
Part II

Specific Handling Methods and Data for 236 Genera

Pinaceae—Pine family

Abies P. Mill.

fir

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Growth habit, occurrence, and use. The name *Abies* is derived from “abed,” the Old World Latin name for the silver fir (Dallimore and Jackson 1967; Weber 1987). Theophrastus (371–286 BC) wrote of “silver firs” from Mt. Ida (today’s Kaz Dag, Turkey) being used in shipbuilding, which may have been the lumber of *A. equi-trojani* (Thanos 2003b), but also may have been in reference to *A. cephalonica* Loud. and/or *A. pectinata* DC. (now *A. alba* P. Mill.) (Amigues 1993, cited in Thanos (2003b). The name *Abies* first appeared in Pliny the elder’s *Historiae Naturalis* from about AD 77 (Liu 1971).

Firs are long-lived, on average achieving reproductive maturity at 20 years, with an average life-span of 60 years (Jacobs and others 1984). Fir trees in excess of 400 years old have been recorded in several species (Earle 1999), and noble firs 600 to 700 years old are known (Arno and Hammerly 1977; Franklin 1979; Franklin and Dyrness 1973), but such life spans are modest compared to those of other tree genera. Siberian fir (table 1) rarely, if ever, survives more than 200 years because the main stem decays out (Vidakovic 1991). In numbers of species, fir is second only to pine but lags behind spruce (*Picea* spp.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in terms of overall importance (Franklin 1982a).

All fir species are indigenous to the Northern Hemisphere (table 1), being widely distributed over the Eastern and Western Hemispheres (Liu 1971) chiefly in the temperate and frigid regions, from sea level to altitudes of 4,700 m. More than 70 species have been variously described (Liu 1971), although the number of those currently recognized is between 39 (Liu 1971) or 40 (Vidakovic 1991), 46 (Farjon 1990), ~50 (Welch 1991), and 55 (Rushforth 1987), depending on placements into varietal categories. Firs are found in 4 extensive regions (Franklin 1974b; Liu 1971; Miller and Knowles 1989; Welch 1991; Young and Young 1992):

- North America (Alaska to the Mexican border)—9 species
- Central America (Mexico, Guatemala, Honduras, and El Salvador)—8 species (Martinez 1948) or 6 species (Liu 1971)
- Mediterranean Basin, as well as lands bordering it, including southern and central Europe to the north, western Asia (Asia Minor, Caucasia, Syria, and Lebanon) to the east, and northwestern Africa (Morocco, Algeria, and Tunisia) to the south—8 species
- Siberia and eastern Asia (Amur, China, Korea, Japan, Taiwan, and the Himalayas)—17 species

The latitudinal range stretches some 53 degrees, from north of the Arctic Circle (north of 67°N, almost to Arkhangel’sk, Russia, on the White Sea) with Siberian fir (Liu 1971), to south of the Tropic of Cancer (south of 15°N, in El Salvador) with Guatemalan fir (FAO, in Anon. 1986). Fir has a long history in Mexico, with pollen from the middle Pleistocene Epoch (5 million years ago) (Graham 1999). The most widely distributed species is Siberian fir, then balsam fir, followed by subalpine fir (Liu 1971). Globally, some species—including Algerian fir (FAO, in Anon. 1986), bristlecone fir (Legg 1953; Little 1975; Talley 1974), Bulgarian fir (see table 1 footnotes for scientific name), Grecian fir, Spanish fir, (FAO, in Anon. 1969), Sicilian fir (Arena 1959a&b, 1960; FAO, in Anon. 1986); Gramuglio 1962; Köstler 1957) and Guatemalan fir (Anon. 1986; Donahue and others 1985; FAO, in Anon. 1986; Salazar 1991; Veblen 1978)—have restricted ranges or are rare and, in some ecosystems, endangered and threatened with extinction. No longer found on the island of Corsica, “silver fir” was described by Theophrastus (Thanos 2003b) as growing taller and better there than anywhere else in central and southern Italy. In 1986, 21 wild trees of Sicilian fir, a species that was considered extinct in 1900, were reported growing at Monte Scalone, Sicily; other plants grown from

Table 1—*Abies*, fir: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
A. alba P. Mill. <i>A. argentea</i> DC.; <i>A. candicans</i> Fisch. <i>A. nobilis</i> A. Dietr.; <i>A. Pardeii</i> Gauss <i>A. pectinata</i> DC.; <i>A. picea</i> Lindl. <i>A. taxifolia</i> Desfont.; <i>A. vulgaris</i> Poir.	European silver fir , common silver fir, silver fir, Swiss pine	Mtns of central & S Europe, S to Corsica (~52°–38°N & ~3°W–27°E)
A. amabilis (Dougl. ex Loud.) Dougl. ex Forbes <i>A. grandis</i> A. Murr. <i>A. grandis</i> var. <i>densiflora</i> Engelm.	Pacific silver fir , lovely fir, amabilis fir, Cascades fir, white fir, silver fir, <i>sapin gracieux</i>	SE Alaska, coastal British Columbia, Coastal & Cascade Ranges of Oregon & Washington & rarely in Klamath Mtns of California (41°–56°50'N)
A. balsamea (L.) P. Mill. <i>A. aromatica</i> Rafn. <i>A. balsamifera</i> Mich. <i>A. minor</i> Duham. ex Gord.	balsam fir , balsam, Canada balsam, eastern fir, balm of Gilead, blister fir, fir pine, silver pine	Labrador & Newfoundland & S to New York to central Wisconsin & Minnesota, N & W to Alberta (59°–38°50' N & 117°–53°W; generally S of 55°N, except in Alberta & Saskatchewan)
A. bracteata (D. Don) D. Don ex Poit. <i>A. venusta</i> (Dougl.) K. Koch	bristlecone fir , Santa Lucia fir, silver fir, fringed spruce	Santa Lucia Mtns, Monterey Co., California (37°–36°N)
A. cephalonica Loudon <i>A. panachaica</i> Heildr.; <i>A. lusombiana</i> Loudon <i>A. peloponesica</i> Haage	Grecian fir , Greek silver fir, Cephalonian fir, Mt. Enos fir	Higher mtns of continental Greece from Epirus & Thessaly S to Lagonia in Peloponnesos & SE to the Euboea; Turkey
A. cilicica (Antoine & Kotschy) Carrière <i>A. selinusia</i> Carrière	Cilician fir	Turkey (Cilicia), N Syria, & Lebanon
A. concolor var. concolor (Gord. & Glend.) Lindl. ex Hildebr. <i>A. lowiana</i> (Gord.) A. Murr. <i>A. grandis</i> var. <i>lowiana</i> (Gord.) Hoopes <i>A. concolor</i> var. <i>lowiana</i> (Gord.) Lemm.	white fir , white balsam, balsam fir, Rocky Mountain white fir, Colorado white fir, <i>piño real blanco</i> , concolor fir	Rocky Mtns from S Idaho & W Wyoming to S New Mexico W to N Baja California, Mexico, & S California N to central & NE Oregon (44°45'–30°N & 124°–105°W)
A. concolor var. lowiana (Gord. & Glend.) Lemmon <i>A. lowiana</i> (Gord.) A. Murr. <i>A. concolor</i> (Gord. & Glend.) <i>A. concolor</i> var. <i>lasiocarpa</i> Engelm. & Sarg. <i>A. grandis</i> var. <i>lowiana</i> Mast.	Sierra white fir , Low white fir, Low silver fir, California white fir, Pacific white fir	Sierra Nevada of California & Nevada, Mt. Shasta, Siskiyou Mtns in SW Oregon, from about the divide between the headwaters of Umpqua & Rogue Rivers, Oregon, to mtns of Baja California Norte
A. firma Sieb. & Zucc. <i>A. bifida</i> Sieb. & Zucc.; <i>A. momi</i> Sieb.	Japanese fir , <i>momi</i> , <i>momi</i> fir, Japanese silver fir	Mtns of central & S Honshu, Shikoku, & Kyushu, Japan (39°–30°N)
A. fraseri (Pursh) Poir. <i>humilis</i> La Pilaye	Fraser fir , southern balsam fir, she-balsam, double fir balsam, double spruce, healing balsam	Appalachian Mtns of West Virginia, S Virginia, W North Carolina, & E Tennessee
A. grandis (Dougl. ex D. Don) Lindl. <i>A. amabilis</i> A. Murr.; <i>A. excelsior</i> (Franco) <i>A. gordoniana</i> Carr. <i>A. lasiocarpa</i> Lindl. & Gord.	grand fir , lowland white fir, white fir, balsam fir, great silver fir, Oregon fir, western white fir, western balsam, <i>sapin grandissime</i> , <i>sapin du Vancouver</i>	W Montana & N Idaho to S British Columbia, Vancouver Island, S to Sonoma Co. in coastal California & E Oregon
A. guatemalensis Rehd. <i>A. tacamensis</i> Lund. <i>A. guatemalensis</i> var. <i>tacamensis</i> (Lund.) Mart. <i>A. guatemalensis</i> var. <i>jiliscans</i> Mart.	Guatemalan fir , Guatemala fir, <i>paxaque</i> , <i>pinabete</i> , <i>romerillo</i>	Mtns of Guatemala, S Mexico, El Salvador; Honduras (19°30'–14°50'N & 104°–91°W)

Table 1—*Abies*, fir: nomenclature and occurrence (continued)

Scientific name & synonym(s)	Common name(s)	Occurrence
<i>A. holophylla</i> Maxim.	Manchurian fir , needle fir, Sino-Korean fir	Khingan Mnts, & N part of Hebei* (N China Highlands), China; S. Sikhote Alin Mnts, Russia; Korean peninsula including Cheju Island (33°30'–49°N) Mtns of central Honshu & Shikoku, Japan (37°–33°30'N)
<i>A. homolepis</i> Sieb. & Zucc. <i>A. brachyphylla</i> Maxim.	Nikko fir , <i>urajiro-momi</i> , <i>Dake-momi</i> , <i>Nikko-momi</i>	Confined to the volcanic island of Cheju & the Chiri-san Mtns, South Korea
<i>A. koreana</i> E.H. Wilson <i>A. nephrolepis</i> Nakai	Korean fir	
<i>A. lasiocarpa</i> (Hook.) Nutt. <i>A. bifolia</i> A. Murr.; <i>A. sub-alpina</i> Engelm. <i>A. sub-alpina</i> var. <i>fallax</i> Engelm.	subalpine fir , alpine fir, balsam fir, white fir, <i>piño real blanco de la sierra</i> , <i>sapín concolore</i>	W Northwest Territories, Yukon, & SE Alaska, S through British Columbia, SE Alberta to Oregon & in Rocky Mtns to Arizona & New Mexico; local in N California & NE Nevada (64°30'–32°25'N & 105°–145°W)
<i>A. lasiocarpa</i> var. <i>arizonica</i> (Merriam) Lemmon <i>A. bifolia</i> (A. Murr.); <i>A. sub-alpina</i> Engelm.	corkbark fir , Rocky Mountain subalpine fir, Rocky Mountain alpine fir, alamo de la sierra, Arizona fir	SE Arizona E to S central New Mexico, & N to SW Colorado; reported locally in central Colorado
<i>A. magnifica</i> A. Murr. <i>A. campylocarpa</i> A. Murr. <i>A. nobilis</i> var. <i>magnifica</i> Kell.	California red fir , red fir, golden fir, white fir, red bark fir, magnificent fir	Sierra Nevada, S Cascade Range, & N Coast Range in California & adjacent Nevada (43°35'–35°40'N)
<i>A. mariesii</i> Mast. <i>A. mayriana</i> Miyabe & Kudo	Maries fir , <i>Toddomatsu</i> fir, <i>Aomori-todo-matsu</i> , <i>O-shirabiso</i>	Mtns of N & central Honshu, Japan (41°–35°N)
<i>A. nebrodensis</i> (Lojac.) Mattei <i>A. pectinata</i> Gilibert var. <i>nebrodensis</i> Lojac. <i>A. alba</i> Mill. var. <i>nebrodensis</i> (Lojac.) Svob.	Sicilian fir , <i>Abete delle Nebrodi</i>	Monte Cervo, Polizzo; Monti Nebrodi & Monte Scalane, Sicily
<i>A. nephrolepis</i> (Trautv. ex Maxim.) Maxim. <i>A. sibirica</i> var. <i>nephrolepis</i> Trautv. <i>A. gracilis</i> Kom.	Manchurian fir , Khingan fir, Siberian white fir, Amur fir, Hinggan fir	E Siberia, through Lesser Khingan Mtns, Manchuria, W to Kansu of China & S to Chiri-san, South Korea (54°54'–35°30'N & 113°–140°30'E)
<i>A. nordmanniana</i> (Steven) Spach <i>A. leioclada</i> (Stev.) Gord. <i>A. pectinata</i> var. <i>leioclada</i> (Stev. ex Endl.) Carr.	Nordmann fir , Caucasian fir, Crimean fir	W Caucasus & mtns connecting Caucasus with Armenian Highlands (44°–40°N & 46°–38°E)
<i>A. nordmanniana</i> ssp. <i>equi-trojani</i> (Asch. & Sint. ex Boiss.) Coode & Cullen <i>A. bornmuelleriana</i> Mattf.	Turkey fir	Mt. Olympus, Bithynia (NW Turkey) to Paphlagonia (N Turkey), Asia Minor (~39°–42°N & 26°–38°W)
<i>A. numidica</i> de Lannoy ex Carrière <i>A. pinsapo</i> var. <i>baborensis</i> Coss. <i>A. baborensis</i> Letourn.	Algerian fir , Algerian silver fir,	Kabylie Range, near summits of Mt Babor & Mt Thabador, Kabylie, NE Algeria
<i>A. pindrow</i> (D. Don) Royle <i>A. webbiana</i> Brandis	west Himalayan fir , west Himalayan silver fir, Pindrow fir	W Himalayas, India & Pakistan, N Afghanistan to Nepal & Tibet
<i>A. pinsapo</i> Boiss. <i>A. hispanica</i> De Chamb.	Spanish fir , Spanish silver fir	Mtns of Malaga & Granada provinces, S Spain; Morocco (var. <i>marocana</i>)
<i>A. procera</i> Rehd. <i>A. nobilis</i> (Dougl. ex D. Don) Lindl.	noble fir , red fir, white fir, noble red fir, feather cone fir, Oregon larch	Washington Cascade Range S through Cascade Range & high peaks of coast ranges to SW Oregon & NW California (48°30'–41°N)
<i>A. recurvata</i> Mast. <i>A. ernestii</i> Rehd.; <i>A. beissberiana</i> Rehd. & Wilson	Min fir , <i>Min-kiang</i> fir	Mtns of Ming River Basin between Min-kiang & Sungpan Districts, Sichuan† Province; SW & C Kansu, NE Yunnan, China (~28°–39°N & 100°–106°E)

Table 1—Abies, fir: nomenclature and occurrence (continued)

Scientific name & synonym(s)	Common name(s)	Occurrence
A. religiosa (Kunth) Schtdl. & Cham. <i>A. glaucascens</i> Roetzl.; <i>A. hirtella</i> Lindl. <i>A. lindleyana</i> Roetzl	sacred fir , sacred Mexican silver fir, Mexican silver fir, <i>oyamel</i> , <i>pinabete</i>	Mtns of central & S Mexico, C. Michoacan to Veracruz & N & W Guatemala (~24°–15°N)
A. sachalinensis (Fr. Schm.) var. sachalinensis Mast. <i>A. akatodo</i> Miyabe <i>A. veitchii</i> var. <i>sachalinensis</i> Fr. Schm.	Sakhalin [or Sachalin] fir, Japanese fir, <i>todo-matsu</i> , <i>akatodo</i>	Sakhalin & Kurile Islands; Kamchatka, Russia; Hokkaido, Japan (53°34'–41°30'N)
A. sachalinensis (Fr. Schm.) Mast. var. mayriana Miyabe & Kudo <i>A. mayriana</i> Miyabe & Kudo	Mayr Sakhalin fir , <i>Ab-todomatsu</i> , <i>todomatsu</i> , <i>aatodo</i>	Hokkaido, Japan; Sakhalin & Kurile Islands of Russia (53°34'–41°30'N & from 10 m @ 45°N to 1650 m @ 44°N)
A. x shastensis (Lemmon) Lemmon <i>A. shastensis</i> (Lemmon) Lemmon <i>A. nobilis</i> var. <i>robusta</i> Mast. <i>A. magnifica</i> var. <i>shastensis</i> Lemmon	Shasta red fir , Shasta fir, silvertip fir, golden fir, yellow-fruited fir	Oregon Cascade Range (~44°N), S through N Coast Ranges & S Cascade Range, California, & in S Sierra Nevada, California
A. sibirica Ledeb. <i>A. heterophylla</i> K. Koch; <i>A. pichta</i> Forbes <i>A. semenovii</i> Fedtsch	Siberian fir , Siberian silver fir, pitch silver fir	N & E Russia, Siberia to Kamchatka & Amur region, Alai Mtns & Turkestan; NE China (67°40'–42°15'N & 160°–40°E)
A. squamata Mast.	flaky fir , <i>linpi lengshan</i>	High Mtns SW China, SE Xizang, W Sichuan, S Gansu & S Qinghai Provinces (26°–34°N & 98°30'–104°E)
A. veitchii Lindl. <i>A. eichleri</i> Lauche; <i>A. sikokiana</i> Nakai	Veitch fir , Veitch silver fir, <i>shirabe</i> , <i>shirabiso</i> , Chinese silver fir	Mtns of Honshu & Shikoku, Japan (37°45'–34°N)

Sources: Anon. (1998), Dallimore and Jackson (1967), Donahue and others (1985), Earle (1999), Farjon and Rushforth (1989), Franklin (1974b), Liu (1971), Puri and Gupta (1968).
* Spelling of Chinese place names has changed over time. This name is given as Hopeh in Liu (1971) but is currently Hebei.
† Formerly spelled Szechuan or Szuchuan (Liu 1971).

Note: The following recognized fir species are not included in the table for lack of sufficient data (common names are given when known):

CENTRAL AMERICA: *A. colimensis* sp. nov. Rusht.; *A. durangensis* Mart. (Durango fir); *A. flinckii* sp. nov. Rusht.; *A. hickelii* Flous et Gauss. (Hickel fir); *A. hidalgensis* sp. nov. Debr., Rácz & Guiz.; *A. neodurangensis* sp. nov. Debr., Rácz & Salaz.; *A. zapotekensis* sp. nov. Debr., Rácz & Ramir.; *A. vejarii* Mart. (Vejar fir).

EAST ASIA: *A. beshanzuensis* Wu (Baishan fir); *A. chengii* Rusht. (Cheng fir); *A. chensiensis* Van Tiegh. (Shensi fir); *A. delavayi* (Van Tiegh.) Franch. (Yunnan fir, or Delavay fir); *A. densa* Griff. (Sikkim fir); *A. fabri* (Mast.) Craib (Faber fir, sometimes also Yunnan fir); *A. fanjingshanensis* Huang, Tu et Fang (Fanjingshan fir); *A. fargesii* Franch. (Farges fir); *A. forrestii* Coltm.-Rog. (Forrest fir); *A. kawakamii* (Hay) Ito (Taiwan fir); *A. spectabilis* (D. Don) Spach (east Himalayan fir or Webb fir); *A. yuanbaoshensis* Lu et Fu (Yuanbaoshan fir); *A. ziyuanensis* Fu et Mo (Ziyuan fir).

MEDITERRANEAN BASIN: *A. x borisii-regis* Mattf. (Bulgarian fir, sometimes Macedonian fir, or King Boris fir); *A. marocana* Trab. (Moroccan fir); *A. tazaotana* Cheval. (Tazaotan fir).

seeds or grafts have been established in various parts of Europe (FAO, in Anon. 1986). Bristlecone fir is found in sufficient numbers, and is distributed widely enough, that the potential for extinction remains low (Smith and Berg 1988), and research on genetics and population viability is underway (USDA FS 1992). The sacred fir, or *oyamel*, of Mexico is logged heavily. However, since 1975 it has become generally known that the bulk (the populations east of the Rocky Mountain crest) of North American monarch butterflies (*Danaus plexippus* L.) overwinter on the cool slopes of the transvolcanic ranges west of Mexico city forested with *oyamel* (Pyle 1992, 1999). Thus, the *oyamels* may be preserved to protect the monarchs. The arboreal altitude record, 4,700 m, is held by flaky fir, with its distinctive reddish-brown bark that exfoliates in thin papery scales, found in the very dry regions of China near Tibet (Rushforth 1987).

Firs are easily distinguished from all other conifers by their disk-like leaf scars and erect, oblong-cylindrical, or cylindrical seed cones. These are borne in the uppermost regions of the crown and are essential to species identification (Farrar 1995). At maturity, the terminally winged seeds, ovuliferous scales, and bracts are shed (Dallimore and Jackson 1967; Farrar 1995), leaving the cone axis—the rachis—as a persistent, erect spike, a unique and distinctive feature of all firs (Hosie 1969). *Abies* is considered to be most closely related to the genus *Keteleeria*; species of this genus have upright, cylindrical cones that resemble those of firs, but *Keteleeria* cones do not disintegrate at maturity (Rehder 1958).

Nine fir species are native to North America; 7 introduced Asiatic and European species have become common in their use as ornamentals or Christmas trees (table 1) and others are being tested (Girardin 1997a). Table 1 is not a complete list of all fir species but covers only those firs for which widely accepted cone and seed information was available at the time of this revision. Brief descriptions, including cone and seed morphology, for nearly 2 dozen other firs found outside North America are available in a website maintained by Earle (1999). Older, still-valid descriptions of fir species with dates of introduction into North America (Rehder 1958) are used frequently by growers of exotic conifers, but readers should be aware that species nomenclature has changed in numerous cases. Information on 22 fir species recognized in China can be found in the *Flora of China* (Cheng and Fu 1987).

Firs play an important role in European forestry, although only European silver fir is distributed widely enough to be of more than local value (Handley 1982).

Several North American firs, including white, grand, and noble firs have been planted in Europe but are only locally important (Handley 1982); subalpine fir is grown in Scandinavia (Dietrichson 1971), especially at high elevations in Norway (Hansen and Leivsson 1990). Introduction of the genus to New Zealand began in the mid-19th century; of some 30 fir species now grown there, white, grand, California red, Nordmann, Spanish, noble, and sacred firs have been suggested as “contingency” species, that is, alternatives to Monterey pine (*Pinus radiata* D. Don) (Miller and Knowles 1989).

