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Bulletin 66

Choice of Seed Origins for the Main Forest Species in Britain

R Lines

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R. Lines
Silviculturist,
Forestry Commission

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Enquiries relating to this publication should be addressed to the Technical Publications Officer, Forestry Commission, Forest Research Station, Alice Holt Lodge, Wrecclesham, Farnham, Surrey GU10 4LH.

FRONT COVER: Sitka spruce seed origins planted in demonstration rows at Bush Nursery, near Edinburgh. In foreground, Annette Island, Alaska, then in decreasing latitudinal order and increasing tree height to Crescent City, California. *(R. Lines)*

Contents

Acknowledgements

The author acknowledges the valuable assistance he has been given by colleagues in the Research Division who are too numerous to name. Thanks are also due to the large number of overseas researchers who have provided me with information and guided my visits over the last 30 years. The maps were drawn by Mr J. Williams.

Foreword

As afforestation in Britain is based predominantly on wide ranging exotic species, choice of seed origins is a crucial constituent of its success. Research in this field, encompassing not only indistinct demarcation between native populations but also variation within them, has to be based on well designed long-term experiments. It is thus fortunate that the author of this Bulletin, Roger Lines, has been responsible for the Commission's extensive provenance investigations for more than half of the six decades since the first project plan was drafted. Over this period he has become recognised as an international authority.

This Bulletin is directed at both manager and researchers. The former are succinctly guided to appropriate seed origins for their site conditions and objectives, and equally importantly warned off unsuitable sources. It is very much in the grower's interest that he should be sufficiently knowledgeable to specify his preferred, acceptable or unacceptable seed origins. Researchers, who may wish to investigate seed origin variation in greater detail, are led into the extensive literature which supports this neccessarily condensed publication. The several more precise means of species improvement now being developed will long continue to rely on this essential first screening of genetic variation.

S.A. Neustein
Chief Research Officer (North)
Forestry Commission
May 1986

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Silviculturist,
Forestry Commission

Introduction

Choice of seed origin can be a very critical stage in forest management, in some cases resulting either in flourishing plantations or else in complete failure. The problem is confounded by the large site differences which exist even in our small country, which may require selection of a different origin in Argyll from that used in Hampshire, or even on different site types within the same region. In broad terms site types in Britain may be linked with the European north temperate forest zonation to give two main types: a northern zone similar to the boreal coniferous forests and a southern zone similar to the West European mixed conifer and broadleaved forests. The former would equate with Regions of Provenance 10 and 20 and the latter with Regions 30 and 40 (see map opposite, from Forestry Commission, 1973). This map emphasises that Britain is split also into western and eastern sectors, which for some site factors may be just as important as the north/south split.

The objects of management will also affect the choice; thus the Christmas tree grower will require a different shape of Norway spruce tree (and so a different origin), from that required by the forest manager, whose aim is rapid growth of good saw-timber. Choice of seed origin has been more difficult in Britain than in the major forested countries of the world, since in the past we have had to import most of our seed and because we tend to grow a wider range of species than any other country of similar size. The British native conifer flora contains only one productive species, Scots pine, due to our isolated geographical position at the end of the Pleistocene glaciation. In Europe the main mountain chains run east and west, thus forming a barrier to migration of tree species during periods of glaciation. In NW America, species were able to recolonise to the north along the mountain chains which run in that direction, thus giving a wide range of productive conifers at the same latitude as Britain.

European Economic Community definitions

Provenance: the place in which any stand of trees (whether native or not) is growing.
Origin: the place in which a stand of native trees is growing, or the place from which a non-native stand was originally introduced.

In general forestry use, the term 'provenance' is commonly extended to mean not only the geographical source of the seed, but also the trees raised from it. This is the meaning which accords with the definition in the standard work on forest terminology (Ford-Robertson, 1971).

It is important to use the EEC definition of 'origin' correctly. For example, if seed was imported from Vancouver Island to form a stand in Hampshire the origin is 'Vancouver Island'. If this stand later produces seed the *origin* is still 'Vancouver Island' but the *provenance* is 'Hampshire'.

Advice on choice of origins

The reliability of advice on choice of origin will depend on the information available from existing trials. Fortunately, seed origin or provenance trials were started in Britain over 50 years ago. We can also learn from studies in NW European countries, although caution must be exercised in interpreting their results for conditions here. Vilmorin planted different provenances of Scots pine at Les Barres, France in 1823 and the first international experiment with this species was started by International Union of Forest Research Organisations in 1908 (unfortunately Britain did not take part in this trial). The cost of seed is a relatively insignificant part of the cost of establishing forest and Faulkner (1962) has shown that an increase of only one half per cent in the value of the final crop justifies a 50 per cent increase in the price of seed.

There are a few basic factors governing the choice of seed origin (see Lines (1965) for a more detailed discussion):

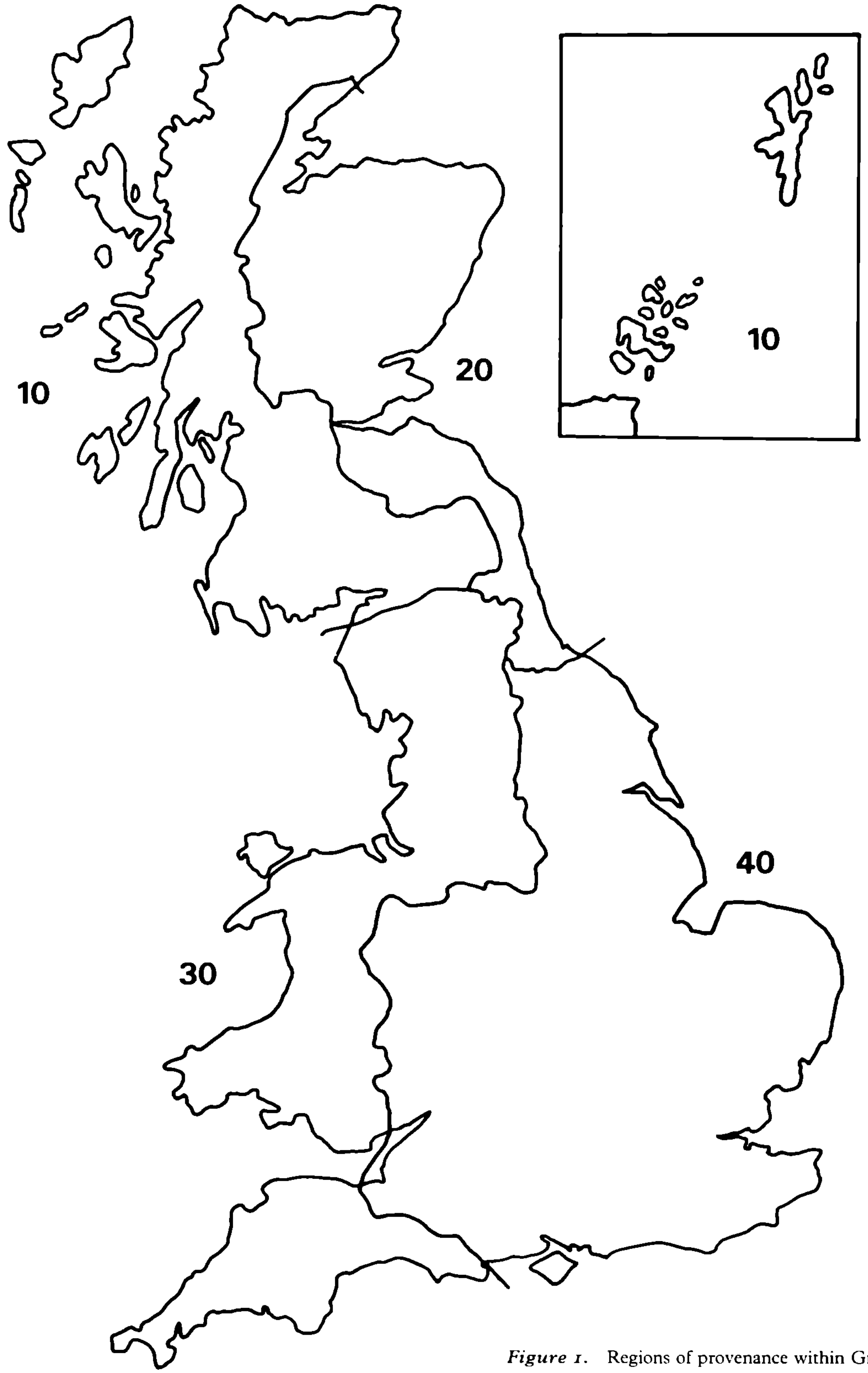


Figure 1. Regions of provenance within Great Britain.

a. **Broad climatic matching** is generally required between the origin and the site on which it is to be planted. In general, our maritime climate does not match well with the continental climates of eastern North America or the Alpine climates of Europe. For example, Alpine seed origins of European larch *(Larix decidua)* flush early and their shoots frequently suffer dieback. The extremely continental Siberian larch *(L. sibirica)* cannot be grown anywhere in Britain because it flushes so early that it is damaged by late winter frosts every year. Some NE American broadleaved species do not enjoy sufficient summer heat to harden their tissues fully in our cool summers.

However, the principle of climatic matching should not be too strongly emphasised. It is surprising how well a species such as Japanese larch grows in Britain, since in Japan it occurs at high elevations (up to 2500 m) and at the same latitude as Algiers. With European Silver fir *(Abies alba)* the best climatic match is with stands in Normandy, yet these perform poorly and the fastest growth in Britain is that of seed origins from a Mediterranean mountain climate in Calabria (the toe of Italy), (Lines, 1979);

b. **Day length** at the place of origin usually exerts a strong influence on flushing and growth cessation. Hence northern seedlots (e.g. Lodgepole pine from the Yukon) flush early and shoot growth ceases at the beginning of our long growing season. Conversely, the most southerly origins of many species (e.g. Sitka spruce, Douglas fir, Red alder) tend to continue growth so late into the autumn that they are especially liable to frost damage. There may be some compensating effect of elevation on this day length effect. Thus several conifers from high elevations in the southern Cascade mountains are inherently acclimatised to a short growing season and cease growth earlier than low elevation seed origins with the same photoclimate;

c. **Edaphic factors** may have some influence, for example Lodgepole pine from poorly drained muskeg (bog) sites appears to tolerate soil conditions in British peatlands better than seed origins from the hot, dry interior of British Columbia, although some of the effect may be due to climate rather than soil.

Some insect pests are confined to a single species, e.g. *Adelges cooleyi* on Douglas fir. Where the insect shows a preference for particular seed origins, details are given in the text. Insects which attack a wide range of species, e.g. *Hylobius abietis,* without showing any apparent preference among origins are omitted. Similarly, the evidence for differential susceptibility among origins to *Heterobasidion (Fomes)* butt-rot is non-existent, though resistance of certain groups of species is known to differ. Pines are resistant, Douglas fir, Noble and Grand firs are relatively resistant and the common spruces, larches, Western hemlock and Western red cedar are relatively susceptible (Aldhous and Low, 1974).

Prior to 1950, Forestry Commission advice on choice of seed origins was published in the forestry journals as results became available, e.g. Macdonald (1937) for European larch, and since 1950 in the annual Reports on Forest Research of the Forestry Commission. The first major attempt to cover a wide range of species was the publication of *Exotic forest trees in Great Britain* (Macdonald *et al.,* 1957). In the 1964 revision of Forestry Commission Bulletin 14 *Forestry practice,* a section of provenance choice was added for the first time. Further information came from Lines (1970) and Kennedy (1974), but it was felt that increasing knowledge available from experimental results justified fuller treatment in a publication which would bring together the information from a variety of sources. This has been done in the following sections for the species of most importance in British forestry, and prescriptions have been kept as short as possible for the use of busy forest managers. Those who wish to investigate seed origin variation in more detail can consult the references provided, as it would have been quite impossible to summarise all the results given in these publications.

As many of our species come from NW America, maps of the Tree Seed Zones for Washington and Oregon prepared by the Western Forest Tree Seed Council (Figure 2), and for British Columbia prepared by the BC Forest Service (Figure 3) are included, together with the Forestry Commission map of Seed Collection Regions in NW America (Figure 4). This has formed the basis of the seed identity code since 1956. These numbers are based on the Oxford System of Decimal Classification.

Each year the Forestry Commission includes in its annual *Seed catalogue* notes on the particular seed origins offered for the main species. If more guidance is required, please consult the Forestry Commission, Northern Research Station, Roslin, Midlothian, telephone 031 445 2176.

Figure 2. Tree seed zones for Washington and Oregon, USA.

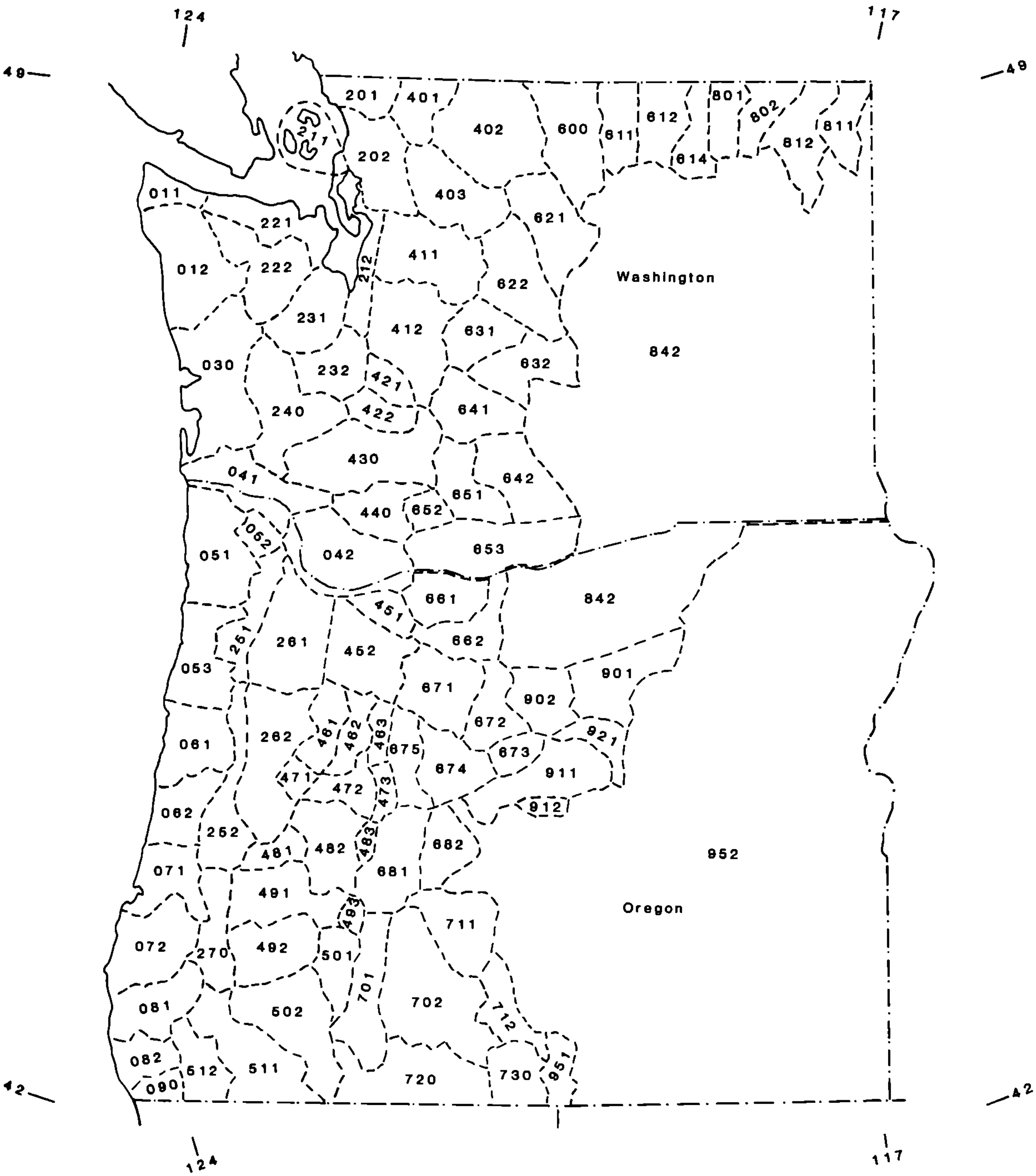


Figure 3. Tree seed zones for British Columbia, Canada.

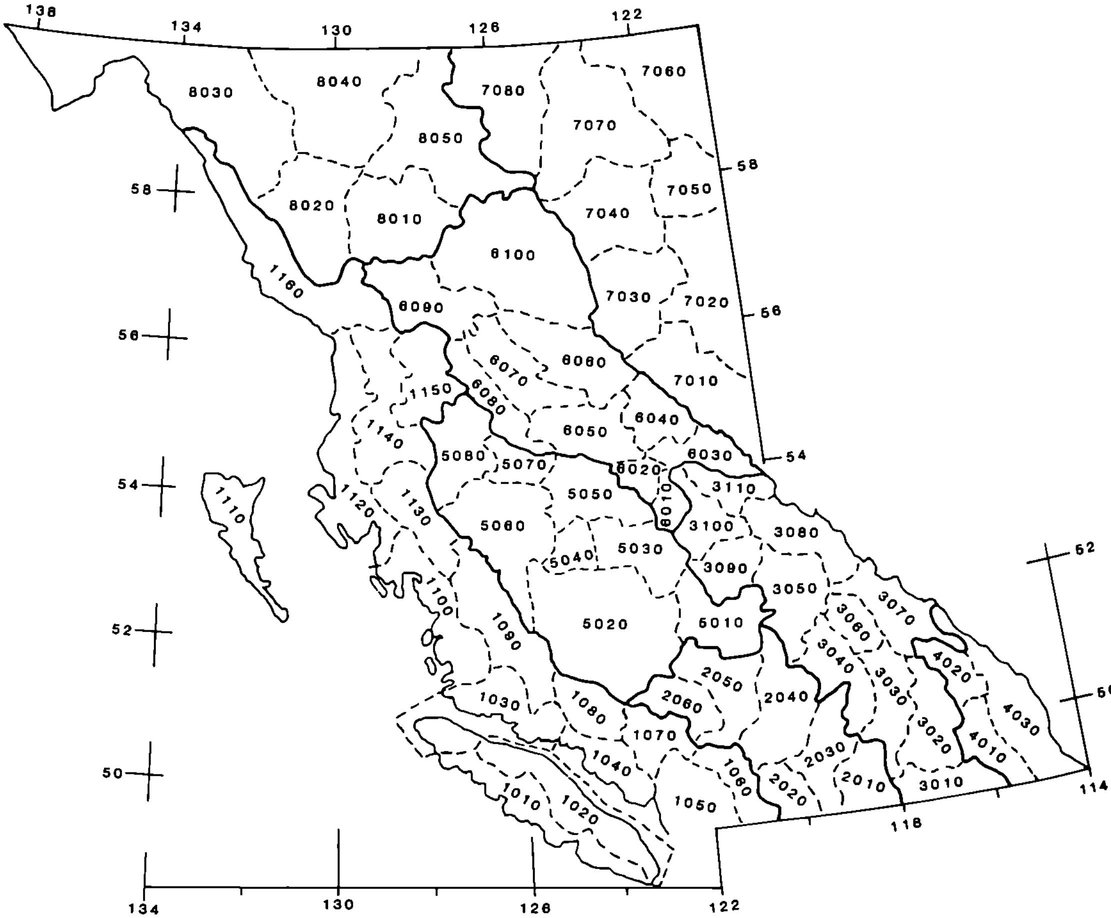
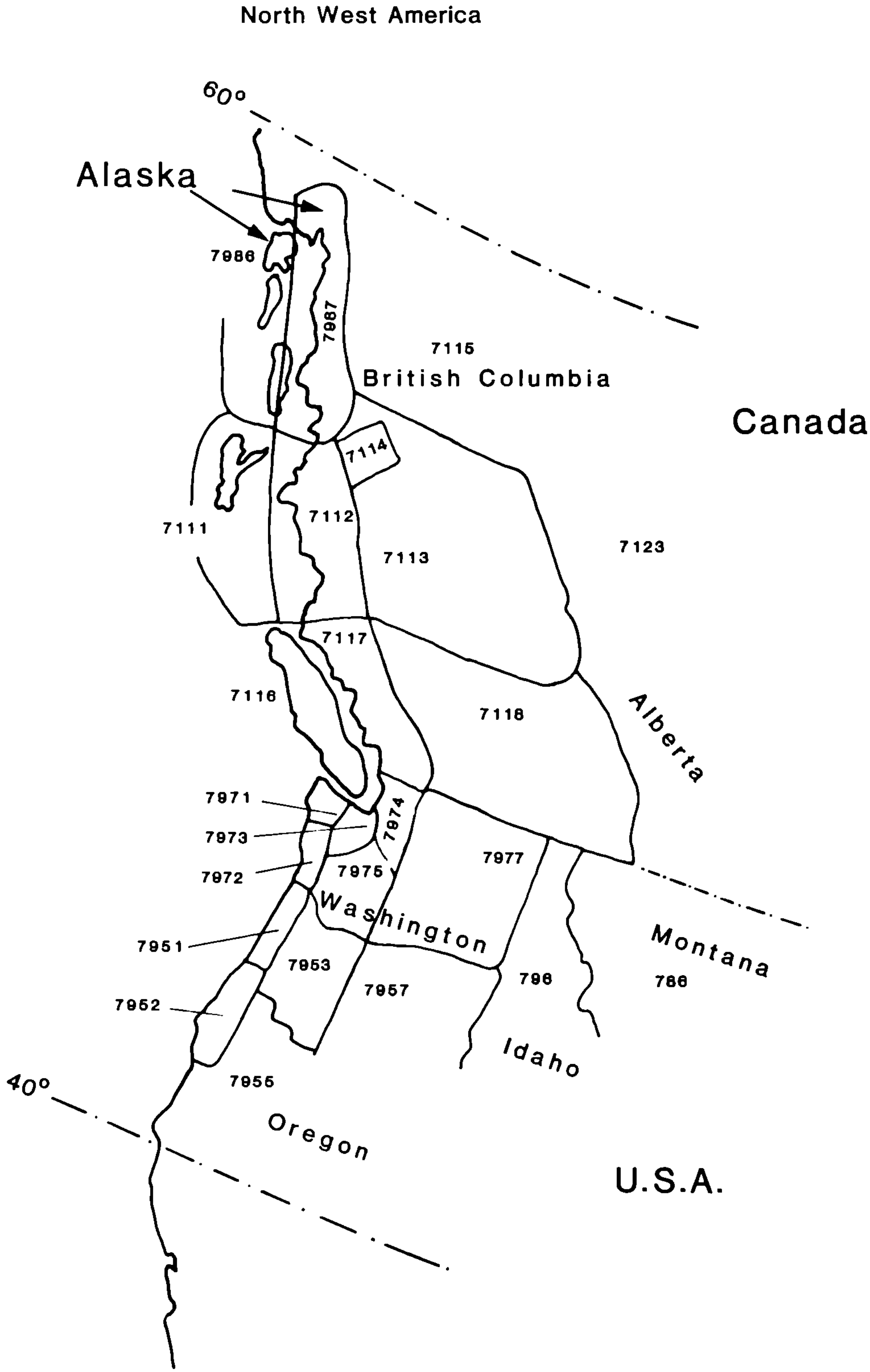


Figure 4. Seed collection regions in NW America.



