Science Foundation grant (DEB-9107419) to S. T. Gower and P. B. Reich.

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Tyner Lake Stand of Western Larch Near Merritt, British Columbia

Dennis Lloyd and Alan Vyse

Within Canada, western larch (*Larix occidentalis* Nutt.) is restricted to the mountains and plateaus of the southeastern portion of British Columbia with the exception of a small outlier in southwestern Alberta. Within that area it grows in a wide range of habitats from valley floor to relatively high elevations and in four of the 12 forested biogeoclimatic zones in the province. The eastern continental limit can be explained by the arid climate of the midwestern grasslands, but there are no obvious reasons for the northern and western limits of its range. Snow breakage has been noted in areas with heavy and wet snowfalls. There is a high incidence of needlecast (*Meria* spp.) in wet climates, and the species seems susceptible to frost damage when flowering and in the seedling and sapling stages. However, the species has been planted in many places beyond its present range, and growth is usually rapid in comparison with local species.

The Tyner Lake stand of *L. occidentalis* adds to the puzzle. It is remarkable because of its size (approximately 500 ha) and its isolated position in relation to the main distribution of the species. The nearest population of western larch is approximately 150 km away.

We set out to provide a full description of the site to support an application for permanent conservation and to encourage further study of the ecological factors limiting the distribution of western larch in the province.

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SITE DESCRIPTION

The stand is at 1,300 m on the Thompson Plateau in south-central British Columbia, at upper elevations of the dry, cool interior Douglas-fir biogeoclimatic subzone. It is about 25 km northwest of the town of Merritt. The mean annual precipitation of the site is about 440 mm, of which 30 percent falls as snow. The frost-free period of 86 days is relatively short, and spring and fall frosts are common. The mean annual temperature is a little over 6 °C. The soils of the site are derived from glacial tills overlying grano-diorite and quartz-diorite bedrock. The rolling topography supports a variety of plant communities from depressional sedge meadows and riparian forest dominated by hybrid spruce to rock outcrops and talus slopes. The mixed *Larix-Pinus* forest has developed on the rapidly to moderately well-drained sites.

STAND HISTORY

We examined the portion of the stand where large western larch dominate. The stand seems to have been started by a large-scale disturbance about 230 years ago. The disturbance was probably a stand-destroying fire as we have yet to find survivors of the previous stand. Following the fire, the stand was probably composed of a mixture of codominant larch and pine, but the larch began to outgrow the pine after 30 years, or 200 years before the present, and the stand developed into a stratified mixture.

Shortly after that stratification stage, a few Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) and interior spruce (a probable hybrid of *Picea glauca* and *P. engelmannii*) entered the stand. About 60 years before the present, a ground fire killed a small proportion of the pine and scarred a proportion of the remaining pine and larch. An outbreak of mountain pine beetle (*Dendroctonus ponderosae* Hopk.) removed approximately three-quarters of the largest subdominant pine at about the same time. The thinning effect of the fire and insect attack stimulated the growth of the surviving pine and some of the dominant larch. A large number of pine and smaller number of larch have regenerated beneath the dominant stems since the fire, giving the stand a distinctive three-storied appearance.

Table 1—Statistics from the larch-dominated portion of the study stand

Measurement	Larch	Pine	Others	Total
Number of stems/ha	970	107	7	1,084
Basal area m^2/ha	24.8	3.9	0.2	28.9
Live volume m^3/ha	218.6	17.1	1.1	231.8
Dead and down volume m^3/ha	15.1	47.3		62.4

STAND STATISTICS

About 50 percent of the 500 ha stand is in a larch-pine mix with larch dominating and the remainder in pine-dominated stands with minor components of larch and Douglas-fir. Table 1 summarizes survey results from the larch-dominated portion of the stand.

CONCLUSIONS

The survival, growth, and reproduction of western larch on the Tyner Lake site suggest that it should be considered for introduction on similar sites. The risks associated with expansion seem to be low based on the good performance of the species outside its range in other parts of the province. In addition, we found that the Tyner Lake site is not unique in any respect other than the presence of larch, which remains a biogeographical puzzle. The area for introductions is large, and the potential benefits justify further silvicultural and biogeographical research.

The area should be secured as a permanent reserve status as soon as possible. The British Columbia Forest Service has already collected plant material for clone bank and breeding purposes.

Stem Taper Equation for Japanese Larch

Søren Fl. Madsen

During the last decade compatible stem taper and volume equations have been developed for eight conifer species in Denmark by Madsen (1985, 1987, 1992) and Madsen and Heusèrr (1992). Japanese larch (*Larix kaempferi* [Lamb.] Carr.) has been included in the project, and separate equations have been developed for this species.

BASIC MATERIAL

The basic material consists of 515 Japanese larch trees, from eight permanent sample plots, representing fertile regions in Denmark. Within most of the plots the various trees have been sampled over decades from several cutting operations. Therefore, within plots, the trees represent variation in tree size and stem form in the year of measurement and developments of dimension and stem taper by age.

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The range of tree diameter at breast height (d) is 0.05 to 0.60 m, of tree height (h) 6 to 30 m, and of stand diameter (D_g) 0.07 to 0.52 m. All trees have been measured section-wise according to Oppermann's method (4 + 10 sections).

COMPATIBLE VOLUME FUNCTION

From the basic material, total stem volumes (v_o) above stump height (h_s) have been calculated and used in a logarithmic model describing volumes within and between sample plots:

$$\ln(v_0)_{ij} = \mu + A_j + \Sigma_i \beta_i x_i + \epsilon_{ij}$$

where

μ is the general level of the tree species
A_j is the general level of the sample plot
β_i are coefficients
x_i are single tree parameters
ε is the residual value

Using weighted regression with weights $w_2 = 1\text{-}d/2$, a mean value of the sample plot levels, and stump heights (h_s), which equal 0.12 + d/4 m, the equation for total stem volume above stump height is:

$$\hat{v}_0 = \exp_e(-2.308702 + 1.760821 \cdot \ln(d) + 1.351809 \cdot \ln(h) + 0.646612 \cdot \ln(h/(h-1.3)) - 0.606762 \cdot D_g^2 + 0.001373/w_2)$$

Analyses show that the standard deviation of the sample plot levels practically equals 0, and the single tree standard deviation within the sample plot equals 5.5 percent of v_0.

STEM TAPER EQUATION

A stem taper model giving stem volumes compatible with the previous volume equation has been developed. The basic model (in short notation) is:

$$d_l^2 = \frac{\hat{v}_o}{(\pi/4)h} \sum_{i=1}^{10} \beta_i \left(\frac{l}{h}\right)^{i-4} + e$$

where

- d_l is stem diameter outside bark in l m above ground level
- $\hat{v}_o$ is volume according to the above stem volume equation
- h is total tree height above ground level
- β_i are coefficients
- ε is a residual value

Using restricted regression on 513 Japanese larch trees of the basic material, six fixed coefficients of the stem taper equation valid for the height interval above 0.49 m above ground level have been calculated:

$b_1 = 6.163678 \cdot 10^{-5}$
$b_2 = -6.23778 \cdot 10^{-3}$
$b_3 = 2.479618 \cdot 10^{-1}$
$b_8 = -3.471702 \cdot 10^{2}$
$b_9 = 2.257603 \cdot 10^{2}$
$b_{10} = -5.820606 \cdot 10^{1}$

For the height interval between h_s and 0.49 m, $\hat{d}_l$ equals $\hat{d}_{0.49}$

The above mentioned restrictions are as follows:

- Rotation of the stem taper line around stem axis gives the same volume ($\hat{\hat{v}}_0$) as found by the previous volume equation ($\hat{v}_0$); or the volumes are compatible.
- $d_l = d$ for $l = 1.3$ m.
- $d_l = 0$ for $l = h$.
- The derivative of $\hat{d}_l^2$ with respect to l equals zero for $l = h$, which means nice stem taper courses near the tip of tree.

The remaining four coefficients, b_4, b_5, b_6, and b_7, are variable coefficients; that is, they vary from tree to tree to fulfill the restrictions. The variable coefficients are calculated from the given d, h, and D_g values per tree. Details can be found in Madsen (1985, 1992) and in Madsen and Heusèrr (1992).

EXPLOITATION

The above stem taper equation gives various possibilities of calculation. The stem diameter ($\hat{d}_l$) may be calculated directly from the given d, h, D_g, and l values per tree. The height (l) corresponding to a given stem diameter ($\hat{d}_l$) may be calculated by iteration. The stem volume ($\hat{v}_a$) between stump height (h_s) and the height (l) aboveground where d_l = a can be calculated as (compare Madsen 1985):

$$\hat{\hat{v}}_a = \hat{v}_o \left[\Sigma_i b_i \left(\frac{1}{i-3}\left(\frac{l}{h}\right)^{i-3} + \left(\frac{0.49}{h}\right)^{i-3}\left(\frac{i-4}{i-3} - \frac{h_s}{0.49}\right)\right) + b_3\left(\ln\left(\frac{l}{0.49}\right) + 1 - \frac{h_s}{0.49}\right)\right]$$

where i = 1, 2, 4, 5, 6, 7, 8, 9, 10.

FIT

The stem taper equation of course should only be used within the ranges of the basic material. Here the average fit seems good, as mean stem diameters of all trees in all relative heights above ground level are close to the measured ones (deviations below 1 percent) and the standard deviations between measured and predicted diameters in all heights are between 2.1 and 5.9 percent. In addition, pooled calculations for seven tree species have shown practically insignificant bias in the majority of various d/h-classes (d = diameter at breast height).

Compatibility with the stem volume function for $\hat{v}_o$ implies that the stem taper describes the variation of stem taper with varying tree size in the stand in 1 year and, further, the development of stem taper with increasing age within the same sample plot.

Figure 1 is an example of the stem-taper equation.

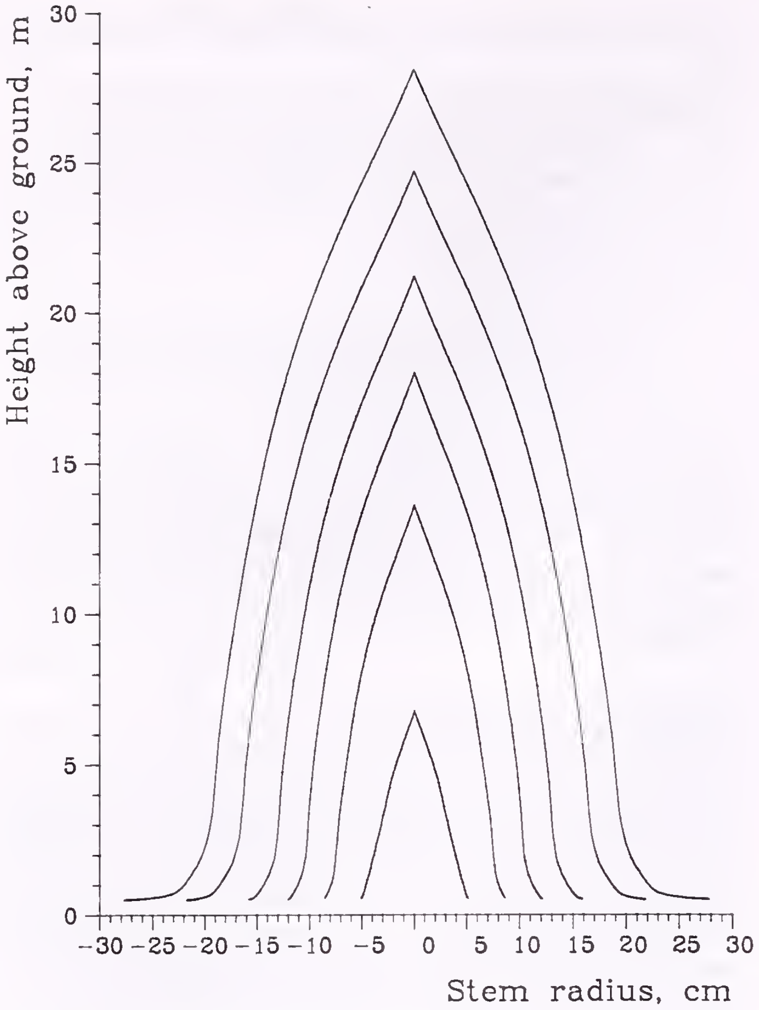

Figure 1—Stem taper equation for Japanese larch by development in tree size as for tree 349 in the permanent sample plot GV, Giesegaard estate, in every 10 years of the period 1915 to 1965.

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Effect of 20 Years of Regulated Stand Densities on Bole Form of Young Western Larch

Ward W. McCaughey, Wyman C. Schmidt, and Jack A. Schmidt

Because of economic factors such as increasing mill costs and diminishing wood supplies, accurate tree volumes and dimensional characteristics are essential if our wood resources are to be fully utilized. And because utilization standards are constantly being adjusted toward use of smaller stems, a bole form or taper function equation is an important factor in tree volume calculations.

Bole form varies considerably between species within the Intermountain West (Amidon 1984; Van Hooser and Chojnacky 1983). Volume equations for western larch (*Larix occidentalis* Nutt.) have been developed using a variety of bole form equations, but they did not account for spacing effects (Plank and Snellgrove 1978). In this paper, we describe a study designed to evaluate bole form differences between three spacing levels at four locations in western Montana. Girards and Absolute form quotients were used as measures of bole form.

METHODS

This study complements a larger study on spacing effects on the growth and development of western larch

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(Schmidt and Seidel 1988) and was initiated to evaluate the effects of three spacings on the bole form of "young" western larch in western Montana. In 1961, four study areas were established in western Montana—two on the Coram Experimental Forest and one each on the Flathead and Lolo National Forests. Each location contained extensive overstocked stands of young, 7- to 9-year-old, western larch reproduction with minor components of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco). These young stands at each location were thinned in 1961 to a wide range of densities. From these, three initial stand densities of 704 (1740 TPA), 360 (890 TPA), and 146 (360 TPA) trees per hectare of pure western larch were selected for evaluating bole form.

After growing at these stand densities for 20 years, the study plots were thinned again in early 1982 to wider spacings at the four locations, and felled trees were sampled for this study (table 1). Ten thinned trees in each 0.04 ha plot were randomly selected for bole form measurements. Sample trees were marked at 13 locations along the bole, and outside bark diameter and bark thickness was measured and recorded (fig. 1). Outside bark diameters were measured with a diameter tape to the nearest 0.25 cm. Bark thickness was measured with a Swedish bark gauge to the nearest 0.13 cm. Total height was also measured on sample trees and recorded to the nearest 0.3 m.