It is in western North America that firs attain their greatest ecological and economic importance (Franklin 1982a). They are major vegetation components, especially in the boreal, Pacific Coast coniferous, and western montane/alpine coniferous forests. They are critical as cover for watersheds where heavy winter snowpack accumulates—this cover modifies snowmelt so that runoff continues throughout the spring and into summer (Franklin and others 1978; Laacke and Fiske 1983)—and the maintenance and regulation of high-quality streams (Hunt 1993). Firs provide cover, and their seeds and leaves are important as food for various birds, including northern spotted owl (*Strix occidentalis*) (Ripple and others 1991), osprey (*Pandion haliaetus*), and bald eagle (*Haliaeetus leucocephalus*) (Hopkins 1979) and mammals including mule (*Odocoileus hemionus*) and white-tailed (*O. virginianus*) deer, elk (*Cervus elaphus*), and black (*Ursus americanus*) and grizzly bears (*U. arctos*), moose (*Alces alces*), and mountain goat (*Oreamnos americanus*) (Agee 1982; Cooper and others 1987; Leach and Hiele 1956; Peek 1974; Steele and others 1981). Some of these animal species are sensitive, rare, or endangered (Laacke and Fiske 1983). Excellent sources of information on wildlife-cover values of fir forests are available (FEIS 1996).

Firs are found at all elevations, from sea level (grand fir on the Pacific Coast and balsam fir on the Atlantic Coast) to timberline (noble and subalpine firs); they attain their maximal development on relatively cool, moist sites (Franklin 1974b). Noble fir is one of the most windfirm trees (Earle 1999). The form, texture, and color of fir trees add to the high scenic values of their growing locations, many of which have become important recreation areas. Their attractive, highly symmetrical appearance make many species, particularly Fraser and Pacific silver firs, valuable in urban horticultural plantings, where their slow growth can be an advantage. Whereas the original *Woody-Plant Seed Manual* (USDA FS 1948) mentioned only 5 fir species used “to a very small extent” in reforestation in the United States,

9 species—Pacific silver, balsam, white, Fraser, grand, subalpine, red, Shasta red and noble firs—are now in regular use throughout their native ranges.

With 2 exceptions—Fraser fir, the remaining stands of which are extremely valuable for watershed protection as well as for their scenic beauty (Beck 1990), and the rare bristlecone fir—all North American firs have become commercially valuable as timber and/or pulp species. In general, fir wood is soft, odorless, and light in color and weight; it lacks resin ducts and usually kiln-dries without checking or collapse (but tends to warp). It is easily worked and finished to a good surface, and it takes paint and polish well (Dallimore and Jackson 1967). Although generally of low durability (Franklin 1982a) unless treated with preservative, fir wood can be used in projects that do not require high structural strength; balsam fir is used extensively for cabin logs. Noble fir wood (sometimes marketed as “Oregon larch”) is the strongest (along with red fir) of fir woods and is more durable than that of most firs. The frames of Royal Air Force Mosquito fighter planes of World War II were built with noble fir (Pojar and MacKinnon 1994). Grand fir knots, steamed and carved, were made into fish hooks (Turner 1998). The many other products made in North America of fir wood include quality veneers, paneling, construction plywood, crates, container veneers, poles (after preservative treatment), moldings, window sash and door stock, Venetian blinds, ladder rails, and aircraft framing (because of its high strength-to-weight ratio) (Bakuzis and Hansen 1965; Frank 1990; Franklin 1974b, 1982a, 1990; Smith 1982). In the late 19th century, clear lumber of red fir was known as “butter wood” because, when made into boxes for cheese and butter, it did not influence their flavor (Young and Young 1992).

Japan, which imports large quantities of noble and Pacific silver firs for construction (Franklin 1982a), uses its indigenous Japanese fir for making boards, roof shingles, door plates, matches, wooden clogs, musical instruments, household utensils (furniture, packing boxes, and coffins), as well as using it in ship-building and cooperage (Liu 1971). The Yunnan and Faber firs (*A. delavayi* and *A. fabri*, see table 1 footnotes) are used for temple construction in the high mountains of Sichuan Province, China (Earle 1999). European silver fir is widely used throughout Europe also for construction, joinery, musical instruments, and (after preservative treatment) for poles. Guatemalan fir faces extinction in parts of its range (Donahue and others 1985; Salazar 1991) through overuse for building materials, roof shingles, interior paneling, weaving looms and “low-density” furniture, shipping crates, charcoal, firewood (Anon. 1998;

Donahue and others 1985; Salazar 1991), and Christmas trees and boughs (FAO, in Anon. 1986). In Guatemala, sheep and other livestock destroy nearly all regeneration (Veblen 1978).

Fir pulp is used extensively for making printing papers and high-grade wrapping paper, with Pacific silver fir the mainstay in the Pacific Northwest and balsam fir in the northeastern United States. Red fir is preferred for sulfite and thermomechanical pulping (Laacke 1990b; Smith 1982). Wood residues not utilized elsewhere are considered to be an energy source (Smith 1982).

Fraser fir (in the East) and Pacific silver, white, red, and noble firs (in the West) are prized also for Christmas trees (Hopkins 1982; Laacke 1990a&b) and typically command high prices (Franklin 1974b; Young and Young 1992). The farm-gate value of Fraser fir Christmas trees cut in North Carolina in 1993 was 80 to 100 million dollars (Blazich and Hinesley 1994, 1995). Noble fir boughs account for some 75% of fir bough harvest in the Pacific Northwest (Douglass 1975; Murray and Crawford 1982), as well as in Denmark (Bang 1979 & Holstener-Jorgensen and Johansen 1975, both cited by Murray and Crawford 1982; Franklin 1982a). Guatemalan fir also provides yuletide greenery and Christmas trees in its native range (FAO, in Anon. 1986; Salazar 1991). The sacred fir, or *oyamel*, is so named because of its heavy use as greenery for celebrating religious events in Mexico. Throughout Europe, but particularly in Denmark, Nordmann fir is prized as an ornamental, for its decorative foliage, and for Christmas tree production (Gosling and others 1999; Poulsen 1996); seeds from sources from the northern Caucasus (Republic of Georgia) are preferred (Godwin 1997).

From bark resin blisters, oleoresin (known commercially as Canada balsam and Strasbourg turpentine) is obtained for varnishes, the mounting of light microscopy specimens and medicinal purposes (Dallimore and Jackson 1967; Frank 1990; Lanner 1983). After distillation to yield fine turpentine oil, the crude residue is sold as rosin (Liu 1971). The pitch and bark of subalpine fir were a very important source of medicines for native peoples of the interior of British Columbia (Pojar and MacKinnon 1994); the pitch also made an effective insect repellent (Turner 1998). The fragrant needles of balsam fir are stuffed into souvenir pillows sold in New England (Frank 1990). North American native peoples pulverized fir needles for use as a body scent (sometimes to mask their human scent to reduce the risk of being attacked by large predators) or as a perfume for clothing; used powdered fir needles (particularly those of subalpine fir) mixed with deer grease as a hair tonic and tint; sprinkled

finely ground needles on open cuts; boiled white fir needles to make a tea; and boiled bark resin to make an antiseptic for wounds or as a tea for colds (Hart 1976; Hopkins 1982; Pojar and MacKinnon 1994; Turner 1998). The Straits Salish of Vancouver Island made a brown dye for basketry of grand fir bark and a pink dye by combining it with red ochre (Turner 1998). Cone scales of east Himalayan fir (see table 1 footnote) have been used to make a purple dye (Rushforth 1987).

Most commercial “pine” scents are essential oils distilled from fir foliage (Hunt 1993); foliar loppings of European silver fir in Czechoslovakia yield 1,380 tonnes (13,612 tons) per year of essential oils (Cermak and Penka 1979). “Pine” aromatherapy and other perfumery oil is steam-distilled from Siberian fir foliage (Luebke 1994–2000). The essential and fatty oil contents of west Himalayan fir seeds are suitable also for commercial exploitation in India (Jain and others 1988). Oil chemistry of other fir seeds has been studied intensively (Carrillo and others 1994; Guo and others 1984; Hasegawa and others 1987; Iwai and Nishioka 1945; Kaneko and others 1985; Rutar and others 1989).

Geographic races. The genus *Abies* was established by Miller in 1754, but Spach, in 1842, made the first attempt at a generic classification (Farjon and Rushforth 1989). Taxonomically, it is a difficult genus (Liu 1971), with extensive genetic variation (Libby 1982) that is reflected in at least 14 formal classification attempts (and several other groupings of species) made in the past 160 to 175 years. Two earlier, more-notable monographic revisions of *Abies* (Franco 1950; Gaussen 1964) were superceded in the early 1970s by a more widely accepted classification (Liu 1971) using 2 subgenera. In this scheme, the subgenus *Pseudotsuga* has a single section for the species *A. bracteata*, while the subgenus *Abies* is divided into 14 sections, 3 of which contain continuously variable forms. Section *Grandes* contains the North American species *amabilis*, *concolor*, and *grandis*; section *Nobiles* contains *magnifica* and *procera*; and section *Balsameae* contains *balsamea*, *fraseri*, and *lasiocarpa*. However, this scheme has been criticized for its unrestrained use of geographical and ecological characters that grouped species merely because they occur together, producing artificial associations (Farjon and Rushforth 1989).

More recently, a new classification scheme based on the morphology of fruiting and vegetation that puts together species with similar ecological preferences from adjoining geographical regions has been proposed. This scheme divides the genus into 10 sections, 4 of which are further

divided into a total of 9 subsections, including 3 new subsectional names (Farjon and Rushforth 1989); an historical review plus an evaluation of other attempts to classify firs are included. The new scheme is diagrammatically represented in table 2.

For North American firs, section *Bracteata* retains the single species *A. bracteata* as the type species, whereas section *Amabilis* includes *A. amabilis* as the type species. Section *Balsameae*, subsection *Laterales* (type *A. kawakamii*), includes *A. balsamea*, *A. bifolia*, and *A. lasiocarpa*, whereas subsection *Medianae* (type *A. sachalinensis*) includes *A. fraseri*. Section *Grandes* includes *A. grandis* (type) and *A. concolor*, as well as the Central American species *A. guatemalensis*, *A. durangensis*, and a new species *A. flinckii* (Rushforth 1989). Section *Nobiles* includes *A. procera* (type) and *A. magnifica*. Section *Oiamel*, which is divided into subsections *Religiosae* and *Hickelianae*, includes the other known Central American firs, including another new species *A. colimensis* (Rushforth 1989).

Note that this scheme places Fraser fir (*Abies fraseri*) in subsection *Medianae* and balsam fir (*A. balsamea*) in subsection *Laterales*; this separation is based on whether bract scales are exerted and the seed scales reniform (*Medianae*, Fraser fir), or bract scales are included and seed scales are cuneate-flabellate (*Laterales*, balsam fir) (Farjon and Rushforth 1989). Natural hybrids between these 2 species have been reported (see below) and bracts in balsam fir are not always completely “included” (hidden) (Lester 1968), so this separation does not appear to be justified.

Detailed taxonomy (as well as descriptions of cones, pollen, seeds, and seedlings) of 11 European fir species can be found in a recent monograph (Schutt 1991), whereas a more general text (Vidakovic 1991) includes 26 fir species. Other descriptions and drawings are available (Cope 1993; Rehder 1958; Rushforth 1983, 1984, 1986; Farjon 1990; Debreczy and Rácz 1995).

In North America, 2 sets of genetic complexes—grand and white firs, and noble and California red firs—create significant taxonomic confusion for students, foresters, and land-managers (Franklin 1982a). The geographic variation of the first set—grand fir and white fir (section *Grandes*, Farjon and Rushworth 1989; section *Grandes*, Liu 1971)—has been extensively studied. Although these 2 species are morphologically, ecologically, and chemically distinct, they are genetically plastic and intergrade and hybridize freely over a wide area (Daniels 1969; Foiles and others 1990; Hamrick 1966, cited by Franklin 1974b; Hamrick and Libby 1972; Klaehn and Winieski 1962; Laacke 1990a; Lacaze 1967; Steinhoff 1978). The variation can be continuous—

Table 2—*Abies*, fir: schematic of new infragenetic classification system

Section	Subsection	Species
<i>Abies</i> P. Mill.	—	<i>Abies alba</i> (type) <i>A. cephalonica</i> , <i>A. cilicica</i> ¹ , <i>A. nebrodensis</i> , <i>A. nordmanniana</i> ² , <i>Abies x borisii-regis</i>
<i>Piceaster</i> Spach emended Farjon & Rushforth	—	<i>Abies pinsapo</i> (type) ³ <i>A. numidica</i>
<i>Bracteata</i> Engelman emended Sargent	—	<i>Abies bracteata</i> (type)
<i>Momi</i> Franco emended Farjon & Rushforth (type: <i>Abies firma</i>)	<i>Homolepides</i> (Franco) Farjon & Rushworth <i>Firmae</i> (Franco) Farjon & Rushforth	<i>Abies homolepis</i> (type) ⁴ <i>A. recurvata</i> (includes <i>A. recurvata</i> var. <i>ernestii</i>) <i>Abies firma</i> (type) <i>A. beshanzuensis</i>
<i>Amabilis</i> (Matzenko) Farjon & Rushforth	<i>Holophylae</i> Farjon & Rushforth	<i>Abies holophylla</i> (type) <i>A. chensiensis</i> ⁵ , <i>A. pindrow</i> ⁶ , <i>A. ziyuanensis</i> <i>Abies amabilis</i> (type) <i>A. mariesii</i>
<i>Pseudopicea</i> Hickel emended Farjon & Rushworth (type: <i>Abies spectabilis</i>)	<i>Delavayanae</i> Farjon & Rushforth	<i>Abies delavayi</i> (type) ⁷ <i>A. chengii</i> , <i>A. densa</i> , <i>A. fabri</i> ⁸ , <i>A. fargesii</i> ⁹ , <i>A. forestii</i> ¹⁰ , <i>A. fanjingshanensis</i> , <i>A. spectabilis</i> , <i>A. yuanbaoshanensis</i>
<i>Balsameae</i> Engelman emended Farjon & Rushforth (type: <i>Abies balsamea</i>)	<i>Squamatae</i> E. Murray <i>Laterales</i> Patschke emended Farjon & Rushforth <i>Medianae</i> Patschke emended Farjon & Rushforth	<i>Abies squamata</i> (type) <i>Abies kawakamii</i> (type) <i>A. balsamea</i> , <i>A. bifolia</i> , <i>A. lasiocarpa</i> , <i>A. sibirica</i> (includes var. <i>semenovii</i>) <i>Abies sachalinensis</i> (type) (includes var. <i>mayriana</i> = <i>A. mayriana</i>) <i>A. fraseri</i> , <i>A. koreana</i> , <i>A. nephrolepis</i> , <i>A. veitchii</i> (includes var. <i>sikokiana</i>)
<i>Grandes</i> Engelman emended Farjon & Rushforth	—	<i>Abies grandis</i> (type) <i>A. concolor</i> (includes var. <i>concolor</i> & var. <i>lowiana</i>), <i>A. durangensis</i> ¹¹ , <i>A. flinckii</i> (= <i>guatemalensis</i> var. <i>jaliscans</i>), <i>A. guatemalensis</i>
<i>Oiamei</i> Franco (type: <i>Abies religiosa</i>)	<i>Religiosae</i> (Matzenko) Farjon & Rushforth <i>Hickelianae</i> Farjon & Rushforth	<i>Abies religiosa</i> (type) <i>A. colimensis</i> , <i>A. mexicana</i> ¹² , <i>A. vejarii</i> <i>Abies hickelii</i> (type) ¹³
<i>Nobiles</i> Engelman	—	<i>A. procera</i> (type) <i>A. magnifica</i> (includes var. <i>shastensis</i>)

Source: (Farjon and Rushforth 1989).

1 Includes *A. cilicica* ssp. *isaurica*.
2 Includes *A. nordmanniana* ssp. *equi-trojani*.
3 Includes *A. pinsapo* var. *marocana*, and var. *tazaotana*.
4 Includes *A. homolepis* var. *umbellata*.
5 Includes *A. chensiensis* ssp. *salouensis*, and ssp. *yulongxueshanensis*.
6 Includes *A. pindrow* var. *brevifolia* = *A. gamblei*.
7 Includes *A. delavayi* var. *nukiangensis*.
8 Includes *A. fabri* var. *minensis*.
9 Includes *A. fargesii* var. *sutchuensis*, and var. *faxoniana*.
10 Includes *A. forrestii* var. *georgi*.
11 Includes *A. durangensis* var. *coahuilensis*.
12 *A. mexicana* = *A. vejarii* var. *mexicana*.
13 Includes *A. hickelii* var. *oaxacana*.

hybrids between grand and white firs are intermediate in most characteristics—and white fir is usually referred to as “grandicolor” from northwestern California through central Oregon. However, regional races have evolved (Daniels 1969) and the major geographical units have been summarized (Franklin 1974b) as follows:

Species	Geographical location
<i>A. grandis</i>	Coastal lowlands of southern British Columbia, Washington, Oregon, and California, including lower elevations on the western slopes of the Cascade Range
<i>A. grandis</i>	Eastern slopes and higher elevations in the Cascade Range north of about 44° to 45°N latitude
<i>A. grandis</i>	Northern Idaho and interior of southern British Columbia
Intergrade	Klamath Mountains and Cascade Range of southwestern Oregon and northern California
Intergrade	Blue, Ochoco, and Wallowa Mountains of northeastern Oregon, west central Idaho
<i>A. concolor</i> *	Sierra Nevada, California
<i>A. concolor</i>	Southern Rocky Mountains and southern California

*Now recognized as Sierra white fir (table 1).

No varieties of grand fir have been established, but 2 forms—the green coastal and the gray interior (Foiles and others 1990), reduced from the 5 climatic forms (Muller 1935, 1936, cited by Franklin 1974b)—are usually recognized. White fir is a highly variable species, the variation being significantly correlated with latitude of seed source for most morphological and growth characteristics (Hamrick and Libby 1972). At least 4 major morphological divisions—(a) central Oregon and northwestern California, (b) south-central Oregon and central and northeastern California, (c) southern California and Arizona, and (d) eastern Nevada and western Utah—have been designated (Hamrick and Libby 1972).

White and grand firs, as well as red and noble firs, are chemically distinguishable by their seedcoat terpenoids (von Rudloff 1976; Zavarin and others 1978, 1979), a method useful for identifying seed provenances (Zavarin and others 1979). Other chemo-systematic comparisons of leaf- and twig-oil terpenes have expanded the knowledge of geographic variation of Pacific silver, balsam, grand, and subalpine firs (Hunt and von Rudloff 1974; von Rudloff 1976; von Rudloff and Hunt 1977), and Greek (or Grecian) fir (Koedam 1981; Mitsopoulos and Panetsos 1987).

Noble, California red, and Shasta red firs form the second important interfertile complex of species (Franklin and others 1978; Sorensen and others 1990). Noble and California red firs readily produce hybrids (Barbour 1988; Little 1979) with seed and seedling characteristics similar to Shasta red fir where the ranges overlap (Franklin and others 1978; Sawyer and Thornburgh 1977; Silen and others 1965; Sorensen and others 1990). Populations in southern Oregon and northwestern California may represent hybrid swarms between the 2 species (Franklin and others 1978). Phenotypically, trees in southern Oregon to northwestern California often resemble noble fir but behave ecologically as Shasta red fir (Løfting 1966 and 1967, cited by Franklin 1974b). A latitudinal gradient in the Cascade Range, with a major discontinuity around 44°N, has been discerned (Franklin and Greathouse 1968a). The 2 species can be artificially cross-pollinated without difficulty as long as red fir is the female (ovuliferous) parent (Zavarin and others 1978). Noble fir exhibits high self-fertility that does not appear to affect germination but which can depress height growth (Sorensen and others 1976). Although no races of noble fir are known within its natural range, population differentiation and variation is reported (Maze and Parker 1983). Three horticultural varieties—*cv. glauca*, *cv. prostrata*, and *cv. robustifolia*—are recognized (Franklin 1990). When noble, Sakhalin, Maries, Japanese, and Grecian firs were used as female parents, height, dbh, and crown area were greater in the interspecific crosses than in intraspecific crosses (Mergen and Gregoire 1988).

Of all the interspecific crosses, progeny of Maries fir (as the female parent) showed the greatest growth; this species also had the least, whereas Sakhalin fir had the greatest, inbreeding depression (Mergen and Gregoire 1988). Effects of these crosses on seed and seedling characteristics were reported earlier (Mergen and others 1965). Geographic similarity (especially among Japanese, Korean, Maries, and Sakhalin firs) was suggested as a positive influence on hybrid survival and performance (Mergen and Gregoire 1988). Earlier, it had been suggested that a geographical, rather than genetic or physiological, separation occurred as the genus *Abies* evolved (Klaehn and Winieski 1962). Possible causes for incompatibility and results from other European inter- and intraspecific crossing experiments are reported (Kantor and Chira, 1965, 1971, 1972). However, many of the reported artificial crosses between noble fir and other true firs including balsam, white, subalpine, Min (or Min-kiang), and Sakhalin firs have not been repeated, and

their validity is questionable (Franklin 1990). Unsuccessful attempts to hybridize white and grand firs with European silver, Algerian, Nordmann, and Grecian firs indicate strong reproductive isolation between the North American representatives of the genus and their European counterparts (Kormutak 1997).

Pacific silver fir has an extensive range, occupying many soil types, and it can exist in areas of deep snow and minimal summer droughts (Packee and others 1982). Yet it is not a highly variable species, and no artificial hybrids with any other species have been described, although there is a cultivated dwarf form, Pacific silver fir var. *compacta* (Crawford and Oliver 1990). Despite this apparent lack of variation, strong family differences in germination responses among populations of Pacific silver fir on Vancouver Island, with important implications for maintaining genetic diversity in nursery seedling crops, have been reported (Davidson 1993; Davidson and others 1996).