Scots pine
(Pinus sylvestris L.*)*

Natural range

Scots pine has a very wide range, from Spain across the whole of northern Europe, and continuing across Siberia almost to the Pacific Ocean. It is thus a mainly continental species which occurs in Scotland at the most maritime part of its range. Several local varieties have been distinguished. The variety *scotica* is native in Aberdeenshire, Argyll, Inverness-shire, Perthshire and Wester Ross. On the continent it is found from sea level to 2400 m (Steven and Carlisle, 1959) and in Scotland it formerly occurred up to 1000 m. At present, scattered natural seedlings can be found at 640 m in the Cairngorms (Pears, 1967).

Silvicultural characteristics

A typical pioneer species in that it is a marked light-demander, it is frost-hardy, with fast early growth, low demands on nutrients and moisture and it produces fertile seed at an early age. However, it can remain healthy for over 200 years under the most suitable conditions. Stem form can be very variable, from slender, rather narrow-crowned individuals, to coarse, heavy-branched trees with twisted stems. Its crown shape is often deformed by strong winds and, where also exposed to sea spray, foliage browning is frequent. It is unstable on heavy wet mineral soils and has a short life on shallow calcareous soils, especially chalky rendzinas.

Introduction and use

Scots pine invaded Britain during the Boreal Period about 10 000 years ago, before the English Channel was formed. There is some evidence that it came via two routes which might explain the apparent differences in terpene types within the present native range (Forrest, 1982). By 5000 years before present it seems that Scots pine died out completely south of the Highland Fault Line except for possible remnants in the Lake District and the Brecklands (Birks *et al.*, 1975). It was reintroduced to sandy areas in England many centuries ago and now behaves like a native on the heathlands of Norfolk, Surrey and Hampshire. Elsewhere, it was planted very extensively, e.g. at Drummond Hill, Perthshire, more than 300 years ago (Steven and Carlisle, 1959). In the latter part of the 19th century conifer planting increased greatly, the most popular species being Scots pine. Unfortunately, this was also a time when nurserymen paid scant attention to seed origin and as the collection cost of pine seed was much lower on the continent, there was a flood of cheap imported seed. From 1919, the Forestry Commission obtained most of its seed from home sources, though this came mainly from well-grown stands of unknown origin. In the period up to 1955, 47 per cent of the seed came from East Anglia (Lines, 1964a). Part of this came from stands thought to have originated in Scotland and part from continental sources – probably Germany. Over the years the proportion of Scots pine used in afforestation has dropped, partly being superseded by Lodgepole pine, but mainly by the spruces, as afforestation progressed on to less well-drained sites.

Scots pine represented 20 per cent of all species planted by the Forestry Commission in the year 1946, compared with 36 per cent for Sitka spruce. By 1975 Scots pine made up only 1.5 per cent of all species used, while Sitka spruce was 71 per cent of the total. The 1980 Census showed that 12 per cent of the total area of Coniferous High Forest was Scots pine.

Seed origin experiments

There are 28 experiments containing about 150 seedlots. This species was one of the earliest to be tested by the Forestry Commission, with 11 experiments established by 1931. The older experiments are described by Lines and Mitchell (1965). Although suffering from poor experimental design, the results are clear. They confirm the overall superiority in height and appearance of seedlots collected in Scottish stands when planted in Scotland. Seedlots from northern Scandinavia, southern Spain and the Caucasus all failed. In one experiment in East Anglia, French and German origins grew faster than Scottish or the local Thetford provenance. Trials to find suitable seed origins for use in the extreme west of Scotland were only partly successful; origins from W Norway grew poorly, while even the best ones from Wester Ross grew only moderately well.

Recommendations

1. Seed orchard seed should normally be the first choice. In recent years, improved seed from seed orchards has been available in substantial amounts. The current orchards are composed of a mixture of tested and untested clones and shortly even higher quality seed will be available from second generation orchards. The older orchards contain clones from a particular area, e.g. Deeside or east England and it is best to return seed broadly to its origin. The newer orchards, however, contain only tested clones which originate from several areas but have shown a wide degree of adaptability.

Figure 5. Natural range of Scots pine, *Pinus sylvestris* L.

2. If seed from orchards is not available, then the next choice would be from selected sources in the UK, i.e. from Registered Seed Stands.

3. Finally, seed from selected EEC seed sources is a third alternative. The preferred EEC sources are northern France, Germany and the Benelux countries.

Corsican and Austrian pines *(Pinus nigra* var. *maritima* (Ait.) Melville and var. *nigra* Harrison)

Natural range

The four varieties of European Black pine recognised by Röhrig (1957) extend from Spain to the Crimea and are silviculturally distinct. Only the two varieties above are important in British forestry. Vidaković (1974) gives a recent account of its taxonomy and genetic variation. Corsican pine (var. *maritima)* occurs in Corsica, Sicily and in the Calabrian region of southern Italy. In Corsica it is found from 800 to about 1600 m above sea level and either pure or mixed with beech or Silver fir. Soils are freely-drained gritty loams, over granite (Brown, 1960). In Calabria the elevation range is similar, with stony or sandy loams derived from granite, gneiss and mica-schists (Röhrig, 1957). Climatic records from these mountain forests are sparse. Annual precipitation is about 1500 mm, much of it falling as snow in the winter. The length of the summer drought is much less than at coastal stations at sea level in Corsica and bright sunshine occurs far more often than in Britain.

Austrian pine (var. *nigra)* has a limited natural distribution in Austria, growing mainly on low limestone hills between the eastern end of the Alps and the town of Wiener Neustadt. Seed from this area was used extensively to plant the poor gravel plains nearby. It appears that the seed imported to Britain has come from this area, rather than from the more extensive patches of this variety in northern Italy and Yugoslavia, shown on the map of Lee (1968). The Austrian stands are at only a few hundred metres above sea level; elsewhere this variety may be found up to 1500 m. Wheeler *et al.* (1976), on the basis of performance in world-wide provenance trials, group all these northern, Balkan, Greek and Turkish populations together as var. *nigra.*

Silvicultural characteristics

Corsican pine is a potentially fast-growing tree (maximum Yield Class recognised in British yield tables is 20 compared with 14 for Scots pine) and is as tolerant of poor dry sandy soils as Scots pine. It grows better than Scots pine on coastal sand dunes with salt spray. It tolerates a range of soils, including heavy clay soils in south and east England, where the form of Scots pine can be very poor. It can be a difficult species to establish and to avoid early losses careful planting of either paperpot seedlings or good 1+1 transplants in February-March is recommended. Stem form is usually excellent but branching can be heavy. It suffers dieback in the late thicket stage associated with *Gremmeniella (Brunchorstia)* when planted on sites in upland and northern Britain. The borderline between sites where it can grow healthily and sites where it will fail from dieback is difficult to determine without evidence from past or existing plantations. As a rough guide, 300 m in SW England is probably safe. Wetter, upland sites (over 150 m in north England and progressively diminishing with latitude to even lower elevations further north) carry some risk of dieback, although it can grow well at sea level in the far north of Scotland. Corsican pine is rarely attacked by the Pine tortrix *Rhyacionia buoliana,* which can cause severe damage to Scots pine in East Anglia. It was also noticed at an early date as being one of the conifers most resistant to air pollution. It grows better than Scots pine on shallow soils over chalk, and will resist lime-induced chlorosis for 5-10 years longer than Scots pine on shallow chalk rendzinas.

Austrian pine is slower growing and heavier branched. It is very exposure resistant and as such has been used mainly for shelterbelts. It is much more resistant to lime-induced chlorosis than Scots pine when planted on chalk sites.

Introduction and use

Corsican pine was introduced in 1759 and Austrian pine in 1835 (Mitchell, 1972). They were planted mainly for ornament until 1870 when Corsican pine began to be used on a wider scale, often in mixture with other conifers. Its superior volume production compared with that of Scots pine on poor sandy soils encouraged its widespread use in the early years of the Forestry Commission. In fact, it was extended on to unsuitable sites where it suffered from unseasonable frosts, and to high rainfall, upland sites where it established well, only to be killed later by *Brunchorstia* (Steven, 1934). In the 1947 Census there were 15 582 ha of Corsican pine in Forestry Commission and private woodlands together. By 1980, this area had risen to 47 250 ha. In England the Forestry Commission area of Corsican pine was 30 560 ha making it the most extensively used species after Sitka spruce and Scots pine.

Most of the seed for existing plantations was imported from Corsica (Brown, 1960) or later from selected British stands. However, during the period 1927-28, three batches of seed totalling 3500 kg were bought from a Corsican seed merchant, G. Ursuline. Although stated as being of Corsican origin these seedlots were detected as being atypical at the nursery stage and later studies of needle morphology have shown that they were probably imported to Corsica from Italian stands of the var. *nigra* (Lines, 1985b).

Figure 6. Natural range of European black pine, ***Pinus nigra*** Arnold.

Seed origin experiments

In the 1930s seed origins from Corsica were considered to be best, based purely on early observations of plantations from different commercial importations. However, Steven (1934) believed that critical experiments should be established. The earliest trials in 1951 contained only four seedlots on three sites in north Wales. A home collected (Corsican) lot was tallest at two sites, but poor at Clocaenog, where one from Calabria was outstanding. A Spanish seedlot grew poorly on all sites.

In 1960-62 a second set of trials with 9-13 provenances was planted at three sites in the Pennines and two on sandy heathlands. The Pennine sites were affected by air pollution (Lines, 1985b). However, there was little evidence of a provenance x site interaction between the 'clean' and 'polluted' sites. Height growth was best for a Belgian provenance (Forêt de Koekelare) originally from Calabria (Gathy, 1957), followed by seedlots from English stands of Corsican origin, while those direct from Calabria in Italy were almost as slow growing as those from Austria and Turkey. Basal area production at 20-23 years showed a different pattern, with seedlots collected in Belgium and France (originally from Calabria) giving better results than the more slender trees of Corsican type. The somewhat heavier crowns of these Calabrian types may give more knotty timber. The Pennine experiment at Haslingden, which is on a higher and wetter site, has now been destroyed by *Brunchorstia* (Lines, 1985b) while the other three, which are 120 m lower, with less that 900 mm of rain, have not been affected.

A third series of experiments with up to 33 seedlots was planted in 1965-66. Successful growth was obtained on two sites overlying calcareous formations (to test for provenances resistant to chlorosis), one on sandy heathland and one in the industrial Pennines. The pattern of results after 6-19 years is rather similar, despite the large variation between the sites. Tallest origins were from Corsica, with those of Corsican type from northern Europe (including lots from Denmark, France, Italy and northern England) almost as tall. Origins from Calabria were intermediate, while Austrian types (var. *nigra)* were shortest. Earlier results from the Pennine experiment (South Yorks 5, P66) have already been published (Lines, 1985b). So far, the experiments on calcareous parent material have not shown chlorosis.

Seed origin variation in *P. nigra* has been studied overseas ever since Vilmorin's trial of four varieties of *P. nigra* at Les Barres in 1830 (Price, 1959). The most comprehensive experiments are in New Zealand (Wilcox and Miller, 1974), USA (Wheeler *et al.,* 1976) and W Germany (Röhrig, 1966; Stephan, 1984). In France, Arbez and Millier (1971) studied the variation in needle characters of 3-year-old plants of 16 origins. In Germany and in the USA winter frost was responsible for injury to Corsican origins. This seldom occurs under our milder climate, so that the New Zealand results are of greater interest here. After 20 years, the tallest seedlots were from New Zealand stands of Corsican origin, followed by those from Corsica and from English stands of Corsican type. As in Britain, the Calabrian seedlots had relatively high volume for their height.

Recommendations

Corsican pine

1. For southern sites in low rainfall areas, home collections from registered ('select') stands of Corsican origin are best.

2. Seed from registered EEC stands in Corsica, French region 01 (2A) or 01 (2B), is the next choice.

3. For planting north of the Midlands, the two sources above will also grow well, though for higher volume production, seed from second generation stands of Calabrian origin, e.g. Koekelare in Belgium, or Les Barres in France or, if available, seed from healthy stands of Corsican type in northern Britain are suggested. Incidence of *Brunchorstia* appears related more to site than to choice of seed origin, so that in wetter upland areas Corsican pine should not be planted.

Austrian pine

There is observational evidence that on thin soils over chalk or limestone, Austrian seedlots may be more healthy and more resistant to chlorosis than those from Corsica, but with poorer volume production. Austrian pine has a role in shelterbelts and in situations of severe coastal exposure. Preferred origins are EEC registered stands.

Lodgepole pine (*Pinus contorta* Douglas ex Loud.)

Natural range

Lodgepole pine is distributed along the Pacific coast from Yakutat, Alaska (59° 30′ North) to Point Arena, California (39° N). Its range in the interior is even greater, from 64° N in central Yukon, to 31° N in Baja California, Mexico. It grows from sea level to 3350 m in the Rocky Mountains and on sites which have an annual rainfall from 280 mm at Atlin Lake, BC in the rain shadow of the Coast Range near the Yukon border, to over 4000 mm on the Alaskan coast. Coastal stands are mainly on muskegs in the north and on rocky sites or sand dunes in the south. It grows on a range of poor mineral soils in the interior; where it occurs following huge fires, it blankets a range of soil types from valley bottom to near the treeline. It is very tolerant of soils poor in nutrients or moisture and is found on limestone in the Rocky Mountains as well as on very acid soils (pH 2.8-3.9) and on serpentines in California.

It is a highly variable species which has become adapted to a complex set of environmental conditions by forming three distinct groups of subspecies (Critchfield, 1957) or races (Critchfield, 1980). These are:

P. contorta ssp. *contorta:* Pacific coast

P. contorta ssp. *murrayana:* southern Cascades, Sierra Nevada and mountains of southern California

P. contorta ssp. *latifolia:* Rocky Mountains and Inter-Mountain region, northern Cascades.

There is also a distinct population on the Mendocino White Plains of California, ssp. *bolanderi,* which is of no forestry interest in Britain.

Silvicultural characteristics

These vary so much with seed origin that it is difficult to generalise. It is nearly always an aggressive pioneer following fire, though in Oregon it forms extensive climax forests on pumice soils (Franklin and Dyrness, 1973). It is intolerant of shade, and over-dense natural regeneration may stagnate in the pole-stage or earlier. It is sexually precocious and produces large quantities of seed, which can travel long distances. In North America the ssp. *latifolia* has predominantly closed (serotinous) cones, which open only after fire. In British stands, serotinous cones are rare. Its ability to grow on very infertile soils is one of its major assets for afforestation in Britain. However, small amounts of phosphate are necessary for establishment and it responds to top-dressing with phosphate and potash on the poorest peats. Lodgepole pine is more tolerant of waterlogging than Sitka spruce (Coutts and Philipson, 1978) and thus helps to dry out deep peats and hasten the development of fissures. All except the most southerly coastal origins withstand frost; many also tolerate cold blasting winds in winter rather well and show some resistance to salt spray (see exceptions in Table 1). On many sites the heavy-crowned south coastal origins are very susceptible to damage from heavy wet snow in the thicket stage. This causes breakage of individual branches or often the whole crown is broken at about 2-3 m above the ground.

Rapid early growth in height of planted stock is characteristic of several origins and this carries the penalty of instability, particularly on compact mineral soils or on soft peat (Lines, 1980a). Because of its fast early growth, a stand of Yield Class 10 will have a top height of nearly 4 m at age 10. Sitka spruce at the same age would have to grow at a rate equivalent to yield class 16 to keep up in height. It is therefore essential to use inherently slow-growing origins when these species are planted in nursing mixtures.

Lodgepole pine never attains the great age or large dimensions of other species in NW America. Critchfield (1980) notes few over 33 m in height and none exceeding 86 cm in diameter, except in the southern Sierras. The largest surviving specimen tree in Britain is at Culcreuch Castle, near Stirling, and is 29.5 m tall and 69 cm in diameter, though one which blew down at Bicton, Devon was 31 m x 106 cm.

Introduction and use

No trees resulted from David Douglas' first seed collection of 1825, the first successful introduction being in 1853 by the Oregon Association. That seed came from the Siskyou Mountains – now known to grow poorly here. Later introductions followed from both the coast of Washington and the interior of British Columbia, e.g. at Bodnant in 1876 ssp. *contorta* and 1888 ssp. *latifolia.* The oldest plantation was in the Ruttle Wood, Beaufort Estate near Inverness, planted about 1912, and it was used in forest experiments from 1922. Lodgepole pine was not regarded highly by Forestry Commission top management (Macdonald, 1954), so that prior to 1947 only 1300 ha of plantations were established in both Forestry Commission and private woodlands. In Eire it was used more widely from the 1930s, with 40 000 ha established by 1963.

In Britain, afforestation of poor peatland and moorland sites increased dramatically in the 1950s and 1960s with 20 million Lodgepole pine trees planted by the Forestry Commission alone in 1964, so by 1972 there were 73 200 ha of Lodgepole pine plantations in Forestry

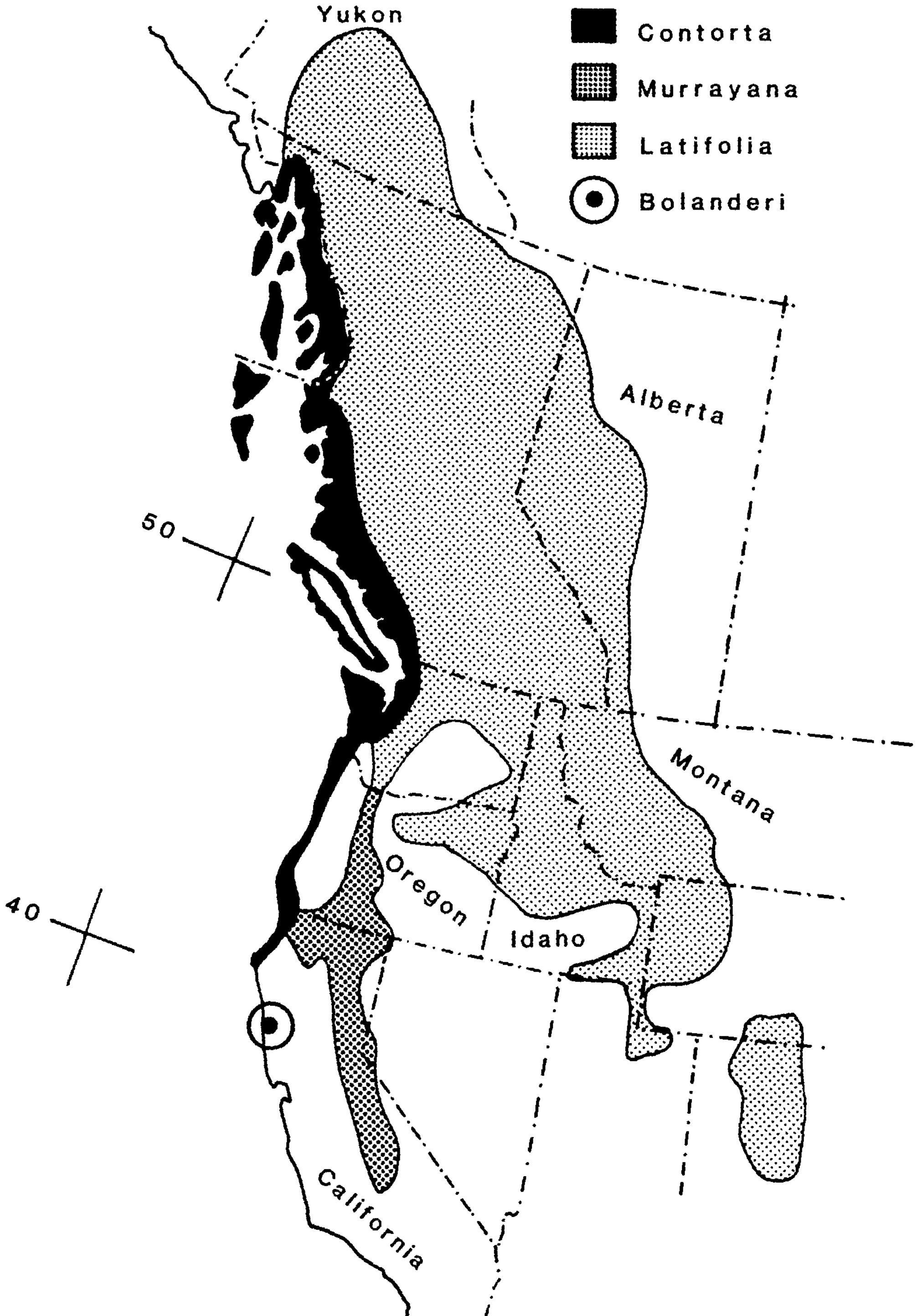


Figure 7. Natural range of Lodgepole pine, ***Pinus contorta*** Douglas ex Loud., indicating the occurrence of four sub-species.