Outside bark diameter and bark thickness measurements were taken on each sample tree at the following locations along the bole:

1. 1.37 m aboveground, diameter at breast heigh (d.b.h.)
2. 4.9 m aboveground
3. One-half total height above 1.37 m
4. Deciles of total height (base of each section)

Inside bark diameters were calculated by subtracting twice the bark thickness from the outside bark diameter value at each measurement location. Decile measurements were used to construct graphic representations of average bole forms. Bole form quotients (Girards and Absolute) were computed and evaluated for their between-spacing differences. Analysis of variance from the SAS computer statistical package was used to analyze spacing effects on tree heights, outside bark diameters, Girards (GFQ), and Absolute (AFQ) form quotient. All significance tests were computed at the $p \leq 0.05$ level. Equations used to compute GFQ and AFQ were:

Table 1—Thinning schedule for 0.04 ha plots at two locations on the Coram Experimental Forest and one location each on the Flathead and Lolo National Forests

Years of thinning	Spacing interval	Trees per hectare	Number of trees cut
	m		
1961	1.5 x 1.5	704	
1981	2.4 x 2.4	275	106
1961	2.1 x 2.1	360	
1981	3.4 x 3.4	146	53
1961	3.4 x 3.4	146	
1981	4.6 x 4.6	81	16

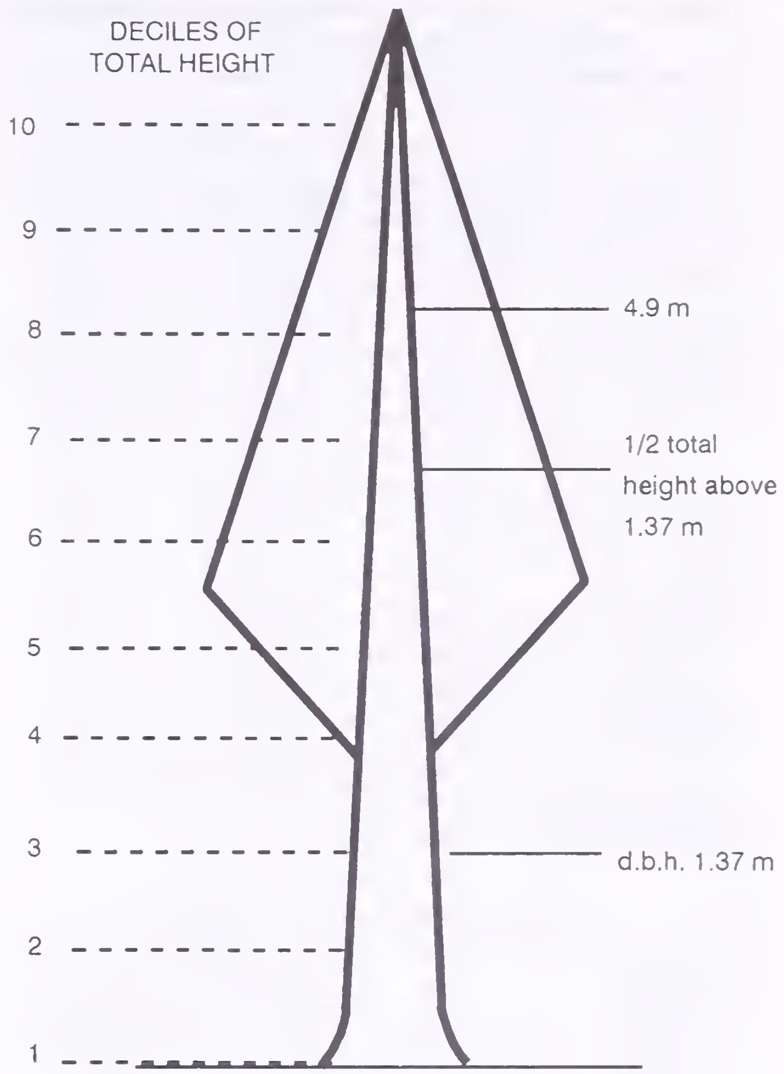

Figure 1—Location of bole form measurements on young western larch. Measurements were taken at base of each decile section.

$$\text{Girards form quotient} = \frac{d_1}{D_1} \times 100$$

where d_1 = diameter inside bark at 4.9 m
D_1 = diameter outside bark at breast height

$$\text{Absolute form quotient} = \frac{d_2}{D_2} \times 100$$

where d_2 = diameter inside bark at
D_2 = at one-half total height
D_2 = diameter inside bark at breast height

RESULTS

Mean tree heights and outside bark diameters generally increased as stand density decreased from 704 to 360 to 146 trees per hectare (TPH) (table 2). Outside bark diameters at the 146 TPH stand density were always significantly larger than the 704 and the 360 TPH stand densities.

Table 2—Mean total height and outside bark diameter at breast height (d.b.h.) of western larch grown under three spacing levels at four locations in western Montana

		Mean	
Area	Spacing level	Total height	Outside bark d.b.h.
	Trees per ha	*m*	*cm*
Coram 1	704	7.5 A[1]	5.9 A
	360	9.2 B	9.2 B
	146	12.6 B	14.6 C
Coram 2	704	8.7 A	6.9 A
	360	9.4 A	9.0 B
	146	10.8 B	13.4 C
Cottonwood Lakes	704	4.1 A	4.1 A
	360	6.6 B	7.1 B
	146	6.6 B	8.9 C
Pinkham Creek	704	9.2 A	7.8 A
	360	9.0 A	8.9 A
	146	11.4 B	13.6 B
All areas combined	704	7.4 A	6.2 A
	360	8.6 B	8.5 B
	146	10.3 C	12.6 C

[1] Different letters within a column, by individual area, denote significant differences at the $p \leq 0.05$ level.

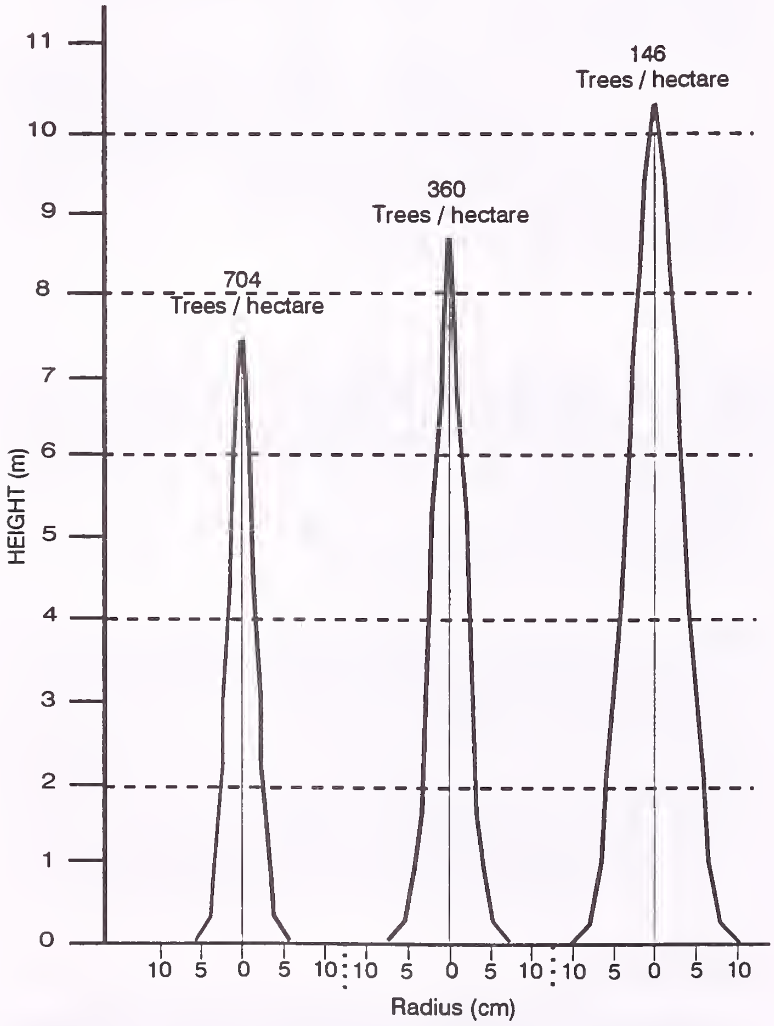

Figure 2—Visual representation of bole configuration for western larch trees growing at 146, 360, and 704 trees per hectare. All four study locations have been pooled and averaged.

The 360 TPH stand density had significantly larger diameters than the 704 TPH stand density with the exception of Pinkham Creek, which still showed an absolute but not significant increase. Figure 2 demonstrates average bole configuration for western larch trees growing at 146, 360, and 704 TPH for all four study locations. An opposite relationship exists between high and low values for GFQ and AFQ. A high GFQ value indicates a more buttressed tree form in comparison to a lower GFQ value, while a high AFQ value indicates a less buttressed tree form in comparison to a lower AFQ value.

Results from analysis of variance for Girards form quotient (GFQ) for the four study locations showed that Cottonwood Lakes was significantly different from Coram 1, Coram 2, and Pinkham Creek. Stand density differences using GFQ were analyzed separately for Cottonwood Lakes and pooled for the other three study locations. Girards form quotient could not be computed for the 704 TPH stand density at Cottonwood Lakes because sample trees were less than 4.9 m tall. There was no significant difference in GFQ between the 360 (GFQ 34.6) and 146 (GFQ 31.2) TPH stand density at Cottonwood Lakes.

The GFQ of 64.8 for the 146 TPH stand density was significantly greater than the GFQ of 57.5 for the 360 and the GFQ of 50.2 for 146 TPH stand densities for the combined data set of Coram 1, Coram 2, and Pinkham Creek. There was no significant difference in the GFQ between the 360 and 146 TPH stand densities for the three combined areas.

The AFQ value for Coram 2 was significantly different from Coram 1, Cottonwood Lakes, and Pinkham Creek, which were not significantly different from each other. Density differences using AFQ were analyzed separately for Coram 2 and pooled for the other three study locations. The AFQ of 56.3 for the 146 TPH stand density was significantly lower than the AFQ of 61.3 for the 360 TPH and the AFQ of 59.7 for the 704 TPH stand densities at Coram 2. The AFQ values for the two denser spacings at Coram 2 did not differ significantly. There were no significant differences in AFQ values between the three densities for the pooled areas. However, there was an absolute increase in AFQ as stand densities changed from 704 (AFQ 56.5) to 360 (AFQ 57.5) to 146 (AFQ 58.6) TPH.

DISCUSSION AND CONCLUSIONS

These bole form data describe the dimensions of trees that could be used in thinning from below. Thinning from below is a practice commonly used in young western larch stands and best fits the biology of this highly shade-intolerant species. As a result, most trees removed in early thinnings, such as trees in this study, are potentially those that would be used for small diameter wood products.

Only trees removed by thinning were sampled for this study, and as with any thinning, they generally were the slowest growing trees. In spite of that, relative differences in bole form between stand densities are evident as shown by differences in visual appearance of bole form (fig. 3), mean height and outside bark diameter measures (table 2), and in Girard and Absolute form quotients. Trees growing under a low stand density of 146 TPH, compared to higher densities, are significantly taller, have larger outside bark diameters, and have GFQ and AFQ values consistently larger or smaller, respectively.

The visual representation of bole form for the 146 TPH stand density indicate that trees appear to be blocky with more taper than trees growing under the 360 or 704 TPH stand densities. This is due to less competition from other trees, more growing space, and greater crown retention by this highly shade-intolerant species. Crown development was not a part of this supplemental study but will be evaluated in the main study on spacing effects on the growth and development of western larch.

It appears that spacing affects bole form of "young" western larch, and these differences should be considered when evaluating stands, from initial and subsequent intermediate thinnings, for potential wood products such as posts and poles. Further study of crop trees is needed to evaluate bole form differences over a variety of age, site, and stand densities and for development of volume equations specific to spacing levels. By using the full complement of trees in the stand, volume equations describing growth and bole form should be developed.

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Growth of 19 Larch Provenances in Croatia

Steve Orlic and Marijan Ocvirek

Research of European larch provenances in Forest Research Institute, Jastrebarsko, was started in 1965 (Dokus 1975). Seed samples were obtained from Czechoslovakia, Poland, Germany, and Croatia. The quantity of seed or plants was limited. Field trials were established on pilot plots in three ecologically characteristic regions of continental Croatia. Because of the limited quantity of plants, larch was planted with Weymouth pine in inter-rows. In addition to the 18 European larch provenances, the trial included one provenance of Japanese larch from southern Korea.

The aim of the researchers was to determine the European larch variability, to define the provenance that would be best for this environment, and to see what increment could be expected from this economically interesting conifer species. It is known that European larch has a wide area of natural distribution in Europe, both horizontally and vertically, and diverse edaphic and climatic conditions.

Pintaric (1966) established international larch provenance trials on Igman in Bosnia in 1961. The research included 11 provenances of European and one provenance of Japanese larch. The trials were established in the region of sessile-flowered oak, in a common hornbeam community, and a montane beech forest. During the first 5 years the best was Krnov provenance from Czechoslovakia. Pintaric (1966) points out big differences between trees of the same provenance. These differences are sometimes bigger than the ones between the provenances themselves.

MATERIALS AND METHODS

The research program included 18 European larch provenances—13 provenances from Czechoslovakia, one from Poland, two from Bavaria, Germany, and two from Croatia—and 1 Japanese larch provenance from southern Korea. The 19 provenances were:

Bruntal, Razova, Czechoslovakia
Albrehtice, Czechoslovakia
Sabinov, Brezovacka, Czechoslovakia
Liptovsky, Mikula, Czechoslovakia
Nizbor, Drevic, Czechoslovakia
Jeromerice, Czechoslovakia
Ruda, Raskov, Czechoslovakia
Rajec, Czechoslovakia
Pozorice, Czechoslovakia
Jihlava, Hencov, Czechoslovakia
Blizyn, Svinia gora, Poland
Durdevac, Croatia
Vujnovic brdo, Gospic, Croatia
Tanap, Visoka Tatri Czechoslovakia
Baden-Würtenberg, Germany
Litovel, Usov, Czechoslovakia
Ruda on Moravi, Czechoslovakia
Amorbach, Kirchell, Germany
Yongwol-kun, Southern Korea

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Unfortunately, apart from data on provenance name, other data on locations (longitude, latitude, height above sea-level, relief, plant community) were not available. Further references to each provenance in this paper are by first name of the location.