For balsam fir, the most widely distributed fir in North America, apparently-continuous variation along altitudinal and geographic gradients has been reported (Lester 1968; Myers and Bormann 1963) in which the putative variety *phanerolepis* (bracted balsam fir) is most important (Myers and Bormann 1963), but var. *fraseri* and var. *balsamea* have also been recognized (Frank 1990). The variety *phanerolepis* is most common in maritime Canada, the St. Lawrence Valley, and at higher elevations in mountains of the northeastern United States (Fernald 1909; Myers and Bormann 1963), although its taxonomic validity has been questioned (Myers and Bormann 1963). Natural hybrids have been discerned between balsam and Fraser firs (Myers and Bormann 1963; Robinson and Thor 1969), 2 closely related relics of an ancestral taxon (Robinson and Thor 1969; Jacobs and Werth 1984) that may have exhibited north-south clinal variation, although balsam fir var. *phanerolepis* is unlikely to be of hybrid origin (Robinson and Thor 1969; Jacobs and Werth 1984). Balsam fir var. *phanerolepis* and Fraser fir have been shown to be closely related and recently segregated taxa, with balsam fir var. *phanerolepis* being more closely related to balsam than to Fraser fir (Clarkson and Fairbrothers 1970). Using viable seed production as the criterion, balsam × Fraser fir and reciprocals, Fraser × bracted balsam fir and reciprocals, and bracted balsam × subalpine fir were found to be fully crossable (Hawley and Dehayes 1985a). This suggests that geographical rather than genetic isolation is likely more responsible for the taxonomic variation in these 2 firs (Hawley and Dehayes 1985a). After growing for 7 months indoors, hybrids from all these combinations were verifiable, with the hybrid seedlings not being

characteristically intermediate between parents, but mostly resembling—but still distinguishable from—the paternal parent (Hawley and Dehayes 1985b). Interspecific crosses between balsam fir (as the maternal parent) and 10 other fir species (as paternal parents) have been claimed (Chiasson 1967), even though subsequent germination was very poor. A cultivar of balsam × Fraser fir (Fraser fir var. *prostrata*) is a dwarf shrub with horizontally spreading branches that is used ornamentally (Beck 1990).

Subalpine fir, the second most widely distributed fir in North America (covering 32 degrees of latitude), exhibits considerable variation, so much so that an (unsuccessful) proposal was made to reclassify it as a subspecies of balsam fir (Boivin 1959). In the West, subalpine fir was previously recognized as a separate, single species possessing 2 varieties, var. *arizonica*, the corkbark fir found only at the southern end of the range, and var. *lasiocarpa*, the typical subalpine fir, the remaining non-corky-barked trees (Fowells 1965; Little 1953). Differences in morphology, foliar volatile oils, and other factors have been cited as reasons for returning to the original designations of alpine fir as 2 species—that is, the subalpine fir (*A. lasiocarpa* Hooker) growing in the Cascade Range and the Rocky Mountain fir (*A. lasiocarpa* var. *arizonica*), growing in higher elevations in the interior—which are believed to have hybridized extensively (Hunt and von Rudloff 1979, 1983). It has been suggested (Hunt and von Rudloff 1979) that at the southernmost end of its range, coastal subalpine fir possibly hybridizes with noble fir, but no evidence for this has been reported.

Currently, corkbark fir is included under Rocky Mountain fir; corkbark fir seeds are about 70% larger than subalpine fir seeds (Fowells 1965). In central Alberta, on its eastern boundary where the range of Rocky Mountain fir meets and overlaps with that of balsam fir (Fowells, 1965, Hosie 1969), some studies obtained evidence of hybridization (Moss 1955; Roller 1967), whereas others suggested Rocky Mountain fir is a variety of balsam fir (Bakuzis and Hansen 1965). The controversy over the subalpine fir–Rocky Mountain fir–balsam fir complex (Hunt and von Rudloff 1979, 1983; Parker and Maze 1984; Parker and others 1981) continues.

The only unique populations of coastal subalpine fir are found in Alaska, at lower elevations, and appear to be isolated with no reported introgression between them and coastal mainland populations (Harris 1965; Heusser 1954). The Prince of Wales Island population has distinctive terpene patterns, but it is not known how, or if, these differ from those of neighboring populations (Hunt 1993). Three horti-

cultural and ornamental varieties of subalpine fir have been recognized—subalpine fir cv. *beissneri* (a dwarf tree with distorted branches and twisted needles), subalpine fir cv. *coerulescens* (with intensively blueish needles), and subalpine fir cv. *compacta* (a dwarf tree of compact habit) (Alexander and others 1990). Other fir varieties are described by Welch (1991).

Based on the mean yield of germinable seeds per cone as the crossability criterion in a study of 6 firs native to California (not including noble fir), plus 4 Eurasian and 2 Mexican firs, the long-held view that western true firs hybridize freely was challenged by Critchfield (1988). The only truly successful cross was white × sacred fir (from Mexico), species from 2 different taxonomic sections (independent of the classification scheme). Seedlings from white × grand fir were easily identified as hybrids, but crosses with Eurasian firs were uniformly unsuccessful. Nevertheless, the white × sacred fir cross, like several other successful crosses mentioned above, suggests that taxonomic sections in firs are not separated by reproductive barriers (as in *Pinus*), and that fir classifications should be reconsidered (St.-Clair and Critchfield 1988).

European experiences have been similar. In Germany, combinations of Veitch × European silver fir, white × Nordmann fir, white × grand fir, and white × noble fir showed marked hybrid vigor (heterosis effect) that was obtained almost always when white fir was a parent. Hybrids with long, green needles had the greatest growth vigor, needle color being a criterion of growth vigor even in seedlings (Rohmeder 1960a; Rohmeder and Eisenhut 1961; Rohmeder and Schönbach 1959). Seedlings from white × grand fir, Grecian × Nordmann fir, and Spanish × European silver fir crosses outgrew the offspring of the maternal species after 1 year (Kormutak 1991). Several of these crosses are between species from different taxonomic sections, providing support for the absence of reproductive barriers and/or the need to reconsider taxonomic sections (mentioned earlier). As in noble fir in North America, relative self-fertility of European silver fir in Germany is very high (0.72) (Moulalis 1986). Successful controlled crossings, unsuccessful controlled crossings, natural hybrids, intermediate populations, putative spontaneous hybrids, and putative controlled hybrids in firs have been summarized by Vidakovic (1991). The genetics and breeding of European silver fir have been thoroughly reviewed by Korpel and others (1982) and genetic variation in this species was further reported on by Bergmann and Kownatzki (1987). Since the 1980s, studies on fir genetics have gained momentum in Central America (Furnier and other 1996; Aguirre-Planter

and others 2000), Europe (Fady and Conkle 1992, 1993; Fady and others 1991, 1992; Giannini and others 1994; Kormutak and others 1982, 1993; Mitsopoulos and Panetsos 1987; Parducci and others 1993, 1996, 1999, 2000; Parducci and Szmidt 1997, 1998, 1999) and Asia (Kawamuro and others 1995; Suyama and others 1992, 1996, 1997; Tsumura and others 1994; Tsumura and Suyama 1998). All of the reports cited here and throughout this chapter refer to other studies that are too numerous to include.

Elsewhere, Turkey fir (*A. bornmuelleriana*); the possible Grecian × Turkey fir hybrid (*A. equi-trojani*) (Liu 1971); and Nordmann fir are so variable in Turkey that *A. bornmuelleriana* and *A. equi-trojani* should be regarded as only races or ecotypes of *A. nordmanniana* (Arbez 1969a&b). Nordmann and Turkey fir can be distinguished in the nursery based on needle and bud characteristics (Arbez 1967). Bulgarian fir is recognized as one of several spontaneous hybrids (European silver × Grecian fir), as is Cilician fir (Grecian × European silver fir) (Korpel and others 1982). A monograph on Grecian fir is available (Panetsos 1975). Two varieties of European silver fir, var. *chlorocarpa* and var. *erythrocarpa*, are recognized in Bulgaria (Doikov 1973). Populations of Siberian fir in the former USSR have been differentiated on the basis of cone scale morphology (Vetrova 1992). Four species—west Himalayan fir, east Himalayan fir, Sikkim fir (often included with east Himalayan fir but quite distinct [Farjon 1990]), and Yunnan fir—are common in the Himalayas. A fifth—Faber fir, a Chinese species discovered in northeast Myanmar (Burma) on the Burma—Yunnan border, possibly a form of Yunnan fir—is not so common (Puri and Gupta 1968). Faber and Yunnan firs are closely related and were previously regarded as different forms of the same species (Dallimore and Jackson 1967) or as synonyms for the same species (Liu 1971). However, they have currently been given separate-species status (Farjon and Rushforth 1989). Other species have been described, such as Webb fir, which may be the western, high-altitude form of Sikkim fir, adding to the confusion (Puri and Gupta 1968). The high-altitude east Himalayan fir and the low-altitude west Himalayan fir are known to hybridize freely, forming intermediate populations with introgression at middle altitudes (Jain 1976).

Fir taxonomy in Mexico also is confused. Although *A. hickelii* has been suggested to be a synonym for *A. guatemalensis* (Dvorak 1997), others (Farjon and Rushforth 1989; Farjon 1990) classify it as a distinct species. Three more new species from western Mexico have been described (Debreczy and Rácz 1995). Levels and patterns of genetic variation in the firs of southern Mexico and

Guatemala have been reported (Aguirre-Planter and others 2000).

Because taxonomy remains confused in several instances, and because hybridization is probable, until the patterns of variation are better understood, the use of fir seed sources local to the reforestation site is the best practice. However, the specific or varietal name applied to the local population should not be relied on (Franklin 1974b). Geographic source has long been known to affect cone and seed characters in many fir species. Numerous studies have reported—sometimes contradictorily—that cone dimensions and (to a lesser extent) seed weight, germination, and seedling yields (as well as mineral contents in some species) may be under strong genetic control and related to provenance (Gambi and Stradajoli 1971; Giannini and Marinelli 1977; Gvozdikov 1980; Kociova 1974a&b; Laffers 1979; Singh and Singh 1981; Singh and others 1991; Ujiie and others 1991). For seeds of noble and Shasta red firs, the strong latitudinal gradients (or clines) in cotyledon number and in seed weight were considered promising indices of seed source/provenance (Franklin and Greathouse 1968b). Provenance selection is a key issue in Christmas tree production of noble, grand and Shasta red firs (Hupp 1984).

Isozyme analysis has effectively identified provenances of European silver fir (Konnert 1991) and has been used to study geographic variation of firs in Europe and to make comparisons with North American fir species (Konnert 1991; Kormutak 1988; Moller 1986; Schroeder 1989a,b&c). Thus, it was concluded that although European silver fir survived the last glaciation in 5 refugia, the species migrated to its present range from only 3 of them (Konnert and Bergmann 1995). By use of enzyme systems, Pascual and others (1993) showed that there is genetic divergence between Spanish and Moroccan populations of Spanish fir and that several true varieties of this species may exist. Enzyme linkages in balsam fir similar to those in other conifers might be used for taxonomic purposes (Neale and Adams 1981). A mating system study in balsam fir was described by Neale and Adams (1982). An isozyme study of Fraser fir on Mt. Rogers in Virginia revealed little or no population differentiation (Diebel and Feret 1991). Isozyme markers have revealed low levels of genetic variation within and high levels of genetic differentiation among Central American populations of Guatemalan fir, sacred fir, *A. flinkii*, and *A. hickelii* (see table 1 footnotes) (Aguirre-Planter and others 2000).

Flowering and fruiting. Fir strobili are unisexual and are typically borne on the uppermost branches. Both male (microsporangiate) and female (megaspore-bearing) strobili in grand fir develop from axillary buds (Owens 1984). The

minimum age for production of female strobili is 20 years, that of male strobili, 35 years (Eis 1970). Usually, female strobili occur singly or in small groups on the upper side of the previous year's twigs on the highest branches, whereas male strobili cluster densely along the undersides of the previous year's twigs lower down in the crown. This arrangement promotes cross-fertilization but may reduce pollination (Singh and Owens 1982). However, both male and female strobili may be found on the same branchlet. Seed production in most fir species typically begins on trees 20 to 30 years old (table 3), although individual trees may produce some cones at a younger age, for example, 12 years in noble fir (Franklin 1974b) and 15 years in balsam fir (Roe 1948a). However, heavy cone production in noble fir begins when trees are 30 to 35 years old (Franklin 1982b). Seed production by Spanish fir in Czechoslovakia does not begin until trees are 50 years old (Holubcik 1969).

All firs require 2 years to complete their reproductive cycles; detailed descriptions of the cycles have been published for balsam, Pacific silver, grand, and subalpine firs (Owens and Molder 1977a&b, 1985; Powell 1970; Singh and Owens 1981, 1982), as well as descriptions of factors affecting seed production (Owens and Morris 1998). In Pacific silver fir, microscopic primordia are initiated in the axils of leaves inside vegetative buds during May of the first year; bud differentiation occurs about 2 months later, with bract initiation in mid-July and ovuliferous scales in mid-August; seed-cone buds become dormant in November. Microsporophylls are initiated between mid-July and early September, whereas microsporangia begin differentiation in September and are dormant by mid-October. Development of pollen-cone and seed-cone buds resumes early in April of the second year. While the single, large megaspore mother cell in each ovule is undergoing meiosis in early May, mature 5-celled pollen is forming (Owens and Molder 1977a&b).

Strobilus production, male and female, in balsam fir has been related to shoot vigor, the lowest number of female strobili occurring on whorl branches, and the most male strobili on internodal branches (Powell 1972). Even where the zones of male and female bearing overlap, the 2 sexes usually occur on different types of branch; when on the same branch, male strobili are confined to the weaker shoots. As the trees age, they appear to maintain a potentially female zone of constant size (number of whorls and internodes), while the uppermost boundary of the potentially male zone rises with increasing tree height. If the leader is lost, the male zone continues to rise while the female zone gets smaller, and the apical part of the crown can eventually become male (Powell 1972).

Table 3—Abies, fir: phenology of flowering and fruiting, and major characteristics of mature trees

Species	Location & elevation (m)	Flowering	Fruit ripening	Seed dispersal	Tree ht (m)	Age (yrs)*	Interval (yrs)
<i>A. alba</i>	Europe	May–mid-June	Mid-Sept–mid-Oct	Mid-Sept–mid-Oct	25–45	25–30	2–3†
<i>A. amabilis</i>	W Washington & Oregon (150–400) Vancouver Is., British Columbia (500) Lewis Co., Washington (1,600)	Late Apr–May Mid-May–June June	Late Aug Mid-Sept	Late Aug–Sept	35–65	30	3–6
<i>A. balsamea</i>	— Minnesota	Mid–late-May Late Apr–early June	Late Aug–early Sept	Mid-Sept Early Oct	10–20	20–30	2–4
<i>A. bracteata</i>	Sta. Lucia Mtns, Monterey Co., California	Late Apr–early May	Late Aug	Mid-Sept	10–35	—	3–5
<i>A. concolor</i> var. <i>lowiana</i>	— Stanislaus NF, California (2,000) Fremont NF, Oregon (1,600)	May–June Late May	Sept–Oct	Sept–Oct Late Sept–late Oct	25–60	40	3–9
<i>A. firma</i>	Japan	Mid-May–early June	—	—	—	—	—
<i>A. fraseri</i>	Roan Mtn, North Carolina	Late Apr–mid-May	Mid–late Oct	Late Oct–early Nov	30–45	—	4–6
<i>A. grandis</i>	Northern Idaho (750–1,100) W Washington & Oregon (100–400) Linn Co., Oregon (1,600)	Mid-May–early June Mid-June Mid-April–mid-May	Sept–mid-Oct Aug	Sept–early Nov Early Sept	10–25 35–65	15 20	3 2–3
<i>A. guatemalensis</i>	Mendocino Co., California (65)	Early–mid-June	—	Late Aug–mid-Sept Early Oct	—	—	—
<i>A. homolepis</i>	Guatemala, S Mexico, Honduras, & El Salvador	Late March–early Apr	Oct–mid-Dec	Nov–mid-Dec	20–30	—	2–3‡
<i>A. lasiocarpa</i>	Japan San Francisco Peaks, Coconino Co., Arizona Northern Idaho (950) Eastern Montana (2,100) Linn County, Oregon (1,750)	Mid-May–mid-June Late June Late June–early July Early–mid-July Late May–early July	Mid–late Sept Mid-Sept–early Oct Mid-Aug Late Aug	Mid–late Sept Late Sept–early Oct Mid-Sept Early Sept Early Oct	20–30 10–35 10–35	— 50 20	5–7 2–3 2–4
<i>A. magnifica</i>	—	Late May–early June	Aug	Sept–Oct	30–55	35–45	2–3
<i>A. mariesii</i>	Japan	Mid–late June	Mid–late Sept	Late Sept–early Oct	10–25	—	5–7
<i>A. nordmanniana</i>	—	—	May After Oct 1	Sept–Oct	40–60	30–40	2–3
<i>A. pindrow</i> §	Russian Georgia	Late Apr–mid-May	Sept–early Oct	Oct–Nov	—	30–40	2–4
<i>A. pinsapo</i>	Himalayas	—	—	—	—	50	—
<i>A. procera</i>	Czech Republic & Slovakia Benton & Linn Cos., Oregon (1,350–1,550) Lewis Co., Washington (1,600)	June June–early July	Mid–late Sept Late Sept	Early Oct Early Oct	45–80	12–15	3–6
<i>A. sachalinensis</i>	Hokkaido, Japan	May–June	Sept–Oct	Oct	—	—	2–4
<i>A. x shastensis</i>	SW Oregon (1,850–2,000) N. California coast ranges (2,000) Shasta Co., California (1,700–2,000)	Mid–late June	Late Sept Late Sept	Late Sept–mid-Oct Early–mid-Oct	30–55	30–40	2–3
<i>A. sibirica</i>	W Siberia	—	—	Mid-Oct	—	—	—
<i>A. veitchii</i>	Japan	June	Sept–early Oct	Sept–Oct	20–25	30	2–8 5–6

Sources: Ahlgren (1957), Anon. (1950b, 1998), Bakuzis and Hansen (1965), Baron (1969), Beck (1990), Dallimore and Jackson (1967), Ebell and Schmidt (1964), Eis (1970), Eis and others (1965), Enescu (1960), Fowells (1965), Fowells and Schubert (1956), Franklin (1968, 1974b), Franklin and Ritchie (1970), Gordon (1978), Haig and others (1941), Hetherington (1965), Hughes (1967), Laacke (1990a&b), Laacke and Fiske (1983), Legg (1953), Leloup (1956), Little and DeLisle (1962), Lofting (1961), MacDonald and others (1957), MacLean (1960), Morris (1951), Munz and Keck (1959), Owens and Molder (1977b), Pearson (1931), Puri and Gupta (1968), Rudolf (1952), Sato (1940), Schmidt and Lotan (1980), Singh and Singh (1984a&b), Talley (1974), Tulstrup (1952), USDA Forest Service (1948), Wappes (1932), Zon (1914).

* Minimum age for commercial seed bearing.

† At higher elevations in central Europe, 4 to 6 years.

‡ Occasionally (Talley 1974).

§ Includes *A. delavayi*, *A. densa*, and *A. spectabilis* (Puri and Gupta 1968).

Thinning promoted fruiting in 150- to 170-year-old stands of Siberian fir in Siberia (Zelenin 1991), and best Sakhalin fir seeds occurred after heavy thinning (Sato 1940). In contrast, after a commercial thinning in a younger Siberian fir stand, the remaining trees produced such small amounts of pollen that seed quality was greatly reduced (Okishev and Pugachev 1983). Strobilus production in a Nikko fir seed orchard in Japan increased slightly following application of gibberellins $GA_{4/7}$ and GA_3 , but girdling at the branch base was ineffective (Katsuta and others 1981).

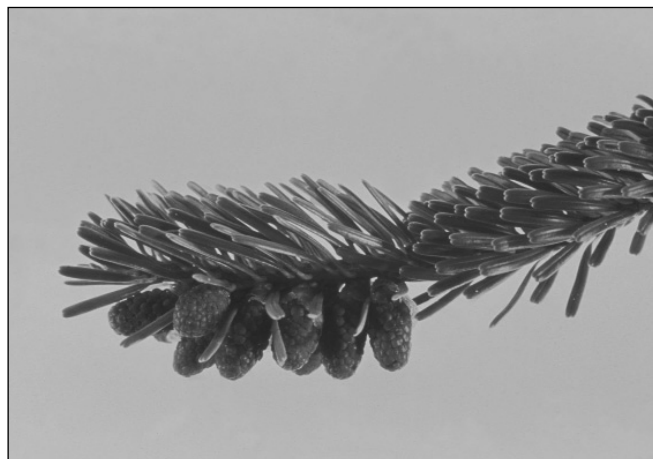
Following bud burst in early spring, female strobili quickly elongate, and initially the bracts are highly conspicuous (figure 1). Enlarging male strobili have a miniature raspberry-like form (figure 2) until pollen is shed, when they become elongated and tassel-like. Wind-pollination in Pacific silver fir occurs by late May (Owens and Molder 1977a&b). Pollination durations may vary widely, from 18 days in a Nikko fir seed orchard in Japan (Ito 1975) to a month in a Spanish fir forest in Spain (Arista and Talavera 1994a). Fir pollen is relatively heavy, so that pollination distances greater than 60 m may be the limiting factor for viable seed production in fir (and other coniferous species); although isolated trees may show an apparently good cone crop, the seedcrop may be poor (Anon. 1950a; Arista and Talavera 1994b). Parthenocarpy is known in balsam fir (Anon. 1950a) and Siberian fir (Nekrasova 1978a); without pollen, cones can be of normal size but what seeds form are without embryos. Controlled pollination techniques have been described for Fraser fir (Miller 1983), and fir pollen can be stored for at least 2 years under carefully controlled conditions (Kravchenko and others 1974; Lowe 1974).

For Pacific silver fir on Vancouver Island, development of the female gametophyte is complete at the end of June and fertilization occurs in mid-July. Embryonic meristems

Figure 1—*Abies amabilis*, Pacific silver fir: female strobili at the receptive stage (courtesy of D. Pigott).



Figure 2—*Abies procera, noble* showing the typical “raspberry” form (courtesy of Y. Tanaka.) fir: male strobili prior to pollen shedding (courtesy of D. Pigott).