Commission forests. In 1971/72, 19.3 per cent of all plants used by the Forestry Commission were Lodgepole pine, while 60.3 per cent were Sitka spruce. Improvements in forest practice, such as chemical control of *Calluna* and aerial top dressing of fertilisers, later resulted in an increase in the use of Sitka spruce and a decrease in Lodgepole pine usage. However, in recent years research has shown an important nursing effect of Sitka spruce by Alaskan origins of Lodgepole pine (Taylor, 1985) and this has once again increased the demand for Lodgepole pine. The current area of Lodgepole pine in Britain at the 1980 Census was 101 390 ha (Forestry Commission) and 25 680 ha (private woodlands).

Until 1976 insect pests did not have a major influence on the use of Lodgepole pine, the most important being the Pine sawfly *(Neodiprion sertifer)* and the Pine shoot moth *(Rhyacionia buoliana)*. The former periodically defoliated young stands and checked growth without causing many deaths. The shoot moth causes such stem distortion that it soon became apparent that it was unwise to use Lodgepole pine on dry sites in the southern half of England. From 1976 onwards severe damage from Pine beauty moth *(Panolis flammea)* had to be controlled in Scotland by aerial spraying. Although this insect shows a greater preference for laying its eggs on South Coastal origins (Leather, 1985) it can destroy stands of any seed origin in a serious infestation. So far, severe outbreaks have occurred entirely on infertile peat soils in north Scotland.

The far more rapid growth of coastal seed origins in comparison with inland ones was recognised as early as 1928 by A.C. Forbes in Eire. In Britain the use of inland sources predominated until 1948 and since the large intraspecific variation was largely ignored in forest practice, much confusion resulted. The greater growth potential of some coastal (i.e. Washington and Oregon) origins combined with a greater stress on their presumed higher economic return, increased the demand for 'coastal' sources. Unfortunately, the most easily procurable seed was from Lulu Island at the mouth of the Fraser River where the rainfall is relatively low. Trees of this origin are 'coastal' in location, but they grow more slowly and are not resistant to exposure. Nearly 1000 kg of seed of this unsuitable origin, (resulting in 100 million plants) were imported in the early 1950s (Lines, 1976a). When large quantities of seed became available from the Pacific coast of Washington and Oregon in the mid 1950s, the improved techniques of ground preparation and heavier application of fertilisers, which were becoming standard practice, resulted in much early instability and basal sweep. In addition, when these origins were used in intimate mixture with Sitka spruce, they soon overtopped and suppressed it, resulting in stands of low value.

In the late 1960s and 1970s planting was extended to poorer ground, with a wide variety of origins being used. As the disadvantages of southern coastal sources became apparent, Skeena River became the preferred seed region. The disastrous Pine beauty outbreak in 1976 caused a marked drop in use of the species, but very shortly afterwards the benefits obtained from mixtures of Alaskan origins with Sitka spruce boosted the demand. In the Forestry Commission this is currently running at about 2.5 million plants of Alaskan and North Coastal seedlots per annum with a smaller use of Skeena River origins. In the private sector, Alaskan sources are also in most demand.

Seed origin experiments

Sixteen experiments were planted before 1940 and 67 between 1940 and 1977, including some 340 seedlots. These cover most of the species' range, though the area to the east of the Rocky Mountains and the Cascades/Sierras is not well represented, since these origins grow poorly here. Coastal parts of the range and the interior of Canada west of the Rockies have adequate cover. Early results were summarised by Macdonald (1954) and Edwards (1954, 1955). Results from later experiments clarified the picture of seed origin variation, e.g. Lines (1966, 1976b and 1980b). Wood (1955) and Aldhous (1976) described the species and its variation within the native range and much light was thrown on the inherent regional patterns of variation by Forrest (1980) using analyses of shoot terpenes. Variations in phenology and bud development of selected origins at the nursery stage (Cannell *et al.*, 1981) led to greater understanding of subsequent growth in the forest. Information on wood properties of different seed origins was summarised by Brazier (1980). The latest summary of results from British seed origin trials (Lines, 1985a) emphasises the point that the fastest growing coastal origins should be used only exceptionally, because of their early instability and liability to snow break in the late thicket or early pole stage. A more comprehensive publication on the species is currently in preparation.

Recommendations

1. Seed origin choice with Lodgepole pine is complex, as often a compromise must be reached between e.g. growth rate and stem form or exposure tolerance. Table 1 allows origins to be selected with whichever characters are considered to be of greater importance by the forester.

2. For use in *mixture* with Sitka spruce:

   a. Alaskan (798) or North Coastal (7111) or (7112) origins are most likely to produce a good nursing effect and have a good chance of resulting in a self-thinning mixture leading to a final crop of pure spruce;

   b. if faster-growing origins, e.g. Skeena River (7114) or Southern Interior of BC (7118) are used, then a higher proportion of the pine is likely to survive into the final crop, unless the pine is thinned or otherwise treated to control its growth.

3. For *pure stands* of Lodgepole pine:

   a. for a combination of good form and volume production, on many sites the choice will lie between Skeena River (7114), Vancouver Island (7116) and Southern Interior of BC (7118) origins (see Table 1). Vancouver Island sources should not be used on very exposed sites and seed from the (7118) region should be from the Wet Belt (Aldhous, 1976);

   b. if good form is of more importance than volume production, then Central Interior of BC (7113), e.g. Prince George or Bulkley River (east part of 7114) origins are indicated.

Table 1. Characteristics shown by progeny of a range of Lodgepole pine seed origins

Origin	Code	Growth rate	Crown density	Stability	Stem form	Exposure tolerance	Tolerance of poor soils	Notes
Coastal Alaska	ALP (798)	4	1	1	1	1	2	Grow best in north Scotland. Ideal for mixture with Sitka spruce.
North Coastal (including QCI and north and west Vancouver Island)	(7111) (7112) (7116) part NLP	3	1	1	1	2	2	Hardy general purpose sources, second choice for mixture with Sitka spruce.
Vancouver (south and east Island and adjacent mainland)	(7116) part	2	2	4	3	4	3	Avoid exposed sites and seed from delta of Fraser River (e.g. Lulu Island).
Puget Sound (rain shadow of Olympic Mountains)	(7973) SLP	2	2	4	3	4	3	Avoid exposed sites. Best in low rainfall areas.
Pacific Coast of Washington	(7971) (7972)	1	1	5	4	1	1	Useful for quick shelter on exposed infertile sites where stem form unimportant.
Oregon Coast	(7951) (7952)	1	1	5	5	1	1	Generally unsuitable, especially in north Scotland.
Inland Yukon	– (7121)	5	5	1	1	2	5	Unsuitable for use in Britain.
Skeena River	(7114) West KLP	2	3	2	2	3	3	General purpose sources for less exposed sites and mineral soils. May grow too fast for use in mixture with Sitka spruce.
Bulkley River	(7114) East	3	4	2	1	3	3	Second choice to Skeena. Stem form on some sources may be superior.
Central Interior of British Columbia	CLP (7113)	4	4	1	1	2	4	Hardy, well proven.
Southern Interior British Columbia (includes NE Washington and Idaho)	ILP (7118)	2	4	3	3	3	4	Variable performance within this group. Forking can be serious. Best ones grow well on many sites.

Sitka spruce
(Picea sitchensis (Bong.) Carr.)

Natural range

Sitka spruce extends in a narrow coastal strip from Kodiak Island, Alaska to Mendocino County, California, a range of nearly 3000 km. Its northern limit is 61° N near Valdez, Prince William Sound and its southern limit 39° N. The strip is widest (210 km) in S Alaska and northern British Columbia, while in S Oregon and California it is strictly confined to the coastal 'fogbelt'. The species is unique amongst spruces in its restriction to humid oceanic conditions. It has been found at elevations above 900 m in S Alaska and BC, but over most of its range it occurs below 300 m. In two parts of its range it overlaps with White spruce *(Picea glauca* (Moench) Voss). In the Kenai Peninsula of Alaska the hybrid is called *P.* x *lutzii* (Little, 1953), while on the Skeena River in British Columbia the introgressed populations have been described by Roche (1969).

Climatic conditions are rather uniform over much of the range, due to rather low sea temperatures right down to California. There is a long frost-free season, high humidity with annual rainfall 1000-3000 mm, and absence of severe frosts. The accumulated temperature (degree-days over 5° C) varies from < 1000 to over 2000, roughly equivalent to the variation between north Scotland and southern France.

Sitka spruce reaches its maximum development on the Queen Charlotte Islands and in the rain forests of the Olympic Peninsula (Ruth, 1958). It grows on a wide range of soils, from coastal sand dunes, through recent glacial outwash gravels to mesic river alluvium and better drained peat soils. It is rare on poor muskegs.

Silvicultural characteristics

Unlike most other spruces, Sitka spruce is a lowland tree which achieves its best growth in super-humid climates. It has less frost resistance than other North American spruces, and is never found where the soil freezes hard, even for a short time. Also known as 'Tideland spruce', it is outstanding for its tolerance of high soil-water sodium levels induced by ocean spray (Krajina *et al.*, 1982). These authors also regard it as a nutritionally demanding tree, which cannot thrive without considerable amounts of available calcium and magnesium. These must be in balance, and on limestone and serpentine bedrocks, where either calcium or magnesium is in excess, it grows poorly. In Britain, calcium never seriously limits growth, but nitrogen and phosphorus are often limiting, especially on heathland or poorer peat soils. *Calluna* can induce severe check in Sitka spruce and this was one of the earliest subjects of Forestry Commission research. By the 1950s Macdonald (1952) noted that "most of the planting of Sitka spruce on upland heaths is now done in mixture with pine".

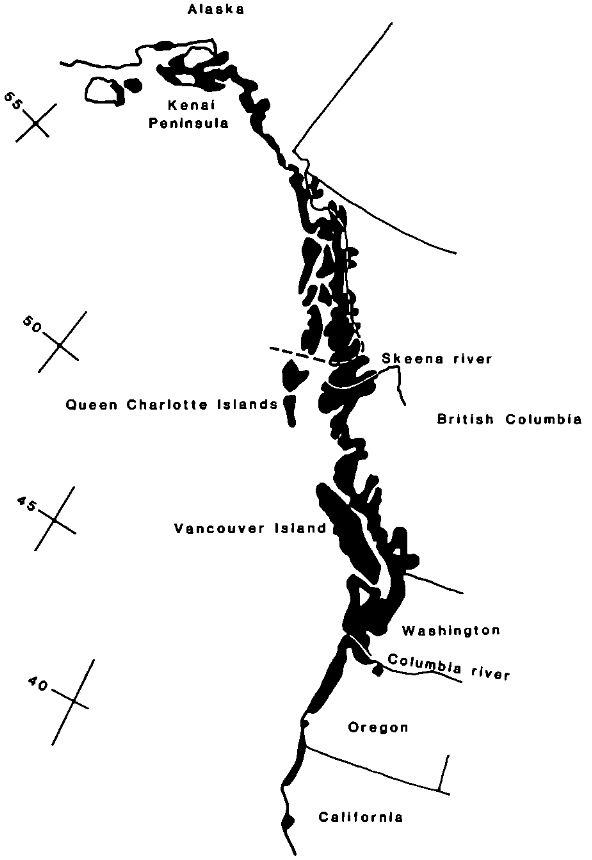
In the 1960s herbicide control of *Calluna* became standard practice on sites where it was known to induce check. There are practical difficulties in achieving good control under some circumstances and as it is easier to treat pure stands of Sitka spruce, planting of pure spruce on these site types increased markedly. The nutritional requirements of Sitka spruce are now better known (Binns *et al.*, 1980; McIntosh, 1983) and it is clear that on some poor heathland sites one or more applications of nitrogen may be required in the first 15 years even where *Calluna* has been eliminated.

The value of nurse species in mixture has recently become better appreciated when it was realised that in addition to helping Sitka spruce through the 'check' phase by 'biological manuring', some slow-growing nurses, like Alaskan Lodgepole pine, would later become suppressed and give the spruce more growing space later in the rotation, compared with pure spruce grown under a 'non-thin' regime (Taylor, 1985). This type of self-thinning mixture was first proposed by Wood (1955).

Temperature does not appear to limit growth anywhere in Britain (Faulkner and Wood, 1957) and Nielson *et al.* (1972) have shown that it still has a healthy rate of net photosynthesis, even when the leaf temperature is 0° C in December. Krajina *et al.* (1982) consider Sitka spruce as less shade tolerant than other spruces, but Hodges and Scott (1968) thought it rather shade tolerant in comparison with other species.

Growth potential of Sitka spruce is very high and it can attain a greater height and diameter than any other spruce. It starts coning at a younger age than Norway spruce, so that natural regeneration follows felling more frequently with Sitka spruce at normal rotation ages in Britain. Sitka spruce roots are incapable of surviving long periods of anaerobic conditions, hence on sites with a high watertable, wide shallow root plates develop, except where lateral rootspread is limited by plough furrows. However, on deeply-rootable soils Sitka spruce roots can penetrate to over 2 m. Sitka spruce is one of the hardiest species as regards resistance to wind exposure on upland sites or in coastal areas. It thrives least on drier sites and if seasonal water stress is strong, the influence of *Elatobium* defoliation can be severe. Defoliation by *Elatobium* may also be frequent and severe in coastal areas as a result of their relatively frost-free winters. Frost in late spring or early autumn often damages this species (Macdonald, 1952). Sitka

Figure 8. Natural range of Sitka spruce, *Picea sitchensis* (Bong.) Carr.



spruce was less tolerant of air pollution than Lodgepole pine in the industrial Pennines, when levels were high in the 1950s (Lines, 1984c).

Introduction and use

One of David Douglas' introductions of 1831, it was unusual in passing quickly through the specimen tree phase and then being planted on poor, high elevation sites such as Durris, Kincardineshire in 1879. In the early years of this century it was extensively planted at Corrour, Inverness-shire, at Moorburnhead, Dumfriesshire and at the Crown Forest of Inverliever, Argyll when this was an experimental area under R.L. Robinson (Macdonald, 1952). The 1947 Census shows that it represented 17 per cent of the total area under conifers and an even larger percentage of Forestry Commission woodlands. By 1981, 47 per cent of the Forestry Commission's coniferous high forest consisted of Sitka spruce. In current planting, Sitka spruce represents 63 per cent of the total. It is mostly planted in the north and west of Britain, in some areas comprising 90 per cent of all trees planted. The total area of plantations in Britain was 525 900 ha in 1980.

Most of the small imports of seed prior to 1922 came from the firm of J. Rafn who obtained seed from Gray's Harbor County, Washington (Barner, personal communication). In 1922, 3000 lbs of seed were sent from the Queen Charlotte Islands and this was supplemented by 468 lbs from the 'USA' in 1923. Thereafter, the great bulk of seed (88 per cent) has come from British Columbia; 50 per cent is known to be from the Queen Charlotte Islands and very likely many of the imports described merely as 'BC' also came from these islands. The only seed import from the USA exceeding 1000 lbs was in 1947, when 3467 lbs were bought. It seems probable that the major collection area was Washington rather than Oregon, and very little came from Alaska. In the 30 years up to 1952, 67 000 lbs of Sitka spruce seed were imported and this was supplemented on a small scale by home collections, the earliest being 1 lb in 1923 from the old stands at Durris near Aberdeen.

Seed origin experiments

There are 47 experiments containing 185 seedlots. These give adequate cover of the natural range and of the range of sites on which this species is used in Britain. The pre-war experiments were rather unsatisfactory (Lines, 1964), while those planted in 1950-59 lacked extensive cover of the range. The series planted in 1960/61 contained up to 13 seed origins ranging from 60.5° N in Alaska to 43° N in Oregon and were planted on 14 sites from Sutherland to Cornwall. Nursery studies of this material were reported by Aldhous (1962) and phenological differences by Lines and Mitchell (1966). Height growth 10 years after planting showed a high interaction between seed origin and site, with northern origins relatively poorer on southern sites and vice versa. The tallest origin overall was from Sooke, Vancouver Island, though another seedlot from Vancouver Island was shorter than the one from the Queen Charlotte Islands on most sites (Lines, Mitchell and Pearce, 1971). An experiment with 37 seed origins planted in 1968 at Glendaruel, Argyll, was the first to show significant differences in height growth within seedlots from the Queen Charlotte Islands region. Their mean height at 6 years was better than the mean height of eight Washington origins (Lines, 1975). However, at 10 years the Washington group was marginally taller than that from the Queen Charlotte Islands.

A major IUFRO series of experiments was planted in 1974/75 with up to 70 seed origins on 18 sites (ten in Scotland, four in England and four in Wales) (Lines, 1980e). Sixty four of these origins were used to study growth patterns and phenology in a nursery trial (Kraus and Lines, 1976). Date of growth cessation was shown to be highly correlated with latitude of seed origin. No overall pattern of flushing could be determined, though individual origins varied strongly. The conclusion from the forest experiments after 10 years (Lines and Samuel, in press) is broadly that height growth is inversely correlated with latitude. However there is a very strong site x seed origin interaction, with the most southerly origins growing poorly on northern and environmentally severe sites, while the northern origins grew relatively better on northern sites. Origins from the Queen Charlotte Islands were found to grow much faster than would be expected from their latitude of origin, while those from the mainland of British Columbia are much less vigorous than would be expected from a simple cline with latitude. On frosty sites the most southerly origins were frequently damaged and had serious losses. Sitka spruce from the middle Skeena River region has grown very slowly.

Sitka spruce is most sensitive to frost as a one year seedling in the nursery, since plants may still be in active growth in October or even November, especially the most southerly origins (Edwards, 1953; Aldhous, 1962). It is recommended that if southern origins are used then the seedbeds should be protected by screens from September onwards. Transplants are less sensitive, as they form terminal buds earlier, although lammas growth increases the risk from autumn frost. Cannell and Sheppard (1982) showed that shoots of 7 to 10-year-old trees varied greatly between seed origins in their level of autumn hardiness. Both decreasing day length and slight frost enhanced hardiness. During November-March all origins could withstand -20° C. However, in March-April frost hardiness diminished in response to higher temperatures, several weeks before budburst. Southerly origins responded to warmth more rapidly than northerly ones. During budburst all seed origins were equally susceptible. The incidence of frost damage in the 18 IUFRO forest experiments was assessed on 17 occasions in 12 experiments. Spring frost damage often showed little variation between seed origins. The southern Oregon and Californian seedlots were frequently worst damaged, but in some experiments Alaskan ones suffered equally and in one experiment Washington origins were least damaged. In April 1981, a peculiar kind of frost damage to the stem cambium affected the experiments at Ratagan and Farigaig (Lines, 1983). Damage was worst on southern origins, but Queen Charlotte Islands sources were also affected. The clinal pattern of damage increasing as latitude decreased was also seen in the rather frequent occurrence of autumn frost damage, and this was correlated with greater production of lammas shoots by southern origins. A fuller account of seed origin variation in Sitka spruce is now being prepared for publication.

Recommendations

1. Most seed collected from well-grown stands of Sitka spruce in Britain will be of Queen Charlotte Islands (7111) origin. This forms a general-purpose seed source which is reasonably frost hardy, very resistant to exposure and well-proven as a producer of acceptable timber. It can be reliably used throughout Britain, and is also the best provenance for very exposed sites.
2. Where sites are less exposed, and particularly on sites in south-west England and Wales, there is a choice between Queen Charlotte Islands and more southerly origins with the latter offering a slightly increased risk of autumn or winter frost damage (particularly in the nursery), but greater timber production. The experiments show that on these more favourable sites north Oregon seedlots from the (7951) seed region grow best, while those from (7971) and (7972) in west Washington and some Vancouver Island (7116) origins grow faster than those from Queen Charlotte Islands. These southern sources also grow well on sites close to the sea as far as 57° N in Scotland. Use of these very fast-growing origins carries a possible risk that the timber density of some trees may be unacceptably low. Deleporte (1984) showed that in Sitka spruce seed origin trials in France, wood density decreased as growth-rate increased.
3. There is no case for using Alaskan (7986) origins in Britain and those from the introgression area in the upper Skeena River should also be avoided.