Plants of different provenances of larch were grown in the nursery of the Forest Research Institute. Sowing was carried out twice, in the spring of 1966 and 1967.

Plants sown in 1966 were used for the establishment of the trial in the territory of forest enterprise Karlovac, forest unit Duga Resa, pilot project "Lokve." Plants sown in 1967 were used for the establishment of the trial in the territory of forest enterprise Vinkovci, forest unit Stari Mikanovci, pilot project "Durgutovica," and in the territory of forest enterprise Bjelovar, forest unit Veliki Grdevac, pilot project "Slatki potok."

Seeds were sown in the nursery beds in small furrows. One-year-old plants were transplanted into beds in a triangular design with a 20 by 20 cm spacing and then left for 2 years. The plants were lifted, balled, and transported to the field.

The larch provenance trial on Lokve pilot project was established in the spring of 1969. Seedlings were 1 and 2 years old. Basic spacing was 2 by 2 m. Larch was planted with 4 by 4 spacing, and Weymouth pine 2 and 3 years old were interplanted. Thirteen provenances from Czechoslovakia, one from Poland, and one from Bavaria, Germany, were planted in this trial. The number of planted trees per provenance was 25 in a 5 by 5 m grid with no replication. Fill-in planting for those seedlings that died was done twice, in spring, 1971 and 1972.

The provenance trial on the "Durgutovica" pilot project was established in the spring of 1970. Ten provenances from Czechoslovakia, one from Poland, one from Bavaria, Germany, two from Croatia, and one provenance of Japanese larch from southern Korea were planted. Plants were 1 and 2 years old. Basic spacing was also 2 by 2 m. Larch was planted with 4 by 4 m spacing and Weymouth pine 2 years old were interplanted between the larch. The trial design was a randomized variant design with four replications. One-hundred plants (5 by 5 by 4 replications) were planted per provenance. Fill-in planting was carried out a year later in the spring of 1971.

In addition to those two trials, in the spring of 1970, pilot project "Slatki potok," forest enterprise Bjelovar, in a trial identical to the one in Durgutovica, was established. Unfortunately, this was destroyed in a fire in 1980.

Survival and height growth of trees in the trials at Lokve and "Durgutovica" were measured each year for the first 5 years and then every fifth year. The last measurement was done in the "Lokve" trial in the spring of 1989 and in the "Durgutovica" trial in the autumn of 1989—the 20th year after the establishment. Survival, height, and diameter at breast height (d.b.h.) were measured. Data from the "Durgutovica" trial were statistically processed using the variance analysis, F test, and Duncan test.

RESULTS

Survival data and average values for total height and d.b.h. in trials of the different provenances of European and Japanese larch are presented in table 1 and figure 1.

Survival and Mortality

Provenances with the lowest survival percentage in the trials were: Ruda on Moravi 19.2 percent, Amorbach 29.3 percent, and Durdevac 54.5 percent. Other provenances had good survival at both localities. Some of the provenances had 80 percent survival at one or the other locality.

In the "Durgutovica" trial, provenance survival ranged from 70.4 to 82.1 percent and averaged 75.4 percent. In

Table 1—Average values of survival, height, and diameter in 20th year.

Cardinal numb.	Mark	Provenance	Survival		Height, m					Diametar, cm				
			D %	L %	"Durgutovica"		"Lokve"		Average	"Durgutovica"		"Lokve"		Average
					h	Variation width	h	Variation width	h	d1,30	Variation width	d1,30	Variation width	d1,30
1.	A	BRUNTAL, RAZOVA, Czech.-Slov.	80,8	92,6	18,17	13,6-20,7	17,18	13,9-19,9	17,68	22,14	14,0-30,3	19,08	9,0-26,0	20,61
2.	B	ALBRECHTICE, Czech.-Slov.	77,5	80,6	17,93	12,5-21,2	17,14	14,3-20,3	17,54	20,73	10,1-28,0	17,72	10,0-26,0	19,23
3.	C	SABINOV, BREZOVIČKA, Czech.-S.	70,4	100,0	16,87	11,6-20,6	16,00	16,0-16,0	16,44	19,83	8,6-32,0	19,00	17,0-21,0	19,42
4.	D	LIPTOVSKY, MIKULAŠ, Czech.-S.	80,5	74,2	17,00	12,8-20,6	15,42	11,8-19,4	16,21	18,89	8,3-24,9	13,52	7,0-22,0	16,21
5.	E	NIŽBOR, DREVIČ, Czech.-Slov.	81,1	70,0	17,71	12,2-21,8	14,50	9,6-18,4	16,11	20,82	11,0-28,1	14,57	7,0-23,0	17,70
6.	F	JAROMERICE, Czech.-Slov.	82,1	73,3	18,11	14,3-21,2	15,20	9,7-18,8	16,66	20,74	14,0-29,4	14,14	6,0-21,0	17,44
7.	G	RUDA, RAŠKOV, Czech.-Slov.	76,6	82,8	17,62	11,1-21,2	15,23	12,3-17,9	16,43	20,33	7,6-29,6	15,83	10,0-29,0	18,08
8.	H	RAJEC, Czech.-Slov.	79,1	68,4	17,73	11,5-20,5	16,03	13,0-18,1	16,88	20,65	8,4-28,0	17,23	12,0-23,0	18,94
9.	I	POZORICE, Czech.-Slov.	-	89,5	-	-	16,97	14,4-19,6	16,97	-	-	17,82	11,0-26,0	17,82
10.	J	JIHLAVA,HENČOV, Czech.-Slov.	78,1	69,2	18,16	12,6-21,3	16,76	14,8-18,9	17,46	20,81	9,8-27,4	17,33	8,0-24,0	19,07
11.	K	BLIZYN, Czech.-Slov.	70,9	71,0	17,10	10,6-19,1	15,41	10,0-19,5	16,26	21,87	9,6-30,5	15,18	6,0-26,0	18,53
12.	L	DURDEVAC, Czech.-Slov.	54,5	-	14,17	9,5-18,9	-	-	14,17	14,50	6,3-27,6	-	-	14,50
13.	M	VUJNOVIĆ BRDO,GOSPIĆ, Croatia	71,2	-	17,11	11,1-20,5	-	-	17,11	19,66	6,9-26,0	-	-	19,66
14.	N	TANAP,VISOKA TATRI, Czech.-S.	81,7	-	17,30	11,2-20,2	-	-	17,30	20,27	9,8-30,0	-	-	20,27
15.	O	BADEN WÜRTENBERG, Germany	76,2	-	18,07	15,0-21,5	-	-	18,07	21,77	10,0-32,0	-	-	21,77
16.	P	LITOVEL, USOV, Czech.-Slov.	-	82,8	-	-	14,95	10,3-19,4	14,95	-	-	14,63	7,0-23,0	14,63
17.	R	RUDA NA MORAVI , Czech.-Slov.	-	19,2	-	-	15,13	13,8-16,4	15,13	-	-	12,40	6,0-17,0	12,40
18.	S	AMORBACH, KIRCHELL, Germany	-	29,3	-	-	12,74	10,5-15,3	12,74	-	-	10,00	6,0-15,0	10,00
19.	T	YONWOL-KUN. J. KOREJA	70,8	-	15,90	12,5-18,2	-	-	15,90	19,23	11,5-28,6	-	-	19,23
Trial average			75,43	71,64	17,26	12,14-20,50	15,62	12,46-18,42	16,31	20,15	9,73-28,83	15,60	8,71-23,00	17,66

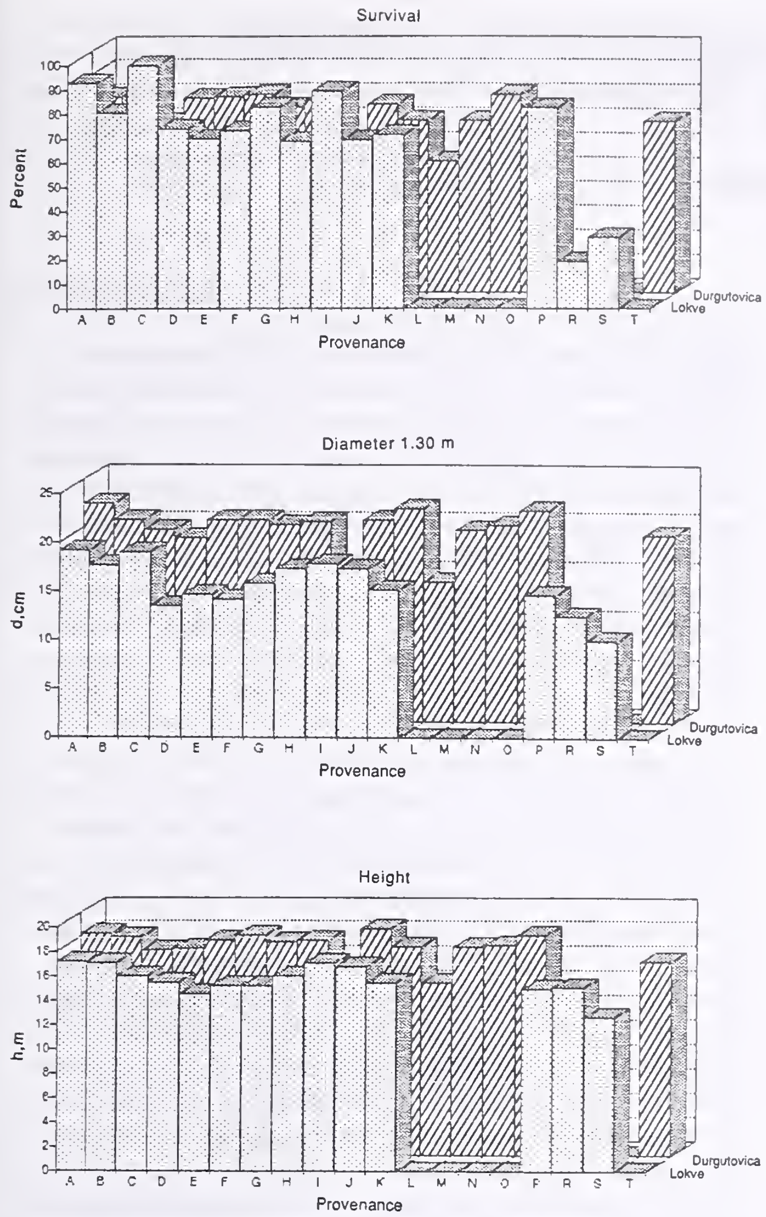

Figure 1—Survival, diameter at breast height (1.3 m), and total height of 19 different provenances of *Larix* at two locations 20 years after planting in Croatia.

the "Lokve" trial it ranged from 19.2 to 100.0 percent, with an average of 71.6 percent. The Japanese larch provenance in "Durgutovica" trial (Yongwol-kun) was among the worst at 70.8 percent.

Certain damage and loss was caused by game (deer) on both localities.

Height

Total height of trees in the "Durgutovica" trial averaged 17.3 m (14.2 to 18.2 m). The best provenances were Bruntal, Jihlava, and Baden-Würtenberg. The worst provenances were Durdevac and Yongwoll-kun. In the Lokve trial, total height averaged 15.6 m (12.4 to 17.2 m) among the best provenances. They were Bruntal and Pozorice. Among the worst were Amorbach and Nizbor.

The last measurement showed that the height and diameter growth of the same provenances was greater on "Durgutovica" than on the "Lokve" locality. This was so for the first few years after the establishment of the trial. The possible reason for this is favorable edaphic conditions. According to the Thornthwaite climate chart and the data of the weather station Vinkovci, the "Durgutovica" locality has subhumid climate with a marked precipitation deficit in the summer months of July, August, and September, but sufficient precipitation is accumulated in winter to maintain favorable soil humidity until the termination of height and diameter tree growth. The "Lokve" locality is situated on the border between the humid and the perhumid climate with no precipitation deficit in the summer months but with marked precipitation up to 430 to 860 mm annually. Closely connected with the precipitation quantity are the temperature relations during the vegetation period, which influences the growth of plants. Luvic soil in "Durgutovica" is favorable for larch, while fern-heath soil in "Lokve" is less favorable.

Diameter

Average d.b.h. in the "Durgutovica" trial was 20.2 cm (14.5 to 22.1 cm). The best provenances were Bruntal, Blizyn, and Baden-Würtenberg. The worst provenance was Durdevac. Trees with d.b.h. of over 30 cm were registered on the "Durgutovica" project. Average d.b.h. in the "Lokve" trial was 15.6 cm (10.0 to 19.1 cm). The best provenances were Bruntal and Sabinov. The worst were Amorbach and Ruda on Moravi. Maximum d.b.h. registered in this trial was 29 cm.

The same provenances in the "Durgutovica" trial have bigger d.b.h. than the ones in the "Lokve" trial, which is also the case with data on height.

PRELIMINARY CONCLUSIONS

Research results from a trial of 18 provenances of European larch and one provenance of Japanese larch indicate the following:

1. The best provenances for Croatian forestry needs are European larch provenances from Sudetic Mountains, Czechoslovakia, and from Bavaria in southern Germany.
2. Japanese larch was satisfactory in these trials, and work with this species should be continued.
3. All researched provenances exhibited faster growth in subhumid climate on luvic soils than in humid-perhumid climate on fern-heath soil.
4. The intensive growth of Weymouth pine in the interrows on fern-heath soil negatively influenced crown development and hence growth rate.

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Western Larch Regeneration in Partial Harvesting Systems

Ed Oswald

Regeneration of western larch (*Larix occidentalis*) in partial harvesting regimes is being examined at three sites in southeastern British Columbia as part of a combined alternative silviculture system/mountain pine bark beetle control project. Two sites (Cranbrook and Parsons) support a *Pinus contorta / Shepherdia canadensis-Mahonia aquifolium / Calamagrostis rubescens* community on an aeolian cap over glacial till at Cranbrook and on a fluvial terrace at Parsons. The third site (Elkford) is higher in elevation and supports a *Picea engelmannii-Pinus contorta / Shepherdia canadensis-Symphoricarpos albus* community on colluvium and till. All three sites are currently dominated by lodgepole pine 80 to 100 years old. Western larch is currently prevalent in the Cranbrook site; the Parsons site is at the northern natural limit of western larch though a few natural stands exist in the vicinity and it has been planted farther north; and the Elkford site is slightly higher in elevation than naturally occurring western larch. The project treatments include spacing to 4 m, spacing to 5 m, clearcut, a control, and fertilization at each tree density. The harvesting treatments were planned for the 1992-1993 winter, with fertilization to follow during 1993.