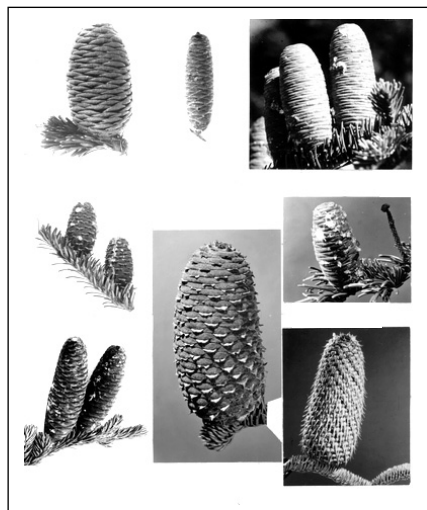


and cotyledons develop in early August and embryos mature late the same month or September. Seed dispersal usually begins mid-late September and most seeds have been shed by November (Owens and Molder 1977a&b). Similar phenologies have been described for grand fir on southern Vancouver Island (Owens 1984) and for Spanish fir in Spain (Arista and Talvera 1994b).

Mature fir cones are 7.5 to 25 cm long and typically ovoid to oblong-cylindrical. In many fir species, the fan-shaped ovuliferous scales outgrow the bracts early in the season, but the bracts remain highly conspicuous in noble fir, nearly covering the entire surface of the cone at maturity (figure 3). Typically, Shasta red fir bracts are also visible on the surface of mature cones, which makes them distinguishable from cones of California red fir, which have bracts that are shorter than the scales (Laacke 1990b). However, north of Mt. Lassen, where red and noble firs hybridize, red fir has exserted bracts (similar to those of noble fir). Adding to the confusion, exserted bracts are found also on a large southern Sierra Nevada population of red fir (Laacke 1990b). The bracts remain so prominent in bristlecone fir as to give this species its name.

Each scale bears 2 seeds on its adaxial (upper) surface, the ovules forming at the base of the scale near the attachment to the cone axis. The membranous wings form over the outer part of the scale. Scales near the tip and base of the cone usually lack fertile seeds. At maturity, seeds separate from the scale on which they form—a useful diagnostic in judging advancing ripeness—and seed dissemination involves abscission of the cone scales from the axis, leaving the rachis, the spike-like axis on the tree (figure 4) that may persist for several years. In Pacific silver fir, the scales become greatly distorted during drying in late summer, and

Figure 3—*Abies*, fir: mature female cones of *A. amabilis*, Pacific silver fir (**top left**); *A. balsamea*, balsam fir (**top middle**); *A. concolor*, white fir (**top right**); *A. fraseri*, Fraser fir (**middle left**); *A. x shastensis*, Shasta red fir (**middle center**); *A. grandis*, grand fir (**middle right**); *A. lasiocarpa*, subalpine fir (**lower left**); *A. procera*, noble fir (**lower right**).

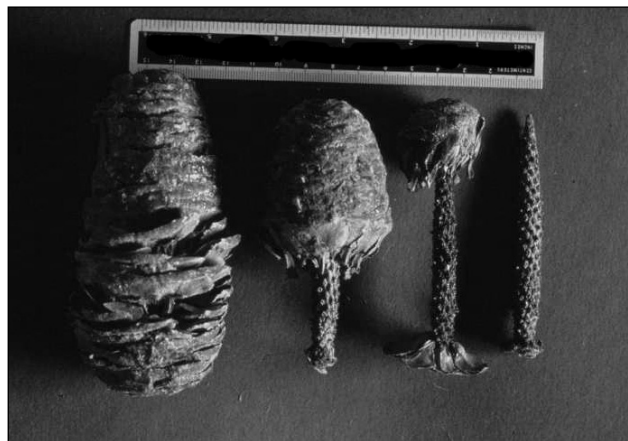


this twisting actively tears them from the axis. No such distortion occurs in noble fir, and seed dissemination requires branch movement by the wind or other agents to disturb the cone (Franklin and Ritchie 1970). Cone disintegration of other species such as grand fir and subalpine fir are intermediate.

Thus, pollination, fertilization, seed ripening, and dissemination all occur in the same season—in as little as 90 to 120 days—following the year of strobilus initiation (Franklin and Ritchie 1970). The chief agent of seed dispersal is the wind; seed rain density decreases as a function of distance from the parent tree, seedling mortality increases, and smaller-seeded species travel further (Carkin and others 1978; Franklin 1982b; Hofmann 1911; Houle 1992, 1995; Isaac 1930b; McDonald 1980; Savchenko 1966; Wolfenbarger 1946).

The majority of fir seeds are normally shed in October/November (table 3). Frequently these have the highest seed weight, maximum germination capacity and lowest occurrence of empty and immature seeds, plus higher seedling survival rates, than seeds shed earlier/later. In several firs, seed dispersal may extend well into winter (Anon. 1950b; Aussenac 1966; Hetherington 1965; Houle and Payette 1991; Roe 1946), the seeds becoming buried in, and germinating in, snowbanks (see also Pregermination treatments). Up to 50% of a Maries fir seedcrop may lodge in the foliage and only fall to the ground over winter (Smirnov 1991). The date of seed-fall of European silver fir in Italy

Figure 4—*Abies grandis*, grand fir: four stages in the abscission of ovuliferous scales from the cone axis (courtesy of D. Pigott)



became later with increasing altitude, but the amount of seeds fallen per square meter was greatest at intermediate altitudes of 900 and 1450 m and lowest at 800 and 1600 m. Seed quality in this species improved with increasing altitude because of a decrease in the percentage of empty and dead seeds (Giami 1970).

Fir seeds are large compared to most conifers, averaging 29, 46 and 83 seeds/g for Pacific silver, grand, and subalpine firs, respectively (Kolotelo 1997). In mature seeds (figure 5), the membranous wings are large—20 to 23.5 mm long in Manchurian fir (Voroshilova 1983)—ovoid or oblong, 1 to 1.5 times the length of the seed, and up to twice the seed width. The wing is usually translucent, uniformly light brown or tan, sometimes with a magenta edge. Seeds are completely covered by the wing on the adaxial face, but only on 2 margins on the abaxial face (Cermak 1987) by narrow flaps (figure 6). The soft seedcoat is brown, tan, or rarely cream and, in the outer, softer parts (sarcotesta) (Cermak 1987) where the seed is covered by the wing, large resin vesicles develop from cavities that differentiate in the outer layers of the integument (Owens and Molder 1977b). Vesicles appear on the seed surface as small, dark patches, their number, character, and placement varying with the species. Vesicle position (figures 7–9) and chemical contents in European silver fir have been described (Cermak 1987). The seedcoat of white fir is thinner than that of red fir and contains more vesicles, the number varying between 5 and 12/seed, although 7 to 9 are more common (Kitzmilller and others 1975). About 20% of the fresh weight of European silver fir seeds is resin (Cermak 1987), 90 to 95% of which is monoterpene hydrocarbons (principally limonene) (Cermak 1987; Cermak and Penka 1979; Penka and others 1977).

Figure 5—*Abies*, fir: mature seeds of *A. amabilis*, Pacific silver fir (**top left**); *A. balsamea*, balsam fir (**top center**); *A. fraseri*, Fraser fir (**top right**); *A. grandis*, grand fir (**bottom left**); *A. lasiocarpa*, subalpine fir (**bottom center**); *A. magnifica*, California, red fir (**bottom right**).

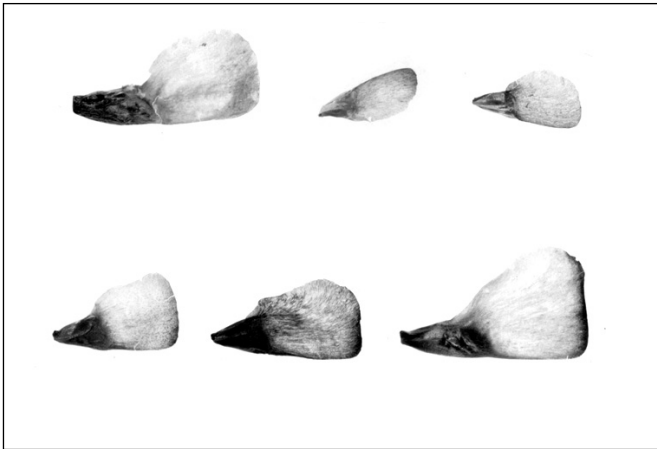
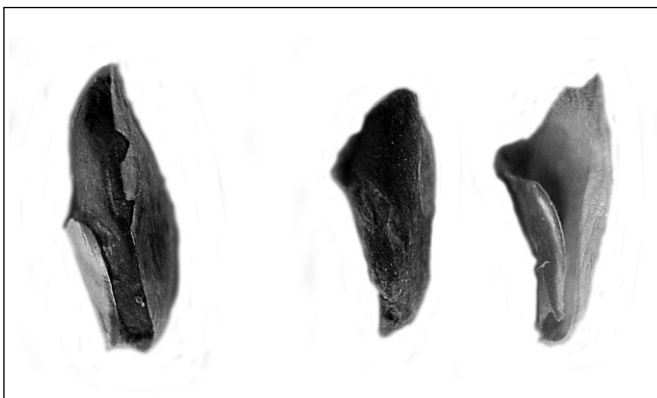


Figure 6—*Abies procera*, noble fir: abaxial view of seed showing (**left**) a seed with wing, but with integument still attached (indicated by the prominent flaps wrapping around the long margins) and which would be regarded as a “pure seed” commercially; a naked seed (**center**) without wing or integument; and the intact integument (**right**) removed from the seed at center. This wing attachment to the seed is typical for fir (Edwards 2002); scale bar is in millimeters.



The role of resin has been linked to inhibiting precocious germination, that is, to promoting dormancy, of mature fir seeds at the time of seedfall (Rohmeder 1951). It might also provide some form of protection for the embryo and megagametophyte against excessive drying (Gunia and Simak 1970). Germination of non-stratified European silver fir seeds was increased after resin removal by low-temperature vacuum distillation (Zentsch 1960), and resin extracted from this species inhibited germination in pine and spruce seeds (Dässler and Zentsch 1959; Rohmeder 1951). Damaging the vesicles during processing of fresh European silver fir seeds and allowing the resin to “contaminate” undamaged seeds reduced their germination (Gunia and Simak 1970). The germination-reducing effect of resin leak-

age in other species was greater when damage occurred before the seeds had been stratified (Arista and others 1992; Kitzmiller and others 1973, 1975), lending support to the suggestion that the resin may be chemically transformed during chilling rather than simply being evaporated (Gunia and Simak 1970). Leaking resin quickly oxidizes and may then be toxic to the embryo (Bouvarel and Lemoine 1958), and/or provide a good medium for mold development (Gunia and Simak 1967, 1970; Kitzmiller and others 1973). Whatever the precise role of the resin, fir requires careful handling of cones and seeds from the time they are picked (Dalskov 1960; Gunia and Simak 1970). Although fragile, the seedcoat can account for up to 60% of the total dry weight in noble fir seeds (Kandya and Ogino 1986).

Most of the bulk in a mature fir seed is occupied by the fleshy, nutritive megagametophyte tissue. Whereas the seedcoat proportion does not vary greatly, the weight of the megagametophyte and embryo varies widely among individual seeds and is more closely correlated with how quickly the seeds germinate (Kandya and Ogino 1986). The embryo extends almost the length of the megagametophyte (figure 10), and this extension—relative to the megagametophyte length—is a good index of seed ripening (Dobbs and others 1976; Oliver 1974) (see also table 6). Embryonic cotyledons, which may vary in number from 3 to 14, are well-differentiated, but the radicle apex is difficult to discern as it is encased by the protective root cap.

Seedcrops large enough to justify commercial collections generally occur every 2 to 4 years (table 3), but inter-

Figure 7—*Abies alba*, European silver fir: diagrammatic view of the adaxial surfaces of a pair of seeds on an ovuliferous scale. **CA** = cone axis; **OS** = ovuliferous scale; **Br** = bract; **S₁**, **S₂** = seeds; **W₁**, **W₂** = wings. A cross section through the seeds (indicated by the dotted line) is shown in figure 8 (after Cermak 1987).

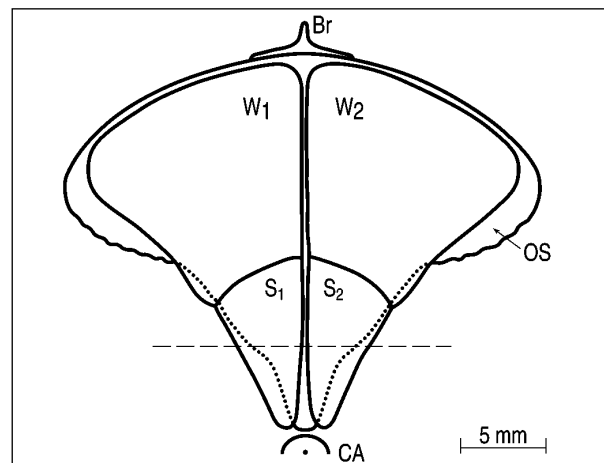


Figure 8—*Abies alba*, European silver fir: diagrammatic cross section of a seed (SI in figure 7). OS = ovuliferous scale; Br = bract; W = wing; m = median plane of the ovuliferous scale; e = embryo; meg = megagametophyte (“endosperm”). A, B, D, and E indicate individual resin vesicles located on the adaxial (ad) or abaxial (ab) surfaces, and medial (med) and marginal (marg) edges of the seed (after Cermak 1987).

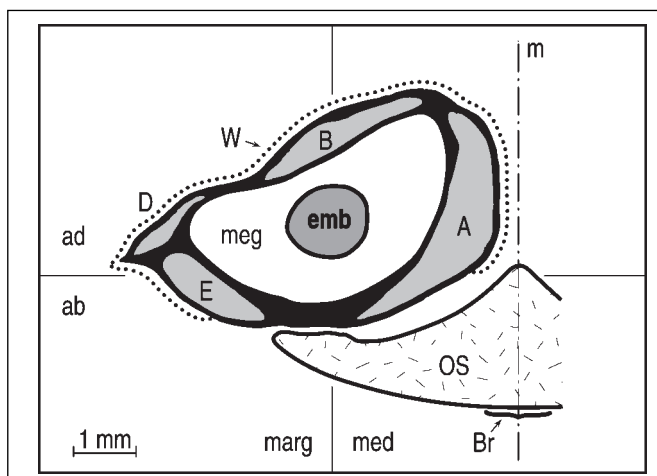
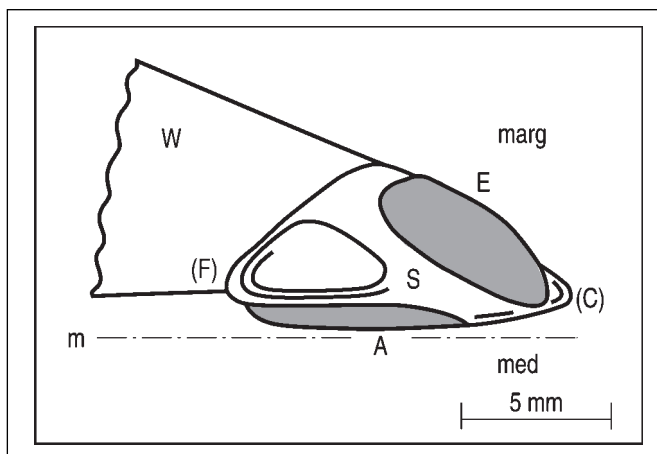
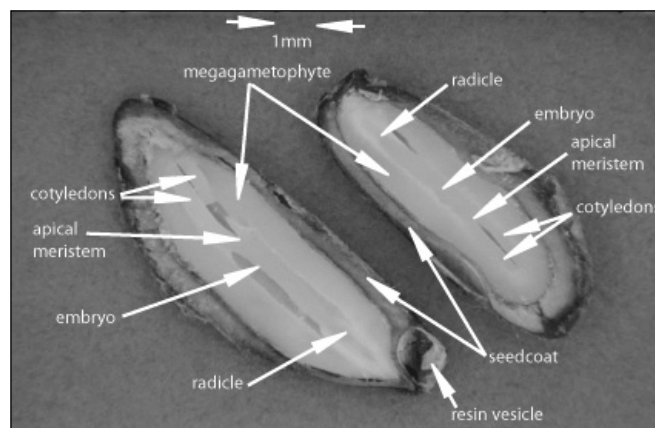


Figure 9—*Abies alba* European silver fir: diagrammatic view of the abaxial surface of 1 seed. W = wing; m = median plane of the ovuliferous scale. Resin vesicles appear on the medial (A) or marginal (E) sides of the seeds, and at both ends (C and F) (after Cermak 1987).



vals may vary considerably due to numerous factors. Strobilus production in balsam (Powell 1977) and Spanish firs (Arista and Talavera 1995) occurs in alternate years. This was previously thought to be due to an endogenous rhythm unrelated to environmental factors (Greenbank 1963), but it has been shown that good cone crops in grand fir require both a cool, moist summer the year before seed maturation and a warm, dry summer the year of seed matu-

Figure 10—*Abies grandis*, grand fir: longitudinally sectioned mature seeds showing embryos (e) occupying 90+% of the corrosion cavity in the megagametophytes (meg) (“endosperm.” C = cotyledons; AP = apical meristem; R = radicle; H = hypocotyl/shoot axis; V = resin vesicle; SC = seedcoat. Scale bar is in millimeters (courtesy of D. Pigott).



ration (Eis 1973). Thus, large crops are unlikely in consecutive years. Other environmental requirements must be met also, which is why lapses of several years between heavy crops is more the rule. For example, the interval between heavy crops of white fir in California is commonly 5 years (McDonald 1992) but may vary from 3 to 9 years (Fowells and Schubert 1956). Henderson (1982) found that for sub-alpine fir, only 1 year over a 28-year period produced a “bumper” crop, whereas 4 other years were “good.” Several true firs in Oregon and Washington produce good crops on a 3-year cycle (Franklin 1968), with noble fir averaging medium or better crops 50% of the time over its range, although some sites may go as long as 6 years without significant cone production (Franklin 1982b). Crop year can have a large effect on seed weight and cotyledon number in noble fir (Sorensen and Franklin 1977); cotyledon number in Sakhalin fir was weakly correlated with provenance (Okada 1966).

Several methods for forecasting cone crops have been devised. One, for Maries fir, is based on bud counts the previous year (Matsuura 1963); another uses visual estimates of the number of cones on individual Sierra white fir trees and the proportion of trees bearing cones (McDonald 1992); a photographic method is more accurate than visual rating for red fir (Gordon 1962). Crop production in grand fir can be estimated using a regression equation that employs the number of cones on the top 2 whorls of the crown, and the num-

ber on the south side of the tree (Kulhavy and Schenk 1976).

Cone length and seed yield are significantly correlated in grand fir (Ching 1960), and cone length and seed weight are correlated with mean temperature during maturation in Sakhalin fir (Okada 1983). The fertile length, or “effective size,” of balsam fir cones ranges from 60% in small cones to 83% in large cones and, because larger cones are borne higher in the crown, the upper branches bear a greater proportion of the potential seed yield than they bear of the cone crop (Powell 1979). The fertile length of a European silver fir cone represents 74% of the total cone length, and the average yield of potentially fertile seeds varies from 122 (small cones) to 272 (large cones) (Nanu 1979a).

Total seed set (including damaged seeds) can be estimated for subalpine fir (Kulhavy and others 1976) and other firs (Douglass 1969) from the number of exposed seeds—sound and insect-damaged—when cones are cut in half lengthwise. The number of filled seeds exposed when cones are cut in half longitudinally is used in British Columbia to judge whether the crop is worth collecting; for Pacific silver fir at least 8 to 12, for grand fir at least 12 to 14, and for subalpine fir at least 4 to 6 filled seeds must be exposed on one cut face of the cone (Edwards 1986a; Eremko and others 1989). These numbers apply just prior to collection, because insects or disease may decrease counts if there is a significant time lag between cone examination and cone collection.

Tree age and size affect seed quality, sometimes in contradictory ways. Best seeds were obtained from younger (40- to 50-year-old) trees of the rare Sicilian fir in Italy (Arena 1960) and balsam fir in Michigan (Benzie 1960), than from trees more than 150 years old. European silver fir trees between 40 and 100 years old were judged best (Magini 1953), but Bosnian sources of this species showed no decrease in fertility with age (Panov 1949). West Himalayan fir at 200 years in Pakistan still produced enough seeds for adequate natural regeneration (Haq 1992), although viable seeds did not exceed 15% of the crop.

Almost 90% of white fir cones are borne on dominant trees, 12% on codominants, and almost none on intermediate and suppressed trees (Fowells and Schubert 1956). In white fir, cone production peaks in trees with 75 cm dbh, then gradually decreases as diameter increases (Fowells 1965). Seed-bearing white fir trees over 60 cm dbh are targets for the fir engraver beetle (*Scolytus ventralis* LeConte), which weakens and damages tops and thus may seriously impair cone production in old-growth stands (Hopkins 1982). Most cones occur on branches of the second and third nodes from the apex of balsam fir trees (Powell 1979).

Similarly, cones occur at the very top of dominant Siberian fir trees over 28 cm dbh (Kolomiec 1950). In Siberian fir, the frequency of fruiting is correlated also with height, diameter, and trunk volume (Nekrasova and Ryabinikov 1978): all trees with a dbh of 24 cm or larger bear cones (Atimetov 1968). For European silver fir, seed numbers per tree generally increase with dbh, whereas the 1,000-seed weight peaks at dbh 40 to 50 cm, then decreases. Nursery seedlings surviving into their second growing season increased with parent-tree dbh up to 50 to 60 cm, so cones should be collected from trees 35 to 50 cm dbh (Souleres 1965). Germination in Himalayan fir seeds is optimal from trees in the 1.3- to 2-m dbh class (Puri and Gupta 1968). Cone diameter, 1,000-seed weight, and germination varied significantly with dbh of west Himalayan fir trees (Arya and others 1994).

Proper form and timing of nitrogen fertilizer has increased the frequency and size of balsam fir seedcrops—producing bigger and heavier cones and better quality seeds—in both natural stands and seed orchards (Arnold and others 1992; Edwards IK 1986; Sheedy 1974, 1978). Similar effects have been reported for European silver fir (Huchler 1956). Foliar levels of phosphorus and magnesium were identified as the nutritional elements most limiting cone yields in a Fraser fir seed orchard; the relative nitrogen status of high-yielding trees was superior to that of low-yielding trees. However, increasing the level of the most limiting nutrient may not increase cone production because other internal and external factors play a more decisive role (Arnold and others 1992).