Norway spruce (*Picea abies* (L.) Karst.)

Natural range

This species has a wide natural distribution in Europe, from near Grenoble, France, through the Juras, the Central Alps of Switzerland and Italy, down through Yugoslavia to nearly 41° N in the Rhodope Mountains, Bulgaria; also in southern Germany, Austria, Czechoslovakia and along the Carpathian Mountains of south Poland and Romania, where it extends into the Transylvanian Alps. Its northern range includes north-east Poland and continues into western USSR, Finland, Sweden and eastern Norway (Schmidt-Vogt, 1977). It reached the Atlantic coast of Norway in a limited area south of the Arctic Circle less than 1000 years ago. Some authors have regarded *P. abies* as a single Eurasian species with the var. *obovata* extending from the Urals to the Sea of Okhotsk. It has been extensively planted outside its native range in countries such as France, north Germany, Denmark, west Norway and Iceland.

Palaeobotanical studies, reviewed by Tallantire (1980) and Moore (1981) have shown a complex pattern of re-invasion of spruce following its retreat to three ice-free refugia during the last glaciation (Lindquist, 1948). These were the Apennines, Romania and central Russia. A brief description of their subsequent spread to form the Alpine, Hercynian-Carpathian and Baltic-Northern groups is given by Lines (1960). Many centuries of planting within and outside its natural range have added to the complexity of the situation. The present geographical pattern of genetic variation has been studied using biochemical, morphological and phenological methods (see references in Schmidt-Vogt, 1977).

Silvicultural characteristics

Although its main range is from areas with a marked continental climate and it should therefore be considered essentially a continental species, in contrast to Sitka spruce, it nevertheless has spread naturally to islands off the south coast of Norway and thus proved a rather adaptable species. It grows well in many parts of Britain and is easy to establish, being more suitable than Sitka spruce on drier, eastern sites. In Britain it has proved very susceptible to salt-laden winds and winter foliage browning is frequent on exposed sites, even below 300 m above sea level. Spring frosts can severely damage (though seldom kill) young trees which are early flushing, though late flushing origins flush much later than Sitka spruce and thus can be used in frost hollows. It can tolerate a range of soils, growing well on the more fertile peat soils and on flushed gleys. The shallow root system which develops on soils with a high water table makes it susceptible to early windthrow, though it can root quite deeply on uncompacted, free draining soils. Norway spruce is a moderate shade bearer which responds strongly to thinning. It has a fairly high growth potential, good seed origins having a General Yield Class of 22 or above on the best sites. Disadvantages are its susceptibility to *Fomes* and deer damage, and the tendency for certain origins to have heavy branch bases and non-cylindrical stems.

Introduction and use

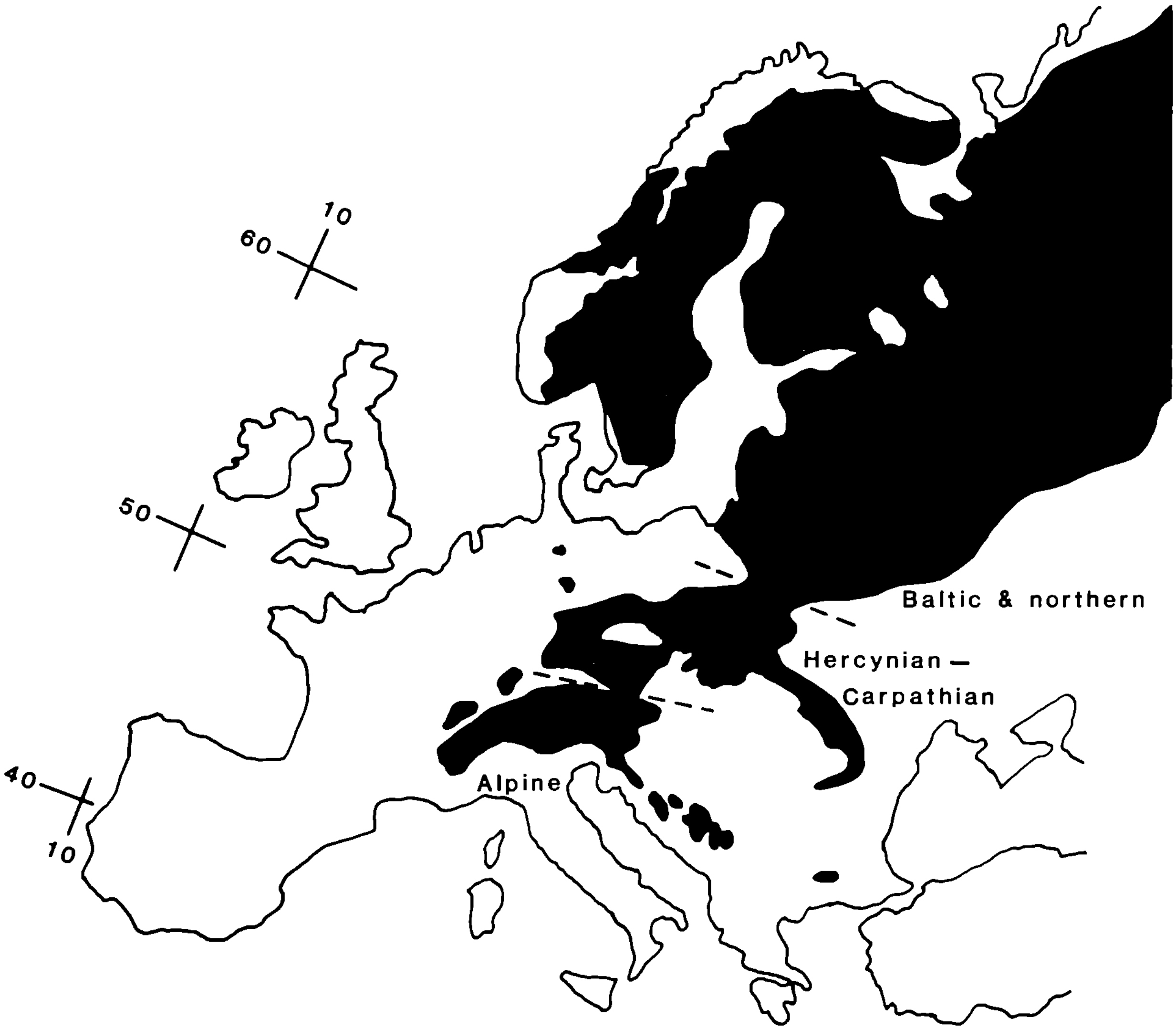
The species was introduced to Britain about 1500 and used widely during the 19th century; in Scotland it was frequently planted in mixture with Scots pine and European larch. In 1979 Norway spruce plantations in Great Britain totalled 116 850 ha, of which 61 per cent was owned by the Forestry Commission. In England the proportion owned privately was nearly 50 per cent whereas in Wales less than 20 per cent of the area was in private ownership. The 1980 Census data show a clear trend towards a peak in Norway spruce planting during the period 1951-60, with a very dramatic fall in the last two decades. For example, in Scotland 15 550 ha were planted in 1951-60, declining in 1971-80 to only 5250 ha. The recent substitution of Sitka spruce for Norway spruce is shown by comparing the areas in the 1931-40 age class in Scotland (7825 ha for Norway spruce, 11 275 ha for Sitka spruce), with those in the 1971-80 age class (5251 ha for Norway spruce and 169 265 ha for Sitka spruce). This represents a fall in the percentage of Norway spruce from 41 to 3 per cent. For the same periods in England the comparison is less dramatic (from 46 to 16 per cent). This could be because Norway spruce is more widely planted for Christmas trees in England.

Although seed has been imported from a wide range of origins, the bulk came from Austria (51 per cent) and Germany (31 per cent) prior to 1939. Italian and Swiss Alps sources represented less than 10 per cent each. Elevation of the collection areas is not always known, but more than 50 per cent is known to have come from areas where the elevation range exceeded 610 m (2000′).

Seed origin experiments

Seed origin variation in Norway spruce has been intensively investigated since Cieslar's (1905) experiments and Dietrichson (1980) notes nearly 300 trials in Nordic countries alone. In Britain the pre-war seed origin trials were described by Edwards (1955).

Figure 9. Natural range of Norway spruce, ***Picea abies*** (L.) Karst., indicating the occurrence of three main groups.



They suffered from fire, frost and in some cases large differences in age and type of plant. The conclusion was that south-east European origins grew most vigorously, followed by those from Germany and the Alps. Scandinavian sources were least successful. The first comprehensive experiment was the IUFRO one at the Bin (Huntly Forest) (Lines, 1960, 1973a). This includes 18 origins representing a large part of the range. Origins from Romania and southern Poland grew best. Some Alpine lots, e.g. Lankowitz (Austria) and Val de Fiemme (Italy) also grew well. In 1968 a IUFRO experiment with 1100 origins was planted at Savernake and smaller experiments at Minard and Drummond Hill included 200 origins at each site. The first results were summarised by Lines (1973b) and detailed results at 6 years from planting were presented at the 1976 IUFRO Congress (Dietrichson, Lines *et al.*, 1976). The general conclusions from this IUFRO trial at 11 years were summarised (Lines, 1980f) and are that two zones of fast-growing origins were distinguishable. One extends from Czechoslovakia, along the Carpathian chain through southern Poland and south-west Ukraine into Romania. The other, more northerly zone, includes the Harz Mountains, some areas such as Denmark and the N German plain where spruce is not native (though it has been planted for centuries), north-east Poland and north-west Russia.

Interest in east European seed origins led to a further series of experiments in 1968/71 at five sites, in which Romanian and Polish origins were compared with French, Swiss, Bulgarian and Austrian sources. Some of the tallest Romanian lots were from Turda, Dorna Cindreni, Toplita, Bicaz and Cimpeni. Polish origins from Szylarska, Istebna and Przerwanki were fast-growing. For Christmas tree production, the fastest growing origins may be unsuitable as they become too lanky, especially on fertile sites.

Flushing time is very variable in Norway spruce, some of the variation being that of individual trees. However, there are large and highly significant differences in flushing between seed origins (Lewis and Lines, 1973; Lines, 1973b). Romanian, Polish and some Russian origins were the last to flush, while Scandinavian and some central Alpine sources were earliest.

Recommendations

1. For commercial forestry, east European origins from Romania, Poland and Czechoslovakia combine fast growth with late flushing times. Some southern Austrian sources also have these characteristics.
2. German origins are rather variable and only the Harz region appears generally suitable.
3. Most French, Alpine and Scandinavian origins are not recommended either because of slow growth, early flushing or both.
4. For Christmas tree production, origins from the Schwabische region of south Germany, Forestry Commission seed region (4347), which is mainly German seed zone 84013, are the first choice.

European larch (*Larix decidua* Miller)

Natural range

European larch occurs in four separate areas of Central Europe:

a. Alps; b. Sudeten Mountains; c. Poland; d. Tatra Mountains (Lines, 1957).

The elevation range in the Alpine area is from 2450 m in the French Alps to 300 m in the Wienerwald. The most extensive stands are in the Alps and this area has provided most of the seed for the large areas of plantations made outside the native range in the 18th and 19th centuries. The Sudeten, Tatra and Polish larch areas are much more restricted and their elevations range from 1200 m in the Tatra Mountains to 150 m in the Lysa Gora region of Poland.

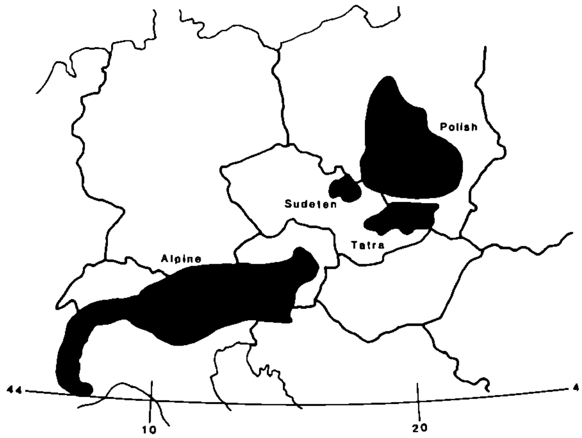
Many excellent plantations occur outside the natural range and these have been used as seed sources for many years. However, there is also a long history of plantation failures from frost, canker and insect attack, due to the use of unsuitable seed origins.

Silvicultural characteristics

European larch is a pioneer species and a strong light demander, which colonises ground freshly bared by landslips or upturned roots following catastrophic windthrow or avalanches. Early seedling growth is rapid, enabling the species to compete effectively with other vegetation. The fast growth rate enabled larch to succeed in the mixture with Scots pine and Norway spruce which was used on a wide scale in 19th century plantations. Anderson (1940) considered it useful for nursing oak, but it can grow too fast for this purpose and currently Norway spruce is preferred as a nurse for oak. Competition among trees within larch stands quickly eliminates suppressed trees or those suffering from disease or insect attack. The light shade cast enables ground vegetation to persist. If brambles are present they can make access difficult. European larch flushes earlier than Japanese larch and as flushing may be well advanced by the end of March it is seriously at risk from spring frosts.

Epidemic dieback is a serious and complex phenomenon (Pawsey and Young, 1969; Buczacki, 1973) and, while often associated with shoot cankers caused by *Trichoscyphella willkommii* and frost, can also be related to the intensity of *Adelges* infestation. Epidemic dieback in the early pole stage can be devastating, particularly on Alpine origins of larch. Because early growth is often

Figure 10. Natural range of European larch, *Larix decidua* Miller, in four main areas of Central Europe.



satisfactory, the vulnerability of these origins on susceptible sites was not realised until large quantities of seed from the Alps had been imported in the 1920s and 1930s.

Differences in crown form attributable to seed origin are well illustrated by Schober and Fröhlich (1967). Stem form in European larch can vary from excellent to appalling and is partly influenced by site factors and most strongly by seed origin (see photos in Schober, 1969). Coning commences at 10-15 years. In some years all flowers may be killed by spring frosts. Seed weight varies from 4.0 g per thousand seeds for some Czechoslovak origins to 11.7 g for French Alpine origins (Heiken and Soegaard, 1962).

Introduction and use

Introduced as a specimen tree in 1629, it was first planted on a large scale by the Duke of Atholl at Dunkeld after 1750. It is likely that the early introductions there formed the seed source for the planting boom which followed, leading to the 'Dunkeld' strain being very widely planted in central Scotland. The oldest trees are clearly of Alpine type. In the early years of the Forestry Commission, much European larch was used but by the 1930s this had been largely replaced by Japanese larch, while European larch continued in popularity longer in private woodlands. In 1947 there was a total of 53 786 ha of European larch. This species represented 21 per cent of all conifers in private woodlands, but only 7 per cent of all conifers in Forestry Commission areas. By 1981 the percentage of European larch in Forestry Commission woodlands had declined to 1.1 per cent and the total area of European larch was then 40 410 ha. The reduction since 1947 is mainly due to replacement of this low yielding species by higher yielding spruces and Douglas fir and where larch was required, by the substitution of Japanese or Hybrid larch.

Undoubtedly the wrong choice of seed origins during the 1920s had an important influence on subsequent Forestry Commission use of European Larch, but poor origin selection was combined with a tendency to plant it on the more testing sites, where serious attacks of canker and dieback occurred. Between 1921 and 1936, 16 887 kg of European larch were imported or collected in Britain. 77 per cent was of Alpine origin, at first mainly from the Italian Tyrol and later from Swiss sources. In 1925, for example, nearly 2000 kg were imported from the Swiss Alps at elevations from 1000-1400 m. Throughout this period, small quantities (4 per cent of the total) of seed came from Silesia, much of it said to be 'Sudeten'. Unfortunately there is doubt as to whether this seed was collected from native stands in what is now Czechoslovakia, or whether it came from the many plantations of Alpine origin in Silesia (Edwards, 1957). 19 per cent of the total was home collected, largely from private estates in north-east Scotland. It is unfortunate that a large amount of seed from 1300 m in the Swiss Alps was still being imported as late as 1947, in view of its poor performance in early provenance trials.

Seed origin experiments

Provenance variation in European larch has been studied for many years on the continent and since the 1930s in Britain (Anderson, 1932; Edwards, 1954, 1962; Lines, 1967). There are 39 provenance experiments planted in 1926-60, with over 200 seedlots, many of which are home collections. No experiments have been planted recently, so that there are no tests which include origins from Registered Seed Stands in EEC countries and few with authentic Sudeten larch from the native area in the Jesenicky Mountains of Czechoslovakia. These trials have emphasised the important interaction between seed origin and site factors, as shown by their survival, growth rate and incidence of canker and dieback. On more favourable sites in England, and on a few in Scotland, all provenances have survived well and grown without serious canker or dieback. Height growth showed clear differences, though seldom more than one or at most two Yield Classes. On these sites, choice of provenance was not critical except in so far as stem form was important. Polish larch had severely distorted stems on some sites (Lines, 1959). On higher elevation, more exposed, frosty and less fertile sites, the choice of provenance could mean the difference between success and total failure. Only Japanese and Hybrid larches proved safe on the worst sites.

Recommendations

The most important characteristics of European larch are: growth rate, stem form, resistance to canker and dieback, and the date of flushing. The main groups of provenances have been ranked for each of these characters (see Table 2).

Table 2. Characteristics of the main groups of European larch provenances

Provenance group	Growth rate (Best = 1 to poorest = 5)	Stem form (Best = 1 to poorest = 5)	Resistance to canker and dieback (Best = 1 to poorest = 5)	Flushing date (Earliest = 1 to latest = 4)
Polish	1	5	1	4
Sudeten/Silesian/Tatra	2	3/4	1	4
'Scottish'	3	2	2	3
'N German lowlands'	3	2	2	3
Eastern Alps (low elevation)	3	1	3	3
Eastern Alps (high elevation)	4	2	4	2
Western Alps (high elevation)	5	3	5	1

1. Registered Seed Stands in Britain should be the first choice but it is often difficult to obtain adequate supplies of European larch from these.

2. Imports from the Sudeten area of Czechoslovakia, or from low elevation plantations outside the native range in Germany (e.g. Schlitz) and Austria (e.g. Wienerwald) are the next choice.

3. Seed from high elevations in the Swiss, French and Italian Alps must be avoided.

Japanese larch *(Larix kaempferi* (Lambert) Carr. *(L. leptolepis* (Siebold and Zuccarini) Gordon))

Natural range

This species occurs only on a group of volcanic mountains in central Honshu, Japan, mainly at elevations from 1200-2400 m, though as a bush to 2800 m on Mt Fuji (Lindquist, 1955). It has been widely planted in central Japan and at lower elevations on the island of Hokkaido, 8° of latitude further north. The climate is wet with annual rainfall 1250-3700 mm, warm summers and cool, rather dry winters.

Silvicultural characteristics

A pioneer species, which colonises recent volcanic ash deposits, it grows well on loose-textured soils low in nitrogen. It flushes later than European larch and high-elevation origins shed their leaves early in autumn. It is remarkable that a mountain tree from Mediterranean latitudes has proved to grow well even in north Scotland. Rapid establishment and early growth, quick vegetation suppression, a degree of fire tolerance, and high amenity value have encouraged wide-scale use over the last 30 years. However, the windy climate of the British uplands, together with the much longer day length here in summer, and often higher nitrogen availability in British soils compared with those in Japan, may induce such poor stem and crown form as to make the tree useless for sawn timber production. This species should not be planted on fertile exposed sites except for amenity or shelter.

Introduction and use

The first seed was collected by J.G. Veitch on the slopes of Mt Fuji in 1861. Its use was confined to ornamental planting until the present century. In 1947 there were 22 280 ha of plantations divided almost equally between private and Forestry Commission woodlands. The 1980 Census showed 111 350 ha (which includes a small proportion of Hybrid larch). The area planted annually peaked in the period 1951-1960 and has since fallen by about two-thirds. In Wales the area of Japanese larch under Forestry Commission ownership represents 78 per cent of the total, whereas in England the Forestry Commission owns only 35 per cent of the total area of Japanese larch plantations.