Planting of western larch, Engelmann spruce, and Douglas-fir (*Pseudotsuga menziesii*) throughout each study area took place in 1993 to permit examination of potential stand conversion species. The amount of light reaching each seedling will be estimated by determining the leaf area index or amount of canopy cover over the seedling, or both. Advance regeneration is abundant on the sites at Parsons and Elkford and sparse at Cranbrook. New regeneration is anticipated at all three sites subsequent to treatments. Lodgepole pine will likely dominate the new regeneration, but some western larch could occur at Cranbrook.

Western larch saplings to a height of about 5 m occur at the Cranbrook site. A few seedlings, mostly up to 0.5 m in height, appear to have good vigor and vitality, but they are insufficient in number to assess vigor in relation to sunlight, competition, and depth of duff. There seems to be a high degree of mortality in saplings 1 to 3 m tall, and those still alive have poor vigor. Saplings 3 to 5 m tall have a relatively small diameter and most often are severely bent over, which is likely the result of snow press. Some of these with crowns lying on the ground serve as "mother trees" to branches that turn upward and take on a treelike appearance, though rooting of these branches was not observed. Even trees in excess of 15 m often had bent tops.

We plan to monitor all forms of western larch regeneration and subsequent development, and how these factors compare with other species following the treatments.

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Flowering in Potted Western Larch Grafts Established from Juvenile Ortets

David Remington

The Montana Department of State Lands, U.S.A., in cooperation with Champion Timberlands, began development of a potted indoor seed orchard for western larch (*Larix occidentalis* Nutt.) in 1989. The primary reason for selecting a potted, greenhouse-based seed orchard was to protect emerging conelets from spring frosts, which Sheared (1990) identified as the major factor inhibiting western larch cone production. However, several other advantages have been cited for potted indoor orchards (Ross and others 1985). The other advantages we anticipate are reduced time from orchard establishment to flowering, better control over pollination, flexible breeding zones, and ease of genetic upgrading.

Grafting onto potted rootstock began in 1990. Ortets were best individuals from best families in Montana western larch progeny tests, planted in fall 1981 by the Inland Empire Tree Improvement Cooperative (IETIC). Pending construction of a permanent 4,500 sq. ft. greenhouse for

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the orchard, stock has been temporarily maintained in other facilities at the Forestry Division complex in Missoula and at Champion Timberlands' facilities in Plains, MT. We anticipate that the orchard will meet Montana western larch seed needs for both the Department of State Lands and Champion Timberlands by the year 2000.

GIBBERELLIN STUDY

In the spring of 1991, 27 clones were selected for a study of the effects of Gibberellin $A_{4/7}$ injection on flowering. A test graft from each clone was randomly chosen and injected with 0.6 mg of $GA_{4/7}$ dissolved in 1.0 ml ethanol. A second graft from each clone was randomly selected as a control. The injections were done when long shoot buds had broken on about half of the grafts in the orchard population.

Mortality during the 1991 growing season, related to root damage and probable gibberellin toxicity, eliminated most of the paired clones from the study. The remaining clones showed inconclusive flowering results.

An additional 37 clones were selected for a second gibberellin study, and injections were done in March 1992. A reduced concentration of $GA_{4/7}$ was used in an attempt to avoid gibberellin-induced mortality. A spray treatment, using $GA_{4/7}$ in an aqueous solution, was also included. Results will be evaluated in spring 1993.

STOCK MAINTENANCE

The major problem with potted stock maintenance so far has been winter damage affecting root systems. The stock experienced sever cold spells while they were outdoors in December 1990 and October and November 1991. Effects became apparent early the next growing season in both cases when damaged grafts flushed but then declined in vigor and died. Construction of a permanent greenhouse for the orchard, tentatively planned for 1993, should prevent these problems from recurring.

There have been some occurrences of root diseases, larch casebearer, *Meria* needlecast, and drought damage. Close monitoring is essential to ensure proper irrigation and to detect and treat disease problems before they become severe.

Stock maintenance practices have included a combination of liquid and granular fertilizer application and annual pruning to maintain compact crowns. It will be necessary to maintain stock at a height of no more than 6 to 7 ft and in pots no larger than 5 gal.

Table 1—Flowering summary of 2-year-old grafts, spring 1992

Type of flowering	Male	Female	Total
Grafts flowering (n = 196)	12 (6%)	11 (6%)	18 (9%)
Clones flowering (n = 78)	10 (13%)	9 (12%)	15 (19%)
Families flowering (n = 43)	7 (16%)	9 (21%)	11 (26%)

FLOWERING OF 2-YEAR-OLD GRAFTS

A few grafts done in 1990 flowered in 1991. In 1992, 9 percent of the 1990 grafts flowered, representing 19 percent of the clones and 26 percent of the families (see table 1). Male and female flowering were in nearly equal proportions. The number of flowers ranged from one to 15 female strobili per graft and from one to 25 male strobili per graft. These results include the surviving gibberellin-treated grafts, but only two of the 19 flowering grafts were treated. The winter damage sustained in 1990 may have stimulated flowering by mimicking a root pruning treatment.

These results suggest that substantial western larch flowering can occur only 2 years after grafting using juvenile ortets, even with only minimal effort at flower induction. It is also noteworthy that both male and female flowering was substantial. We have been concerned that pollen production may be a serious limiting factor with grafts established from juvenile ortets.

ACKNOWLEDGMENTS

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Ecology and Silviculture of Western Larch at its Southern Limits

Robert Steele and Kathleen Geier-Hayes

DISTRIBUTION

Western larch (*Larix occidentalis* Nutt.) extends southward to about latitude 44° 15' in Idaho and slightly farther south in the Blue Mountains of eastern Oregon (Little 1971). In Idaho, the southernmost known *Larix*, now dead (Brock 1993), was disjunct from the main distribution by about 22 mi (35.4 km) and was located at about the same latitude as the southernmost limits in Oregon.

In Idaho, *Larix* is restricted to areas of stronger maritime climatic influence and possibly soil conditions with greater moisture and deeper volcanic ash layers. *Larix*, however, extends farther south than some maritime indicator species such as *Tsuga heterophylla*, *Thuja plicata*, *Taxus brevifolia*, *Asarum caudatum*, and *Clintonia uniflora*. As *Larix* extends southward, it becomes restricted to sites where *Abies lasiocarpa* and *Abies grandis* are climax and *Vaccinium globulare* and *Linnaea borealis* are prevalent in the undergrowth. In eastern Oregon, the environmental range of *Larix* expands to include many drier sites where *Pseudotsuga menziesii* is climax but the volcanic ash is more extensive (Johnson and Clausnitzer 1992). Here *Larix* extends beyond the dry limits of *Abies grandis*, *Vaccinium globulare,* and *Linnaea borealis*.

CULTURE

Larix growth rates are somewhat reduced near its southern limits and maximum sizes are less than in areas to the north. Average height at 50 years is about 65 ft (19.8 m) in central Idaho (Steele and others 1981; Steele and Geier-Hayes 1987) as compared to 80 ft (24.4 m) on the most favorable sites in northern Idaho (Cooper and others 1991) and northwestern Montana (Pfister and others 1977). In central Idaho, timber yields are comparable to *Pseudotsuga menziesii* growing on the same site.

A seed tree cut is the preferred silvicultural method for regenerating *Larix* naturally and regeneration is most successful on either exposed mineral soil, moss mats, or moist rotten wood (Steele and Geier-Hayes 1992). However, while some *Larix* seed tree cuts have successfully reproduced *Larix*, many others have failed. The primary reason for failure appears to be lack of seed due to late spring frosts and cone feeding insects (Shearer 1990).

Because of the uncertainty of natural regeneration, *Larix* seedlings have been planted in some areas. Survival and growth is usually adequate where competition has been effectively reduced. Some *Larix* has been planted intermittently beyond its natural range as far east as Driggs, Idaho. Generally, growth rates are poor on these offsite plantings but the planting east of Driggs is on an *Abies lasiocarpa* stream terrace and is growing remarkably well.

SUCCESSIONAL STATUS

Larix is a shade intolerant early seral species throughout central Idaho. It is easily replaced by *Pseudotsuga*, *Picea*, and *Abies*. Due to its longer life span (Minore 1979), *Larix* persists longer in the stand than *Pinus contorta* even though *P. contorta* is more shade tolerant.

Larix seed is relatively small and light. It is easily dispersed by wind and is well adapted for establishing on mineral soil following extensive stand-destroying wildfire. The moister segments of *Abies grandis* and *A. lasiocarpa* forests where *Larix* grows are conducive to this type of fire. Fire-killed *Larix* can produce viable seed if mature cones are present at the time of the fire (Shearer and Stickney 1991). However, since cone crops often fail due to late spring frosts, long distance dispersal from less frost prone terrain can be critical for regenerating burned areas.

Larix sites support several fast-growing shrub species which compete with *Larix* seedlings. The *Larix*, however, is the fastest growing conifer seedling in central Idaho and often reaches 4.5 ft (1.4 m) in 6 years.

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Culturing 1-0 Western Larch Seedlings at J. Herbert Stone Nursery

David Steinfeld and Steve Feigner

The demand for western larch (*Larix occidentalis*) seedlings for reforestation in the Western United States has been steadily increasing over the past decade. Since the mid-1980's, the J. Herbert Stone Nursery has been supplying between 1 and 2 million seedings annually to the effort. Situated in the Rogue Valley of southern Oregon, this nursery is in an ideal location for producing a plantable seedling in 1 year. The warm summer and fall temperatures create optimum conditions for shoot and root growth. The following synopsis describes the general nursery culturing guidelines developed for this site.

STRATIFICATION

Seed is soaked for 48 hours in cold running water and spread on open trays, a half inch deep, before moving into stratification rooms. The temperatures are maintained at 1 °C, and fogging nozzles keep the seed constantly moist. Seed is kept in these rooms for 80 days. After this period, the seed is dried down to 25 percent moisture (wet weight) and kept at 1 °C until sowing.

SOWING

In April the seed is sown in eight rows at a density of 16 seedlings per square foot. The seed is pressed into the soil and the entire bareroot bed is immediately covered with a $^3/_8$-inch layer of fresh sawdust mulch. To keep the sawdust from moving off the bed by rainsplash or wind, a stabilizer (tradename Agri-Lock) is applied. Ammonium phosphate and potassium sulfate is banded 4 inches below the seed during the sowing operation.

CULTURING

Sown seed is constantly monitored for moisture. Irrigation is scheduled to ensure that the seeds never dry. Once the seedlings emerge, irrigations are then based on surface soil temperatures and soil moisture conditions. Short bursts of watering during the hot afternoons help to keep the temperatures below 33 °C in July and 35 °C in August. When the soil profile dries below field capacity, entire rooting zone is irrigated.

Approximately 6 weeks after seedling emergence (early May), the first of five fertilizer treatments begins. At 2-week intervals, nitrogen fertilizer, in the form of ammonium nitrate and ammonium sulfate, is applied to the soil surface and irrigated into the profile. The total amount of actual nitrogen applied during this period is 140 lb per acre. After bud set in mid-October, two more applications of ammonium sulfate are made that together total 50 lb of actual nitrogen per acre.

By late August, most of the seedlings have reached the target height of 7 inches. At this point further height growth is discouraged by limiting the number of irrigations and allowing the root zone to dry. It is also necessary to stress the seedlings through wrenching, where an

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angled blade is pulled below the seedlings at a depth of 12 inches. This action stresses the seedlings by breaking some of the small feeder roots. It also serves to loosen the soil, creating an ideal rooting environment for fall root growth.

Once seedlings have set a bud, the rooting zone is moistened to field capacity and the roots are vertically pruned. Predawn plant moisture stress (PMS) is kept below 5 bars throughout the fall with irrigations. The low moisture stress coupled with the warm fall climate allows several months of rapid root growth .

PEST MANAGEMENT

Weeds, insects, and pathogens are managed through an Integrated Pest Management (IPM) program. The only disease affecting the larch at this nursery is dampening-off. This is controlled by fumigating with Basamid at 350 lb per acre several months before sowing. The major damage from insects is caused by the lygus bug (*Lygus hesperus*). This insect injects digestive enzymes into growing shoots causing tip mortality and the production of several tops. Damaged seedlings tend to be much smaller than undamaged seedlings. The insect is controlled with a bug vacuum similar to those used on lettuce and strawberries. In addition, chemical control with the insecticide Pydrin is used when flightless insect stages are present. Weeds are controlled by hand weeding.

LIFTING AND PROCESSING

The seedlings are lifted, graded, and packed during the first several weeks of December. The minimum grading specifications are 4 inches tall and 3 mm stem caliper. Roots are usually pruned between 9 and 12 inches. Seedlings are then placed in bags or boxes and stored in cold refrigeration until they are frozen in early January.

Geographic Variation in Modulus of Elasticity of Tree Trunks Among Japanese Larch Planted in Hokkaido

Katsuhiko Takata, Koji Ueda, and Akio Koizumi

Japanese larch (*Larix leptolepis* Gord.) is endemic to the central part of Honshu Island, Japan, and has been planted extensively in the northern area of Japan. Initially, the plantation larch forests had been managed in short rotation to produce timber for civil engineering and packing. However, silvicultural policy is recently shifting to produce timber for structural use in long rotation because economic circumstances and market demands have been changing.

The international Japanese larch provenance trial was organized by Dr. W. Langner (Langner 1958), and 25 seed sources were selected by Japanese Government Forest Experiment Station (present name: Forestry and Forest Products Research Institute) in 1956. Forty-four parallel trials were established in nine European countries, the U.S.A., Canada, New Zealand, and Japan.

In this paper, we present results on two of these trials established in Hokkaido, Japan. The objectives were to estimate geographic variation of wood quality among and within provenances and to find the most promising seed sources for planting in the northern area of Japan.