Causes of reduced seed production. Despite producing abundant amounts of pollen, firs typically are poor seed producers, the reasons (in decreasing order of importance) being infrequent cone initiation, insect infestation, frost damage to cones and ovules, inadequate pollination, and several other minor causes (Owens and Morris 1998). The main factor affecting the number of cones produced is the proportion of initiated female strobili that develop into fully mature cones (Eis 1970; Nekrasova 1974; Owens and Molder 1974, 1977a&b; Owens and Morris 1998; Powell 1973; Shea 1989a&b). In a good crop year, an average grand fir tree produces over 40 cones (Foiles and others 1990). Cool wet weather may interfere with pollen dispersal (Franklin 1974a). Lack of pollination, incomplete development, and abortion, in balsam fir may cause more empty seeds than insect damage (Fye and Wylie 1968). Self-pollination in noble fir may reduce seed yield by 31%; although seed weight, germination, and seedling survival are not affected, seedlings of selfed parents show a 24%

inbreeding depression of 3-year height growth (Sorensen and others 1976). Late frosts up to 6 to 8 weeks after bud burst, that is, late May and early June (Fowells and Schubert 1956; Franklin and Ritchie 1970) may cause total abortion of female strobili in several species. Additionally, some primordia may become latent or differentiate as vegetative structures, depending on environmental and physiological factors during their development. Aerial contaminants may reduce seed yields also (Loffler 1988; Sidhu and Staniforth 1986).

High percentages of empty seeds have been observed in collections of numerous fir species (Franklin 1974b; Keen 1968; Khutortsov 1987; Nanu 1979b). The proportion of empty seeds increases in poor seed years, up to 90% in Siberian fir (Nekrasova 1978b) and to 63% plus 36% insect damaged in noble fir (Scurlock and others 1982). Cone crops of noble fir must be medium size or larger for sound seed to exceed 10% (Franklin 1982b).

The proportion of high-quality germinable seeds is often reduced by frequent infestations of insects that damage both cones and seeds (Hedlin 1974; Hedlin and others 1980). Insect predators appear wherever firs grow worldwide and about 50 insect species have been identified as damaging agents to fir cone and seedcrops (table 4). Tortrix moths are a major pest in China (Zhang 1982). Damage caused by cone midges, moths, maggots, and seed chalcids (*Megastigmus* spp.) usually is extensive, but cone moths (*Barbara* spp. and *Dioryctria* spp.) (figure 11) and cone maggots (*Earomyia* spp. and *Hylemya* spp.) that mine through the cones, injuring more than 1 seed (Hedlin 1966; Hedlin and Ruth 1974; Keen 1968; Pfister and Woolwine 1963) cause the most conspicuous destruction. The insect

Figure 11—*Abies grandis*, grand fir: almost-mature cones attacked by the insect *Barbara* spp. (courtesy of D. Pigott).



complex colonizing white fir cones comprises 3 feeding guilds—cone and seed miners, seed miners, and scale and bract feeders (Shea 1989a&b). These include at least 11 different insects (Shea 1989a&b):

- cone and seed miners—*Dioryctria abietivorella* Grote, *Eucosma* probably *siskiyouana* (Kearfoot), *Cydia* probably *bracteata* (Fernald), and *Barbara* spp.
- seed miners—*Megastigmus pinus* Parfitt, *M. rafni* Hoffmeyer, and *Earomyia abietum* McAlpine
- scale and bract feeders—*Asynapta hopkinsi* (Felt), *Dasineura* probably *abiesemia* Foote, *Resseliella conicola* (Foote), and *Lasiomma (Strobilomyia) abietis* (Huckett)

Seed-mining guild insects cause the major seed damage in most years and, as cone crop size decreases, the proportion of cones with more than 1 insect species increases, together with an increase in co-occurrence of members of different guilds (Shea 1989a&b). In contrast, the larvae of seed chalcids (figure 12), which are the most common insects destroying coniferous seeds across the North American continent (Speers 1974a), destroy 1 seed each (Nanu 1980; Speers 1967). By means of seed x-radiography, not only can the degree of damage be estimated readily (Kulhavy and others 1976; Overhulser and Tanaka 1983; Speers 1967; Tanaka 1982), but larvae of *Megastigmus* spp. can be distinguished from those of *Resseliella* spp. (Gagov 1976).

In poor seed years, insects may totally destroy seedcrops of white fir in the western United States (Keen 1968), Fraser fir in the eastern United States (Speers 1968), and Siberian fir in western Siberia (Kolomic 1950). Damage generally is

Figure 12—*Abies*, Fir: seed chalcid.



Table 4—Abies, fir: insects affecting cone and seed production

Insect*	Common name	Host tree species
<i>Adelges piceae</i> Ratz.	balsam woolly aphid	<i>A. balsamea</i> , <i>fraseri</i>
<i>Argyresthia fundella</i> F.R.	—	<i>A. alba</i>
<i>Asynapta</i> spp.†	bract feeder	<i>A. concolor</i> , <i>lasiocarpa</i>
<i>Barbara</i> spp.	fir cone moth	<i>A. alba</i> , <i>concolor</i> , <i>grandis</i> , <i>lasiocarpa</i> , <i>magnifica</i> , <i>nephrolepis</i>
<i>Camptomyia</i> spp.	—	<i>A. alba</i>
<i>Cartodere</i> spp.	—	<i>A. alba</i>
<i>Cryptophagus (micrambe) abietis</i> (Pay.)	—	<i>A. alba</i>
<i>Cydia bracteatana</i> Fernald	fir seed moth	<i>A. concolor</i>
<i>Dasineura</i> spp.	fir seed midges	<i>A. concolor</i> , <i>grandis</i> , <i>lasiocarpa</i> , <i>procera</i>
<i>Dendroctonus</i> spp.	—	<i>A. guatemalensis</i>
<i>Dioryctria</i> spp.	cone moth	<i>A. alba</i> , <i>amabilis</i> , <i>balsamea</i> , <i>A. cephalonica</i> , <i>A. concolor</i> , <i>A. grandis</i> , <i>nephrolepis</i> , <i>nordmanniana</i> , <i>A. pindrow</i> , <i>pinsapo</i>
<i>Earomyia</i> spp.	seed maggot	<i>A. alba</i> , <i>concolor</i> , <i>grandis</i> , <i>lasiocarpa</i> , <i>magnifica</i> , <i>A. nordmanniana</i> , <i>procera</i>
<i>Epinotia nigricana</i> H.-S.	—	<i>A. alba</i>
<i>Eucosma siskiyouana</i> Kearfott	cone and seed miner	<i>A. concolor</i>
<i>Evetria margarotana</i> Wocke	—	<i>A. alba</i> , <i>borisii-regis</i> , <i>cephalonica</i> , <i>sibirica</i>
<i>Hylemya</i> spp.	cone maggot	<i>A. bracteata</i> , <i>concolor</i> , <i>grandis</i> , <i>lasiocarpa</i> , <i>nephrolepis</i>
<i>Lasiomma</i> spp.	fir cone maggot	<i>A. concolor</i> , <i>grandis</i> , <i>lasiocarpa</i> , <i>nephrolepis</i>
<i>Laspeyresia</i> spp.	—	<i>A. alba</i> , <i>borisii-regis</i> , <i>cephalonica</i> , <i>concolor</i> , <i>magnifica</i>
<i>Leptoglossus occidentalis</i> Heid.	western conifer seed bug	<i>A. grandis</i>
<i>Lestodiplosis holstei</i> L.	—	<i>A. alba</i>
<i>Lonchea viridana</i> Meig.	—	<i>A. alba</i> , <i>borisii-regis</i> , <i>cephalonica</i>
<i>Lycoriella cellaris</i> Leng	—	<i>A. alba</i>
<i>Megastigmus</i> spp.	seed chalcid	<i>A. alba</i> , <i>amabilis</i> , <i>balsamea</i> , <i>borisii-regis</i> , <i>A. bracteata</i> , <i>cephalonica</i> , <i>concolor</i> , <i>fraseri</i> , <i>grandis</i> , <i>guatemalensis</i> , <i>A. lasiocarpa</i> , <i>magnifica</i> , <i>bornmuelleriana</i> var. <i>equitrojana</i> , <i>A. sibirica</i> , <i>pinsapo</i> , <i>procera</i>
<i>Pegohylemia</i> spp.	—	<i>A. alba</i> , <i>balsamea</i>
<i>Ptilinus fur</i> L.	—	<i>A. alba</i>
<i>Resseliella</i> spp.	cone scale midge	<i>A. alba</i> , <i>borisii-regis</i> , <i>cephalonica</i> , <i>cilicica</i> , <i>concolor</i> , <i>A. grandis</i> , <i>nordmanniana</i>
<i>Spermatolonchaea viridana</i> L.	—	<i>A. cilicica</i>
<i>Zeiraphera rufimitrana</i> Foote	—	<i>A. alba</i>

Sources: Androic (1960, 1976), Annala (1982), Arista and Talavera (1995), Bess (1946), Blais (1952), Bradley and others (1981), Bryant and Hudak (1968), Canakcioglu (1969), Donahue and others (1985), Durzan (1979), Eremko and others (1989), Fang and others (1988, 1989), Fedde (1973a&b), Gagov (1976), Gonzalez and others (1983) [in Donahue and others 1985], Gordon (1970), Greenbank (1963), Hall (1981), Hedlin (1966), Hedlin and Ruth (1974), Hedlin and others (1980), Hussey (1954, 1957, 1960), Hussey and Klinger (1954), Jespersen and Lomholdt (1983), Kailidis and Georgevits (1970, 1972), Kayacik (1964), Keen (1968), Koerber (1963), Kolomic (1950), Kulhavy and Schenk (1976), Kulhavy and others (1976), Lanz (1942, 1943), Legg (1953), Mackay (1949), Matic (1972), Miller (1986), Miller and Ruth (1989), Moody (1988), Nanu (1979b), Nanu and others (1986), Nekrasova (1978b), O'Connor and O'Connor (1984), Overhulser and Tanaka (1983), Pfister and Woolwine (1963), Powell (1973), Pribylova (1975), Puri and Gupta (1968), Rahman and Chaudhry (1986), Schooley (1975, 1976, 1978), Scurlock and others (1982), Shea (1989a&b), (Skrzypczynska 1982, 1984, 1985, 1989a&b), Skrzypczynska and others (1988, 1990, 1995), Speers (1968, 1969), Talley (1974), Tanaka (1982), Toth (1973), Woodwell (1961).

* Insect names, in alphabetical order, are listed as cited by sources. No attempt has been made to rationalize synonyms, because sources rely on different nomenclature authorities.

† For simplicity and conciseness, where several species in a single genus have been identified, insects are grouped by genus, for example, *Asynapta* spp.

higher in poor crop years (Speers 1967), because adult female insects have fewer cones on which to concentrate (Lanz 1943). Even in good cone crop years, the number of emerging adult insects may be positively correlated with the flowering intensity of the food plants, with the most important factor influencing the size of the insect population being the amount of seeds produced (Annala 1982). Little in-depth research on the biology, ecology, and effective control of fir seed and cone insects has been done (Gara 1982).

Although cone and scale midges cause no significant loss, seed or gall midges may reduce seed yields (up to 72%) (Skrzypczynska 1985) by fusing seeds to the scales, although germinability of galled noble fir seeds was not reduced (Franklin 1974b). Likewise, larvae of *Spermatolonchaea viridana* L. (table 4) cause deformations on the cone scales and seed wings of Cilician fir in Turkey but do not affect the seeds (Kayacik 1964).

Most insects damage seeds directly, but the spruce budworm—*Choristoneura fumiferana* (Clemens), a defoliating insect—also attacks balsam fir by feeding on pollen in

developing male strobili (Bess 1946; Blais 1952; Greenbank 1963). Also, the budworm girdles the basal parts of developing female strobili (Powell 1973), thereby reducing the formation of female buds and hence the cone crop for the following season (Powell 1973; Woodwell 1961). Severe defoliation decreases tree vigor, food reserves, and cone production (Hall 1981; Schooley 1975, 1976, 1978), and the trees become susceptible to secondary attacks (by root rot and beetles), a condition referred to as Stillwell syndrome (Moody 1988).

In some localities, Douglas squirrels (*Tamiasciurus douglassi*) and red squirrels (*T. hudsonicus richardsoni*) cut and cache large quantities of cones of Pacific silver, grand, and subalpine firs. They may sever the twigs that support the current cones, and also those that bear the female buds for the next year's crop (Franklin 1964; McKeever 1964; Smith 1968). In the Northeast, voles and mice (*Clethrionomys gapperi*, *Peromyscus maniculatus*, *P. leucopus*, and *Microtus pennsylvanicus*) prefer spruce (*Picea glauca*, *P. rubens*)

and pine (*Pinus strobus*, *P. resinosa*) seeds to balsam fir seeds, even in extreme hunger (Abbott 1962; Abbott and Hart 1960). However, a titmouse (*Parus ater*) is known to eat European silver fir seeds, causing many problems in Slovakian nurseries (Bauer and Tichy 1960). Titmice, voles (*Clethrionomys rutilus*), mice (*Apodemus* spp.), and shrews (*Sorex* spp.) can destroy 60 to 80% of the Siberian fir seed-crop in Siberia (Vladyshevskii and Shtarker 1982).

Several fungi associated with fir seeds usually make their presence apparent during stratification and germination (table 5), but it has not been shown if the cones become infected before harvest or during harvest, handling, transporting, or processing. The fungal pathogen *Caloscypha fulgens* (Pers.) Boud. was found in 25% of stored grand fir seedlots, but not in Pacific silver fir (Sutherland 1979). Dwarfmistletoes (*Arceuthobium* spp.) attack firs, especially red and white firs, to such an extent that stand control measures can be required (Hawksworth and Wiens 1965; Parmete and Scharpf 1963). Infected trees show less growth and

Table 5—Abies, fir: fungi and other organisms isolated from fir cones and seeds

Organism	Host tree species
<i>Alternaria</i> spp.	<i>Abies</i> spp.*
<i>Aspergillus</i> spp.	<i>Abies</i> spp.
<i>Botrytis cinerea</i> Pers.: Fr.	<i>A. amabilis</i>
<i>Caloscypha fulgens</i> (Pers.) Boud.	<i>A. grandis</i>
<i>Cephalosporium</i> spp.	<i>Abies</i> spp.
<i>Ciboria rufo-fusca</i> (O. Weberb.) Sacc.	<i>A. alba</i> , <i>nordmanniana</i>
<i>Cladosporium</i> spp.	<i>A. grandis</i> , <i>magnifica</i> , × <i>shastensis</i>
<i>Cylindrocarpon</i> spp.	<i>A. amabilis</i> , <i>sibirica</i> , <i>Abies</i> spp.
<i>Fusarium culmorum</i> (Wm.G. Sm.) Sacc.	<i>Abies</i> spp.
<i>Fusarium moniliforme</i> J. Sheld.	<i>A. grandis</i> , <i>nordmanniana</i>
<i>Fusarium oxysporum</i> Schlechtend.: Fr.	<i>A. grandis</i> , <i>procera</i>
<i>Fusarium roseum</i> Link: Fr.	<i>A. grandis</i> , <i>procera</i>
<i>Fusarium semitectum</i> Berk.& Ravenel var. <i>majus</i> (Wollenweb.)	<i>A. amabilis</i>
<i>Fusarium</i> spp.	<i>Abies</i> spp.
<i>Geniculodendron pyriforme</i> G.A. Salt	<i>A. amabilis</i> , <i>grandis</i>
<i>Heterobasidion annosum</i> (Fr.:Fr.) Bref.	<i>Abies</i> spp.
<i>Lirula macrospora</i> (R. Hartig) Darker	<i>Abies</i> spp.
<i>Melanospora zamiae</i> Corda	<i>Abies</i> spp.
<i>Mucor</i> spp.	<i>Abies</i> spp.
<i>Papulospora</i> spp.	<i>A. amabilis</i> , <i>grandis</i>
<i>Penicillium</i> spp.	<i>A. amabilis</i> , <i>grandis</i> , <i>magnifica</i> , × <i>shastensis</i> , <i>procera</i>
<i>Phoma</i> spp.	<i>Abies</i> spp.
<i>Rhacodium therryanum</i> Theum.	<i>A. sachalinensis</i>
<i>Rhizoctonia solani</i> Kühn	<i>A. balsamea</i> , <i>fraseri</i> , <i>grandis</i>
<i>Sclerotium</i> spp.	<i>A. mariesii</i> , <i>Abies</i> spp.
<i>Trichoderma</i> spp.	<i>A. amabilis</i> , <i>grandis</i> , <i>Abies</i> spp.
<i>Tricothecium roseum</i> (Pers.:Fr.) Link	<i>A. grandis</i>
<i>Truncatella hartigii</i> (Tub.) Steyaert	<i>Abies</i> spp.
Virus-like particles	<i>A. alba</i> , <i>homolepis</i>

Sources: Anderson (1985), Bloomberg (1969), Buchwald and others (1961), Edwards and Sutherland (1979), Eremko and others (1989), Flachmann and others (1990), Hayashi and Endo (1975), Heit and Natti (1969), Kolotelo (1994), Littke and Browning (1991), Ono (1974), Prisyazhnyuk (1960). Fungal nomenclature mainly according to Farr and others (1989).

* Individual tree species not determined.

vigor (Laacke 1990a&b) and produce fewer seeds with lower viability (Hawksworth 1978).

Collection of cones. Fir seeds ripen in 2 recognizable phases, the first being the accumulation of organic materials, and the second involving metabolic changes within the seeds, so that germinative capacity continuously increases up to (or almost up to) seed dispersal (Edwards 1969; Franklin 1974b; Pfister 1967; Speers 1962; Weyerhaeuser 1958; Yanagisawa 1965). In noble fir, germination increases to a peak, accompanied by an increase in seed dormancy (Edwards 1969, 1982a), then levels off before seed dispersal (Edwards 1969; Franklin 1965; Rediske and Nicholson 1965); a similar trend occurs in Turkey fir (Beskok 1970). In contrast, in grand (Pfister 1966; Snyder 1976) and Fraser firs (Speers 1962) germination continues to increase right up to seed dispersal. For this reason, seeds should not be removed from fir cones—particularly cones collected early—immediately after collection, because low seed viability may result (Edwards 1969; Rediske and Nicholson 1965; Speers 1962) due to curtailment of the second phase of ripening.

The period for cone collection, from the time organic accumulation ends until seed dispersal begins, typically ranges from 4 to 6 weeks, depending on location. Calendar dates are unreliable and vary with locality—especially elevation—and weather patterns, but if cone storage facilities are available, collections in the West may begin by mid- to late-August. Knowledge of local ripening conditions (degree-day summations are useful) and the use of the few known ripeness indices (table 6) can aid the decision to begin collecting (Edwards 1982a).

Judging when to start cone collection can be a major difficulty. In many tree genera, not all fruits mature simultaneously, maturation date varying among cones on the same tree (cones on the southern aspect of the crown generally ripening earlier), among trees within the same stand, from stand to stand in the same year, and from one year to the next (Edwards 1980a; Franklin 1965). The extent to which collections can be made in advance of seed dispersal is largely governed by the fact that fir seed development ceases if the cones are detached from the parent tree too soon, especially if the primary organic-accumulation phase is incomplete. Early-collected cones are more sensitive to handling method, but this sensitivity declines in later collections (Edwards 1980a). Cone maturity indices are very important for firs, therefore.

In firs, cone and seed color (common maturity indices in many conifers) may be more closely related to seed source and to individual parent tree than to ripeness. For example, mature cones of white fir may be either green or purple,

with green cones having (on average) 25% fewer viable seeds, and the seeds weighing 15% less, than seeds from purple cones, although there were significant interactions with elevation of the seed source (Farris and Mitton 1985). Similarly, in the former Yugoslavia, mature seeds of white fir from violet cones germinate better than those from yellow cones (Stilinovic and Tucovic 1971). Quality of Siberian fir seeds is better from trees with light-green cones than that of trees with dark-green cones (Kirgizov and Mosin 1980). Progressively southern sources of European silver fir in Bulgaria have darker colored and more germinable seeds (Gagov 1973).

Nevertheless, workable indices of fir maturation have been devised for some species based on changes in cone color, seedcoat color, or the development of color in the seed wing (table 6), although this remains subjective and depends on the experience of the collector (Rudolf 1940). When cones of noble fir in Denmark begin to change from green to yellowish brown and bend down the branches because of their weight, natural seedfall is 2 to 3 weeks ahead; thus at the first signs of cone scale separation, the cones are collectable (Dalskov 1960).

Two interrelated parameters—cone moisture content and cone specific gravity—are more objective and reliable indices (Rediske 1961). There is some general agreement (table 6) that maturity is reached when specific gravity of cones has fallen below 0.9, indicating a moisture content below 50%. Either of these 2 parameters must be measured only on freshly picked cones, and because cone moisture content is not easily determined in the field, specific gravity is usually the measurement of choice. Thus, if cones of white and red firs (and of other conifers) float in kerosene, a 50:50 mixture of kerosene and linseed oil, or any mineral/lubricating oil of specific gravity 0.85 to 0.80, the crop is ready to be picked (Lanquist 1946). However, cone specific gravity is of little use in judging maturity in Japanese fir (Yanagisawa 1965).

Although no documented use of the following attribute has been found outside British Columbia, one criterion for judging when to begin fir cone collections is to allow a sample of longitudinally cut seeds to dry out overnight at room temperature. Then, if the megagametophyte tissue shows very little or no shrinkage away from the testa in most (if not all) of the seeds, they are sufficiently well developed for cone collections to begin (Dobbs and others 1976; Edwards 1980a, 1982a; Eremko and others 1989). Shrinkage of the megagametophyte indicates that the seeds are still high in moisture content and that collection should be delayed.