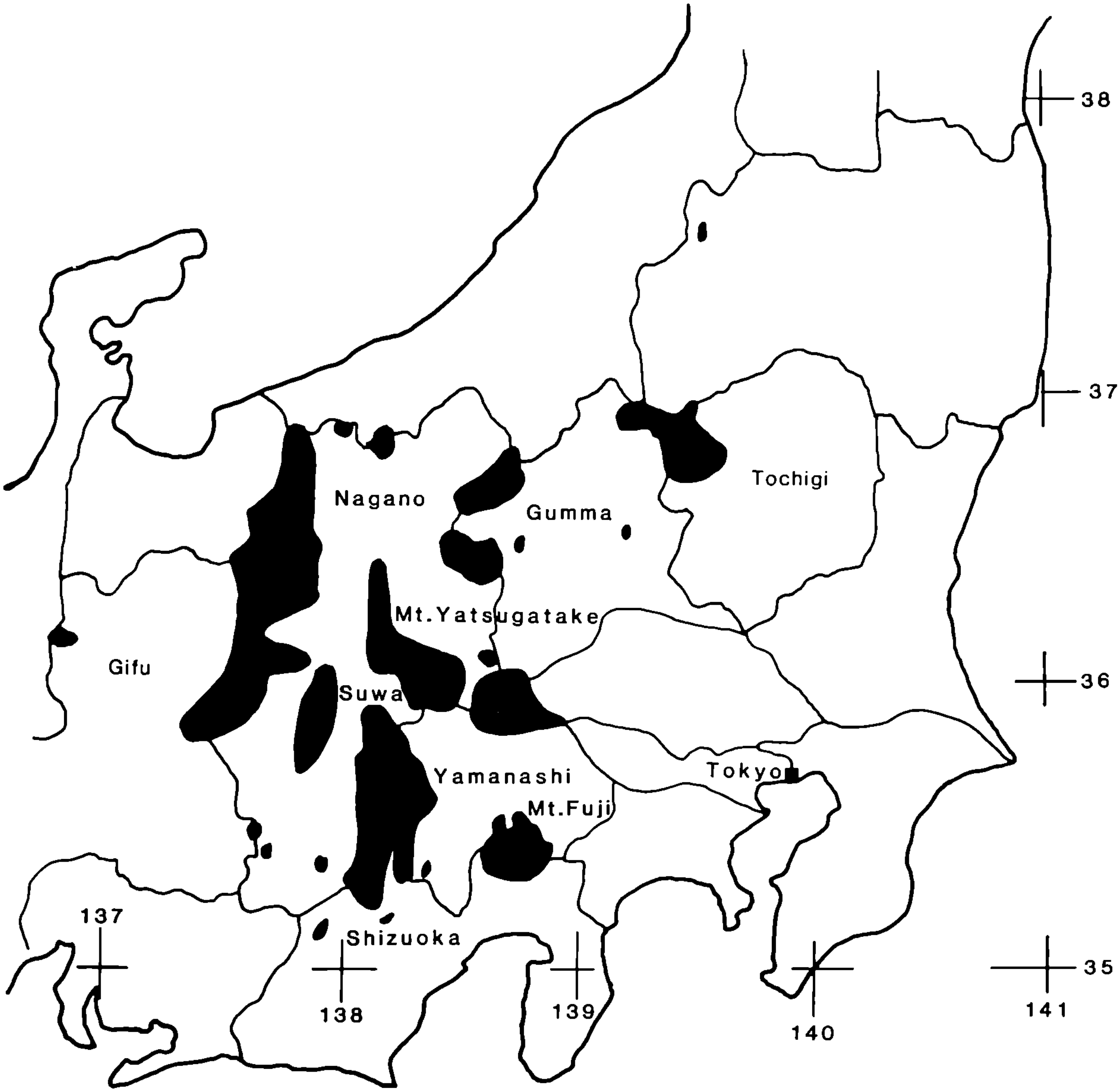
Most of the seed used in Britain has come from the Nagano Prefecture of Japan, though large imports came also from plantations in Hokkaido (probably originating in Nagano). Careful investigations of individual seedlots which have produced a poor quality stand on one site have shown that the same seed on another site has produced an acceptable crop.

Seed origin experiments

The earliest experiments in Britain were planted in 1934 on four sites with six seed origins. No consistent differences were found for height, stem or crown form (Edwards and Pinchin, 1953). In 1939/40, three more experiments were planted with 12 progeny lots from four districts in Nagano Prefecture (Wood and Edwards, 1950). Another progeny lot from a high elevation (2300 m) failed in the nursery. These experiments show that differences in branch form of individual trees were highly heritable, but not characteristic of a particular local population (Lines, 1962).

In 1956, a collection from 25 stands throughout the natural range was sent by Professor Iwakawa to Professor Langner in Germany who distributed the seed to 10 countries (Langner, 1958). Eleven experiments were planted in Japan (Toda and Mikami, 1976), 13 in Germany (Hattemer, 1968, 1969; Krusche and Reck, 1980), and 21 in USA and Canada (Farnsworth *et al.*, 1972; Genys, 1972; Park and Fowler, 1983). In Britain 25 of these seed origins were planted at Fetteresso, Grampian, 20 at Broxa, N Yorkshire and 15 at Ystwyth, Dyfed. Results after 10 years (Lines and Mitchell, 1969) showed that the tallest origins were from the Suwa region of Nagano Prefecture, which includes Mt Yatsugatake, and from the lower slopes of Mt Fuji. The best seedlots came from an elevation range of 1650-1850 m. Rank correlations for height between the British sites were poor, as they were for many sites overseas. Later assessments show a few seed origins as being fairly consistently fast-growing, while others, especially those from above 1900 m, were consistently slow. There was little correlation between scores for stem form at Fetteresso and in the Japanese experiments. At Fetteresso and Broxa commercial seedlots from Nagano and Hokkaido grew as well or better than the research collections of Professor Iwakawa. The difference between the tallest and shortest origins was about 35 per cent.

Figure 11. Natural range of Japanese larch, *Larix kaempferi* (Lambert) Carr.



Recommendations

1. The best source is likely to be seed from selected British plantations, as these will have been thinned to remove individuals with poor stem and crown features. This seed may have a proportion of natural hybrids with European larch.
2. For Japanese seed, the Suwa region of Nagano (elevation 1500-1800 m) remains the first choice.
3. Acceptable origins would be the Nikko region, Tochigi Prefecture (elevation 1500 m) and the plantations on Hokkaido.
4. Seed collected above 1800 m and from outlying areas in Honshu should be avoided.

Douglas fir *(Pseudotsuga menziesii* (Franco) Mirb.)

Natural range

The full range of this species (including the Colorado Douglas fir, var. *glauca* (Beissn.) Franco) is from Takla Lake, British Columbia at 55° N to below 20° N in Mexico and from the Gardner Canal (128° W) in British Columbia in the west to 105° W in the Rocky Mountains of Colorado. For commercial forestry in Britain only seed sources from British Columbia, Washington and Oregon have practical value. The map shows this part of the range. Wood (1955) points out that Douglas fir in North America generally experiences summers with higher temperatures and much greater seasonal moisture stress than anywhere in Britain. His comparison of accumulated temperatures in Canada and Britain shows that where Douglas fir reaches its northern limit on Vancouver Island at Quatsino Sound, the accumulated temperature is 2300 day degrees. This value is found in the English Lake District at an elevation of 160 m (500′) and at sea level in the Borders. Yet Douglas fir grows well near Ullapool, 3° of latitude further north. Nevertheless, it is clear from studies of root regeneration potential (P.M. Tabbush, personal communication) that low soil temperature at planting can result in poor survival, and autumn or late spring planting into warmer soil is recommended.

Silvicultural characteristics

Douglas fir is a fast-growing (GYC up to 24+) moderate shade-bearer, which requires reasonably sheltered conditions for long-term healthy growth. There is much variation in tolerance of seasonal frost and severe winter cold between seed origins. Macdonald (1952) considered that for rapid growth the mild, moist conditions of the west were essential. Wood (1955) on the other hand, believed that its moisture requirements were overestimated and that its best growth would lie in southern regions of Britain with moderate rainfall (not exceeding 1150 mm). Krajina *et al.* (1982) say that of all the species in British Columbia it is the one least tolerant of flooding and this is certainly true in Britain. They considered that its nutritional requirements in British Columbia are moderate in relation to Sitka spruce and it is found in Canada on a wide variety of soils, including those over limestone. In Britain, experience shows that its nutritional threshold is apparently higher than in North America, roughly equal to that of Sitka spruce (Wood, 1955) to achieve a fair rate of growth. Douglas fir is notoriously unstable on poorly drained, heavy-textured gley soils at the late establishment stage, and may require staking. It should be restricted to well-drained brown earths and more fertile sandy podzols.

One of its serious handicaps is a tendency towards stem sinuosity in the thicket and pole stages in British plantations. British foresters visiting NW America (e.g. Wood, 1955) have sought to find areas where this feature was displayed and thus avoid them as seed sources, but it is not obvious anywhere within the native range. It appears that some elements of the British climate – perhaps our frequent summer rainfall, higher wind speeds or long day length at latitudes beyond its native range – encourage this defect. It is worst here on moist, fertile sites and there is little evidence for it in France and Germany. The main insect pest is *Adelges cooleyi* which can check leader growth for a few years at age 5-10 years on coastal origins, though those from the interior of British Columbia are much less affected. Douglas fir does not grow well on exposed sites in Britain, and trees emerging above the canopy in mixtures with other species show one-sided crowns.

Introduction and use

Although it must have been seen by Captain Cook when he stopped at Nootka Sound, Vancouver Island in 1778, its discovery is attributed to Archibald Menzies during his visit to Nootka in 1792. David Douglas was the first person to send seed back, but its exact source is uncertain. It was probably from near his base on the Columbia River at Fort Vancouver, Washington, across the river from the present day city of Portland, Oregon. Specimen trees from Douglas' seed grew so well that they excited considerable interest and, as soon as they started to cone, more seed was collected from them, especially from one tree at Lynedoch, Scone Estate, in Perthshire. This was the source for the first plantation at Taymount in 1860. Of the two trees at Lynedoch, one always coned heavily and according to estate records, the two trees yielded 200 000 cones between 1850 and 1870 (Forestry Commission internal report). Several million plants could have resulted from these and it is known that many stands in Perthshire and some in Argyll derived from this source. Other early collections were made by Hartweg in California and Lobb shortly afterwards. These produced many specimen trees, but neither seedlots produced such vigorous progeny as Douglas' seed (Matthews, 1953). It is clear that many of the 19th century plantations resulted from home collections, perhaps largely derived from the original Douglas collection. At Cavers Estate near Hawick, Roxburghshire it is recorded that there was wide-scale

Plate 1 Sitka spruce seed origin demonstration, 10 years old. Arranged in decreasing latitude from right to left: Annette Is., Alaska; Derrick Lake, Nass R.; Kitwanga, Skeena R.; Jedway, South Q.C.Is.; Dinan Bay, North Q.C.Is.; Vedder, Fraser R.; Muir Creek, South Vancouver Is.; Big Qualicum R., East Vancouver Is.; Naselle, S. Coast Washington; Shelton, Puget Sound; Newport, Oregon; Crescent City, California. Bush near Edinburgh. **(N5925)**

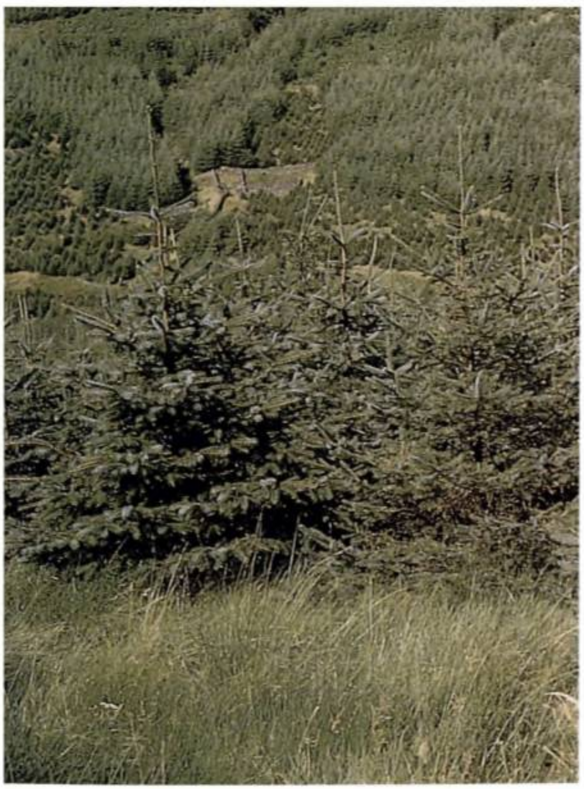


Plate 2 Sitka spruce from Lawing, Alaska. 10 years old. Note slow growth, dense crowns with long branches and blue needles. Loch Goil, Argyll. **(N2176)**

Plate 3 Sitka spruce from Gold Beach, southern Oregon. 6 years old. Note very rapid growth, narrow crown and dull green needles. Tree on right shows characteristic lammas shoots near tip. Site is an exposed plateau at 440 m in the South Wales Coalfield at Rhondda. **(N5151)**

Plate 4 Corsican pine from Corsica, showing good form, with light branching, through which the stem can be seen. Poor sandy site at Stenton, East Lothian. **(N2666)**

Plate 5 Corsican pine of Calabrian type. Note heavier cro which hides the stem. Very good needle retention, resulting earlier canopy closure. Stenton, East Lothian. **(N2667)**

Plate 6 Lodgepole pine from Salmon Arm, Southern Interior of British Columbia, aged 48 years. Note rather thin crowns; some trees with slight basal sweep, even after several thinnings; some with rough lower bark. Site originally heather moorland. Wykeham, N. Yorks Moors. **(N6103)**

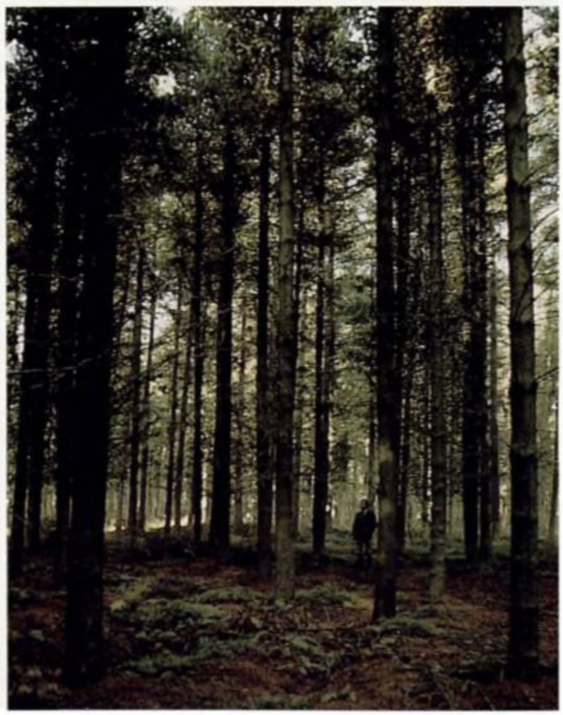


Plate 7 Lodgepole pine from Hazelton, Skeena R., Britis Columbia, aged 48 years. Note denser crowns, good stem fo and smooth lower bark. Wykeham, N. Yorks Moors. **(N61**

Plate 8 In front of figure: Japanese larch from Rengeyama, a high elevation (2350 m) site, showing slow growth after 8 years on an upland heath at Fetteresso, Grampian Region.
Behind figure: Japanese larch from Mt. Fuji, at 1440 m, showing much faster growth though with somewhat poorer form. **(N1429)**

Plate 9 European larch from a high elevation origin, Münsterthal, Switzerland. Aged 23 years. Note slow growth and straight stems. Die-back and canker reduced total basal area to 17.8 m^2 per ha at 33 years, on an upland heath at Clashindarroch, Grampian Region. **(N71)**

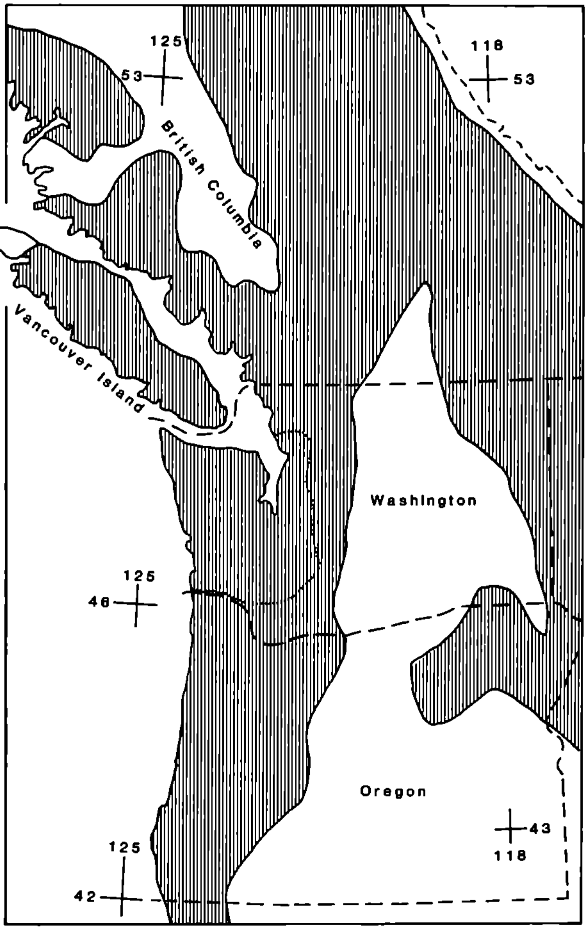
Plate 10 European larch from the Sudeten region at a low elevation, aged 23 years. Note rapid growth and sinuous stems. This origin was more resistant to canker and die-back, with a total basal area of 36.5 m^2 per ha at 33 years. **(N72)**

Plate 11 Foreground: Douglas fir from Waldport, Oregon, showing poor survival and growth after 8 years at Dunkeld, Perthshire. Background: Douglas fir from Enumclaw, Washington, showing high survival and fast growth. **(N3975)**

Plate 12 In front of figure: Grand fir from Clackamas R., Oregon. Mean height 1.89 m at 6 years. Brendon, Somerset. Background: Grand fir from Elwha, Washington. Mean height 2.73 m at 6 years. **(N5968)**

Plate 13 Grand fir from Big Spring, on the east side of the Oregon Cascades. Note the upswept needle tips, which are characteristic of trees from this introgression zone with *Abies concolor*. Drummond Hill, Perthshire. **(N5368)**

Figure 12. Natural range of Douglas fir, *Pseudotsuga menziesii* (Franco) Mirb.



vegetative propagation from the two trees there.

New large-scale imports date from 1870-1880, when the seed firm of C.H. Manning are known to have supplied seed at first from the lower Columbia River and later from their offices at Roy, near Tacoma, Washington. It is likely that some seed came from British Columbia in the late 19th century. The first seed imported by the Forestry Commission in 1921 was 913 lbs, reputed to be from Washington. The following year 4000 lbs came from the lower Fraser River. Thereafter most seed up to the 1950s came from both these sources. Small amounts came from the Shuswap Lake area in the interior of British Columbia, from Oregon or from undefined sources in 'USA' or 'BC'. During the next 30 years a few seedlots came from Vancouver Island and Oregon, but the great bulk was from Washington. Of the total of 50 747 lbs imported, 77 per cent came from the USA and 23 per cent from British Columbia.

Douglas fir now forms 3 per cent (25 400 ha) of Forestry Commission coniferous woodlands, and 4 per cent (20 490 ha) of the total area of private coniferous woodlands. In view of its high timber value, rapid growth and resistance to butt rot it is likely to be used on an increasing scale as the emphasis swings away from afforestation of bare ground to replanting of more sheltered valley sites, e.g. those currently carrying better quality Scots pine or larch.

Seed origin experiments

Seed origin differences have been studied for 75 years in the USA (Munger and Morris, 1936; Isaac, 1949) reporting on trials planted in 1912 and in Germany, Münch's trial of 1912 reported by Rohmeder (1956). Schober (1963) summarised results from experiments in Germany, Denmark, Belgium and Holland. In Scotland and northern England, 11 experiments were planted with 82 seedlots and in southern England and Wales 19 experiments were planted with 118 seedlots between 1928 and 1972. There are two main series:

a. one planted in 1953/54 with 13-19 seedlots (Bonded Seed) from the Manning Seed Company, restricted to Washington and Oregon, and
b. a IUFRO series planted in 1970-72 with 44 seedlots, covering the main part of the range from central British Columbia to California.

A further series of experiments planted in 1959/60 tested the progeny from well grown older stands in Scotland, many of which derived from the David Douglas introduction to Lynedoch, Scone Estate. Results from some stands were disappointing, with a rather high proportion of trees showing malformed individuals and slow growth (Lines, Mitchell and Low, 1967). It now appears that because of the very small genetic base of the older stands (seed collected from only one or two trees) the progeny show inbreeding depression. Progeny from Scottish stands known to result from a large seed import do not show these features.

With Douglas fir early growth rate is only one of several characteristics which strongly influence choice of seed origin. For example, some southern origins grow fast in the nursery, but later suffer severely from frost. At 20 years of age experiments in Scotland showed small differences in top height, but much larger differences in volume (Lines, 1977).

Differential resistance to *Adelges cooleyi* was noted in 1951 (Lines, 1956) and in the 1953/54 series of experiments the only consistent resistance to this pest was shown by a seedlot from Shuswap Lake, interior British Columbia. Mejnartowicz and Szmidt (1978) showed that resistant origins among 59 of the IUFRO seedlots were all from east of the Cascade Mountains in USA and the Coast Range in British Columbia. On the other hand, many of these interior seed origins showing resistance to *Adelges* suffered needle cast from *Rhabdocline pseudotsugae* (Lines and Aldhous, 1961; Stephan, 1980). As regards early survival and resistance to blasting winds in winter, these interior sources are undoubtedly superior to those from the southern coastal part of the range, as was demonstrated by the severe winter of 1962/63. However, they offer a poor long-term prospect and are overtaken in height growth and volume production by the better coastal origins within 15-20 years of planting.

The IUFRO collection gives the best information on growth rate up to 10 years. Nursery results are given by Lines and Mitchell (1970) and results after 6 years in the forest by Pearce (1980) for the five southern experiments and by Lines (1980c) for the three Scottish experiments. The 10-year height and diameter assessments show that the tallest origins were from the Pacific coast and foothills of the Olympic and western Cascade Mountains of Washington. Some low elevation Oregon sources also grew well, while Vancouver Island origins had moderate growth rates. Those from northern (above 50° N) or southern (below 44° N) latitudes grew poorly, as did those from above 800 m elevation. The pattern of diameter growth was similar to that for height. Although statistically significant, the interaction between seed origin and site was much less than with Sitka spruce, so that the choice of different seed origins for different parts of Britain is less critical (Lines and Samuel, in press).