MATERIALS AND METHODS

The study was undertaken in two trial stands—Esashi trial established in fall 1959 and Shimizu trial established in spring 1960. The Esashi trial and the Shimizu trial included 25 and 19 origins, respectively. The experiment was in a triple lattice design in both trials, which had 25 plots in each block and replicated three times. Each plot contained 126 trees from a provenance planted at 1.8 by

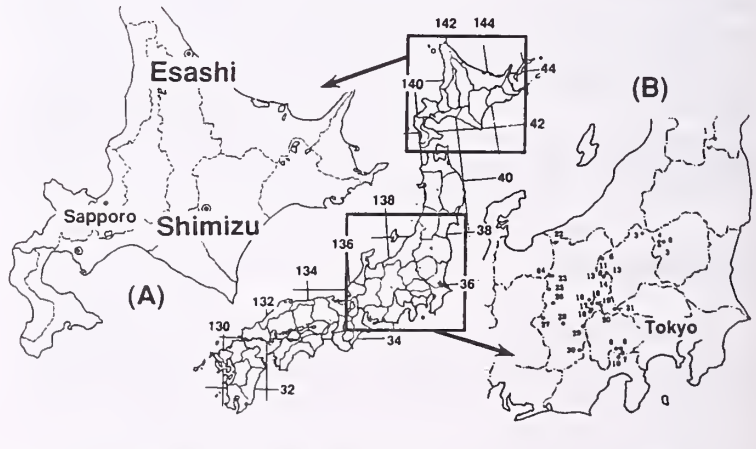

Figure 1—Locations of trial stands (A) and natural forests (B) from which seed were collected. Index numbers are Japanese numbers in table 2.

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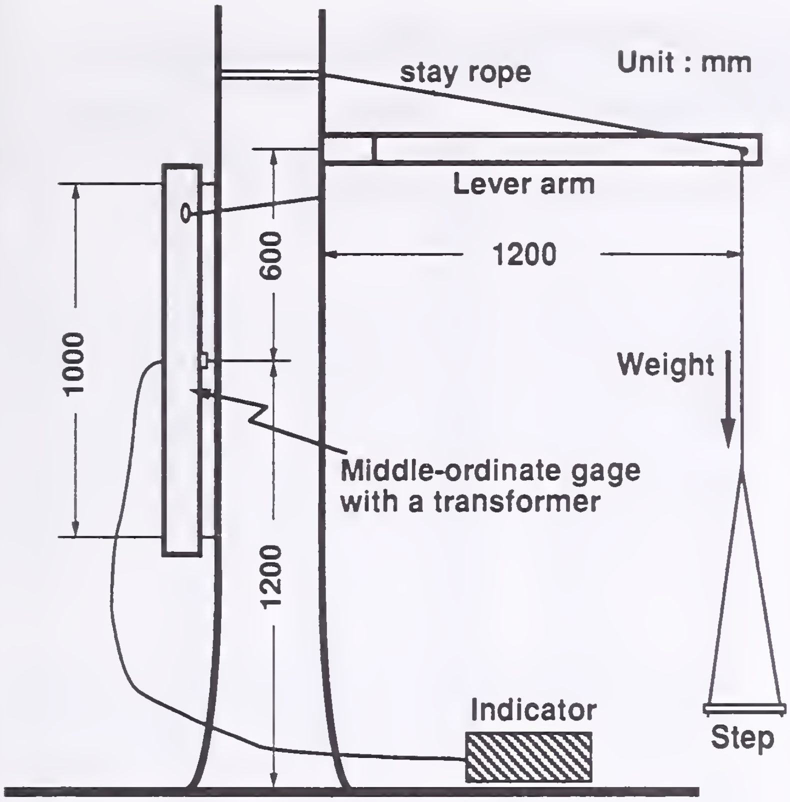

Figure 2—Setup of the tree-bending test to evaluate modulus of elasticity of a tree trunk.

1.8 m spacing. Locations of trial stands and natural forests from which seed were collected are shown in figure 1.

We measured the diameter at breast height (d.b.h.) and modulus of elasticity of tree trunks (trunk MOE). A method of tree-bending test developed by Koizumi and Ueda (1986) was applied to evaluate trunk MOE. The setup of the tree-bending test is shown in figure 2. When an operator gets on a step hung on one end of a lever arm, the person's weight is converted into a bending movement acting on a stem. The deflection caused by the bending movement is measured by the middle-ordinate gauge with a transformer of 1-µm sensitivity set on the opposite side of the stem at breast height. The nondestructive measurement is made twice per tree in two directions at the right angle to each other. The obtained figures are averaged to compensate the error caused by uneven shape of cross sections. The trunk MOE is calculated upon the applied movement, and the movement of intertia of the trunk is determined from the circumference and the bark thickness at breast height. Theoretical and experimental studies indicated that the error in MOE evaluation caused by irregular form of stem and other factors was negligible (Koizumi 1987).

Table 1—Outlines of two trial stands. Numbers in parentheses are of provenances used for the tree-bending test

Location	Established year	Tested year	Number of provenances	Number of tested trees per provenance
Esashi	1959	1990	25(24)	12
Shimizu	1960	1986	19(19)	6

The tree-bending test was carried out at Shimizu trial in 1986 and at Esashi trial in 1990. The sample trees for the tree-bending test were selected so that they showed average growth in each plot and had straight stems without obvious knots or wounds around breast height. Two trees were selected per plot for 19 provenances in each of three blocks at Shimizu trial. Three trees were selected per plot for 24 provenances in each upper two blocks at Esashi trial, where additional two trees per plot in each of three blocks were felled, cut into logs, and submitted to static bending test to evaluate trunk MOE. The two trial plantations are outlined in table 1.

RESULTS AND DISCUSSIONS

Mean values and coefficients of variation for d.b.h. and trunk MOE are shown in table 2. The provenance means for d.b.h. range from 19.3 to 22.0 cm for Esashi trial from 16.2 to 18.3 cm for Shimizu trial. Matsuzaki and others (1991) reported the 30 years' performance for growth characteristics at Esashi and Shimizu trials, in which the ranking of mean d.b.h. calculated from diameter measurements were nearly in agreement with our ranking. The provenance means for trunk MOE range from 103.2 to 122.9 tonf/cm^2, a difference of 20 percent, for Esashi trial, and from 70.4 to 98.7 tonf/cm^2, a difference of 40 percent, for Shimizu trial. The overall mean for trunk MOE at Esashi trial is 115.4 tonf/cm^2, which is 1.3 times as great as that at Shimizu trial. The experimental design and silvicultural treatments are almost the same at both trials, so that the difference between them may be attributed to the site effect.

Table 3 shows the results of analysis of variance for trunk MOE. The differences among provenances were highly significant at 1 and 5 percent level for Esashi and Shimizu trial, respectively. The replication and provenance interaction is significant at 1 percent level for Esashi trial. These results for Esashi trial indicate a strong environmental influence within each replication, which is due to the occurrence of a shallow gully in Esashi trial.

Comparison of mean MOE's for provenances common to Esashi and Shimizu trials is shown in figure 3. The correlation between the two trials is weak, and correlation coefficient is not significant (r = 0.45). However, some groups of provenances (circled) had a same tendency in trunk MOE ranking at each trial. It must be noted that the provenances included in each circle are in adjacent seed-stands. The provenance and environmental interaction may be weak for these provenances.

No correlation is found between trunk MOE and environmental variables such as latitude, longitude, and elevation of the provenances. This result agrees with others reported mainly for growth characteristics (Stairs 1965 and many others).

Based on our observations on trunk MOE, we recommend the provenances of Sangoome and Tenzine Pass for planting in the northern area of Japan to produce timber for structural use.

Table 2—Average values and coefficients of variation for MOE and d.b.h. for tested provenances at two trials

Prov. Jpn.[1] No.	Sch.[2] No.	Provenance name	MOE (tonf/cm^2) Esashi Ave.	MOE Esashi C.V.	MOE Shimizu Ave.	MOE Shimizu C.V.	D.b.h. (cm) Esashi Ave.	D.b.h. Esashi C.V.	D.b.h. Shimizu Ave.	D.b.h. Shimizu C.V.
3	13	Akanuma	122.9	13.3	77.7	15.1	20.3	12.6	17.6	7.6
4	14	Kootoku	119.7	14.6	—	—	19.5	5.9	—	—
5	15	Yasyuubara	119.3	10.3	—	—	20.8	8.6	—	—
6	16	Manza	112.5	10.9	80.7	13.1	20.9	7.1	16.1	5.1
8	1	Tenjin pass	121.1	12.5	95.3	15.9	21.0	8.3	16.8	3.6
9	2	Sangoome	120.7	10.0	98.7	6.0	20.4	8.2	18.1	5.8
10	—	Sizuoka	103.7	21.0	84.8	13.1	21.1	10.8	18.0	6.7
12	17	Lower Mizunoto	113.5	15.9	81.6	8.0	21.1	7.1	17.2	9.3
13	18	Kutukake	117.9	15.0	86.9	8.2	22.0	5.6	17.2	9.7
14	19	Oiwake	113.6	10.0	—	—	20.7	8.6	—	—
15	7	Tadesina	114.2	14.0	83.9	14.6	21.1	9.1	17.1	6.9
16	8	Toyohira	118.3	9.8	92.7	8.2	20.8	10.7	18.3	7.1
17	10	Upper Tatusawa	121.6	9.4	91.2	12.7	19.3	8.8	17.6	4.3
18	9	Lower Tatusawa	114.8	7.5	90.6	9.0	19.5	9.7	17.0	6.9
19	5	Inago	113.3	15.0	88.1	9.3	20.9	12.9	17.7	4.9
20	6	Uminokuti	117.1	12.7	94.1	16.2	19.9	8.5	18.0	8.7
21	4	Mt. Kobusidake	119.2	11.7	98.0	8.5	21.0	8.2	17.3	7.6
24	22	Lower Takasegawa	103.2	10.8	84.8	8.1	21.0	12.4	17.3	7.8
25	20	Kamikooti	124.4	5.0	—	—	20.7	8.1	—	—
26	25	Mt. Hatimoriyama	115.4	13.8	80.7	9.4	20.0	10.7	17.1	9.2
27	24	Mt. Ontake	111.5	10.5	70.4	15.3	20.3	6.6	17.8	4.5
28	23	Mt. Kiso-komagatake	111.0	11.5	78.6	12.3	20.0	11.1	17.2	4.9
29	11	Mt. Kai-komagatake	111.9	14.8	80.7	12.4	20.5	11.0	17.3	11.2
30	12	Mt. Akaisi-oosawadake	107.7	13.7	—	—	20.1	9.7	—	—
		Overall means	115.4	13.5	86.3	14.4	20.6	9.8	17.4	7.8

[1] Japanese number
[2] Schmalenbeck number

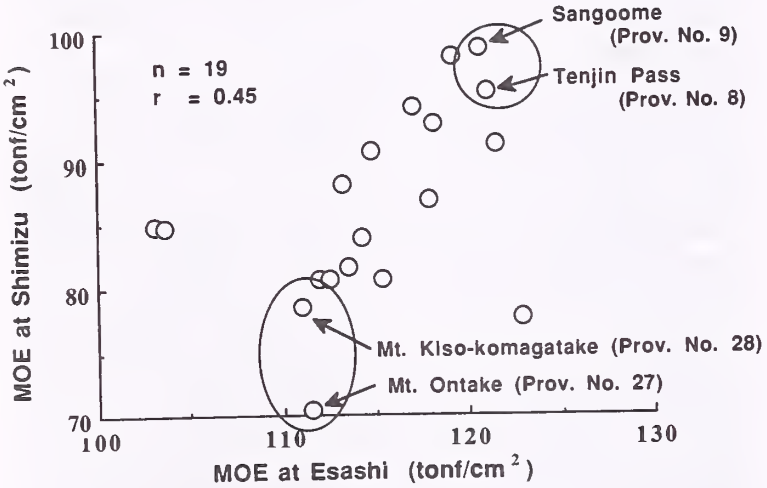

Figure 3—Correlation of mean MOE between Esashi and Shimizu trials.

Table 3—Results of analysis of variance for trunk MOE at Esashi and Shimizu trials

Location	Sources of variation	Degrees of freedom	Mean squares	F values
Esashi	Replications	2	784.1	3.86[1]
	Provenances	23	373.6	1.84[1]
	R x P	46	343.5	1.69[2]
	Error	217	203.2	
Shimizu	Replications	2	272.5	2.66
	Provenances	18	340.7	3.33[2]
	R x P	36	143.2	1.40
	Error	56	102.3	

[1] Significant at the 5 percent level
[2] Significant at the 1 percent level

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Maintaining Bird Diversity in Western Larch/ Douglas-fir Forests

Bret W. Tobalske, Raymond C. Shearer, and Richard L. Hutto

Abstract—Bird occurrences were evaluated under four stand conditions in western larch/Douglas-fir forests: clearcut, partial cut, unlogged (fragmented), and contiguous forest. Frequencies were noted for foraging guilds, tree gleaners, flycatchers, nesting guilds, tree drillers, and primary cavity nesters. Managers should consider a diversity of habitat conditions if maintaining habitat for bird species is an objective.

We studied the influence of tree harvests on the community of birds inhabiting a western larch (*Larix occidentalis*)/Douglas-fir (*Pseudotsuga menziesii*) forest on Coram Experimental Forest in northwestern Montana (Tobalske and others 1991). We evaluated bird occurrences under four stand conditions: clearcut, partial cut, unlogged (fragmented), and contiguous forest. There were five clearcuts ranging from 14 to 35 acres (6 to 14 ha). The largest partial cut unit was 70 acres (28 ha), and eight others ranged between 5 and 40 acres (2 and 16 ha). Fragmented forest consisted of 330 acres (134 ha) interspersed with the clearcuts and partial cuts. Contiguous forest was 837 acres (339 ha) in the Coram Research Natural Area.

The most recent harvest, a seed-tree and overstory removal, occurred in the winter of 1988 to 1989. The cut units were initially harvested from 1942 to 1944. Based on guidelines for the management of cavity-nesting birds in McClelland and Frissell (1975), snags of all tree species, along with living paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), and black cottonwood (*P. trichocarpa*), were retained in the cutting units during the recent harvest.

During the breeding season, between June 1 and July 7 each year (1989-1991), the senior author of this paper censused bird populations with fixed-point counts, 328 ft (100 m) in radius. Counts were performed at 10 randomly selected points within each of the four stand conditions in the study area. Each point was visited 3 days each year. Counts were done between one-half hour after sunrise and 10 a.m., for ten minutes each. Species detections were by sight or sound, including birds in flight over the plot.