Table 6— <i>Abies</i> , fir: cone and seed maturity indices identifying earliest collection date		
Species	Cones	Seeds
<i>A. amabilis</i>	Green with yellow tinge, turning gray or purple	Seedcoat cream or tan; wing light brown/pale purple, with brown margin; megagametophyte opaque & firm; embryo yellow/yellow-green, 90% extended; rudimentary cotyledons well developed*
<i>A. balsamea</i>	Turning purple; moisture content < 60%	—
<i>A. concolor</i>	Specific gravity 0.85–0.96	Wing uniform brown, deep magenta edge; seed detached/loosely attached to cone scale; embryo pale yellow-green, 9 of 10 fully elongated
<i>A. firma</i>	Turning yellow-brown, losing luster	—
<i>A. fraseri</i>	Blue-green turning brown	Distinct seedcoat color visible
<i>A. grandis</i>	Light brown; specific gravity <0.90 In BC: turning gray or purple.	Wing purple-brown (green-colored cones only); seed detached from cone scales In BC: seedcoat cream or tan; wing light brown/pale purple, with brown margin; megagametophyte opaque & firm; embryo yellow/yellow-green, 90% extended; rudimentary cotyledons well developed
<i>A. guatemalensis</i>	Turning dark green or purple; resin droplets visible on exterior	Wings yellow
<i>A. homolepis</i>	Turning yellow-brown & losing luster	—
<i>A. lasiocarpa</i>	Green with yellow tinge, turning gray or purple	Seedcoat cream or tan; wing light brown/pale purple, brown margin; megagametophyte opaque & firm; embryo yellow/yellow-green, 90% extended; rudimentary cotyledons well developed
<i>A. magnifica</i>	Specific gravity < 0.75.	Wing uniform brown, deep magenta edge; detached/loosely attached to cone scale; embryo pale yellow-green, 8 of 10 fully elongated
<i>A. mariesii</i>	Turning brown & losing luster.	—
<i>A. procera</i>	Light brown; specific gravity < 0.90	Wing uniform brown; detached from cone scale; embryo 90% extended & firm; crude fat content 25 mg/g dry weight †
<i>A. sachalinensis</i>	Turning brown & losing luster	—
<i>A. veitchii</i>	Turning brown & losing luster	—

Sources: Anon. (1998), Bakuzis and Hansen (1965), Donahue and others (1985), Eremko and others (1989), Franklin (1965, 1974b), Oliver (1974), Pfister (1967), Snyder (1976), Speers (1962), Stoeckeler and Jones (1957).
* Using 10 × lens.
† Rediske and Nicholson (1965).

The ratio of embryo length to the length of the cavity in the megagametophyte (figure 10) is also widely employed in British Columbia for judging when to collect (Eremko and others 1989). Embryos do not have to be fully elongated to be germinable, but seeds with embryos less than 50% extended germinate less vigorously and predictably. This extension can be determined readily by field personnel equipped with a sharp knife, a 10 × lens and a little training (Dobbs and others 1976; Eremko and others 1989), and it can be recorded easily on x-ray film. Thus, when a majority of the embryos—94% in white fir seeds (usually some 3.5 weeks before seedfall) and 84% in red fir (2 weeks before seed dispersal)—are fully elongated, provided other criteria are satisfactory (table 6) the cones are ripe enough to collect (Oliver 1974).

Because megagametophyte tissues do not mature as quickly as the embryos, collections should be delayed until these tissues have achieved a firm consistency (similar to the meat of a coconut), that is, they have lost their earlier watery, translucent appearance. Megagametophyte tissues will then exhibit little or no shrinkage or curling and retain a relatively firm, fresh appearance when longitudinally sliced seeds are left uncovered overnight at room temperature. The current prescription is to delay collections until embryos are at least 90% extended (figure 10), by which time the megagametophyte tissue has matured sufficiently also (Edwards 1982a; Eremko and others 1989) (table 6). As previously mentioned, another useful criterion of seed maturation is the degree to which the seeds have abscised/detached from the ovuliferous scales on which they developed. Seed

detachment indicates that they have ceased, or have greatly reduced, the accumulation of organic materials and that the seedcoats are undergoing the final stages of their development and becoming impermeable, usually signaled by the attainment of a distinct seedcoat (and seedwing) color.

Chemical indices of maturity have been explored. The crude fats and lipids that—together with protein bodies—are the main storage structures in fir seeds (Kovac and Wrischer 1989) reach high levels in mature seeds of several fir species (Bennett 1966). At a seed crude-fat content of 250 mg/g (dry weight), noble fir cones were judged to be ripe enough to collect, but that some artificial ripening (the “after-ripening” phase) prior to seed extraction was required to achieve maximum seed quality (Rediske and Nicholson 1965). A later study on maturing noble fir seeds was unable to substantiate the pattern of crude fat accumulation (Edwards 1969). Metabolism of fir seed lipids during germination has been linked to the glyoxalate cycle (Firenzuoli and others 1968).

As a general recommendation, no single criterion should be relied on when judging maturity of fir seeds. Rather, several characteristics such as seedcoat and wing color, seed detachment from cone scale, and embryo color and extension should be assessed before large-scale cone collections are undertaken (Oliver 1974; Snyder 1976).

Because fir cones disintegrate and seeds disperse at maturity, then making cone collection impossible, it is necessary to collect in advance of full seed ripeness. Collections may be by hand from standing (Seal and others 1965) or recently felled trees, or from squirrel-cut cones on the ground or from squirrel caches. Extensive collections in the western United States used to be made by climbing open-grown trees in 40- to 70-year-old stands, and some cones are still collected this way, but caution is required because fir stems are relatively brittle and tops may break out (Franklin 1974b). Cones collected by climbing should not be thrown to the ground, even in sacks, because of the danger of resin vesicle damage discussed earlier. Collections made close to the time of natural seed dispersal—when the cones are lighter (drier), the seeds are riper, and the seedcoats tougher—still require care to avoid resin vesicle injury (Dalskov 1960).

Synchronizing cone collections with felling operations, so that cones can be collected from newly felled trees reduces this danger, but the cones may disintegrate upon impact with the ground (making gathering time consuming) and may be difficult to separate from the branch debris (Pigott 1994). Squirrel-cut or -cached cones are easier to collect and the seeds are more likely to be ripe for 2 reasons: squirrels in the Pacific Northwest (at least) do not

begin to cut in quantity until cones are approaching maturity, so that full seed development can be achieved because the cones are typically cached in cool, moist microsites (Franklin 1974b; Halvorson 1986; Pedro White and White 1986). However, red squirrels in the Rocky Mountains and Douglas squirrels in the southern Cascades have been seen to cut and begin caching white fir cones before they were fully mature (Fowells and Schubert 1956; Lanner 1983); red squirrels also cut immature subalpine fir cones (Lanner 1983). The high crude-fat content of conifer seeds, especially that of fir seeds, probably resists spoilage in the caches (Halvorson 1986). Although there is no direct evidence that seeds collected in this way are inferior, some squirrel-cut fir cones may have been bruised, and the seeds damaged, on impact with the ground. Also, the parent trees from which they were cut will not be known. Because squirrels collect far more cones than they can eat, they later fail to find all the cones they have cached. Thus only a portion of the caches are found by human collectors and there is no danger of depriving the animals of their winter food supply (Pedro White and White 1986).

Shooting-out cone-laden tops of fir trees with a rifle has been used with some degree of success, with smaller crews collecting many (if not more) cones than by climbing. However, there are inherent dangers in this technique, especially in the vicinity of other work crews, and/or near urban areas (Dobbs and others 1976). Cone harvesting by mechanically shaking the trees was unsuccessful on both noble and grand firs (Anon. 1970).

One technique developed in the past 2 decades is the aerial cone-rake, a device designed to be lifted by helicopter and lowered over the crowns of cone-bearing trees (figure 13). In the process of retrieving the device, cones and cone-laden branches are raked from the tree by a circle of tines and collected in a basket (figure 14). When the basket is full, the device is lowered to a cone-dump site and the cones and slash sorted by hand (Wallinger 1986) (figure 15). By this means, larger volumes of cones per day—up to 10 hl (28 bu) of Pacific silver fir, 10 hl or more of grand fir, but only 2 to 5 hl (5 to 15 bu) of subalpine fir—can be collected in a much shorter time than by traditional methods (Eremko and others 1989; Portlock 1996), making the technique economically viable. There are additional advantages in that cone collection can begin closer to seed dispersal, that is, full maturity, and cones can be collected from areas that have no road access. The technique works best on tree species (such as fir) that bear cones in the upper third of the crown. Cone rakes have been used to collect over 90% of all fir cones collected in British Columbia (Wallinger 1986). All aspects

Figure 13—*Abies procera*, noble fir: aerial collection using a cone rake (courtesy of D. Pigott).



Figure 14—*Abies procera*, noble fir: cones collected by aerial cone rake (courtesy of D. Pigott).



of the application of the technique, as well as aerial clipping/sawing, and aerial topping for cone collection, have been comprehensively reviewed (Camenzind 1990).

Cone and seed processing. Seed germinability of a number of species, including white (Oliver 1974), grand (Pfister 1966), Nordmann (Muller 1971), and noble firs (Edwards 1969; Franklin 1965; Rediske and Nicholson 1965) can be improved by storing the cones under cool, moist conditions for several weeks after collection. In contrast, cones of red fir need to be collected as close as possible to seed fall (Oliver 1974). Artificial ripening of early-collected seeds allows cone collections to be started sooner, thus extending the collection period, so that immature cones from logging operations can be used (Edwards 1982a). The maximum period of collection prior to the onset of natural seed dispersal appears to be around 6 weeks, but it is safer

to think in terms of only 4 weeks. Warmer, drier summers (after pollination) may allow earlier starts to cone collection than cool, wet summers. In most years, the beginning of August is probably the earliest any cones should be collected, and only then if storage facilities can provide the cool, slow-drying conditions required. Because water loss is an intrinsic part of the maturation process (Pollock and Roos 1972) in orthodox seeds (see chapter 1), the cones need to be dried, preferably slowly, so that mold build-up and heating are avoided.

The period of cone storage is governed by the natural disintegration of the cones; once they have fallen apart they can be regarded as fully mature (Edwards 1969; Muller 1971). Well-spaced (not stacked) sacks of cones should be stored for periods of several weeks or months in drying sheds with good air circulation, for cones mature best in cool (<10 °C), shaded conditions (Edwards 1969; Franklin 1965; Rediske and Nicholson 1965). Storing grand fir cones with their bases in water or nutrient solutions gave higher seed weights and increased germination (Pfister 1966), but storing grand and noble firs cones in damp peatmoss was deleterious (Franklin 1965; Pfister 1966). For immature cones that are high in moisture, rebagging the cones as they arrive at the storage station and reducing by half the amount of cones in each sack will promote good curing. Periodic inspection for deterioration and turning the material within the sacks are good cone storage practices. Spreading balsam fir cones on mesh-bottomed trays is advantageous also; cones should not be more than 6 cm deep and they may

Figure 15—*Abies grandis*, grand fir: bagging aerially collected cones at a dump site; note the wooden box by picker's knee, this is a cone-volume measuring device (courtesy of D. Pigott).



need turning at least once each day, especially if they settle onto the trays in a compact mass (Carman 1953). No deterioration in seed quality was found when Pacific silver fir cones were stored for 6 months (October to March), either in a covered shed exposed to ambient external temperatures or in a refrigerated compartment at 2 °C prior to seed extraction, provided the cones had been properly handled in the field (Leadem 1982). Therefore, fir cones may be among the last to be scheduled for seed extraction, December or even later, by which time full seed maturity has been achieved and the cones have completely disintegrated, making seed extraction simpler. It cannot be over emphasized that fir seeds should not be extracted from the cones immediately after collection, especially from early-collected cones, otherwise viability is likely to be low.

Cones should be placed in proper storage facilities as soon as possible after harvesting and on no account should they be left untended at the collection site or in a vehicle for more than a few hours. Especially for premature collections, interim collection facilities in the field are essential to allow for continuing maturation (Dobbs and others 1976; Eremko and others 1989; Stein and others 1974; see also chapter 3). Incompletely ripened fir seeds store poorly, with serious losses in germinative capacity (Muller 1971; Yanagisawa 1965). Even when collected close to full maturity, fir cones that are not placed in suitable interim storage which will permit continued loss of moisture, the heat of respiration is liable to cause an increase of the surrounding temperature and non-dormant seeds may sprout before the cones can be processed. Such viviparous germination has been observed in subalpine fir (figure 16 and 17) and in other conifer species (Edwards 1980a). Although interim storage is a minor component of seed collection costs, it is important and yet is often poorly addressed (Pigott 1994). Cones should be moved to a more permanent storage location as soon as other operations permit, but for reasons similar to the above, long-distance transportation should be avoided. Turpin (1963) recommended field extraction using an inexpensive, easily erected structure so that only the extracted seeds of European silver, white, grand, and Sierra white firs are shipped.

Processing fir cones (table 7) is similar to processing cones of other conifers, except that if the fir cones have been stored for 2 to 3 months, they will have disintegrated naturally, the seeds will have separated from the scales, and the kiln-drying and tumbling steps can be dispensed with. In British Columbia, storage of the cones of Pacific silver, grand, and subalpine firs not only conditions the cones, but also, if the cones are dried to a target-moisture content of

Figure 16—*Abies lasiocarpa*, subalpine fir: viviparous germination, with seeds germinating in the cone before they could be extracted (courtesy of D. Pigott).

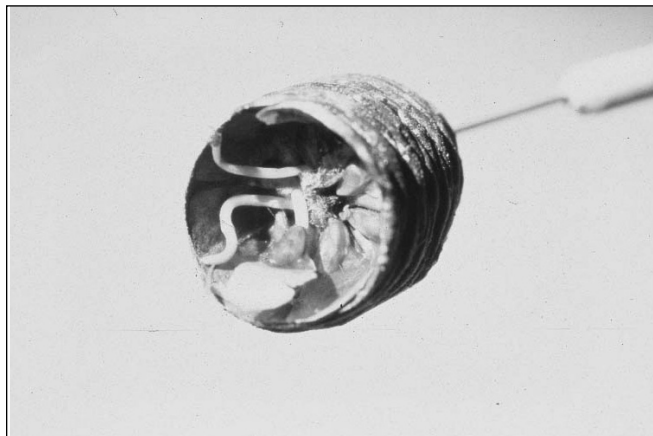


Figure 17—*Abies lasiocarpa*, subalpine fir: viviparous germination, with seeds germinating while still attached to the ovuliferous scales (courtesy of D. Pigott).



15%, damage through seedcoat abrasion is reduced and makes the seed wings become more brittle and easier to break off (Rooke 1997).

When additional drying is required, cones should be air-dried for 3 weeks or more at 20 to 30 °C (Franklin 1974b) where ambient conditions permit. If kiln drying is absolutely necessary, temperatures between 30 and 38 °C for up to 14 hours are used (table 7), but care must be taken to avoid damage through too rapid or prolonged drying. When possible, kiln-drying should be avoided so that any possibility of heat damage to the seeds is eliminated.

Partially or wholly disintegrated cones are tumbled or passed over vibrating screens (Carman 1953; Rooke 1994) to separate the seeds from the cone axes, scales, and bracts.

Table 7—*Abies*, fir: cone drying schedules

Species	Air-drying* period (days)	Kiln-drying period	
		Time (hr)	Temp (°C)
<i>A. amabilis</i>	60–180	6–14 †	30–38
<i>A. balsamea</i>	20–30	0	—
<i>A. concolor</i>	7–14	0	—
<i>A. firma</i>	14	(‡)	48
<i>A. fraseri</i>	30–45	0	—
<i>A. grandis</i>	60–180	6–14 †	30–38
<i>A. guatemalensis</i>	< 60§	0	—
<i>A. homolepis</i>	14	(‡)	48
<i>A. lasiocarpa</i>	60–180	6–14 †	30–38
<i>A. magnifica</i>	8–21	0	—
<i>A. mariesii</i>	14	(‡)	48
<i>A. procera</i>	60–180	6–14 †	30–38
<i>A. sachalinensis</i>	14	(‡)	48

Sources: Anon. (1998), Edwards (1982a), Franklin (1974b), Heit (1968a), Heit and Eliason (1940), Jones (1962), Leloup (1956), Speers (1967).
* At ambient air temperature; cooled (<10°C) conditioning facilities are superior.
† If air-drying not possible, but cones should not be processed immediately after harvest.
‡ In a rotary kiln; seeds removed from heat as soon as they fall through the tumbler mesh.
§ In the shade.

Screening is more gentle and less damaging to seedcoat resin vesicles. Nordmann fir seeds can be extracted by passing the cones between series of rotating and fixed teeth, the spacing of which gradually decreases (Saralidze and Homeriki 1964). The separated seeds are then de-winged, a step during which fir seeds can be easily damaged (Allen 1958; Franklin 1974b; Roe 1948b; Weyerhaeuser 1957), thereby exacerbating losses of viability during storage (Rediske 1967). Small lots are best de-winged by hand (Roe 1948b), but even this can rupture some vesicles in noble fir (Edwards 1982a). Grand fir seeds de-winged by hand germinated significantly better than those commercially processed (Wang 1960). When mechanical processes must be used on large lots, one common technique for true firs is to break the wing at or near the point that it extends beyond the seedcoat, relying on friction in a mass of seeds agitated by gentle rolling of the seed mass (Rooke 1994). Using a spiral screw or auger, or drawing the seeds through tubing connected to a vacuum cleaner, may achieve the same goal. Some machines employ rotary screens that permit the wing, but not the seed, to protrude and to be broken by a brush. Some wings may be removed during the initial vibratory-screening to separate seeds from other cone parts (Carman 1953). Special processing and sowing machinery designed for European silver fir in Poland are based on morphological measurements of the seeds (Czernik 1993).

All these methods, which are performed on dry seeds and can be quite effective in breaking the seedwing, provide for impact damage to the resin vesicles and to the seedcoat itself. Prolonged de-winging, or de-winging fir seeds in a

mixture that includes a considerable amount of hard, sharp debris such as cone scales, can cause considerable injury. When subalpine fir seeds were run through a brush de-winger 3 times, 50% of their original viability was lost (Allen 1958). A simple, efficient 2-step process using a scalper treatment followed by pneumatic separation was recommended for white and red fir seeds by Kitzmiller and others (1975). The scalper did less damage than hand de-winging, and although the pneumatic separator inflicted some injury, it eliminated most of the impurities remaining after the scalper treatment.

As described earlier, the fir seedwing forms on the adaxial (upper) surface of the developing seed and is attached to the seed by an integument. Two narrow flaps wrap around the long margins of the seedcoat toward the abaxial surface, thereby gripping the seed (figure 6). Most integuments remain attached to dry seeds after normal de-winging but often loosen and separate from the seedcoats when they become wet during a germination test. This suggests that the seeds might be de-winged when wet, but no documented use of the method is known for fir seeds.

Gravity table cleaning can be very efficient and gentle (Rooke 1994). An aspirator sorter works well for cleaning and for separating filled and empty seeds of Pacific silver, grand, and subalpine firs (and other conifer seeds), although small-filled seeds generally accumulate in the empty seed fraction, whereas large-empty seeds separate out with the filled seeds (Edwards 1979). Prior seed sizing improves the efficiency of this technique.

The IDS (incubating-drying-separating) method (see chapter 3) works well on seeds of other Pinaceae (Bergsten 1993; Karrfalt 1997; Simak 1984) and has been used to remove seeds infested with *Megastigmus spermotrophus* Wachtl. (Sweeney and others 1991). A variant of the IDS method known as density separation processing (DSP) is used to upgrade seed quality of Pacific silver and subalpine firs in British Columbia. In 12 seedlots of Pacific silver fir, an average gain in germination of 24% and an increase in potential seedlings of 48% was obtained, but gains in seedlots of subalpine fir were smaller (Kolotelo 1993). The method does not work on all seedlots, especially those with a high proportion of immature seeds, and seedlots from sources above 1,000 m elevation (Kolotelo 1994); the reasons for this are not known. Another approach to flotation sorting has been described (Edwards 1978). Separation in other liquids, such as petroleum ether (Lebrun 1967) or absolute alcohol (Simak 1973) cannot be recommended because the ether is highly flammable and alcohol is phytotoxic to true fir seeds (Edwards 1980b).

Another advantage of processing fir cones late in the year during cold weather is that low temperatures solidify any resin that has leaked from the vesicles in the seedcoat or may be present as an impurity from other sources. This makes the resin less likely to gum-up processing machinery as well as making it easier to separate from the seeds. Resin/pitch is relatively dense, so it sinks and seeds float in a water separator. Seeds may be chilled as a first step in cleaning to reduce resin problems, but additional chilling may be required as the seeds warm up (Rooke 1994). When de-winging and cleaning to the desired level of purity are complete, seed moisture contents should be checked, adjusted as required, prior to cold storage. In the past, recommended processing standards of 20 to 35% viability used to be common for commercial lots of North American fir species (WFTSC 1966), and fir seed quality traditionally was low, rarely exceeding 50% germination (Franklin 1974b). This was often the result not only of poor (by present standards) seed processing methods that failed to remove many unfilled or partially filled seeds, but also of inadequate methods for overcoming dormancy.

Typical cone and seed yields and numbers of fir seeds per unit weight are listed in table 8.

Seed storage. Fir seed storage has been intensively researched (Barton 1961; Holmes and Buszewicz 1958, 1962; Magini 1962; Wang 1974) and is summarized in table 9. Fir seeds are orthodox in storage behavior, meaning that they store well at low temperatures and moisture contents.

Most experts agree, however, that the seeds lose viability quickly unless special precautions are taken, possibly because of the high oil and resin contents that (when oxidized) may be toxic to the embryo (Bouvarel and Lemoine 1958). Guatemalan fir seeds have been found to lose their viability in a few weeks; one report states that they cannot be dried below 12% moisture content and are considered recalcitrant (Anon. 1998). However, other workers recommend drying them to 6 to 8% moisture, which permits storage for nearly a year (Donahue and others 1985) (table 9). The embryonic radicle usually dies first in stored European silver fir seeds (Gogala and Vardjan 1989).

One decision that must be made is whether the seeds are to be stored for a few months or for a year or more, because lower temperatures will be required for longer periods (Tocci 1966). For example, it may be pointless to store large volumes of seeds for periods longer than the interval between good cone crops (Edwards 1982a). Although the superiority of sub-freezing conditions as low as -17°C has been amply demonstrated (they are commonly used for long-term storage of fir and other orthodox seeds), higher temperatures (never above 4°C) can suffice for short-term storage. Fir seeds store well for 3 to 10+ years in sealed containers (Allen 1957; Gradi 1966), but such containers are not a panacea if the seeds have not been properly prepared (Gradi 1966; Tumbarello 1960). Experiences with fir-seed storage durations and conditions have been amply reported (Allen 1957; Carrillo and others 1980; Isaac 1930a, 1934; Issleib 1956; Larsen 1922; Roe 1948b; Rohmeder 1953; Rudolf 1952; Schubert 1954; Vilmorin 1944; Vlase 1960), and cryopreservation of fir seeds also has had some success (Jorgensen 1990; Neuhoferova 1994; Stanwood and Bass 1978).