Recommendations

1. The most vigorous seed origins come from a U-shaped area along the western foothills of the Cascade Mountains in Washington, westward along the 46th parallel to the low coastal range and north as far as Forks in Clallam County, i.e. from US Regions 202, 403, 411, 412, 240, 041, 222 and 012.

2. Trees from Coquille, Oregon (072) grow well on a range of sites, but the more southerly Oregon sources should be avoided in Scotland.

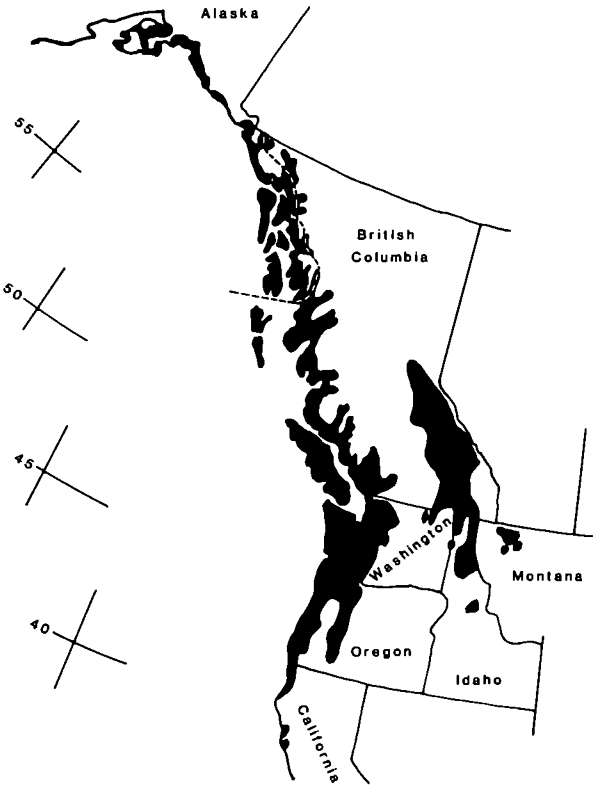
3. Some Vancouver Island sources, e.g. Jeune Landing (1030), grow well in Scotland and quite satisfactorily in England.

4. Little seed is now available from the Lower Fraser River area, which supplied much of the seed 50-60 years ago, as these stands have now been cleared. Seed from registered British stands dating from this era are a good choice anywhere in Britain, but supplies are very limited.

5. Origins from the interior of British Columbia north of 50° should be avoided.

Western hemlock (*Tsuga heterophylla* (Raf.) Sarg.)

Figure 13. Natural range of Western hemlock, ***Tsuga heterophylla*** (Raf.) Sarg.



Natural range

Western hemlock has a very wide range in NW America extending along the Pacific coast from Alaska down to northern California and inland to the Coast Range and Cascade Mountains. Further inland still it occurs in the Selkirk Mountains of British Columbia and extends into north-east Washington, north Idaho and north-west Montana. On the coast, its northern limit is 62° N, its range almost mirroring that of Sitka spruce in Alaska, though excluding Kodiak Island and the west side of the Cook Inlet. At these cool northern latitudes (around 60° N) its maximum elevation is about 800 m and at sea level the average annual temperature is only 4° C and there are only 132 frost-free days per annum (Fowells, 1965). At a more typical site on the coast of Washington, the average annual temperature is 10.6° C with 208 frost-free days. In the Rocky Mountains the absolute minimum temperature may reach -34° C and the species is found up to 1800 m.

Silvicultural characteristics

In NW America its shade tolerance is regarded as second only to that of Pacific silver fir (Krajina *et al.*, 1982). It responds well to release of the overstorey (Fowells, 1965).

Frost resistance is very low and Krajina (loc. cit.) states that its distribution is limited to areas where the ground is well covered by snow before the soil can freeze. This eliminates it from the driest parts of the interior Douglas fir region. However, it can tolerate very low air temperatures in winter after snow has fallen. In Britain, upper shoots of young trees are frequently killed back by strong winds on exposed sites, whereas trees in sheltered areas, even frost hollows, are untouched by severe winters, though they may be damaged by spring frosts.

Hemlock can withstand periods of flooding better than Douglas fir (Krajina loc. cit.) and it can tolerate poorer levels of soil nutrients than most conifers. In fact, Krajina *et al.* state that nutrient-rich seepage may kill Western hemlock seedlings. It is particularly well adapted to regenerating on rotten wood, old stumps, etc., which have very low nitrogen availability. Wood (1955) also emphasises its markedly lower requirements for fertility and moisture compared with Sitka spruce.

Macdonald (1952), acknowledging its capacity to grow on drier eastern sites, stresses its higher productivity in the wetter north-west of Britain. It does not tolerate limestone sites. On the most suitable sites General Yield Class 24 may be attained. A rotation of 50-60 years is normal in Britain; trees as old as 1000 years are known in British Columbia. Establishment as an understorey or on sheltered sites is relatively easy and early growth is rapid.

On exposed upland sites the tree tends to form a bush with many leaders and grows only slowly until canopy is formed. Height growth then increases rapidly, but the stand may have so many trees with multiple stems that its value is low. Deer and hares may cause a similar bush formation on sheltered sites. On the coast of Alaska, stem fluting is a common defect. It is also seen in some stands in Britain, though there is little evidence yet from British seed origin trials that Alaskan origins are worst affected.

Introduction and use

Introduced in 1851, it was not planted as a forest tree until 1888 at Balantyre, Inveraray (Faulkner and Stewart in Macdonald *et al.*, 1957). Before 1939 only 219 kg of seed were imported, which resulted in 245 ha of Forestry Commission plantations (Aldhous and Low, 1974).

Between 1953 and 1971, 2475 kg were imported and by 1967 there were 7225 ha of Forestry Commission plantations. The most recent data show a total of 11 200 ha, of which about 3000 ha is in private woodlands. In many, if not most of these plantations, Western hemlock was used in underplanting or for enriching derelict or poor quality broadleaved woodlands. After the publication of Forestry Commission Bulletin 49 (Aldhous and Low, 1974) there was a reduction in the use of this species.

Seed origin experiments

Unlike some NW American species, different origins of Western hemlock have no obvious morphological or colour differences, except for an Alaskan lot from Juneau which appeared a darker green than other origins in experiments. Early seed imports came mainly from the coast of British Columbia. The performance of the few imports from interior British Columbia, Washington and Oregon went unremarked, so that it can be assumed that they grew normally. Wood (1955) considered that as a climax species it probably varied less than pioneer species. He suggested the Queen Charlotte Islands as a reliable general seed source, based mainly on climatic matching and on several seed imports in the 1930s. Wood also suggested Alaskan origins for colder and more exposed sites. During the last 35 years the main sources have been Vancouver Island and the Queen Charlotte Islands.

Three experiments were sown in 1959 with 16 seedlots from the native range, supplied by the Manning Seed Company, together with two from stands in the British Isles (Avondale, Co Wicklow and Inveraray, Argyll). The latter was from the earliest plantation noted above. Reports were made on the nursery stage (Lines and Aldhous, 1961, 1962) and on the forest stage (Lines and Aldhous, 1963; Lines and Mitchell, 1969; Lines *et al.*, 1972). The nursery experiments showed that southern origins had a longer growing season and grew taller than the northern ones, though the former were more at risk from autumn frosts. Similar results were found in controlled conditions by Kuser and Ching (1980). The very delayed bud formation of the Inveraray provenance suggests that it had a southerly origin, while the Avondale one probably came from further north. Nineteen forest experiments were planted in 1961 and 1962. The winter of 1962/63 was exceptionally severe, resulting in the failure of three experiments and serious dieback on those planted without side or overhead shelter. Several other experiments were closed at 10 years because of low survival. There was a clear pattern of higher survival and growth of the northern origins on exposed sites, while on sheltered sites, southern origins (including the Inveraray provenance) grew best. Because of small plot size and the difficulty of assessing height in dense, polestage stands, only eight experiments have been measured at 20 years. These show fairly small changes in height ranking from those at 10 years, with basal area or diameter following a similar pattern. Because of the strong interaction between seed origin and site there is no seed source which is outstanding on all sites. Rather variable results were also found for 15 seed origins grown on four sites on Vancouver Island (Pollard and Portlock, 1986).

These experiments have shown that Western hemlock is an unsuitable species for new afforestation on exposed upland sites. It is also a doubtful choice for second rotation sites where the stumps have butt-rot.

Recommendations

1. Vancouver Island sources, e.g. Courtenay (BC Region 1020), are good general purpose origins, while on dry sheltered sites in the south and east of England, Camano Island, Washington (Region 212) grows very well.

2. For sheltered sites in northern Britain, Alaskan origins are the hardiest, but may later grow less fast than those from the Queen Charlotte Islands.

Western red cedar (*Thuja plicata* D. Don).

Natural range

This species is widely distributed from nearly 57° N in southern Alaska to 40° N in northern California, along the coast and into the Coast Range and Cascade Mountains. It is also widespread further inland, in south-east British Columbia and in northern Idaho and north-western Montana. It occurs mainly in areas with high humidity, where the annual precipitation ranges from 800 mm to over 2000 mm. The interior part of the range is characterised by relatively dry summers and heavy rain in spring and autumn. In Alaska it is found from sea level to nearly 1000 m, while further south and inland it is occasionally found up to 2000 m, though mainly below 1500 m (Fowells, 1965).

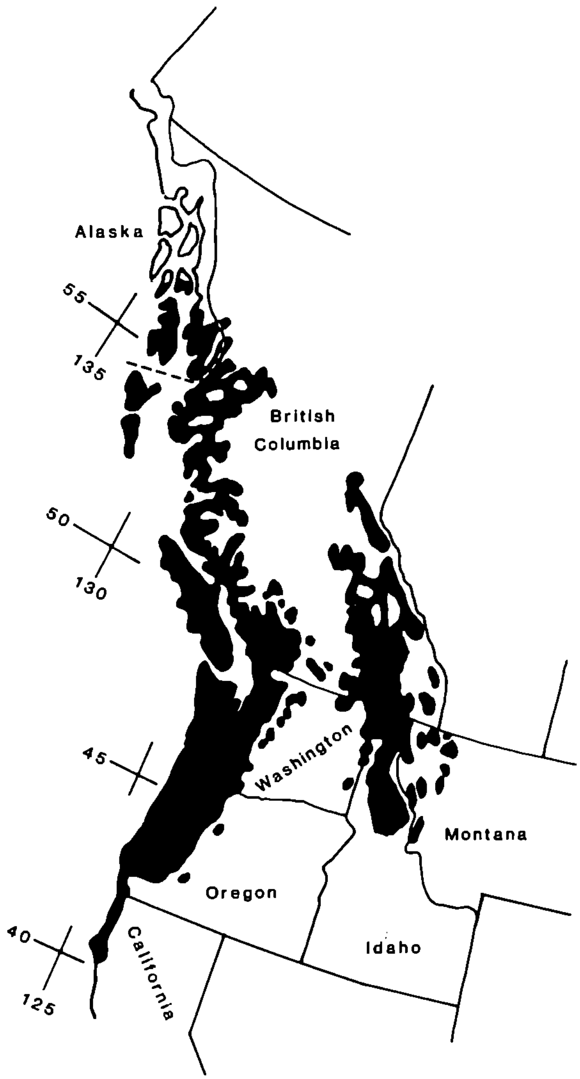
Silvicultural characteristics

In its native range it is seldom found in pure stands, being commonly associated with Western hemlock, Sitka spruce and Pacific silver fir on the coast, while inland it is mixed with Douglas fir, Western hemlock, Grand fir and Western white pine. On poorer sites it occurs with Lodgepole pine, especially on muskegs, where it grows well for some years before dying back to produce characteristic dead 'spire' tops. Over much of its range it is the natural climax species, partly because it remains healthy to a great age and is able to survive fire and mechanical injuries (Wood, 1955). It is very tolerant of shade, though growth responds strongly to increased light, e.g. when an overstorey is removed. Early height growth is rather slow, except on very favourable sites. Later volume growth on the latter can reach Yield Class 24. Young stands are susceptible to spring frost damage and winter blasting. The foliage can turn bronze in winter without permanent injury. It cones quite early and regenerates naturally on suitable sites free from browsing.

Introduction and use

One of the late introductions to Britain, by William Lobb in 1853 from Oregon, it was at first used for ornamental purposes and for hedges. It was rarely planted as a forest stand: prior to 1950 there were only 158 ha in private woodlands and 148 ha in Forestry Commission ownership. The 1980 Census showed 3000 ha on Forestry Commission ground, 2280 ha of which were in England. 2320 ha were privately owned, nearly all in England.

Figure 14. Natural range of Western red cedar, ***Thuja plicata*** D. Don.



Its presence on North American muskegs has led to several attempts to establish it on British peat bogs. Zehetmayr (1954) considered it was worth further trial, particularly in mixture with pine. These attempts have very seldom been successful in comparison with the growth of other species such as Lodgepole pine or Sitka spruce. It has grown quite well on shallow soils over chalk and can tolerate a range from acid to alkaline soil conditions. It has been widely used for underplanting larch or broadleaved species and appears to attain its maximum growth in the south-west of Britain. Home-grown timber of mature Western red cedar is similar to imported timber and very resistant to decay, though small roundwood presents marketing difficulties because of problems of barking and acceptability for the processes used in British pulpmills (Aldhous and Low, 1974). Despite its high growth potential, its use is unlikely to expand appreciably.

Seed origin experiments

Seven experiments were planted in 1962/63 with 13 seed origins. These were mainly from coastal regions, from the Queen Charlotte Islands south to Vernonia, Oregon, with one inland seedlot from Shuswap Lake, British Columbia. One experiment on a frosty flat at Cannock (Stafford) failed at an early stage (Lines and Aldhous, 1964). The remaining experiments cover a wide range of site conditions from a high rainfall area in Argyll to a low rainfall area in East Anglia. The pattern of variation in growth rate among the seed origins was rather similar at all sites, except for Vernonia, Oregon, which grew well at Alice Holt (Hampshire) and Thetford (Norfolk) and poorly elsewhere. Sooke, Vancouver Island was also erratic. The tallest group of origins was from low elevations on the northern slopes of the Olympic Mountains in Washington (Joyce and Sequim), followed by the Shuswap Lake origin. Apart from Sooke, the three other Vancouver Island origins grew well, especially one from Ladysmith, while those from the Washington Cascades also had satisfactory growth rates. Poorest were those from the Queen Charlotte Islands and the Skeena River, near Terrace. Infection by *Didymascella thujina (Keithia)* was assessed in the experiments at Radnor, Thornthwaite and Benmore. Origin differences were highly significant and consistent between sites. Vernonia was worst infected, followed by the Vancouver Island origins (except for Alberni), Shuswap Lake and Joyce, Washington, while the northern origins from Terrace and Queen Charlotte Islands were least infected. There was little correlation between infection at 6-8 years and later height.

Recommendations

1. First choice is the north slope of the Olympic Mountains, Washington (US Zone 221) below 150 m in elevation.

2. Some Vancouver Island seed sources (e.g. Ladysmith, BC Zone 1020) show promise.

3. The interior origin from Shuswap Lake (3040) grew well, except at Benmore.

4. Ashford (US Zone 422) is acceptable and showed high resistance to *Didymascella* in the forest.

Where the nursery has a history of *Didymascella* infection, fungicidal treatment with cycloheximide (Forestry Commission, 1983) is still necessary for any seed origin.

Grand fir
(*Abies grandis* Lindl.)

Natural range

Grand fir is a tree of low to middle elevations, within a latitudinal range from 50° N on the east side of Vancouver Island to 30° 30′ N on the coast of California (Steinhoff, 1980). In addition to this coastal distribution it is also found on both sides of the Cascade Mountains of Washington and north Oregon. There is a wide gap between these populations and those further inland in the Lake Kootenay area of south-eastern British Columbia, north-east Washington, north Idaho, west Montana and the Bitteroot Mountains of Oregon. Grand fir is able to hybridise with *Abies concolor,* whose main western distribution is further south in southern Oregon and California at higher elevations. Where these two species meet, there is a zone of introgression (distinguished as *A. concolor* var. *lowiana* (Gordon) Lemmon by some authors), which has been studied by Daniels (1969) and Zobel (1973) on a morphological basis and by Zavarin *et al.* (1977) using differences in the cortical terpenes. Lacaze and Tomassone (1967) were able to separate different populations of *A. grandis* and intermediate populations using a combination of morphological and growth characters. While the terpene differences give a clear picture of the phylogenetic differences, they do not show any significant difference within the pure Grand fir populations. Thus seed origins from north Idaho and the Pacific Coast of Washington, which have very different growth rates in Britain, have very similar terpene patterns. On the other hand, terpenes provide a reliable way of distinguishing pure populations of *A. grandis* from populations of *A. concolor* var. *lowiana* in areas to the east of the Cascades, not only in Oregon, but as far north as 46° 38′ N in Washington Zone 641.

The area covered by the IUFRO seed collections of 1974/76 was divided into nine regions by A.M. Fletcher, see map in Lines (1979). On the coast of British Columbia Grand fir is found at sea level to 300 m elevation, while in the interior of the province it is confined to valley bottoms. The same is true for most locations in western Washington, though it occurs at 850 m on the east slopes on the Olympic Peninsula. At higher elevations it is replaced by Pacific silver fir (*Abies amabilis* (Dougl.) Forbes). In south-west Oregon, Grand fir is a lowland tree, while in the Cascades it is found at middle elevations up to 1600 m (Fowells, 1965), though it is likely from the studies of Zavarin *et al.* (1977) that some of the highest stands are of the introgression form.

Silvicultural characteristics

Grand fir shows healthy growth over a wide climatic range in Britain. It responds best where the annual rainfall exceeds 1100 mm, but is not as demanding as Sitka spruce in its moisture requirements (Wood, 1957). In British Columbia it is considered a mesothermal species, restricted to areas where the mean temperature exceeds 10° C for 5-7 months (Krajina *et al.*, 1982). It is very sensitive to cold drying winds on exposed sites, though the needles can withstand very low temperatures (-55° C) when dormant (Parker, 1955). It is markedly less exposure-resistant than Noble fir. Nutritional demands are now considered much lower than was thought to be the case in the 1930s and it has grown reasonably well on poor heathlands in Yorkshire and also on *Molinia* peatland in Scotland and the Borders. It is unsuited to heavy clays and waterlogged soils. It is useful as a replacement species for larch crops suffering from *Fomes* butt-rot, since it has relatively good resistance to this fungus (Pratt, 1974). Shade tolerance is fairly high, exceeding that of Douglas fir, but much less than Western hemlock or *Abies amabilis.* Stem form is excellent with fewer coarse dominants than Douglas fir.

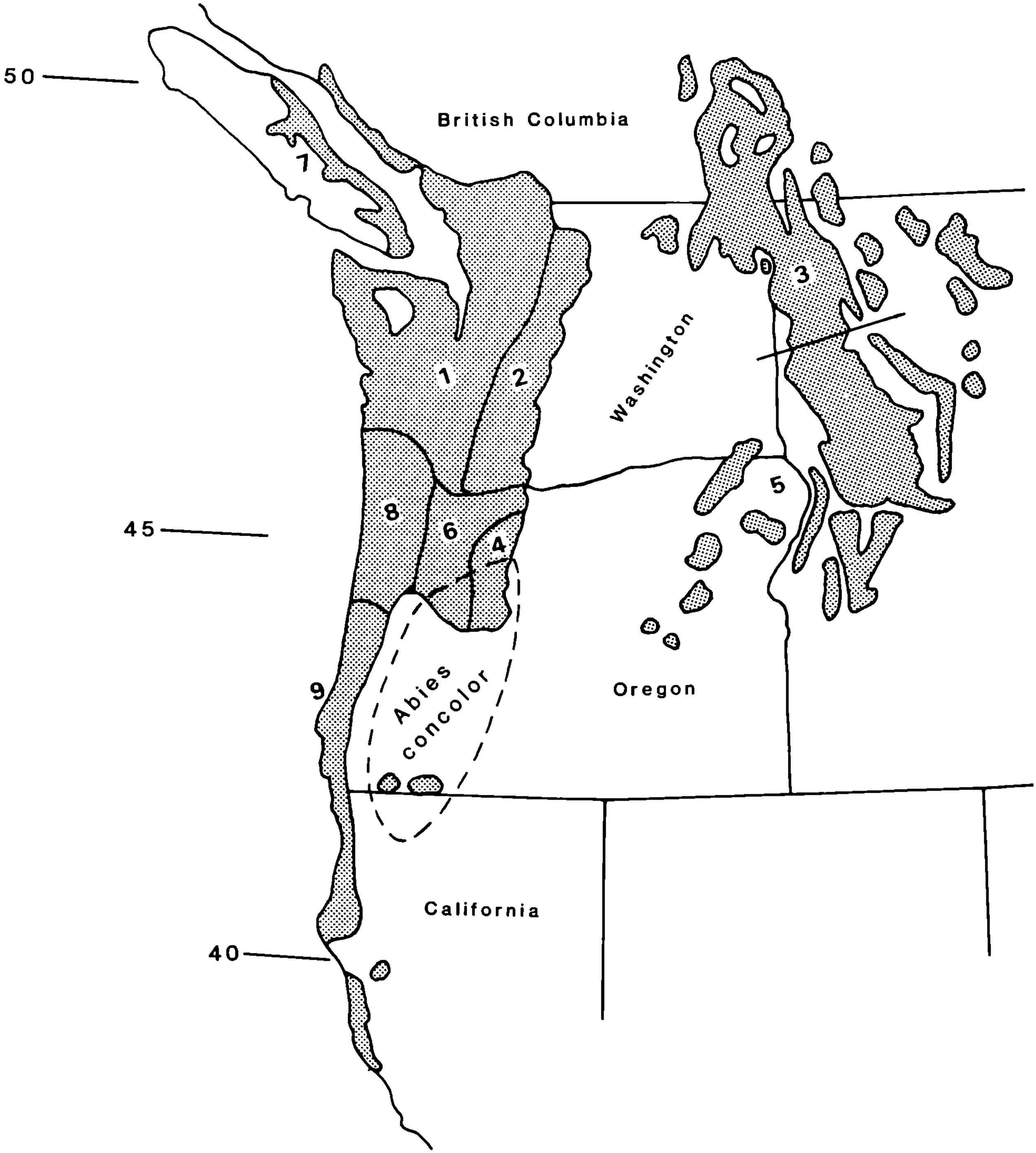
Its potential rate of growth is the highest of any common species, although not always achieved due to past use of inferior seed origins. The most vigorous stand on record is one of Local Yield Class 34 in the Craigvinean section of the Dunkeld Forest in Perthshire. Its rapid growth often means that it stands above surrounding crops and is thus more at risk from gales. Although fairly late flushing, it can suffer badly from spring frosts. Other hazards are infestations of *Adelges piceae* which causes timber defects (Aldhous and Low, 1974) and drought crack, which often appears more serious than it is in fact (Greig, 1969). The timber of Grand fir grown in Britain has low specific gravity and would be useful only in place of lower grades of imported 'whitewood' and not for house construction.