The guidelines of the Ocular Method in Hahn and Jensen (1987) for sampling vegetation were followed. Tobalske sampled vegetation once each year during July at 10 points in each stand condition selected for bird censusing. Tobalske observed 56 bird species. For analysis, species were grouped into guilds (Diem and Zeveloff 1980) based upon shared nesting or foraging habits (table 1). To test the effect of stand condition and year upon the relative abundance of each guild, we used two-way analysis of variance (ANOVA) (SPSS Inc. 1990). Likewise, two-way ANOVA was used to examine variance in vegetation components (table 2). Statistical significance in all tests was $P < 0.05$, employing the Bonferroni adjustment to control for experiment-wise error rate (SPSS Inc. 1990). Differences among means were tested for significance using the Scheffe method (SPSS Inc. 1990).

RESULTS

Among foraging guilds, foliage foragers were less abundant in clearcuts than in other stand conditions (table 1). Tree gleaners were least abundant in clearcuts and partial cuts. In contrast, flycatchers were most abundant in clearcuts, and ground foragers were most abundant in clearcuts and partial cuts. Among nesting guilds, conifer-tree nesters were significantly less abundant in clearcuts. The ground nesting guild was most abundant in harvested areas.

In spite of their dependence upon trees for foraging and nesting, the abundance of tree drillers and primary cavity nesters (essentially woodpeckers) did not differ among stand conditions. Keeping cutting units relatively small and reserving western larch snags along with living paper birch and quaking aspen (McClelland and Frissell 1975) appeared to mitigate the effects of extensive tree removal for at least one woodpecker in these guilds: the red-naped sapsucker (*Sphyrapicus nuchalis*) (Tobalske 1992).

Several vegetation components differed among stand conditions (table 2). Tree cover was least in clearcuts, intermediate in partial-cut units, and highest in contiguous forest. Tree basal area and average d.b.h. was least in harvested areas. Total shrub cover was least in clearcuts and partial cuts. Total forb cover was highest in contiguous forest.

MANAGEMENT RECOMMENDATIONS

If maintaining habitat for bird species is a management objective in western larch/Douglas-fir forest, we suggest that diversity in habitat conditions will promote diversity of bird species because patterns of relative abundance vary among guilds (table 1) and among species within guilds (Tobalske and others 1991).

Tree-dependent bird species, such as foliage foragers and conifer-tree nesters may be most sensitive to clearcutting. The foliage foraging guild is the largest within

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Table 1—Mean number of birds, by guilds, counted per census point within the four stand conditions at Coram Experimental Forest, 1989-1991.

		Stand condition				
Guild[1]	Number of species	Clearcut[2]	Partial cut[2]	Fragmented forest	Contiguous forest	Probability[3]
Foraging						
Foliage forager	26	2.4^{A}	5.2^{B}	4.8^{B}	5.1^{B}	0.001
Flycatcher	5	0.9^{A}	0.3^{B}	0.1^{B}	0.0^{B}	.001
Tree driller	4	0.8	0.6	0.7	1.1	.242
Tree gleaner	5	0.6^{A}	1.1^{AB}	1.5^{BC}	2.0^{C}	.001
Ground forager	15	3.7^{A}	3.0^{AB}	1.8^{BC}	1.6^{C}	.001
Total	55					
Nesting						
Conifer tree	10	0.9^{A}	2.6^{B}	2.5^{B}	2.8^{B}	.001
Conifer or broadleaf tree	11	1.7	2.4	2.1	2.2	.859
Shrub or small tree	10	1.6^{A}	1.6^{AB}	1.0^{AB}	0.8^{B}	.001
Primary cavity	5	1.0	0.8	0.8	1.3	.154
Secondary cavity	10	1.4	1.2	1.5	2.0	.110
Ground	9	1.7^{A}	1.7^{A}	0.9^{B}	0.5^{B}	.001
Total	55					

[1] Guilds adapted from Diem and Zeveloff (1980).

[2] Snags of all species and living paper birch left standing where possible.

[3] Low probability values indicate significantly different means among stand conditions, Bonferroni adjusted to control for experiment-wise error; superscript letters group similar means for each guild (SPSS Inc. 1990).

Table 2—Estimates of vegetation components within each of the four stand conditions at Coram Experimental Forest, 1989-1991.

	Stand condition				
Vegetation component	Clearcut[1]	Partial cut[1]	Fragmented forest	Contiguous forest	Probability[2]
Tree basal area (ft^2/acre)	7^{A}	35^{A}	111^{B}	104^{B}	0.001
Tree d.b.h. of dominant tree (inches)	3^{A}	7^{A}	14^{B}	15^{B}	0.001
Tree total cover (percent)	2^{A}	24^{B}	59^{C}	66^{C}	0.001
Pole and larger (percent)	1^{A}	19^{B}	45^{C}	49^{C}	0.001
Sapling (percent)	1^{A}	5^{A}	13^{B}	13^{B}	0.001
Seedling (percent)	0	1	2	3	0.240
Shrub total cover (percent)	17^{A}	40^{AB}	44^{B}	44^{B}	0.001
Tall[3] (percent)	0^{A}	8^{AB}	9^{AB}	12^{B}	0.000
Mid[3] (percent)	13^{A}	25^{B}	28^{B}	18^{AB}	0.012
Low[3] (percent)	3^{A}	7^{AB}	12^{B}	13^{B}	0.001
Graminoid total cover (percent)	9	10	4	4	0.288
Forb total cover (percent)	19^{A}	16^{A}	35^{AB}	44^{B}	0.001

[1] Tree snags of all species and living paper birch trees were left standing where possible.

[2] Low probability values indicate significantly different means among stand conditions, Bonferroni adjusted to control for experiment-wise error (SPSS Inc. 1990); superscript letters group similar means for each vegetation component.

[3] Tall shrub, >10 ft (3 m); midshrub, 2 to 10 ft (0.6 to 3 m); low shrub, <2 ft (0.6 m) (Hahn and Jensen 1987).

the community of western larch/Douglas-fir forest birds, accounting for 47 percent of the total number of species we observed. Therefore, this guild may be of particular interest to forest managers. If it is desirable to maintain habitat for foliage-foraging birds within harvested stands, we recommend using partial cuts rather than clearcuts (table 1).

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Siberian Larch (*Larix sibirica* Ledeb.): a Successful Exotic in Finland

Anneli Viherä-Aarnio and Teijo Nikkanen

Native tree species in Finland number low because of the harsh climatic conditions and the relatively late cessation of the glacial period in Northern Europe. Only a few economically important species exist: Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* L. Karst.), and the birches, European white birch (*Betula pendula* Roth), and pubescent birch (*Betula pubescens* Ehrh.).

Siberian larch (*Larix sibirica* Ledeb.) has been introduced to provide more variation to this scanty species composition, and it is the best known and the most promising exotic in Finland. Although it has been cultivated for more than a hundred years, it has not reached a commercially significant scale.

European larch (*Larix decidua* Mill.) has also been cultivated in Finland. However, this species is usually more susceptible to larch canker and its stem quality is worse than its Siberian relative.

NATURAL RANGE OF SIBERIAN LARCH

The natural range of Siberian larch is wide, covering Northeastern Russia and Western Siberia. The western most natural stands of Siberian larch grow only about 200 km to the east of Finland. Within its natural range Siberian larch contains a lot of geographical variation. For instance, populations growing to the west of the River Ob are sometimes regarded as a separate species, *L. sukaczewii* Dylis.

THE FAMOUS RAIVOLA PROVENANCE

Larch timber used to be a highly desired raw material for shipbuilding. When creating the Russian navy, Czar Peter the Great decided to establish larch stands in Karelia, close to St. Petersburg. During the subsequent reign of Czarina Anna, the Raivola larch forest was indeed started, in 1738. This famous forest became the most magnificent stand in Northern Europe and one of the most remarkable forest cultures in the whole of Europe. The volume of the stand in some places exceeded 1,000 m^3 per ha, and many trees were more than 40 m high.

The seed used for the Raivola stand originated from Archangel, Northeastern Russia. Supplementary planting and seeding was done with seed from Ufa, in the southern part of the Ural Mountains. Thus, seed collected today from the Raivola stand is probably of provenance hybrid origin.

The Raivola provenance has been the most successful of all Siberian larch provenances tested in both the southern and northern parts of Finland. In addition, it has even proved to be the best in reforestation trials in Northeastern Iceland, thus showing a surprisingly wide ecological tolerance.

CULTIVATION IN FINLAND

The good growth and quality of the Raivola stand inspired foresters to plant Siberian larch in Finland at the end of the 19th century. As a result, several promising stands were created in different parts of the country. Larch stands were subsequently established in the 1930's. Interest in the cultivation of larch arose again in the 1950's, especially in Northern Finland. However, a considerable number of the stands established at that time failed because seed of unsuitable origin from Krasnojarsk had been

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used. This stand failure resulted in a temporary halt to the cultivation of larch, which started again in the 1970's. At present there are nearly 10,000 ha of larch plantations in Finland. However, larch has not attained any major economical importance.

YIELD

Within its natural distribution Siberian larch can grow on a wide range of sites. To obtain the best possible yield in Finland, fertile sites are recommended: a slope with moist and deep mineral soil would be ideal.

On good sites, larch reaches large dimensions at an early age and produces large-sized timber faster than any other tree species in Finland. On fertile forest sites a larch stand can reach a volume of nearly 1,000 m^3 per ha, which is otherwise rare in Finnish conditions. On the average, larch is as productive as Norway spruce on good sites, whereas it does not attain the same level of growth as domestic conifers on sites of medium and poor fertility.

DISEASES AND PESTS

Siberian larch has been considered rather free of serious diseases or pests. When grown in maritime conditions such as in Western Scandinavia it is, however, susceptible to larch canker (*Lachnellula willkommii*). In recent years, the small spruce gall aphid (*Adelges laricis* Vallot) has damaged young larch plantations by decreasing their growth and even killing the trees, especially in Northern Finland. Localized damage can also be caused by the large larch sawfly (*Pristiphora erichsoni* [Hartig]) and larch casebearer (*Coleophora sibiricella* Falkovitsch).

BREEDING AND SEED PRODUCTION

Seed used for cultivation was earlier collected from the old and good stands already growing in Finland. Since the early 1970's, seed produced in seed orchards has also been available. Seven seed orchards of Siberian larch (49 ha) have been established in Finland. Plus-trees used in the seed orchards have been selected from the larch stands growing in Finland. Selected plus-trees number about 200. To test the plus-trees altogether, 51 ha of progeny trials have been established. The plus-tree material available is inadequate for any long-term breeding program.

Because of the relatively small annual cultivation area of larch and the good performance of the famous Raivola provenance in plantations, intensive breeding of Siberian larch has not been regarded as important. There is, however, continuous interest shown in the cultivation of larch in Finland. A cooperation project of establishing a seed orchard of Siberian larch has been planned to meet the mutual needs of the Nordic countries.

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Early Survival and Growth of Eurasian *Larix* Species in South Central British Columbia

Alan Vyse and Ed Elmes

Two *Larix* species of Eurasian origin, *Larix sibirica* Ledeb. and *Larix gmelinii* (Rupr.) Kuzeneva, were grown from seed and outplanted in a number of locations around the Province of British Columbia. The planning and planting were carried out by two private forest industry companies. Their intent was to compare the survival and growth performance of the exotics with that of native species, and *L. occidentalis* Nutt., which is not native to the trial sites. After establishment of the trials the Kamloops Regional Research Section of the British Columbia Forest Service undertook the task of monitoring seedling performance of those trials located in the Kamloops Forest Region. *Larix laricina* (Du Rois) K. Koch, a species that is restricted to the northeastern portion of the province, was subsequently added to the Kamloops trials.

Seed for the trials was obtained from a variety of sources. Species other than the larches were of local origin. The *L. sibirica* seed was obtained from Finnish researchers; *L. gmelinii* seed was obtained from Chinese Forest Authorities; *L. laricina* and *L. occidentalis* were obtained from sources in northern Alberta and southeastern British Columbia, respectively. All species were planted in 1986 except for *L. laricina*, which was planted in 1988.

RESULTS

On three of seven sites the performance of the exotic *Larix* species so far has been inferior to the best local species. On those sites, second-year survival of the *Larix* was good (70 to 90 percent), but lower than the local pine or spruce (more than 90 percent). Height growth of the *Larix* over 5 years was also satisfactory (80 to 100 cm), but again lagged behind the local species (110 cm). *Larix sibirica* outperformed *L. gmelinii*. *Larix laricina* performed as well as *L. gmelinii*. On two other sites, frost and browsing damaged both the local and the *Larix* species to the point that the test site was abandoned. The herbicide Vision was applied to another site in the course of an operational program to reduce vegetation competition, and all *Larix* species were destroyed. On the seventh site, *L. sibirica* outperformed the local provenance of Douglas-fir in height growth over 5 years (2-year survival was 83 percent versus 84 percent; 5-year height was 94 cm versus 69 cm).

CONCLUSIONS

The results are of curiosity value only. All four *Larix* species are clearly capable of surviving and growing on forest sites beyond their native range, but the design of the test does not allow for any wider conclusions. A far more elaborate long-term trial would be required to evaluate the risk of establishing *Larix* species on a large scale. Information from other similar trials will be required to assess the benefits and costs of undertaking such an expensive venture. It seems an unlikely prospect. However, range extensions of *L. occidentalis* will be more thoroughly tested in conjunction with the provincial tree breeding program.

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Fate of *Larix Gmelini* Seeds in the Soil and Herbivore's Impact in Old-Growth Larch Stands

Yong Ban and Huacheng Xu

Studies were conducted on the of fate *Larix gmelini* seeds in the soil and the role of herbivores on seed survival. The loss of seed viability and seed foraging by animals are the major factors affecting seed loss from the time of seed dispersal to seedling establishment. About 90 percent of the mature seeds germinate under the suitable seedbed conditions in June. This can amount to 475 seeds/m. Ungerminated seeds die due to seed rot induced by high temperatures and moisture in the soil. Although animals, especially rodents which have high populations at the end of August, forage a large number of seeds, the overall seed population is not heavily harmed. Rodents that have a close relationship with *L. gmelini* seeds disperse 90 percent of the seeds and only forage 10 percent. Ants are also good seed disersers. Because of *Larix gmelini* seeds' inherent wide dispersal and raid germination characteristics, the large numbers and small size of the seed, and partial litter cover in these old growth stands, some of the seeds survive and germinate in spite of the predation by rodents and losses due to other factors.

Authors were not able to attend the symposium but did submit this poster. Huacheng Xu is Professor of Forest Ecology, P.O. Box 120, College of Forest Resources and Environment, Beijing Forestry University, 100083, People's Republic of China; Yong Ban, Ph.D., is Research Ecologist, P.O. Box 68, Chinese Academy of Forestry, Beijing, 100091, People's Republic of China.