In principle, storage temperature is of greater significance when seed moisture content is high and, conversely, has less effect when moisture content is low (Barton 1953; Magini and Cappelli 1964a&b). At low moisture contents, seed storage becomes almost independent of temperature, an inverse relationship demonstrated by Danielson and Grabe (1973) in a 2-year trial with noble fir seeds that (a) deteriorated rapidly when moisture content was above 12%, irrespective of storage temperature; (b) maintained viability at 12% moisture when stored at -18°C , but not at $+5^{\circ}\text{C}$ or $+20^{\circ}\text{C}$; (c) maintained viability at 6 to 9% moisture when stored at -18°C and $+5^{\circ}\text{C}$; and (d) maintained viability at 4% moisture when stored at -18°C , $+5^{\circ}\text{C}$, and $+20^{\circ}\text{C}$. For firs in general, the critical safe moisture level appears to lie between 5 and 8% of seed fresh weight (Wang 1974).

Table 8—Abies, fir: cone measurements and yields of cleaned seeds

Species	Cone wt/vol		No. of cones	Seed wt/		Seed wt/ cone vol	Seeds/ cone	Range		Seeds/wt		Samples
	kg/hl	lb/bu		/hl	/bu			g/kg	oz/100lb	/kg	/lb	
<i>A. alba</i>	36	28	—	—	55	89	—	17,400–41,000	7,900–18,600	22,500	10,200	>72
<i>A. amabilis</i>	—	—	—	—	—	—	400	17,200–36,400	7,800–16,500	24,250	11,000	66
	—	—	—	—	—	—	—	21,800–45,900	9,900–20,800	30,450*	13,800*	8
<i>A. balsamea</i>	45	35	2,700–5,500	1,000–2,000	—	—	—	66,150–208,400	30,000–94,500	131,400	59,600	42
<i>A. concolor</i>	39–45	30–35	—	—	32	51	—	18,950–39,100	8,600–17,720	24,500	11,100	46
<i>A. firma</i>	—	—	—	—	—	—	—	20,500–30,900	9,300–14,000	25,150	11,400	>12
<i>A. fraseri</i>	—	—	2,500–2,700	900–1,000	—	—	—	117,950–173,650	53,500–78,750	134,050	60,800	10
<i>A. grandis</i>	—	—	700	250	—	—	—	26,250–63,500	11,900–28,800	40,600	18,400	144
	—	—	—	—	—	—	—	—	—	44,550*	20,200*	12
<i>A. guatemalensis</i>	—	—	—	—	—	—	—	30,000–43,000	13,600–19,500	36,500	16,500	>2
<i>A. homolepis</i>	54–64	42–50	800	300	—	—	—	32,200–49,000	14,600–22,200	43,650	19,800	19
<i>A. lasiocarpa</i>	—	—	—	—	—	—	—	52,700–108,700	23,900–49,300	76,750	34,800	19
	—	—	—	—	—	—	—	—	—	47,600*	21,600*	4
var. <i>arizonica</i>	—	—	—	—	—	—	—	38,800–56,200	17,600–25,500	49,200	22,300	8
<i>A. magnifica</i>	32–39	25–30	—	—	40	64	—	8,800–19,600	4,000–8,900	14,100	6,400	36
<i>A. mariesii</i>	33–41	26–32	850	312	—	—	—	42,100–65,050	19,100–29,500	50,700	23,000	>6
<i>A. nordmanniana</i>	40–50	31–39	—	—	125	196	—	11,550–19,000	5,700–8,600	15,650	7,100	>24
<i>A. procera</i>	—	—	200	80	—	—	—	20,300–42,100	9,200–19,100	29,800*	13,500*	>36
<i>A. sachalinensis</i>	—	—	—	—	—	—	—	65,050–118,000	29,500–53,500	97,000	44,000	>29
<i>A. x shastensis</i>	—	—	—	—	—	—	—	11,250–24,700	5,100–11,200	16,100*	7,300*	36
<i>A. veitchii</i>	—	—	—	—	—	—	—	50,700–173,750	23,000–78,800	99,200	45,000	17

Sources: Anon. (1998), Ching (1960), den Ouden and Boom (1965), Eis and others (1965), Fowells and Schubert (1956), Franklin (1974b), Ghent (1958), Heit (1968a), Lalu (1993), Lanquist (1946), Leloup (1956), MacDonald and others (1957), Rafn (1915), Rafn and Son (nd), Roe (1948b), Seal and others (1965), Sojanik (1950), Speers (1962), Tulstrup (1952), Wappes (1932).

* Seeds were 100% sound, separated by x-radiography.

Table 9—*Abies*, fir: experiences with seed storage conditions (recommended conditions are in **bold face**)

Species	Moisture content (% fresh wt)	Storage temp (°C)	Possible storage period (yr)
<i>A. alba</i>	5–7	–3 to 7	2–6
	5–8	–10 to –17	15
	< 9	–15	4–5
<i>A. amabilis</i>	6–8	–17	> 5
<i>A. balsamea</i>	5–8	+0.5 to +4	5
	6–8	–17	13
<i>A. cephalonica</i>	9–11	+ 4	1–2
<i>A. concolor</i>	5–8	0 to –18	7
	6–10	–18	3
<i>A. firma</i>	—	–2 to –4	> 6
<i>A. fraseri</i>	10–15	–12	—
<i>A. grandis</i>	5–8	–7	> 2
	7–10	–4 to –10	3
	11	–4	10 +
	9–11	+4	1–2
	< 9	–15	> 5
<i>A. guatemalensis</i>	6–8	+3 to +4	<1
<i>A. homolepis</i>	—	–2 to +4	> 6
<i>A. lasiocarpa</i>	5–8	–17	> 5
<i>A. magnifica</i>	9–11	+5	5
<i>A. mariesii</i>	—	–2 to +4	> 6
<i>A. nordmanniana</i>	9–11	+4	2
	< 9	–15	> 5
<i>A. procera</i>	6–9	0 to –18	7
	6–9	–4	> 10
<i>A. sachalinensis</i>	—	–2 to +4	> 6
<i>A. × shastensis</i>	11	–4	> 10

Sources: Allen (1957), Edwards (1982a), Franklin (1974b), Gradi (1966), Heit (1941, 1968b), Hofman and Vackova (1966), Holmes and Buszewicz (1962), Isseib (1956), Jones (1962), Loffler (1985), Machanicsek (1965), Mormann (1956), Radulescu (1968), Speers (1974b), Tillisch (1952), Tokarz (1974).

Pregermination treatments. Dormancy in fir may be both physical and physiological, but it apparently does not reside in the embryo, because embryos excised from unstratified noble fir seeds grow just as well as those from stratified seeds (Edwards 1969). Reasons for fir seed dormancy may be poor oxygen exchange or an inhibitor, because chipping the seedcoat to expose and remove a sliver of megagametophyte was as effective as (or more so than) stratification in stimulating germination of seeds of noble, Pacific silver, and grand firs (Edwards 1969) and European silver fir (Gogala and Vardjan 1989). Stratification also probably overcomes dormancy by reducing the mechanical restraint of the tissues surrounding the embryo (Edwards 1962, 1969; Jones and others 1991; Speers 1962; Wang 1960). Length of treatment is usually 21 to 28 days for laboratory tests (AOSA 1998; ISTA 1993), but other reported periods range from 14 to 120 days, and longer periods are the rule for nursery sowing (table 10). Longer treatments should be approached with care because they may result in more fungal/bacterial damage and premature germination (Edwards

1982a; Grittanuguya 1962; MacGillivray 1955; Zentsch 1960) and are best at lower seed moisture levels, as demonstrated for various hybrid firs (Wright 1950) (see also stratification–redry method below).

As with many tree seeds, dormancy among the firs is quite variable. Although stratification is routinely prescribed for European silver and Fraser firs, there are reports (Speers 1967; Zentsch and Jahnel 1960) that some seedlots of both species show little or no dormancy. The only way to determine whether or not a lot is dormant is to perform 2 germination tests—one with stratified seeds and one with unstratified seeds (Edwards 1962). The response to stratification may be regarded as an indicator of the degree of dormancy in the lot; after stratification, more-dormant seedlots germinate more rapidly than less dormant lots. In some instances, stratification has increased total germination as well as germination rate (Jones and others 1991; Pfister 1966; Speers 1968), although this may have been due partially to the seeds' germinating before development of the

Table 10—Abies, fir: nursery practices

Species	Stratification time (days)	Sowing season	Bare-root production			Container production				
			Seeding density /m ²	Seeding density /ft ²	Sowing depth in cm	Mulch ^a	Stock type	Container type ^b	Stock type	
<i>A. alba</i>	0 30 ^d -80	Fall Mid-Mar-mid-Apr	270-430	25-40	2 ^c	3/4 ^c	Pine needles	—	Styro 2, 5	1+0
<i>A. amabilis</i>	28 ^f — 30 ^d -120 ^h 30 ^d -120 ^h	Mar-Apr — Late Apr-early May Early Jan (1+0) for fall/winter lift Jan-Mar (1+0)	270-540	25-50	0.5-1	1/4-1/2	Straw ^g None	3+0, 3+1 1+0, 2+0, 3+0 3+0, 3+1	—	—
	—	—	330/row	100/row	—	—	—	—	313B, 410A	1+0
	—	—	—	—	—	—	—	—	313A&B, 410A, PCT410, 412A, 415B&D, 615A	1+0, P+1 ³
	—	—	—	—	—	—	—	—	313A, Styro 2, 5, & 7	1+0, 2+0, P+1
<i>A. balsamea</i>	0 30 ^d -120 ^h 30 ^d -120 ^h	Early Mar-early April Apr-early May (2+0) outdoors	220-54	20-50	—	—	—	—	415B, D, 412A	2+0
	0	Fall	—	—	—	—	—	—	—	—
	28-60 ^h	Late Mar-early Apr	—	—	—	—	—	—	Styro 2, 5, 7	1+0, 2+0, P+1
<i>A. bracteata</i>	0	Fall	—	—	0.5	1/4	—	2+0	—	—
	14-28	Feb-Mar	—	—	—	—	—	—	313A, 415B, D, 615A	1+0, 2+0, 2+1, P+1
<i>A. concolor</i>	0	Fall	270-430	25-40	2 ^c	3/4 ^c	Pine needles, peat moss, none	2+0, 2+2, 3+0, P+1	—	—
	28-60 ^f	Spring	220-540	20-50	—	—	Straw ^g , none	1+0, 2+0, 2+1	—	—
	14 ^d -80 ^h	Early Jan (1+0) for fall/winter lift	—	—	—	—	—	—	313B, 410A	1+0
	14 ^d -80 ^h	Feb-mid-Apr	—	—	—	—	—	—	313A, 410A, 415B, D, 412A, 615A, Styro 2, 5, & 7; Leach 1, 2	P+1
	—	Apr-early May (2+0) outdoors	—	—	—	—	—	—	415B, 412A	2+0
<i>A. firmid</i>	3 0-60	Apr-early May	—	—	—	—	—	2+2	—	—
<i>A. fraseri</i>	0 28-60 28 ^d -60 ^h 40-60 28 ^d -60 ^h 28 ^d -60 ^h 28 ^d -60 ^h	Fall Late Mar-early Apr Early Jan (1+0) for fall/winter lift Mid-March-early May Jan (1+0) Feb-early Apr Apr-early May (2+0) outdoors	220-540 270	20-50 25	0.3-0.5	1/8-1/4	Sawdust	3+0, 4+0	—	—
	—	—	—	—	—	—	—	—	313B, 410A	1+0
	—	—	330	100	—	—	—	—	415B, D, 615D	1+0
	—	—	—	—	—	—	—	—	313A, 415B, D, 615D, Styro 2, 5, 7	1+0, 2+0, P+1
<i>A. grandis</i>	0 0-42 ^{fg} 28 ^d -120 ^h 28 ^d -120 ^h 28 ^d -120 ^h	Fall Spring (early Apr-early May) Early Jan (1+0) for fall/winter lift Jan-early Feb (1+0) Early Feb-Apr	270-430 215-270	25-40 20-25	2 ^c 0.5-2	3/4 ^c 1/4-3/4	None, sawdust pine needles	2+0, 2+1, 3+0 1+0, 2+0, 3+0, P+1	—	—
	—	—	—	—	—	—	—	—	313B, 410A	1+0
	—	—	—	—	—	—	—	—	313A, 410A, 415B, D, 615A	1+0
	—	—	—	—	—	—	—	—	313A, 410A, 415B, D, 412A, 615A Leach 1, 2, Styro 2, 5, 7	P+1
	—	—	—	—	—	—	—	—	412A	2+0, P+1
<i>A. homolepis</i>	30-60 60-80	Spring Mid-Mar-mid-Apr	—	—	—	—	—	2+2	—	—
<i>A. koreana</i>	60-80	Mid-Mar-mid-Apr	—	—	—	—	—	—	Styro 2.5	1+0
<i>A. lasiocarpa</i>	0	Fall	—	—	—	—	—	—	Styro 2.5	1+0
var. <i>arizonica</i>	30 ^d -80 ^h	Mid-Mar-mid-Apr	—	—	0.3	1/8	Leaf mold	—	Styro 2.5	1+0, 2+0

A

Table 10—*Abies*, fir: nursery practices (Continued)

Species	Stratification time (days)	Sowing season	Bareroot production			Container production		
			Seedling density /m ²	Sowing depth cm	Mulch ^a	Stock type	Container type ^b	Stock type
<i>A. lasiocarpa</i> var. <i>lasiocarpa</i>	30 ^d –120	Early Jan (1+0) for fall/winter lift	—	—	—	—	313B, 410A	I+0
	30 ^d –120	Jan–to early Feb (1+0)	—	—	—	—	313B, 410A, 415B,D, 615A	I+0
	30 ^d –120	Jan–Mar	—	—	—	—	313A,B, 410A, PCT410,	I+0, 2+0, 2+1, P+1
	30 ^d –120	Early Mar–late May (2+0) (incl outdoors)	—	—	—	—	410A, 412A, 415B,D, 415B, 615A	I+0, 2+0, 2+1, P+1
<i>A. magnifica</i> var. <i>magnifica</i>	30–42 ^f	Mid-Mar–early May	215–430 (330/row)	0.5–1.5	1/4–1/2	None	—	I+0, 2+0, 2+2
	30 ^d –60 ^h	Jan	—	—	—	—	415B,D, 615A	I+0
<i>A. nordmanniana</i>	0	Late Mar–early Apr	—	—	—	—	Styro 2.5,7	I+0, 2+0, P+1
	50–70 ^f	Fall	220–540	2 ^c	3/4 ^c	Pine needles, none	—	—
	14 ^d –80 ^h	Spring	540	1–2.5	3/8–1	Peat moss	—	—
	30 ^d –80	Mid-Mar–mid-Apr	—	—	—	—	Styro 2.5,7	I+0, 2+0
<i>A. pinsrow</i> <i>A. procera</i>	0	Mid-Mar–mid-Apr	—	—	—	—	Styro 2.5	I+0
	0–42 ^f	Fall	220–540	2 ^c	3/4 ^c	Pine needles, none	—	—
	28 ^d –120 ^h	Spring	320–430	0.5–1.5	1/4–1/2	None	—	—
	28 ^d –120 ^h	Early Mar–early May	220–380	0.5–1.5	1/4–1/2	None	—	—
<i>A. sachalinensis</i> <i>A. x strastersis</i>	28 ^d –120 ^h	Early Jan (1+0) for fall/winter lift	—	—	—	—	313B, 410A	I+0
	28 ^d –120 ^h	Jan–early Feb (1+0)	—	—	—	—	313B, 410A, 415B,D, 615A	I+0
	28 ^d –120 ^h	Feb–Apr	—	—	—	—	615A, Styro 2.5, Leach 1,2	P+1
	28 ^d –120 ^h	Early Mar (greenhouse)	—	—	—	—	313A	2+0, P+1
<i>A. x strastersis</i>	30–60 ^k	Apr–early May (2+0) (incl outdoors)	—	—	—	—	415B,D, 412A	2+0
	0–42 ^f	Spring	220–430	1–1.5	3/8–1/2	None	—	2+2
	30 ^d –45 ^h	Late Feb–Apr	—	—	—	—	410A, 412A, Styro 5, Leach 1,2	I+0, 2+0, P+1

Sources: Adkins (1984), Adkins and others (1984), AOSA (1998), Asakawa (1968), Barton (1930), Bongio (1997), Bouvarel and Lemoine (1958), Curtis (1997), Fenimore (1997), Franklin (1974b), Garren (1997), Gates (1997), Hanson (1997), Heid (1964, 1967, 1968b), Heid and Blason (1940), Helson (1997), Henry and Blazich (1990), Holmgaard and Kjaer (1951), ISTA (1993), Kusisto (1997), Lehar (1997), Leloup (1956), MacDonald (1998), Moore (1997), Nagao and Asakawa (1963), NBY (1946), Pelton (1997), Rain and Son (nd), Riskin (1997), Rutar (1991), Snyder (1997), Speers 1962, Stuble 1998, Thompson 1997, Toumey and Stevens (1928), Triebwasser (1997), Trimble (1997), Tuistrup (1952), USDA Forest Service (1948), Vacowicz (1997), Wedman (1997), Wong (1997), Wright (1950), Zemanek (1997).

a Depth of mulch; peat moss, 0.5–1.5 cm (1–1.5 in); pine needles, 3–4.5 cm (1–1.5 in); sawdust, 0.5 cm (1/2 in); straw, 5 cm (2 in).

b Containers are all PSB type; Styro = Styroblocks. PCT = copper treated. The various containers listed have the following volumes: 313A, 52 ml (3.6 in³); 410A & PCT 410, 80 ml (4.9 in³); 415B, 93 ml (6.3 in³); 412A, 126 ml (7.7 in³); 415D, 172 ml (10.5 in³); 615A, 336 ml (20.0 in³); Styro 2, 39 ml (2.3 in³); Styro 5, 77 ml (4.7 in³); Styro 7, 121 ml (7.4 in³); Leach 1, 50 ml (3 in³); Leach 2, 164 ml (10 in³).

c Seeds covered with 1 cm nursery soil plus 1 cm sand.

d For 28–30 days only if intending to stratify.

e Some container transplants grown as P+2, P+3, P+4.

f Stratified in wet vermiculite, wet sand, or 1.5- to 2-day running-water soak and naked stratification.

g Used overwinter on first-year seedlings.

h Some free moisture left in plastic bag for long stratification.

i Light may be beneficial to germination.

j When not stratified, soaked 2 days before sowing.

k Alternatively, bury the seeds in snow for 50 days.

extensive fungal and bacterial molding common to more-slowly-germinating unstratified seeds (Edwards 1969). In noble fir, an increasing response to stratification as the seeds matured suggested that dormancy increased also, and that dormancy and maturity are interrelated (Edwards 1969). Whereas much of the variability in dormancy among seedlots may be attributable to seed origin, crop year, and time of collection, it may also be due to methods of cone processing, seed cleaning, and seed storage (Franklin 1974b; Wang 1960).

Laboratory and nursery stratification is often performed by refrigerating previously hydrated seeds in plastic bags or other containers—the “naked stratification” method (Allen and Bientjes 1954) favored in many nurseries for its ease of seed handling. More traditionally, dry seeds (at storage moisture contents) are placed on a moist medium (filter paper, vermiculite, or wet sand) and refrigerated. The moist filter paper method produced higher germination in noble fir because it was believed that the preliminary water soak that is the first step in the naked stratification procedure damaged the seeds by too-rapid tissue hydration, a phenomenon well-documented in legumes (Jones and others 1991). Soaking temperature in this noble fir study was 4 °C. However, no direct evidence for the damage, particularly its location, was provided. It is unlikely that any damage occurred in the tissues of the embryo. When noble fir seeds were soaked in water at 25 °C, after 48 hours most of the water was still in the seedcoat: the outer region of the megagametophyte had become moist, but the embryo was still dry (Edwards 1969). It was found that noble fir embryos require hydration of between 48 and 72 hours, even at room temperature, before they absorb enough moisture to be safely excised (Edwards 1969). Furthermore, when dry noble fir seeds are placed on a moist medium and refrigerated, they absorb water slowly during the entire chilling period and achieve a higher moisture content than seeds soaked in water at room temperature for the same length of time (Edwards 1971). Thus, in the above comparison, the moisture content of soaked seeds averaged 36%, whereas that of seeds chilled on moist filter paper averaged 43% (Jones and others 1991). This difference, small as it may appear, may have been significant due to the moisture content in soaked seeds possibly being less than adequate for optimal stratification to occur. In the development of the stratification/redry method (see below), it was found that if fir seeds were initially hydrated only to 35% moisture content (the same moisture content achieved after redrying), subsequent stratification was far less effective (Edwards 1986). If noble fir seeds are sensitive to imbibitional damage as claimed (Jones and others 1991), then the stratification/redry method—which involves a preliminary soak at

room temperature—must repair such damage since germination is greatly increased. However, no evidence for this repair, or the initial imbibitional-damage phenomenon, has been documented.

In any event, crop year, seed source, seed vigor (as distinct from seed quality), as well as chilling method and germination temperature played roles in the response of different seedlots of Pacific silver fir to stratification (Leadem 1986). Stratification response of Nordmann fir was also believed to be strongly seedlot dependent (Poulsen 1996). For balsam fir seeds, prolonged soaking in cold water containing a fungicide was deleterious (Kozłowski 1960), but changing the water weekly produced germination similar to that after stratification (Rudolf 1950). Best results with Manchurian fir occurred when soaked seeds were stored in snow for 1 to 2 months (Pavlenko 1972).

Stratification temperature range is often specified as 1 to 5 °C (Franklin 1974b), although testing laboratories typically use a narrower window of 3 to 5 °C. Stratifying grand and subalpine fir seeds at 2 °C was optimal (compared to –2, 5, and 7 °C), especially during extended chilling (Edwards 1982a). Fir seeds will germinate during stratification if left for a sufficient length of time (Allen 1960; Edwards 1969; Blazich and Hinseley 1984; Roe 1948b; Vabre-Durrieu 1956). Such observations reinforce the idea that stratification is incipient germination. In this regard, it should be remembered that late-dispersed seeds of numerous high-elevation firs (plus some other conifers) germinate in snow banks (Anon. 1951; Franklin and Krueger 1968; Gordon 1970; Hetherington 1965; Irmak 1961; Roe 1946; Stein 1951). Snow absorbs 99% of the infra-red (IR) radiation from sunlight, and dark-colored seeds embedded in snow may reach several degrees above freezing by absorbing these IR rays. However, these germinants seldom establish as seedlings when the snow melts (Gordon 1970; Stein 1951).