Introduction and use

Introduced by David Douglas in 1831, it was not used as a plantation tree until this century, when a 0.8 ha plot was planted at Novar, Ross-shire in 1900. It is not mentioned in FC Bulletin 14 *Forestry practice* until the seventh edition in 1958. By 1948 there were still only 255 ha, though by 1976 this had increased to 3067 ha. The total now is 4260 ha of which 1250 ha is privately owned.

Unlike Noble fir, little seed of Grand fir has been collected in Britain. Before 1939 the relatively small amounts of seed imported came from British Columbia

Figure 15. Natural range of Grand fir, ***Abies grandis*** Lindl. Also indicated is the natural range of Colorado white fir, ***Abies concolor*** (Gord.) Hildebrand, with which Grand fir is able to hybridise in the introgression zone.



and from west of the Cascades in Washington. With the expanded planting programme after the war, large imports came either from east of the Cascades in Washington and Oregon, or else were simply labelled 'USA'. At this time the main collecting areas were east of the Cascades and it is most likely that our seed came from this area. In the period 1923 to 1958, 83 per cent of the total seed came from these areas, which have later been shown to produce stands of below-average vigour.

Botanically some of the larger imports were not true *Abies grandis* at all, since they came from southern Oregon, east of the Cascades in Seed Zone 681, which Zavarin *et al.* (1977) showed to be *Abies concolor* var. *lowiana*. Unfortunately several of these seedlots were used in experiments during the 1950s and 1960s. This may well have affected opinions about the potential of this species. It would also have inflated the estimates of establishment costs for this species used by Aldhous and Low (1974).

As this publication on the potential of this species was compiled before the results of modern seed origin trials were available, it may be desirable to reconsider their suggestion that it is only a viable commercial alternative to the common species on the best quality sites and thus has a very low potential (see Lines, 1979, p.101). Since 1960, the bulk of seed imports has been of seed origins noted for above average vigour. As its wood quality is likely to be poorest on the best sites, it may be better to use the potential growth vigour of the best origins on sites of mediocre fertility and on sites which are too dry for spruce.

Seed origin trials

For many years Grand fir was assumed to have rather small genetic variation between seed origins and the large observed differences in growth were attributed mainly to its sensitivity to varying site conditions. However, some Continental seed origin trials (Lacaze and Tomassone, 1967; Gathy, 1970; Gøhrn, 1972) showed that there was a large variation, and this was confirmed by the first small trials in 1967/68 with five seed origins in Britain (Lines *et al.*, 1971; Lines, 1973). These results encouraged further studies and a preliminary trial with 24 commercial seedlots was sown in 1972 (Lines, 1974). Results at 6 years in the forest show the continued good growth of seedlots from the Olympic Peninsula and the Oregon coast (Lines, 1979) and these patterns of growth have now been confirmed by the height assessments at 10 years.

Seed collections organised by IUFRO were made in North America in 1974 and 1976 by A.M. Fletcher and the resulting 36 seedlots were sown in 1976/77. Nursery results show that the tallest origins were from Seed Region 1 (coast of Washington) and a Scottish seedlot originally from Vancouver Island. These were double the height of the poorest lots from Region 5 (Lines, 1980d). These origins were planted on up to 12 sites covering a wide range of conditions from Inchnacardoch in north Scotland to Brendon in Somerset in 1978/80. The results after 6 years have not yet been fully analysed; in general the pattern of growth remains similar to that shown at 3 years (Lines, 1984b). The extent of the differences between the best and the worst origin at any site is very large, e.g. at Mathrafal in N Wales, which represents an average site, the tallest origin (Elwha on the north slopes of the Olympic peninsula) had a mean height at 6 years of 2.20 m, while the shortest (Santiam Summit, east side of the Oregon Cascades) was only 1.18 m. Using Everard's (1974) extended curves for General Yield Class, these heights correspond to *provisional* GYCs of 34 and 16, i.e. suggesting a potential gain of 18 Yield Classes, merely by selecting the optimum seed origin. There is relatively little origin x site interaction, with the same regional groups performing well or badly over all sites.

Recent assessments of Continental experiments using the same IUFRO seedlots in Holland (Kriek, 1982) and Germany (Rau and Weisgerber, 1982; Scholz and Stephan, 1982; Reck, 1983) reinforce the early conclusions drawn from British experiments. Other reports from France (Noel, 1979; Roland and Roman-Amat, 1985) and Denmark (Kjersgard and Gøhrn, 1978) on experiments up to 25 years old with a different range of origins, present a similar picture and add information about wood properties. For example, the Vancouver Island origins had superior wood density, whereas some French provenances (originally from the coast of Washington and Oregon) had poor mechanical strength and would be suitable only for pulpwood or similar end uses.

The regional pattern of flushing in British experiments (from earliest to latest) is Regions 9 > 7 > 8 > 1 > 2 > 6 > 4. This is somewhat different to the pattern in the greenhouse study in Germany (Scholz and Stephan, 1982) where origins from the Vancouver Island, Region 7, were markedly earlier than those from the S Oregon Coast, Region 9. Grand fir flushes about the same time as Sitka spruce and much earlier than *A. procera*, *A. concolor* or *A. amabilis*.

Recommendations

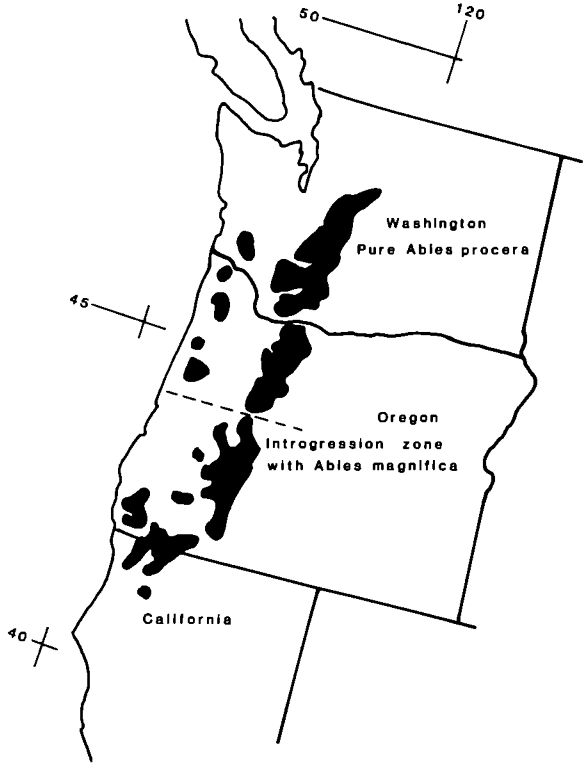
1. Origins from Region 1 (Olympic Peninsula and the Puget Sound) have grown uniformly well on all sites. Within this Region, individual seedlots from Elwha, Louella and Sequim are outstanding.
2. Excellent height growth characterised the two seedlots from the S Oregon coast (Region 9). However, these flush early and they have suffered some die-back on exposed sites and damage has also been reported on these from the Continent.
3. Vancouver Island seed origins (Region 7) are somewhat slower-growing and they are also rather early in flushing. They have the advantage that their use is well proven in Britain, e.g. the stand of Yield Class 34 at Dunkeld is from Campbell Lake, Vancouver Island.
4. On current evidence, all other regions (apart perhaps from 8) are not recommended. Regions 4 and 5 in particular should be avoided.

Noble fir (*Abies procera* Rehder = *A. nobilis* Lindley)

Natural range

Noble fir occurs on the upper slopes (1000-1800 m elevation) of the Cascade Range in Washington and Oregon from the Stevens Pass at 48° N south to about 44° N in central Oregon. Smaller areas are found on isolated peaks, such as Mary's Peak and Laurel Mountain, in the Oregon Coast Range. Below latitude 44° N there is an extensive area in south Oregon where there is introgression with Shasta red fir (*A. magnifica* var. *shastensis* Lemm.) (Franklin *et al.,* 1980). The Continental-type climate can be harsh at these elevations, with low temperatures and very heavy snow fall in winter and much drier summers than anywhere in Britain. The frost-free season is less than 120 days and even less at the highest elevations.

Figure 16. Natural range of Noble fir, *Abies procera* Rehder.



Silvicultural characteristics

In the USA it is a pioneer species following major disturbances such as fire (Fowells, 1965). It is only a moderate shade-bearer, much less so than Grand fir. Morphologically it is well adapted to withstand cold, blasting winds in winter, having stiff, stout twigs with the needles heavily wax coated and the terminal buds covered not only by scales but also by overlapping needles. It is thus far more resistant to exposure at high elevation than Grand fir and much less liable than Sitka spruce to have its leader broken on such sites. Growth is slow at first, but after 5 or 6 years it speeds up and its volume production in middle age can reach a current annual increment of 30 m^3 per hectare with annual shoots of nearly 1 m. It is even more susceptible to heather-check than Sitka spruce on dry *Calluna*-covered sites and less tolerant of 2,4-D as a control measure.

Noble fir is one of the last conifers to flush and ceases height growth early. It bears cones from about 25 years onwards and produces good crops every 3 years. These are so conspicuous that from the 19th century home collection of seed has been common. In 1911 there were 30 000 Noble fir seedlings in the nursery at Ardverikie, Loch Laggan derived from trees planted there 30 years earlier (Stirling-Maxwell, 1911). The seed has a low viability and in home seedlots this may be further reduced by *Megastigmus* damage. It has good resistance to *Fomes* rot, but on some sites suffers badly from drought crack.

Introduction and use

Introduced by David Douglas in 1831, the species became popular in arboriculture after W. Lobb collected seed in Oregon for the nursery firm of Veitch in the 1850s. However, apart from Ardverikie and Corrour Estates, it was not widely used as a plantation species, so that by 1947 there were only 203 ha, about half of which were in the 1-30 year age class (Wood, 1957). Lobb's introductions may have formed an important early seed source, as prior to 1953 almost all Noble fir came from home collections, e.g. as early as 1925, 100 kg of Noble fir seed was collected by the Forestry Commission from Scottish private estates. No doubt similar collections were being made by estates for their own use, as at Ardverikie. In some years, large amounts were collected e.g. 1617 kg in 1951, which largely obviated the need for imports. If in fact a large proportion of the 19th century and early 20th century stands originated from Lobb's limited early collection, then the genetic base may be so small that a degree of inbreeding is inevitable.

Home collections from many small areas proved expensive to organise and from 1953 onwards, seed was also imported from Washington and Oregon. Between 1954 and 1960, 2272 kg came from the Oregon Cascades under the name 'Oakridge'. This town lies to the west of the Divide and it was later confirmed (A.M. Fletcher, personal communication) that the seed was collected in the *Pinus ponderosa* region to the east of the Divide near Odell Butte. It is now clear that trees in this area are in the introgression zone with Shasta red fir. A further 1193 kg came from 'Oregon' which could include seed from this area.

Between 1920 and 1962, 7382 kg of seed was collected or imported. This large quantity of seed had apparently produced only 1808 ha of Noble fir in both Forestry Commission and private forests up to 1967. The latest return shows 2650 ha. The potential of Noble fir for more extensive use came under scrutiny by Aldhous and Low (1974) who concluded: "There appears to be no case for any large-scale planting of this species, because of its slow early growth and low density timber". Since that date there has been increasing interest in it as a high-value Christmas tree and for producing foliage for the horticultural market. Its dramatically distinct appearance and light-coloured foliage have also encouraged greater use for amenity.

Seed origin experiments

Until recently the general view was that this species, with its limited range, showed little variation between seed origins. Table 13 in Aldhous and Low (1974) predicts little gain from tree improvement. Two experiments at Radnor and Thetford planted in 1968 compared seven provenances from Britain and Denmark (all of unknown seed origin) with one direct from Santiam, Oregon. The Santiam and Danish lots grew best, but these results cannot give useful guidance on choice of origin. The only Continental set of experiments with published results is a Danish trial of 24 seedlots collected from the stands planted there between 1880 and 1939 (Barner *et al.,* 1980). The main result of interest is that large differences were found in the proportion of trees suitable for Christmas trees and in foliage quality. Denmark uses 1500 kg of seed annually, largely to grow trees to supply this market.

The 1978 IUFRO seed collection of 19 seedlots was supplemented by 8 lots from the US Forest Service. Differences in height were significant in the nursery and were not correlated with a latitudinal cline. Higher elevation sources were poorer than those from around 1000 m. These origins were planted on seven sites in 1982-84, and establishment has been excellent. It is too early to make predictions about future growth based on very early results. However, the poor growth of trees from Mary's Peak is of concern, as this has been a popular seed source in recent years.

Recommendations

1. The scanty research evidence points mainly at areas to avoid, i.e. the introgression zone south of latitude 44° N and perhaps Mary's Peak, which lies on the border between Seed Zones 061 and 252. However, the Laurel Mountain origin, which is also in the Coast Range, Zone 251, grew well.
2. The most promising source appears to be Larch Mountain, Oregon at 975 m, which lies east of Portland in Zone 451. This is close to the area where David Douglas was prospecting in 1825.

Sessile oak (*Quercus petraea* (Matt.) Liebl.) and Pedunculate oak (*Quercus robur* L.)

Natural range

These species have rather similar ranges in Europe. Sessile oak is not able to grow in the colder north-east parts of Russia and southern Finland. In France, Sessile oak is more common in upland sites (to 1000 m in the Vosges and Juras and to 1500 m in the central Pyrenees). Pedunculate oak occurs in France as the major species on plains and alluvial valleys and on soils which are well provided with moisture, and can tolerate compact soils (Ministère de l'Agriculture, 1977). Oak could not have survived the last glaciation in Britain and during the last 8000 years man's influence may not have allowed it to become genetically fully adapted to conditions here. In the last 500 years there is no doubt that British oakwoods have felt the influence of man more severely than those on the continent. Distribution maps in Perring and Walters (1962) and Fitter (1978) highlight differences in the abundance of the two species in Britain, indicating the more widespread nature of Pedunculate oak, even into the far north of Scotland, while Sessile oak is more common in the west of Britain on more acid and often less fertile sites.

Silvicultural characteristics

Both species of oak are rather slow growing (maximum General Yield Class on the best sites is 8 and the average is around 4). Early annual growth is often 20 cm or less for the first 8 years, though it can be markedly stimulated by use of tree shelters (Tuley, 1983). Although capable of growing on a wide variety of sites, good growth is restricted to the more fertile sites, which historically have usually been converted to agriculture in Britain. Pockets of broadleaved woodland surrounded by arable fields will often be found to have wetter or heavier clay soils which are difficult to cultivate. Sessile oak can tolerate poorer, drier and more acid soils. Neither species should be planted on calcareous soils. Sessile oak often has lighter branching, with better stem and branch form than Pedunculate oak. Both species are light demanders, and do not provide sufficient shade to suppress ground vegetation after about 30-40 years. In Germany and France, where oak silviculture has been developed into a fine art over many centuries, it is standard practice to bring in beech or other shade tolerant species as an understorey, both to control ground vegetation and to provide clean lower boles on the oak. Some seed is produced each year, though characteristically, 'mast' years occur every 3 or 4 years for Pedunculate oak and every 4-5 years for Sessile oak.

Extent and composition

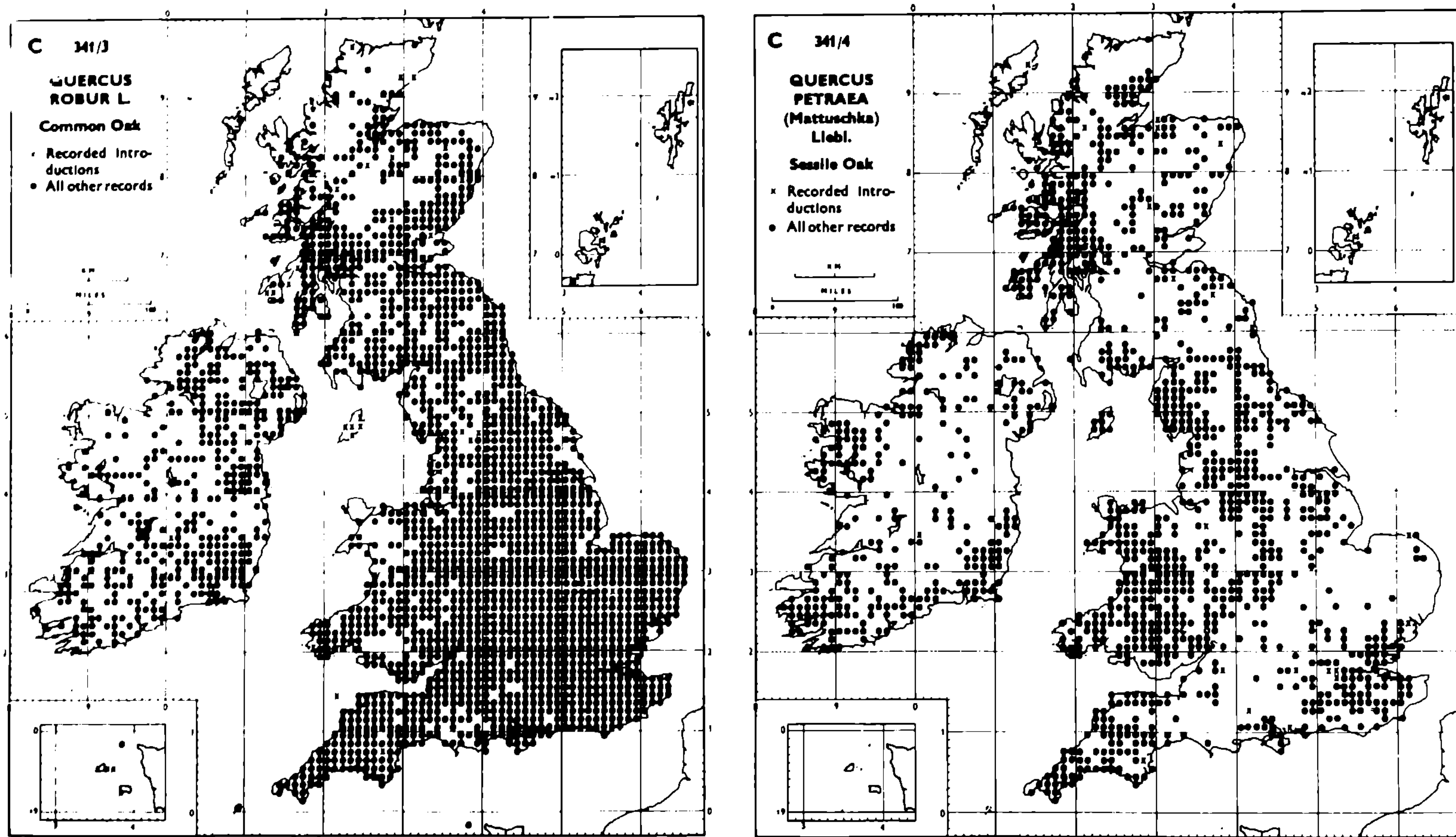
Of the total area of broadleaved high forest in Britain (564 300 ha), 172 000 ha is oak and 93 700 ha of this was planted before 1900. About three-quarters of the total area is not included in formal management schemes.The average Yield Class is 4 in each of the Forestry Commission Conservancies (Evans, 1984). Some of the tallest individuals (over 30 m) occur in the deep glens and wider valley of the eastern Highlands of Scotland (Mitchell, internal report). Oak is grown on a rotation often exceeding 120 years, so that the average age of oak woodlands is greater than for beech and much greater than for other species and very little has been planted since the last war. Between 1919 and 1945 most acorns came from British stands, though between 1929 and 1933, 55 824 lbs of acorns were imported from Germany and Holland. Since 1945, seed has quite often been imported to meet shortages caused by poor seed years in Britain, as it is impractical to store seed for more than one year. Imports of Pedunculate oak seed have come mainly from Holland, Germany and Poland, and those of Sessile oak seed from Austria, Germany and France.