Effects of Intensive and Light Fire Disturbances on *Larix Gmelini* Regeneration Patterns in Da Xingan Ling Mountains, China

Yong Ban and Huacheng Xu

Following an intensive burn and a mast year, *Larix gmelini* regenerates with a remarkable surge the first year, especially on the burned slash of the *Larix gmelini-Alnus mandshurica* plant association. A great number of seedlings also emerge in the second year on the burned areas in the *Larix gmelini-Ledum palustre* association. However, in spite of subsequent mast years, seedling establishment diminishes rapidly on both plant associations in later years because the ecological niche for the seedlings becomes fully occupied. Therefore, seedlings which develop from the wave of regeneration after a fire have a narrow age range. These seedlings will continue to grow and eventually will reach the main canopy layer. This juvenile population of *Larix*, which is improved by having mature trees of the species, presents a notably interesting spacing pattern. There are circle regeneration cohorts in a range of 2 x 2 m and 4 x 4 m on the area around the mature trees where seeds fall down into the soil as a result of severe fire. All of this demonstrates that *Larix gmelini* is a fire adapted species.

There is a 10 year interval between the year of a light fire and the resulting regeneration wave, which is different from that of an intense fire. The regeneration wave resulting from light fire cannot be sustained. Therefore, there is no relationship between fire disturbance that occurred several decades ago and the "inverse J" age distribution and wide range, especially in stands over 200 years old. The wave, which is in dynamic balance with the compensating births and deaths of trees of different ages is typical of advanced regeneration which comprises multigenerational stands. Further development of the understory trees is suppressed by the upper stand canopy. Until there is a canopy disturbance, the understory will not reach into the upper canopy.

Authors were not able to attend the symposium but did submit this poster. Huacheng Xu is Professor of Forest Ecology, P.O. Box 120, College of Forest Resources and Environment, Beijing Forestry University, 100083, People's Republic of China; Yong Ban, Ph.D., is Research Ecologist, P.O. Box 68, Chinese Academy of Forestry, Beijing, 100091, People's Republic of China.

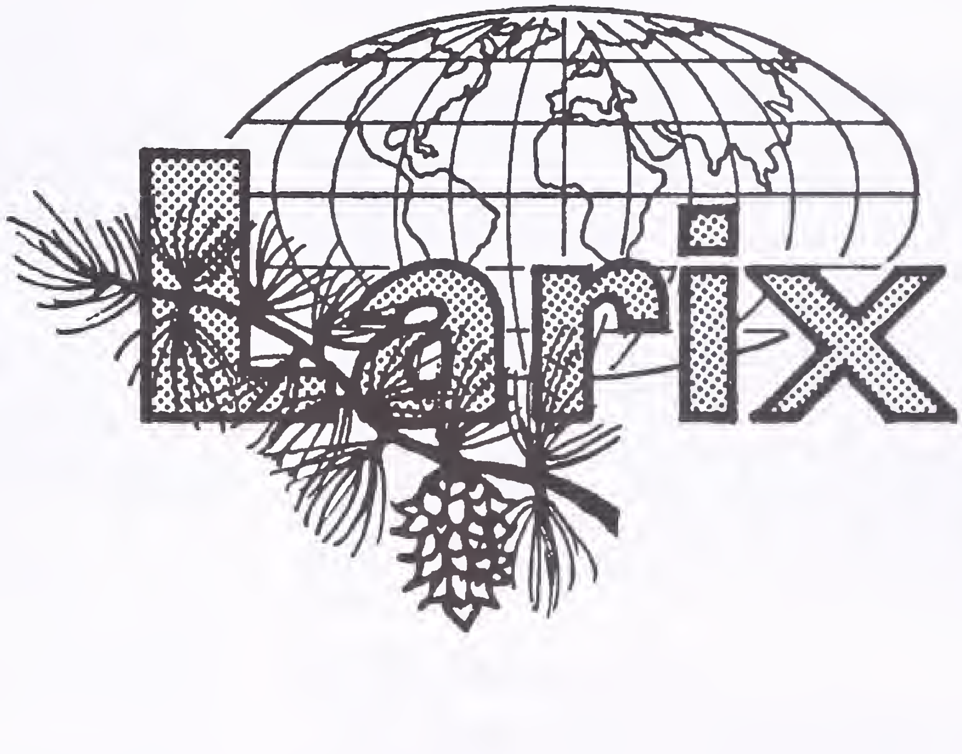
Demography of *Larix Gmelini* Seedling Populations in Old-Growth Larch Stands, Da Xingan Ling Mountains, China

Yong Ban and Huacheng Xu

Demography of *Larix gmelini* seedling populations was studied in old-growth larch forests in the northern Da Xingan Ling Mountains of China from 1988 to 1992. The results showed that after a mast year, a great number of larch seedlings emerge in June of the next year with 100 to 270 individual seedlings/m^2. Most die within a period of 15 days after seedling emergence. The emergence of *Larix gmelini* seedlings in the old-growth stands of the *Larix gmelini-Alnus mandshurica* vegetative association is later in the season than those in the *Larix gmelini-Betula fruticosa* and the *Larix gmelini-Ledum polustre* associations. In the *Larix gmelini-Ledum polustre* association, 48 percent of the seedlings died within 15 days and 97 percent within 3 years. In the *Larix gmelini-Betula fruticosa* association, 29 percent died within 15 days and 66 percent within 3 years, and in the *Larix gmelini-Alnus mandshurica* association it was 33 percent and 69 percent, respectively. Seedlings established early in the season have a prominent advantage in the *Larix gmelini-Betula fruticosa* and *Larix gmelini-Alnus mandshurica* associations—especially in the latter; no advantage was evident in the *Larix gmelini-Alnus mandshurica* associations. Seedlings emerging after July have a very low survival rate. A part of the *Larix* evolutionary strategy includes fully utilizing the transient growth season and rapidly occupying burned, bare land. A great difference in seedling numbers appears among forest types with the most seedlings in the *Larix gmelini-Betula fruticosa*, fewer in the *Larix gmelini-Alnus mandshurica*, and least in the *Larix gmelini-Ledum polustre* associations. Although a great number of seedlings emerge, most will die in the same year, and a high mortality rate will continue in the next 4 years because of the low stability, a characteristic of larch forests.

Authors were not able to attend the symposium but did submit this poster. Huacheng Xu is Professor of Forest Ecology, P.O. Box 120, College of Forest Resources and Environment, Beijing Forestry University, 100083, People's Republic of China; Yong Ban, Ph.D., is Research Ecologist, P.O. Box 68, Chinese Academy of Forestry, Beijing, 100091, People's Republic of China.

VIII. Appendices



Appendix A: Larix Field Tours for the International Larix Symposium

Wyman C. Schmidt

Whitefish, MT, U.S.A., was specifically chosen as the location of the Larix symposium because of its proximity to the three North American species of Larix; *L. occidentalis*, *L. lyallii*, and *L. laricina*. All could be reached within a few hours, and *L. occidentalis* completely surrounded the site of the symposium. Seven tours before, during, and after the symposium were offered, and every tour had many participants.

FIELD TOUR 1: LARCH ECOLOGY AND SILVICULTURE RESEARCH

Tour Coordinators:

Wyman C. Schmidt, Intermountain Research Station, Forest Service, U.S. Department of Agriculture

Gary Gregory, Glacier National Park, National Park Service, U.S. Department of the Interior

This tour visited two Biosphere Reserves: Coram Experimental Forest, a managed reserve, featured over 40 years of ecological and silvicultural research; Glacier National Park, a natural reserve, featured natural ecosystem processes and the interactions with people and wildlife in a park setting.

Coram Experimental Forest

Coram Experimental Forest is an outdoor laboratory dedicated to providing basic information needed to manage western larch-Douglas-fir forests. In general, research emphases have been:

1950's:	Harvesting and natural regeneration
1960's:	Artificial regeneration and stand culture in young forests
1970's:	Environmental effects of new harvest technologies and utilization standards
1980's:	Long-term effects of forest practices on water use, forest development, soil nutrient characteristics, and animal interactions

Stop 1: Coram Overlook—At this stop we discussed the historical background and the ecological, physical, and biological facts about Coram Experimental Forest. We also discussed the cooperative working relationship of the Intermountain Research Station and the Flathead National Forest, the International Biosphere status, and the types of studies that have been conducted at Coram Experimental Forest. This stop was an excellent vantage point for viewing and taking photos.

Stop 2: Residues Utilization and Environmental Effects—We discussed the overall objectives of a residue management study, including treatment effects on vegetation, tree regeneration, water use, soil nutrients, aesthetics, and other factors. Treatments in this multifaceted study included three silvicultural methods and four levels of residue removal. This stop was in a shelterwood that was harvested in 1974.

Stop 3: Larch Spacing Study—We covered the 30-year response of larch forests that were initially thinned at age 9 to a wide range of stand densities. Included were effects of density, thinning interval, and shrub removal on tree growth and mortality, cone production, water use, vegetation response, phenology, and factors such as snow and bear damage to larch. We walked through some of the study plots.

Stop 4: Natural Old-Growth Larch Forest—The discussion centered on research natural areas—the philosophy, system, and status in the West. Presenter Angie Evenden included descriptions of Larix forests represented in the natural area system. Typical flora in a 300-year-old western larch forest was observed on this walk into the forest. Avian and small mammal studies were also covered.

Glacier National Park

Glacier National Park is an outstanding example of a pristine ecosystem in the Northern Rockies. Both western larch and alpine larch occur naturally within the Park and contribute substantially to the visual qualities of this beautiful place, particularly during the fall. Natural ecological processes are allowed to proceed to the greatest extent possible.

Stop 1: Apgar—As we ate lunch on the shores of Lake McDonald, we viewed fire-created mosaics across the lake. The discussion covered the role of fire in maintaining this naturally functioning ecosystem.

Stop 2: Fish Creek—A walk through a frontcountry campground examined the effects of the massive 1929 fire that burned through an old-growth forest in this area. The many surviving western larch are now surrounded by a new forest.

Wyman C. Schmidt was principal organizer of the 1992 International Larix Symposium.

Stop 3: Huckleberry Mountain—This short walk revealed many aspects of vegetation and wildlife changes in a forest burned in 1967. One can compare the young larch in the burned area to an adjacent unburned forest.

FIELD TOUR 2: ECOLOGY AND SILVICULTURE PRACTICES IN LARCH FORESTS OF THE NORTHERN ROCKIES

Tour Coordinators:
Bob Naumann, Northern Region, Forest Service, U.S. Department of Agriculture

Gary Gregory, Glacier National Park, National Park Service, U.S. Department of the Interior

Glacier National Park

Glacier National Park is an outstanding example of a pristine ecosystem in the Northern Rockies. Both western larch and alpine larch occur naturally within the Park and contribute substantially to the visual qualities of this beautiful place, particularly during the fall. Natural ecological processes are allowed to proceed to the greatest extent possible.

Stop 1: Apgar—We viewed fire-created mosaics across Lake McDonald. The discussion covered the role of fire in maintaining this naturally functioning ecosystem.

Stop 2: Fish Creek—A walk through a frontcountry campground examined the effects of the massive 1929 fire that burned through an old-growth forest in this area. The many surviving western larch are now surrounded by a new forest.

Stop 3: **Huckleberry Mountain**—This short walk revealed many aspects of vegetation and wildlife changes in a forest burned in 1967. One can compare the young larch in the burned area to an adjacent unburned forest.

North Fork of the Flathead River Management Area

The North Fork Management Area offered many opportunities to capitalize on the varied resource values. After lunch at Big Creek Campground, this portion of the tour illustrated some of the practices commonly used in western larch forests. Two sites were visited on Flathead National Forest land on the Glacier View Ranger District where silviculture practices were viewed and discussed.

Stop 1—The discussion at the first stop covered management philosophy and objectives as the basis for silvicultural treatments. Forest Plans are the basis for cultural treatments that are applied to serve a number of social and biological needs. Stand level treatments are strongly influenced by ecosystem processes at the landscape level. Treatments are designed through the use of stand data. At this stop, the results of several even-aged silvicultural systems were explained. Examples were shown for regeneration harvest methods, site preparation techniques, regeneration from plantings, aerial seeding, and natural seedfall.

Stop 2—The second stop focused attention at the stand level by visiting a thinning area. The treatment was related to local climate and fire effects. Successional trends were discussed and related to stand development following a 1926 wildfire under both managed and natural conditions. The tour group considered future management options for this western larch stand.

FIELD TOUR 3: FIRE AND HARVEST EFFECTS ON SUCCESSION AND MANAGEMENT OF A *LARIX* FOREST

Tour Coordinators:
Raymond C. Shearer, Intermountain Research Station, Forest Service, U.S. Department of Agriculture

Peter Stickney, Intermountain Research Station, Forest Service, U.S. Department of Agriculture

Debbie Manley, Flathead National Forest, Forest Service, U.S. Department of Agriculture

This tour featured Miller Creek Demonstration Forest, an area designated to protect and encourage long-term research while implementing the Forest Plan and maintaining outputs. The group saw 25 years of research documenting vegetative succession and related resource functions following harvest and prescribed burning, harvest and wildfire, and wildfire in old-growth forests. This tour also visited a lumber mill featuring close utilization of western larch.

Miller Creek Demonstration Forest

In 1967 and 1968, within the Miller Creek Demonstration Forest, 60 4-ha (10-acre) units were (1) clearcut and burned by prescribed fire or wildfire, (2) clearcut and unburned, or (3) uncut and burned by wildfire. Research showed that the first 25 years of vegetation recovery and development manifest marked changes in composition and structure of the seral forest community depending on intensity of the fire and aspect. Herbs (mostly *Epilobium angustifolium*) predominated during the initial stage of succession on sites where the duff layer was substantially reduced by fire. If soil-stored shrub seeds (such as *Ceanothus velutinus*) were present, the cover of shrubs exceeded herbs by the fifth to sixth year. Trees reestablish as early in succession as the first postfire year (such as *Larix occidentalis* and *Pinus contorta*) where on site seed sources were available. On poorly burned sites, herbaceous plants dominated the early seral community longer in the absence of survivor or seed origin shrubs or trees. Clearcutting without fire maintained the predisturbance herb, shrub, and small tree components. Trees established slowly on unburned sites, and most were shade-tolerant species (such as *Abies lasiocarpa* and *Picea engelmannii*).

Recent thinning and weeding reduced the number of conifers on overstocked units to about 1,500 stems per ha (600 per acre). Changes in cover resulting from these treatments were compared at 5-year intervals with untreated controls located on each unit.

Stop 1: Miller Creek Demonstration Forest—We walked on a south-facing slope burned by a late-summer wildfire in 1967 and observed differences in forest vegetation on an area (1) clearcut and prescribed burned before the wildfire, (2) undisturbed by salvage after the wildfire, and (3) salvage-logged and then aerial seed with *Larix occidentalis* after the wildfire. Next, we viewed a spring prescribed fire on a nearby south-facing clearcut that caused a different vegetation response. The final stop compared vegetation on a higher elevation east-facing site made up of (1) virgin forest, (2) unburned clearcut, and (3) prescribed burned clearcut.

Stop 2: Larch Wood Utilization—We observed utilization of western larch for wood products at Plum Creek Timber Co., Inc., Evergreen Mill.

PRE- AND POST-SYMPOSIUM FIELD TOURS

Tour 1: Carlton Ridge (Bitterroot Mountain Range), Saturday, October 3, 1992.

We assembled at the Forestry Sciences Laboratory, Missoula, Montana. Tour Leaders were Clinton Carlson and Steve Arno. This tour took the group to a nearly pure stand of alpine larch on the summit of Carlton Ridge, about 24 km (15 miles) southwest of Missoula, MT. The more adventurous participants were then led to a site below Carlton Ridge where alpine and western larch coexist and hybridize naturally. The alpine larch stand on Carlton Ridge was accessible only by foot trail; about a 5 km (3 miles) walk. The trail started at 1,676 m (5,500 ft) mean sea level, and climbed to 2,590 m (8,500 ft) to the alpine larch stand. The trail was moderately steep but not at all dangerous. There was no trail from the alpine larch on Carlton Ridge to the hybrid site 610 m (2,000 ft) below the ridge. It was a difficult, steep walk and was recommended for only the more hardy participants. Those people wishing to view only the alpine larch stand returned to the transportation via the foot trail. Those visiting the hybrid site continued their descent to a road where they were met by the transportation. The weather in early October in western Montana can be cold and snowy but was mild for this tour. The group was asked to be prepared for a hardy outdoor adventure that would keep Montana on their minds forever! It did.

Tour 2: Link Lake (Whitefish Mountain Range), Sunday, October 4, 1992.

The group assembled at Grouse Mountain Lodge, Whitefish, Montana. Tour Leader was Steve Wirt. This tour took the group into the Upper Whitefish Lake area and beyond into the Whitefish Divide country. It was approximately a 1 hour drive of 60 km (36 miles) from Whitefish, MT, followed by a 1-hour hike of about 2.5 km (1.5 miles) into Link Lake. Link Lake is just one of many lakes in this area and it offered one of the best and most accessible areas to observe alpine larch in the Whitefish Divide. The first half of the trail was a moderate uphill hike over a small divide with the remaining portion, a moderate downhill walk to the lake. The area surrounding the lake had excellent representations of alpine larch. Hiking around the lake and up adjacent ridge tops provided more vistas and additional opportunities for viewing this species.

Tour 3: Preston Park (Glacier National Park), Friday, October 9, 1992.

The group assembled at Grouse Mountain Lodge for the Glacier N.P. Tour. Tour Leader was Gary Gregory. The hike to alpine larch at Preston Park near the Continental Divide covered 10 km (6 miles) and gained 370 m (1,200 ft) elevation. The trail followed Siyeh Creek for a short distance. The creek here had carved through layers of ancient, tilted sedimentary rock. The trail then left the creek and passed through a dense forest of subalpine fir and spruce. Open meadows and avalanche chutes were crossed. This was prime grizzly bear habitat. Preston Park has a landscape of alpine larch and subalpine fir scattered over windswept meadows. There were rewarding views of Going-To-The-Sun Mountain and Matahpi Peak.

Tour 4: Canada Tour—*Larix occidentalis*, *L. lyallii*, and *L. laricina* Ecology, Management, and Silviculture: Southeastern British Columbia and Alberta, Canada, Friday, October 9, 1992.

The group left via bus from Grouse Mountain Lodge for the Canada Tour. Tour Leader was Barry Jaquish. This relaxing 4-day tour explored the spectacular Canadian Rocky Mountains and the southern extent of the Canadian Boreal Forest. The tour featured *Larix occidentalis* management and silviculture in southeastern British Columbia, *L. lyallii* ecology in the Banff National Park/Lake Louise area, and *L. laricina* ecology in west-central Alberta. The tour overnighted in Calgary, Alberta on Sunday, October 11. Those who wanted departed from the Calgary International Airport. The tour terminated Monday, October 12, in Whitefish, Montana. It was a scenic and informative event with something for everyone. Some walking on moderately steep trails was required in Banff.

Appendix B: International Larix Arboretum, Coram Experimental Forest Headquarters, Hungry Horse, Montana, U.S.A.

Raymond C. Shearer
Jack A. Schmidt
Wyman C. Schmidt

The *Larix* Symposium provided the impetus to establish an arboretum that features all *Larix* species of the world (figs. 1 and 2). This International Larix Arboretum, established on a 0.5 ha (1.2 acre) site next to the headquarters of the Coram Experimental Forest and near the Hungry Horse Ranger Station, was dedicated October 7, 1992, with a tree-planting ceremony that had international participation by attendees from North America, Europe, and Asia, and by teachers and students from the nearby Hungry Horse elementary school (figs. 3 and 4). This symbol of global cooperation will not only provide a visual demonstration of larch internationale, but it is designed to provide opportunities for species comparisons and genetics research.

Figure 1—Logo for the International Larix Arboretum at Coram Experimental Forest.

All authors are with the Intermountain Research Station, Forest Service, U.S. Department of Agriculture. For further information about this arboretum, contact Project Leader, Subalpine Silviculture Research Work Unit, Forestry Sciences Laboratory, Missoula, MT 59812.

Figure 2—An overview of the International Larix Arboretum, Coram Experimental Forest, May 1993. Note the shade cards used to increase seedling survival.

Figure 3—Attending the dedication of the International Larix Arboretum at Coram Experimental Forest, Montana, are: (from left to right) Klara Vishnevetskaia, from Moscow, Russia (currently a graduate student at Toronto); Dr. Leonid I. Milyutin, from the Institute of Forests and Wood, Siberian Branch of Russian Academy of Science, Krasnoyarsk, Russia; and, Prof. Dr. Friedrich-Karl Holtmeier, Westfalische Wilhelms-Universitat, Munster, Germany.

Figure 4—During dedication ceremonies of the International Larix Arboretum, Mrs. Sung-Cheon Hong, from Daegu, South Korea, helped plant a tree with Intermountain Station Forester Jack Schmidt, right, and a student from Hungry Horse, Montana, Elementary School.

The arboretum is divided into three equal-sized blocks, about 21.3 m x 70 m (70 ft x 230 ft). Within each block *Larix* seedlings are randomly planted every 1 m (5 ft) in rows 3 m (10 ft) apart. The design calls for 12 trees of each species, subspecies, and hybrids in each of the three blocks for a total of nearly 600 trees. The species, subspecies, and hybrids that are (or will be) planted are:

Common name	Species name	Comments	Date planted
	Larix species		
European larch	*L. decidua*		Sept. 2, 1992
Asian larch	*L. gmelinii*	Includes *dahurica*	Sept. 3, 1992
Sikkim larch	*L. griffithiana*		Not planted
Tamarack	*L. laricina*		Sept. 2 and 8, 1992
Japanese larch	*L. leptolepis*	Formerly *kaempferi*	Sept. 3, 1992
Alpine larch	*L. lyallii*		Sept. 17, 1992
Masters larch	*L. mastersiana*		Sept. 15, 1993
Western larch	*L. occidentalis*		Sept. 17, 1992
Chinese larch	*L. potaninii*		Sept. 16, 1993
Siberian larch	*L. russica*	Formerly *siberica*	Sept. 3 and 8, 1992
	Larix subspecies		
Polish larch	*L. decidua*, ssp. *polonica*		Sept. 3, 1992
Sudetic larch	*L. decidua*, ssp. *sudetica*		Sept. 3, 1992
Olga Bay larch	*L. gmelinii*, ssp. *olgensis*		Sept. 3, 1992
	Larix hybrids		
Dunkeld larch	L. x *eurolepis*	*L. decidua* [pollen] and *L. leptolepis*	Sept. 3 and 8, 1992
Bitterroot larch	L. x occilyal	*L. occidentalis* [pollen] and *L. lyallii*	Sept. 17, 1992
Bitterroot larch	L. x lyalocci	*L. lyallii* [pollen] and *L. occidentalis*	Sept. 18, 1992

Source information for Larix species, subspecies, and hybrids in the International Larix Arboretum, Hungry Horse, Montana

			North latitude		East/West longitude		
Common name	**Species name**	**Provenance**	**Degree**	**Minute**	**Degree**	**Minute**	**Elevation (m)**
		Larix species					
European larch	*L. decidua*		55	49	12	23E	
Asian larch	*L. gmelinii* (includes *dahurica*)	Heilongjiang	47	00	127	00E	
Sikkim larch	*L. griffithiana*	- - - - - - - - - - - - - - - - Not planted yet because no seed received- - - - - - - - - - - - - -					
Tamarack	*L. laricina*	Murray Twnshp	44	12	77	44W	120
Japanese larch	*L. leptolepis* (formerly *kaempferi*)	- -Information not available -					
Alpine larch	*L. lyallii*		46	42	114	11W	2,800
Masters larch	*L. mastersiana*	- -Information not available -					
Western larch	*L. occidentalis*		46	56	113	42W	1,200
Chinese larch	*L. potaninii*	- -Information not available- -					
Siberian larch	*L. russica* (formerly *siberica*)	Krasnoyarsk					
		Larix subspecies					
Polish larch	*L. decidua*, ssp. *polonica*		46	00	77	25E	130
Sudetic larch	*L. decidua*, ssp. *sudetica*	- -Information not available -					
Olga Bay larch	*L. gmelinii*, ssp. Jilin *olgensis*		43	00	126	00E	
		Larix hybrids					
Dunkeld larch	L. x *eurolepis* (*L. decidua* [pollen] & *L. leptolepis*)	- - - - - - - - - - - - - - - Information not available - - - - - - - - - - - - -					370
Bitterroot larch	L. x occilyal (*L. occidentalis* [pollen] & *L. lyallii*)		46	42	114	11W	2,800
Bitterroot larch	L. x lyalocci (*L. lyallii* [pollen] & *L. occidentalis*)		46	56	113	42W	1,200

CEREMONIAL PLANTING—INTERNATIONAL LARIX ARBORETUM, 7 OCTOBER 1992

A seedling of most of the larch species were planted along the north edge of the arboretum at its dedication. Those who planted these trees were:

Larix species	**Planter's name(s)**	**City and country**	**Affiliation**
Larix leptolepis Japanese larch	Fukio Takei	Naganoken, Japan	Nagano Prefectural Forestry Research Center
Larix gmelinii Asian larch	Yeh-chu Wang	Harbin, Peoples Republic of China	Ecological Research Group, Northeast Forestry University
Larix russica Siberian larch	Prof. Leonid I. Milyutin	Krasnoyarsk, Russia	V.N. Sukachev Institute of Forest, Siberian Branch, Russian Acad. of Science
Larix decidua European larch	Friedrich-Karl Holtmeier	Munster, Germany	Landscape Ecology, Westfalische-Wilhelms-Universitat
Larix occidentalis Western larch	Katrine Berg Al Christophersen	Hungry Horse, Montana, U.S.A. Columbia Falls, Montana, U.S.A.	Student, Hungry Horse Elementary School Ranger, Hungry Horse District, Flathead NF
Larix lyallii Alpine larch	Jack A. Schmidt	Missoula, Montana U.S.A.	Intermountain Research Station, FSL, Missoula, Montana, U.S.A.
Larix laricina Eastern larch or tamarack	Joseph Fisher Don Fowler	Hungry Horse, Montana, U.S.A. Fredericton, New Brunswick, Canada	Student, Hungry Horse Elementary School Forestry Canada
Larix occidentalis x *lyallii* Western x Alpine hybrid; WL pollen	Clinton E. Carlson	Florence, Montana U.S.A.	Intermountain Research Station, FSL, Missoula, Montana, U.S.A.
Larix eurolepis European x Japan hybrid; EL pollen	Claudette Berg-Rink Hans G. Schabel	Hungry Horse, Montana, U.S.A. Stephens Point, WI	Student, Hungry Horse Elementary School University of Wisconsin
Larix lyallii x *occidentalis* Alpine x Western hybrid; AL pollen	Bob Muth	Hungry Horse, Montana, U.S.A.	Sixth Grade Teacher, Hungry Horse Elementary School
Larix gmelinii spp. *olgensis* Olga Bay larch	Gabe Buzzell Mrs. Sung-Cheon Hong	Hungry Horse, Montana, U.S.A. Daegu, Republic of South Korea	Student, Hungry Horse Elementary School Kyungpook National University

Note: On September 17, 1993, Susan Colt planted *Larix mastersiana* and Jack A. Schmidt planted *L. potaninii* in the International

A paved road, a sidewalk, and a 1.5 m (5 ft) wide strip planted with native shrubs form a border around the International Larix Arboretum. Shrubs planted in this strip are mostly snowberry (*Symphoricarpos albus*), red-osier dogwood (*Cornus stolonifera*), rose (*Rosa woodsii*), and chokecherry (*Prunus virginiana*), all from the Glacier National Park Native Plant Nursery. The arboretum is enclosed by a 2.4 m (8 ft) high chain link fence that protects the young larch from damage by large herbivores (deer, elk, moose) or by people driving vehicles or snowmobiles across the area.

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Schmidt, Wyman C.; McDonald, Kathy J., comps. 1995. Ecology and management of Larix forests: a look ahead. Proceedings of an international symposium; 1992 October 5-9; Whitefish, MT, U.S.A. Gen. Tech. Rep. INT-GTR-319. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 521 p.

This proceedings is the product of an international symposium on the Larix species of North America, Europe, and Asia. Western larch, an important species in the Western United States and Canada, was featured. The symposium included information on ecology, management, silviculture, regeneration processes, growth, wildlife, vegetation succession, silvics, history, genetics, breeding and provenance testing, physiology, fire, insects and disease, and research needs. This proceedings illustrates the importance of Larix in the temperate forests of the Northern Hemisphere.

Keywords: larch, western larch, *Larix occidentalis*, ecology, international larch management

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