Seed origin experiments

The oak experiments are a mixed bag of species, provenance and progeny trials dating from 1929 to 1954. They include seedlots from Norway, Sweden, Denmark, the Spessart and Darmstadt Forests in Germany, France and the Carpathians. Results are often confounded by poor experimental design. There is little evidence that continental sources were superior to home collections in these trials. The best experiments are a combined progeny and provenance test in 1952 at the Forest of Dean and a well replicated experiment (described by Evans, 1984) with two Pedunculate and nine Sessile provenances planted in 1954 at Penyard, Forest of Dean. Highly significant differences were found for the number of epicormic branches and for height and diameter at 26 years. Differences in stem form were barely significant, nearly all being below what would normally be considered acceptable. The pedunculate provenances had many more epicormics than the Sessile ones.

Faulkner (personal communication) has emphasised the high cost of carrying out a conventional genetic

Figure 17. Distribution of Sessile oak, ***Quercus petraea*** (Matt. Liebl. and Pedunculate oak, ***Quercus robur*** L., in the British Isles. Reproduced from *Atlas of the British flora*, eds. F.H. Perring and S.M. Walters, published by Thomas Nelson & Sons Ltd. (1962). © The Botanical Society of the British Isles.



improvement programme with oak, due to the vagaries of seed years, the long period over which the progenies must be tested and the even longer period before results can be put into mass production. In Germany, oak seed orchards have been abandoned, as it would require an excessively large area to produce the necessary seed.

In Britain there are 14 Registered Seed Stands of Sessile oak covering 150 ha and 33 of Pedunculate oak totalling 187 ha. These currently appear to offer the best prospect for establishing satisfactory oak plantations. An alternative being pursued actively by the National Hardwoods Project team at Oxford University is to use scions from selected 'plus' trees, grafted on to stock plants in a multiclonal tree bank. These would be regularly pruned to produce suitable material for the bulk production of cuttings. The latter would need to be tested over a period to check that they are not affected by the age of the parent tree, the effect of the part of the crown from which the scion was cut and many other problems associated with vegetative propagation.

Recommendations

1. Select whichever oak species is more appropriate for the given site, using Table 17.2 in Evans (1984) as a guide.
2. Use seed from Registered Seed Stands in Britain as a first choice; see Appendix 2 in Evans (1984).
3. If no British seed is available, use seed from Registered Seed Stands in EEC countries such as France or West Germany.
4. If this is not available, obtain seed from trees of good form in a local stand.

Beech
(*Fagus sylvatica* L.)

Natural range

The continental range of beech is somewhat similar to Sessile oak, except that the eastern and southern distribution of beech is much more limited and it is restricted to the higher mountains in the Mediterranean. Although it grows at low elevation from northern France to Poland it is also found at high elevations in the Central Alps and in Bulgaria and Romania up to 1500 m. In Britain it is considered native only in south and east England and south-east Wales, being a late post-glacial immigrant long after oak. It is, however, capable of regenerating naturally in the far north of Scotland and substantial seed collections have been made at Invergordon, north of Inverness. Beech is tolerant of a wide range of soil and climatic conditions. Its ability to grow much better than other species on thin chalk and limestone soils has resulted in wide-scale planting on these formations, where its ability to root deeply into the fissures can exploit the available moisture reserves at depth in these soils during drought periods.

Silvicultural characteristics

Beech is a strong shade bearer with rather slow initial growth. On bare sites this makes the species susceptible to damage from spring frosts and browsing and it can benefit markedly from tree shelters (Tuley, 1983). It has a faster growth rate than oak, averaging General Yield Class 6 over all sites in Britain and with a maximum Yield Class of 10. Moreover, its productivity is higher than for oak of the same Yield Class, as beech reaches its maximum volume increment at an appreciably earlier age.

The major silvicultural disadvantages of beech are that it remains susceptible to squirrel damage over a long period, it suffers disease problems both in the polestage and in the over-mature phase, and it frequently has poor stem and crown form. Brown (1953) devotes a whole chapter to the many factors affecting stem form. Some are under management control, such as initial stocking, use of an overstorey, choice of site. Others, such as frost and insect attack, are less easy to control. Some of the stands of beech with best form are on sites with poor nitrogen availability. Planting at wide spacing on sites with high nitrogen status produces the worst results in stem form. Genetic factors include time of flushing and patterns of lammas growth and branch form. Clonal trials on Danish Plus trees (Larsen, 1956) have shown that the branch pattern is under strong genetic control, but that scions from outstandingly straight trees do not necessarily give grafted trees with above average form when grown at wide spacing. Seedlings from open-pollinated Plus trees give even less reliable results. Beech is also less able to tolerate seasonal waterlogging than almost any other species. Its tendency to produce seed in massive amounts, with varying intervals between 'mast' years is even more extreme than in oak. Edlin (1962) has pointed out that because of the preponderance of poor seed years in Britain and the occurrence of a good seed crop somewhere in Europe every year, it has been the practice to import seed for at least 200 years. Thus many stands in Britain are probably not of native origin.

Extent and composition

Beech covers an area of 73 940 ha, of which 78 per cent is in England; 48 per cent was planted before 1900. Large beech trees are found all over Britain and some of the tallest British specimens found in 1950 were at Yester Estate, East Lothian (Mitchell, internal report). From the earliest days of the Forestry Commission, efforts were made to collect in 'mast' years. For example in 1923, 6981 kg of seed were collected from stands throughout Britain. 1937 was another good year for home collections with 3321 kg. However in 1929, 2400 kg were imported from Czechoslovakia and in 1932, 988 kg came from the Thuringerwald in Germany. Between 1956 and 1981 17 477 kg were imported, mainly from Romania and Bulgaria, with smaller lots from Germany, Poland and Holland to supplement supplies available from British stands. In recent years, when closer control has been exercised over stand quality for home collections, it has been possible to collect about 1000 kg in each good seed year. There is also a high demand for beech for use in hedging and for this purpose multi-branched relatively slow-growing trees are ideal.

Seed origin experiments

The first European experiments were conducted jointly by the Danes and Swiss in 1910 (Holm, 1937). The most comprehensive account of these and other Danish provenance and progeny trials is given by Gøhrn (1972). He presents data on height, diameter and stem straightness and also shows photographs which indicate better form in a long series of provenance and progeny trials than is observed in British experiments. However, the initial spacing used in Denmark was commonly 1 m x 0.33 m, and at this very dense early spacing, competition for light probably reduced any tendency to fork.

In Britain 11 provenance experiments were planted between 1942 and 1955 and between 1953-1974 the Genetics Section established progeny trials testing up to 83 families. Although there were significant differences in height between the best and worst provenances after 15-20 years, differences in stem form were not statistically significant, and none could be described as having really good form. Even those collected from well known parent stands of outstanding form had a high proportion of poor stems 30 years after establishment. There is some evidence that the trees with best form came from the Forêt de Soignes in Belgium and these were also among the most vigorous.

In Britain there are 14 Registered Seed Stands totalling 154 ha and one Seed Orchard based on clones from Kingscote Estate (Evans, 1984).

Recommendations

1. As a first choice, seed from the Forêt de Soignes, Belgium is to be preferred, but this is likely to be in short supply.
2. Use seed from a Registered Seed Stand in Britain as the next choice.
3. If no British seed is available, use seed from Registered Seed Stands in EEC countries such as Belgium, Holland, France or West Germany.
4. If this is not available, obtain seed from trees of good form in a local stand.

Silver birch (*Betula pendula* (Roth.)) and Downy birch (*Betula pubescens* (Ehrh.))

Natural range

Both species are very widely distributed over the whole of northern Europe and parts of western Asia. *B. pendula* extends as far south as the Calabrian Mountains of Italy, while *B. pubescens* extends further north than *B. pendula* in Lapland and is the only tree species of birch found in Iceland and southern Greenland (Schmucker, 1942). In Britain both species occur widely, though *B. pubescens* is more common in the north and west and less frequent in southern England (Perring and Walters, 1962). At one time it was thought that natural hybrids between these two species were common, but chromosome counts (*B. pendula* 2n = 28, *B. pubescens* 2n = 56) show that a very small proportion of supposed hybrids have the intermediate number (2n = 42) of chromosomes (Brown and Al-Dawoody, 1977). Thus there is a considerable overlap in the range of morphological variation within each species which requires fairly detailed analysis (e.g. Gardiner and Jeffers, 1962) to separate them. *B. pubescens* shows an ecological preference for (or perhaps a greater tolerance of) cooler and wetter soils than *B. pendula*, and its occurrence in the far north and west of Scotland beyond the main area occupied by Scots pine during the immediate post-glacial period may represent 'climax' birchwood (Gimingham, 1984).

Silvicultural characteristics

The birches are light demanding, frost tolerant, pioneer species, which tolerate a very wide range of soils, although they only express their best vigour and form on sheltered, fairly fertile sites. On the infertile sandy heaths of the New Forest, south-east Dorset and on the poorer types of heath with ironpan soils of the Yorkshire Moors and Scotland, planted birch often fails where Scots pine succeeds. Birch has the reputation of being a 'soil improver' (Gardiner, 1968). Miller (1984) has investigated the nutrient cycling of birch and found that, compared with other broadleaved species such as ash or sycamore, it was not exceptional. He speculates that birch may have some ability to extract nutrients from intractable soils coupled with some 'quality' factor in the litter.

Even though birch are strong light demanders, many foresters will be aware of how vigorously regeneration can invade and compete with planted Sitka spruce during the thicket stage. In natural birch communities a mosaic pattern develops (McVean, 1964), as birch will not regenerate within an existing wood, but does so very freely on surrounding heathland areas or disturbed sites. Many upland birchwoods contain trees of extremely scrubby form. How much of this appearance is due to early browsing damage and unfavourable site conditions can only be found by taking seed from these stands and growing it on a good site. When this is done, early growth on favourable sites is usually far better, while conversely seed from Plus trees does not produce fast growing straight trees on an infertile exposed site.

Birch is a short-lived tree, slowing down in growth rate after about 30-40 years and often becoming senescent by 60-80 years, although trees up to 200 years have been recorded in Scotland (Philip, 1978). It produces seed freely from about 10 years of age and being very light the seed is widely dispersed. Birch sometimes has high losses after planting, often due to using stock which is too large. Younger plants and those in paperpots are preferable.

Extent and composition

The 1980 Census showed a total High Forest area of 68 130 ha of managed birchwood in Britain. In addition, a further 61 340 ha are 'unmanaged' High Forest. The native scrubby birchwoods of Scotland, comprising a further 41 740 ha, are an important resource, for landscape, animal shelter, conservation and wildlife. Kirby (1984) has recently reviewed Scottish birchwoods and shows maps of their distribution in each 10 km square. Birch is also important for landscape and conservation in many parts of England and Wales, particularly on the poorer sandy soils, where it may be the principal native tree, and for softening the effect of extensive conifer afforestation. About 1 million birches are planted annually in the United Kingdom (Brown and Kennedy, 1981) and in recent years much of the seed and stock used have been imported, with West Germany as the main supplier.

Seed origin experiments

Birch has long been recognised as a potentially valuable producer of high value veneer butts in Scandinavia (Arnborg, 1949). Provenance trials with 42 seedlots planted at four sites in Sweden showed highly significant variation between provenances and a strong interaction between latitude of site and provenance performance (Johnsson, 1976). Northern lots performed badly on southern sites and vice versa. In the Finnish birch tree improvement project, 35 progeny trials covering 68 ha have been established, testing over 5000 families

(Lepisto, 1981). One large plastic greenhouse with 125 widely spaced selected progeny is estimated to be able to supply 50-100 kg of seed annually, enough to provide all the requirements for south and central Finland (Gaggini, 1977).

In Britain the main uses of birch timber are turnery and firewood (Lines, 1984a). Tree improvement in the 1950s centred on selection of 50 Plus trees and the introduction of scions and seed from superior continental stock. Meanwhile, England (1960) was making wide-scale leaf collections of both species to study variation in relation to climatic factors at the collection points. He also collected 10 seedlots and compared them with birch from Norway and Sweden at the Scottish Crop Research Institute near Edinburgh. The Scandinavian lots suffered severely from foliage rusts (see also Mason *et al.*, 1982). A similar trial planted at Devilla, Fife in 1954 with mainly Scottish provenances collected by Dr Berrie, Glasgow University, showed that *B. pendula* was more vigorous than *B. pubescens,* both as seedlings and after 15 years, but none of the seedlots had good stem form. In 1977 a programme for selection and improvement of Scottish birch was started at Aberdeen University (Brown and Kennedy, 1981). This initially concentrated on *B. pendula,* but was later extended to *B. pubescens* (Lines and Brown, 1982). An experiment testing provenance and family variation in the latter species was planted in 1984 on a poor peat at Shin, Sutherland. Researchers from the Institute of Terrestrial Ecology are making detailed studies of variation in both birch species (Pelham *et al.*, 1984) and have found that some of this can be attributed to site-type or 'land-class'. Their studies can be considered as highly intensive provenance trials including several hundred seedlots (Gardiner and Pelham, 1983).

There is good evidence (e.g. Johnsson, 1976; Pelham *et al.,* 1984) that birch seed for forest use should be selected from roughly similar latitudes to those of the planting sites. There is plenty of evidence for the good growth of seed origins from the south of England in Scotland and vice versa, so that a latitudinal shift of up to 5° can be considered acceptable. This urges caution in the use of the selected strains of Finnish birch, which perform so well in their northern latitudes.

Recommendations

1. Decide which species of birch is appropriate for the intended site.
2. Use seed collected from British stands of good appearance taken from similar or slightly more southerly latitude than the planting site.
3. If British seed is not available, use seed from western Europe at similar latitudes to Britain.
4. Avoid northern provenances from Scandinavia, and those from southern Europe. Also avoid those from elevations above 500 m.

Nothofagus spp.

(*N. procera* (Poepp. and Endl.) Oerst. and *N. obliqua* (Mirb.) Blume.)

Natural range

Since little is known about seed origin variation in these two South American species they are considered together. Their ranges overlap in Chile and Western Argentina (Tuley, 1980). *N. procera* extends from 36° S to 40° S, while *N. obliqua* extends a few degrees further in each direction. *N. obliqua* is widespread, occurring mainly between 100 m and 500 m, though it is found above 1000 m at the north end of its range, while *N. procera* is less frequent and is found usually above 500 m and up to 900 m, at which elevation it is displaced by the evergreen *N. dombeyi* (Anon., 1981). Thus they can be considered as coming from low mountains in South Mediterranean latitudes.

Silvicultural characteristics

The genus *Nothofagus* is an ancient one, which spread out from a centre in south-east Asia at a time when land bridges existed between Asia, Australia and South America. The largest number of species is found in New Guinea, which may explain why several species appear ill-adapted to the winter hardening process essential in colder climates. Only *N. antarctica* and *N. pumilio* appear to be fully hardy in Britain. In Chile, *N. procera* can reach a height of 40 m and a diameter of 2 m with a long, straight near-cylindrical bole. It grows faster than *N. obliqua*, it normally forms pure forests and is a strong light-demander. *N. obliqua* often grows in mixture with other species and it regenerates well on cleared areas. It is slightly more shade-tolerant and has poorer stem form than *N. procera*.

In Britain *N. procera* and *N. obliqua* are outstanding for their growth vigour, when compared with beech, oak and other native broadleaved species. The best individuals can grow at a rate of 1 m per annum in height. Stem form, particularly of *N. procera*, is equally outstanding. Their main demerits are:

1. susceptibility to frost damage, and
2. lower timber density than beech, with some degrade in drying.

Frost does not only cause shoot dieback. Basal cankers due to frost are associated with ring shake and entry of decay fungi, which may render the timber valueless several metres up the trunk.

Both species are rarely attacked by Grey squirrels, but they are attractive to deer, which show a distinct preference for *N. obliqua*.

Introduction and use

The oldest specimen trees of these two species date from early this century and the first plots were planted in the 1930s. Only insignificant quantities of seed were imported before 1954, when 17 kg of each species arrived, all except 0.5 kg from Malleco Province, Chile. This seed import was used to establish 191 Forestry Commission plots totalling 25 ha on a wide range of sites (Low, 1967; Nimmo, 1971). Some of this seed was also used by private estates. Between 1954 and 1976 it was again difficult to import seed except in small quantities, and even these had limited information about seed source. In 1976-78 many seedlots were imported, some in substantial quantities. This resulted in further Forestry Commission plantations and wider use in private woodlands. The total area in Britain is still very small.

Seed origin experiments

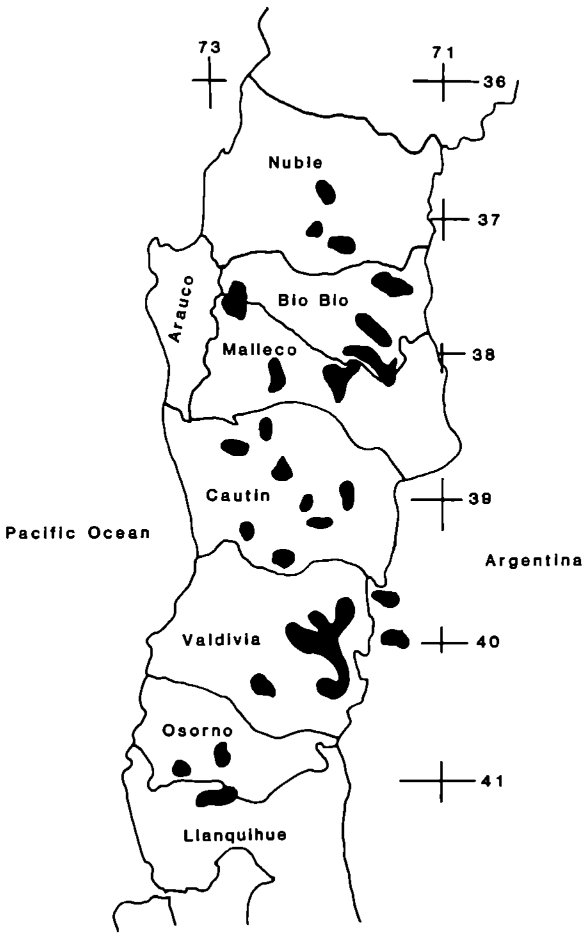
The 1976 collection of 22 imported origins and five home sources was sown in 1977 and planted in 1979 at 11 sites in England, six sites in Scotland and three sites in Wales (Tuley and Lines, 1978). Smaller trials followed in 1981. There was little frost damage in the winter of 1977/78, but in January 1979 when the trees were 1+1 transplants -10°C was recorded at Fleet Nursery, Kirkcudbright, and all seed origins suffered shoot dieback in both species and some trees were killed completely. Similar damage occurred in the Alice Holt Nursery in Hampshire.

In a preliminary trial of these origins, large seedlings were raised in a greenhouse in 1977 and planted in the forest in 1978. Damage from the severe winter in both nursery and forest was described by Tuley and Gordon (1979). In England ring-barking and shoot dieback were common, while in Scotland shoot dieback predominated. It was concluded that the degree of damage should not rule out use of these two species, but seedlots of *N. procera* from Nuble Province, Chile, should be planted only in the mildest areas.

Trials using a freezing chamber to test seasonal variation in frost sensitivity of current shoots taken from some of these seedlots (Murray *et al.*, 1986) confirmed:

1. the greater sensitivity of those from Nuble province;
2. the variation in frost hardiness between individuals within a seed origin;
3. the increase in hardiness with age of tree.

Figure 18. Natural range of ***Nothofagus procera*** (Poepp. and Endl.) Oerst. and ***Nothofagus obliqua*** (Mirb.) Blume., based on Chilean vegetation types.



The winter of 1981/82 was even more severe, causing further dieback on all of the sites planted in 1979, and survival of *N. procera* from Nuble province in nine southern experiments was reduced to 50 per cent (Evans, 1984). Nevertheless, by the end of the fifth growing season, most trees had recovered sufficiently for the best seed origins to average over 2 m in height and survival averaged over 75 per cent on 11 northern sites. Only at Inchnacardoch, Inverness-shire was it below 50 per cent overall. There were significant height differences at 5 years. The tallest *N. procera* were from Cautin and Malleco, Chile and Neuquen, Argentina. The best imported *N. obliqua* were from the southern Llanquihue Province and Malleco. *N. obliqua* was generally shorter than *N. procera,* though a home collection from Benmore, Argyll was outstanding and almost as tall as the best *N. procera.* Assessments of shoot dieback between the different seed origins show the same pattern on many sites, with the worst damage on those from Nuble.

Recommendations

These can only be tentative in view of the short time these seed origins have been under test. However, it should be noted that two exceptionally severe frosts occurred during the critical establishment phase of these trials. They show that both species cannot be planted anywhere in Britain without some risk of frost dámage, but also that many seed origins appear to make a good recovery after the shoots have been frosted.

1. The best single origin of *N. procera* for frost resistance was from Puesco in Cautin Province and this was also tallest in the northern series of experiments.
2. Seedlots from the forests around the towns of Victoria, Temuco and Cunco have grown well.
3. Seedlots from north of latitude 38° S should be avoided.
4. Imported *N. obliqua* shows less seed origin variation. Seed from Llanquihue, Malleco and Cautin provinces in Chile are recommended in that order.

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