Despite the fact that lower than normal levels of seed moisture were known to benefit extended treatments of hybrid fir seeds (Wright 1950), fir seed research continued to focus on stratification temperature and duration and not on moisture level during treatment. Since the 1980s it has been demonstrated conclusively that seeds of Pacific silver, grand, subalpine, and noble firs stratified at 2 to 5 °C in plastic bags for 4 weeks (moisture content 45% or higher), then air-dried to moisture contents between 25 and 35%, can be returned to the same refrigerator for (a) another 12 months (at 25%) without significant decreases in subsequent germination or (b) a further 3 to 6 months (at 35%) with greatly enhanced germination rate and germination capacity (Edwards 1980b, 1981, 1982a,b, &c, 1986b, 1997; Leadem 1986, 1988b, 1989; Tanaka and Edwards 1986). When air-

dried to 35% and refrigerated for a further 3 months, all viable grand fir seeds germinated within 2 weeks (Edwards 1980b). This is the result of achieving a synchronicity in germination achieved by the reduced moisture content that places the embryos under a moisture stress. This stress prevents less-dormant seeds in the mixture from germinating, while allowing more-dormant seeds to achieve a ready-to-germinate state when the extended chilling ends. Subsequently, sowing the seeds on a non-moisture-limiting medium permits all the viable seeds to germinate at the same time (Edwards 1981, 1982b, 1986b). In addition, the reduced moisture content “protects” the energy supplies of the megagametophyte from being respired as rapidly as in seeds undergoing traditional stratification at high moisture content (Leadem 1993).

This process, which has become known as the stratification-redry method, differs from traditional stratification as shown diagrammatically in figure 18. During routine stratification (upper), seeds are soaked for 24 to 48 hours at room temperature, drained, chilled at 2 °C for 4 to 8 weeks in their “fully imbibed” state (moisture content around 45% or higher) until they are sown in the nursery. In the new process (lower), seeds are soaked for 24 to 48 hours at room temperature, drained, and chilled for 4 weeks while fully-imbibed (as in the old method). Then, the stratified seeds are removed from the refrigerator and air-dried to 30 to 35% moisture content. Next, they were returned to the refrigerator for an additional 1 to 3 months of chilling for the most rapid and complete germination. Alternatively, when dried to 25% moisture content and returned to the refrigerator, they can be kept for up to an additional 12 months until they are sown. The procedure has been described in detail (Edwards 1982b, c, 1986, 1997) and is now used operationally in British Columbia (Leadem and others 1990). An almost identical procedure has been described for Nordmann fir seeds (Jensen 1997; Poulsen 1996), and control of moisture level during stratification has been recommended for Guatemalan fir (Donahue and others 1985).

As described above, seeds air-dried to 25% moisture content can be “stored” in the refrigerator for up to a year without losing the beneficial effect of the initial stratification, that is, they remain in a ready-to-germinate state. Stratified seeds of noble and Pacific silver firs have been dried to 5 to 9% moisture content and stored for 1 year, after which they germinated significantly better than the original controls (Hall and Olson 1986). For the seedling grower, these methods allow stratification to begin well in advance of nursery sowing date and/or make the sowing date more flexible (Edwards 1980b, 1981, 1982a, 1986b). Two additional beneficial effects of redrying (to either 35 or 25%) observed in the laboratory were that fungal and bacterial

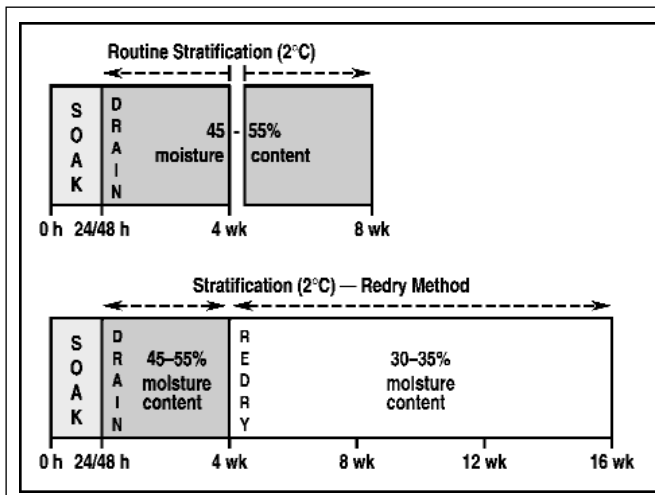
molding of seeds was greatly reduced and that emerging radicles were more positively geotropic than in germinants from routinely stratified seeds. This latter is important in that germination in firs is epigeal (figure 19) and a vigorous healthy radicle is essential for successful seedling establishment.

There is little reported evidence of the use of gibberellins increasing fir seed germination, but a combination of stratification for 40 to 60 days and treatment with 200 ppm GA₃ worked well for Guatemalan fir seeds (Salazar 1991). Use of gibberellin GA₄₊₇ improved dark-germination of Fraser fir at 30/20 °C over a 42-day test but was ineffective (light or dark) at 20/15 °C unless the seeds were first hydrated for 20 hours (Henry and Blazich 1988). The beneficial effect of an auxin has been reported in Sakhalin fir (Yoshida 1960).

Germination tests. Stratification treatments for 10 fir species regarded as consistently dormant are prescribed in seed testing rules (AOSA 1998; Edwards 1987; ISTA 1993), whereas double (paired) tests (with and without stratification) are recommended for 8 other species in which dormancy varies among seedlots. West Himalayan fir might be added to the list of species requiring double tests (Khattak and Ahmad 1980), but Korean fir is consistently dormant (Jakimova 1965). The officially prescribed stratification period for all fir species is either 21 or 28 days, the longer period being favored by the AOSA rules for 6 species.

Alternating temperatures of 30 °C with light for 8 hours and 20 °C for 16 hours without light are standard for most fir species, with 3 notable exceptions. For Pacific silver fir, the current AOSA prescription is for 25 °C (light) for 8 hours and 15 °C (dark) for 16 hours. However, seeds of this species germinate more slowly but more completely at 15 °C (light) for 8 hours and 10 °C (dark) for 16 hours (Leadem 1986). Similarly, subalpine fir seeds stratified for 8 weeks germinate well under a 25/15 °C regime (Hansen and Leivsson 1990; Leadem 1989), whereas Fraser fir seeds stratified for 12 weeks germinate well at 20 °C for 8 hours with light for 1 hour (only) during the latter part of this warm period, followed by 10 °C (dark). If stratified for 8 weeks only, Fraser fir seeds should be tested at the standard 8/16 hours 30/20 °C, with a 1-hour light treatment during the higher temperature (Adkins 1984; Adkins and others 1984; Henry and Blazich 1990). The involvement of phytochrome has been demonstrated in the germination responses of Fraser fir (Henry and Blazich 1990) and is suspected in several other firs (Li and others 1994; Nagao and Asakawa 1963; Messeri and Salvi 1964), making it essential to use fluorescent-only lighting for laboratory tests (Asakawa 1959; Blazich and Hinseley 1984; Nagao and Asakawa 1963).

Figure 18—*Abies*, fir: schematic comparison between traditional stratification (**upper**) and the newer stratification–redry method (**lower**).



The germination substrate is usually kept at its maximum moisture-holding capacity so the test samples are not under any moisture stress but without excess free water present. Full germination of Pacific silver and grand fir seeds was unaffected unless the medium was moistened to below 40% of maximum holding capacity (Edwards unpublished data). However, completeness of germination, and germination rate of west Himalayan fir seeds was highly sensitive to moistening the filter paper with PEG (polyethylene glycol) solution (Singh and others 1986). Many laboratories use a paper/blotter substrate as this allows easy evaluation of the radicles (figure 20), but porous mineral substrates such as perlite, vermiculite, and Sponge Rok[®] may be employed also. Tests conducted according to standard laboratory prescriptions usually terminate after 21 or 28 days, although those on unstratified seeds may continue for 35 or 42 days. As a means of predicting operational sowing requirements in nurseries, some agencies test stratified true fir seeds in fumigated soils at temperatures of around 24 °C during the day and 18 °C at night (Johnson 1984).

By the time newly harvested fir seeds have been processed, there is often insufficient time to complete standard germination tests that require a minimum of 3 weeks for completion, and more than twice this duration if the seeds must be stratified, before they are required for sowing the following spring. To provide more rapid estimates of seed quality, several so-called quick tests have been developed. The simplest is the cutting test, but it is also the least reliable because it fails to detect seeds damaged during handling and processing or that have died during storage.

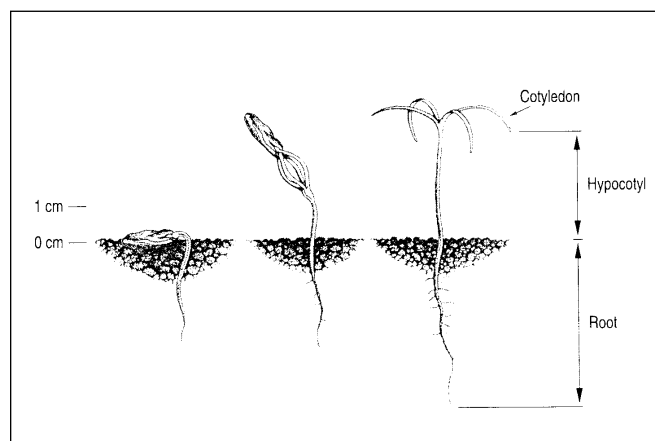
The cutting test invariably overestimates seed quality in grand (Rohmeder 1960b) and European silver fir seeds (Enescu 1968; Ducci and Paci 1986).

Where equipment is available, x-radiography quickly determines percentages of filled seeds of several fir species (Edwards 1982a,b&c; Speers 1967) and provides indirect indications of seed viability (Allison 1980) that are more accurate in fresh than in stored seeds of white fir (Eden 1965). When barium chloride was used as a contrast agent, x-radiography tended to over-estimate the viability of poor-quality seeds and under-estimate that of high-quality seeds of Siberian fir (Scerbakova 1964). When chloroform was used as the contrast agent, there was fairly good agreement with standard tests for seedlots of Pacific silver fir below 30% germination, but in general the germination capacity was over-estimated (Edwards 1982a; Leadem 1984).

Hydrogen peroxide has been used *in lieu* of stratification to stimulate germination in subalpine (Shearer and Tackle 1960), European silver (Simak 1970), and grand firs (Gyimah 1977), but not in Pacific silver fir (Edwards 1982a; Edwards and Sutherland 1979). For a rapid viability test, hydrogen peroxide gives results in 5 to 9 days with viable seeds producing visible radicles. The results correlate well with the standard germination test for noble, grand, and white fir lots between 24 and 64% germination (Ching and Parker 1958), but the method under-estimates germination capacity in lots below 30% (Edwards 1982a; Leadem 1984). As with other rapid viability assessments, the hydrogen peroxide test does not provide any information about the speed of germination, or the requirement for stratification (Johnson 1984).

Official prescriptions for tetrazolium chloride (TZ) staining tests of fir have been developed (AOSA 1998; Buszewicz and Holmes 1957; ISTA 1993; Knierim and Leist

Figure 19—*Abies amabilis*, Pacific silver fir: germinant and seedling development at 3, 5, and 7 days after germination.



1988). Tetrazolium test results often correlate with seedling emergence experienced in nursery sowings (Franklin 1974b). Tetrazolium agreement with standard germination tests can vary among lots of many species (Ducci and Paci 1986; Flemion and Poole 1948; Leadem 1984; Rohmeder 1960b), and a “best estimate” of 2 methods (for example, hydrogen peroxide and TZ) has been proposed for rapid tests (Edwards 1982a). An excised embryo method that requires about 1 week for assessment of European silver fir has been described (Nyholm 1956), but no official prescriptions for fir have been developed. Although “quick tests” may be completed in a matter of hours, or days, compared to weeks required for standard germination tests, not only do they over-estimate (Franklin 1974b; Rohmeder 1960b; Stein 1967) or underestimate (Edwards 1982a; Leadem 1984) viability of fir seeds, they are more time (and labor) consuming, and a single skilled analyst can complete fewer quick tests per month than standard germination tests. They also require a high degree of skill and experience to perform them consistently and well. Their technology was described as unreliable for firs (Edwards 1982a), and it remains so.

Although a number of vigor tests have been devised for agricultural and vegetable seeds (AOSA 1983; ISTA 1995), no tests have been adapted, or are widely used, for firs. However, it is known that stratification broadens the temperature range for optimal germination of Pacific silver (Davidson and others 1984) and grand firs (Wang 1960), and

Figure 20—*Abies lasiocarpa*, subalpine fir: stages in seed germination, from an ungerminated seed (**lower left**) to a 3-day-old germinant (**upper right**) (courtesy of D. Pigott).



that the stratification/redry method (described earlier) broadens the range even further (Davidson and others 1984). This temperature-range broadening is a sure sign of increased vigor (Grabe 1976). One distinction between seed vigor and seed germination can be seen in the effects of long-term seed storage, which causes a reduction in plant percentage in the nursery before it affects germination percentage (Giannini and Murazio 1972; Muller 1977, 1980). Seed vigor was related to germination rate, seed protein levels, and seed respiration, all of which were thought to have potential for development as quantifiable indices of this variable in subalpine fir (Leadem 1988a&b, 1989).

Nursery practice. Fir seedlings are grown as both bareroot and container stock. A 1997 survey found 20 nurseries growing almost 21 million seedlings of 16 (including 6 non-native) fir species for reforestation purposes. Several other exotic firs are grown, especially in the northeastern United States, for Christmas trees (Girardin 1997a&b). For bareroot sowing in the past, most Pacific Northwest and California nurseries stratified for 1 to 2 months (table 10) at 0 to 3 °C, and sowed between mid-April to mid-May (exceptionally as late as June), favoring a seedling density of 270 to 330 seedlings/m² (25 to 30/ft²) (Lavender 1979) (table 10). Bareroot sowing rates for Pacific silver, grand, subalpine, and noble firs in British Columbian nurseries usually were lower—220 to 240/m² or 260 to 300/linear m of seed bed (20 to 23/ft² or 79 to 91/linear ft of seed bed)—to produce more open-grown plants (Arnott and Matthews 1982).

Although seeds of European silver, balsam, and Fraser firs normally may be fall-sown in bareroot beds without stratification (table 10) as are seeds of noble and white firs raised in European nurseries (Franklin 1974b)—spring-sowing of stratified seeds has been recommended for balsam (Roe 1948b), and European silver firs (Neubacher 1959; Paiero and Piussi 1964; Vlase and Iesan 1959). Fall-sowing of freshly collected fir seeds may not be possible because seed processing is incomplete, so sowing the following spring provides the earliest opportunity. Spring-sowing of stratified seeds is the traditional standard for most western North American species (table 10), which minimizes losses from birds, rodents, and adverse weather (Lanquist 1946). Merely soaking grand fir seeds can be beneficial (Hofman 1966). Sowing unstratified seeds of grand and noble firs in January to March or stratified seeds in April gave satisfactory results in the United Kingdom (Faulkner and Aldhous 1959). Most bareroot nurseries use a seedling caliper between 2.5 and 5 mm (metric measure only) for culling purposes.

Fir seedling production in Canadian nurseries is now entirely from container systems (figure 21), a method widely used in the United States also. In container nurseries, sowing usually occurs in the spring, as early as January or as late as June (for stock being grown for 1½ seasons) (table 10). Nearly all container-grown firs are started in greenhouses to provide warm temperatures for germination and early growth and then moved to cooler shadehouses during the hotter part of the summer; alternatively, the greenhouse covers (or sides) may be removed. January-sown seedlings maybe ready for mid-October planting, but more optimal dormancy and frost-hardiness is achieved by delaying planting until mid-November. However, high-elevation sites then may be inaccessible, so cold storage is required to keep stock dormant until spring planting. If noble fir seedlings are to be fall-planted, it is important to switch to cool conditions by mid-summer to achieve adequate cold-hardiness (Owston and Kozlowski 1981). Although stock quality varies widely according to planting site requirements, 1+0 seedlings 7.5 to 10 cm tall with 2.5-mm caliper are acceptable provided the root plugs remain intact on extraction from the containers (Owston 1979).

Many container nurseries stratify fir seeds by soaking them in cold water, then draining them and placing them in large plastic bags. Water temperature is normally uncontrolled and is ambient for the local supply. Seeds to water ratio (by volume) should be at least 1:3. Running water soaks, or water changes during longer soaking periods, are quite common and are used especially to help clean seeds of pathogens (Campbell and Landis 1990). One nursery follows the initial soak with a brief dip in 1% hydrogen peroxide to control fungal infections, but the efficacy of this has not been verified. After draining, no more than 2 to 2.5 kg (5 lb) of seeds are placed in plastic bags that are either loosely tied (Jones and others 1991) or have a breather tube inserted (before the tops of the bags are tied) to ensure gas exchange with the outside air (Johnson 1984). Hanging the bags from a bar in the chilling facility assures that free water will continue to drain to the bottom, and several pin pricks in the bag will allow any excess moisture to drain away. At least once weekly (several times being preferred by some operators) the seeds are rolled within the bags to bring those from the center or bottom of the mass near the top. This provides maximum exposure to the air and ensures that moisture remains evenly distributed and all seeds achieve the chilling temperature. Water is added if the seeds appear to be drying. Several nurseries now use the stratification/redry method (see the section entitled Pregermination Treatments), or a variation thereof, for improving germination in 12

species (table 10). Not every user succeeds with this technique, possibly due to differences in seedlot dormancy, because—as with routine stratification—the stratification/redry method has a greater effect on more-dormant fir seeds, less-dormant lots not benefiting as well.

Container seedlings of grand and noble firs grow quickly and evenly, so that 10- to 15-cm-tall plants can be obtained about 20 weeks after sowing without using extended photoperiods. By artificially increasing daylengths to 18 hours, similarly sized Pacific silver fir seedlings (figure 21) can be produced, but subalpine fir plants generally set bud early and achieve no more than 6 cm of height (Arnott and Matthews 1982; Gates 1994). When 5-month-old container-grown Fraser fir seedlings were naturally chilled outdoors through mid-November (fluctuating temperatures and natural photoperiods), then returned to a greenhouse, at 15 months they were taller than conventionally grown 3+1 and artificially chilled plants (Seiler and Kreh 1987).

Most containers are made of Styrofoam® blocks with cavities (Sjoberg 1974) or trays of individual plastic cells; cavity and cell volumes vary widely (table 10). In general, smaller containers are used for early sowing if the stock is to be transplanted. Later sowings use bigger containers to produce bigger plants, some of which may be transplanted also (table 10). The principles of container nursery technology are well established (Landis and others 1989, 1990a&b, 1992, 1995), and the concept is now widely accepted.

Herbicides are not used at most container nurseries, whereas bareroot facilities employ a range of chemicals; recommendations for some of these (and for damping-off control) have been published (Imai and others 1955; Roe 1948b; Sanftleben 1989; Sato 1962; Singh and Bhagat

Figure 21—*Abies amabilis*, Pacific silver fir: seeds germinating in a container nursery; wooden toothpicks (left-rear of cavities) were used to mark the progression of germination for a research trial (courtesy of C. L. Leadem).



1989). Pesticide use changes over time, so nursery operators should seek the advice of local extension agents for current recommendations.

In bareroot beds, irrigation control may be combined with wrenching, side pruning, and undercutting to assist in achieving seedling dormancy. Undercutting is often repeated, for example at 2-week intervals beginning in late July/early August for 1+0 bareroot stock. For 2+0 seedlings, a combination of sidepruning, wrenching, and undercutting before new growth gets underway (late February/early March), and at other times during the second growth season, is practiced. In contrast, irrigation control is seldom used to regulate the growth cycle in container nurseries because seedlings of many fir species are drought-intolerant. Some nurseries recommend a moist growing regime, as if growing spruce stock, whereas others may reduce irrigation late in the growing season when target heights are assured. Induction of seedling dormancy and better height control are achieved by the use of black-out control (short photoperiods) in several nurseries. Black-out followed by a 4-week rest period and then 1 to several weeks of 23-hour photoperiods may give a slight increase in height growth. Several cycles of black-out and extended photoperiod can induce multiple flushes in 1+0 seedlings of Pacific silver and subalpine firs to ensure that they reach target height as 2+0 crops. However, the second year reflush (in late March as the greenhouse temperature is raised) is sensitive to molding because the emerging new foliage tends to collect a large drop of water.

Extended photoperiods (16- to 23-hour days) during the accelerated growth phase, beginning 4 weeks after sowing for early-sown stock and continuing almost the entire season, are used in many container facilities. Except where high sunlight is encountered, shading usually is not employed. Greenhouse roofs may be removed during the summer to increase light levels and improve cooling. Shading bareroot seedbeds for 2 months after germination and hoeing or hand pulling to control weeds is advised for European silver fir (Vlase and Iesan 1959), but open beds receiving full light are best for noble fir (Schwenke 1956, 1961).

Lifting dates for 1+0 container stock vary from August for "hot" (that is, immediate) planting or transplanting, to mid-November/December for planting the following spring. Depending on weather conditions (such as snowmelt), lifting from bareroot beds may extend from December through March.

Fir seedlings are shippable as 1+0 plugs (85% of total container production), 2+0 plugs, and P+1 (transplanted from containers to outside beds); in addition, some container transplants may be shipped as P+2, P+3, or even older stock (table 10) depending on the species and customer requirements. Plug stock may be transplanted both spring and fall (August), fall transplantation giving larger seedlings but at the risk of damage during the first winter. Bareroot 2+1 seedlings are reported to perform better when transplanted in the fall.

Shippable heights for container seedlings vary between 13 cm (5 in) for 1+0, and 15 cm (6 in) to 26+ cm (10+ in) in 2+0. Transplants from containers may be between 20 cm (8 in) to 46 cm (18 in), averaging 30 to 36 cm (12 to 14 in). Root caliper generally varies from 2.5 to 3.5 mm for 1+0 stock of all fir species and up to 6 mm for 2+0. Sizes of shippable bareroot stock are not well defined, depending largely on contract requirements.

To overwinter stock in bareroot beds, some nurseries find mulches such as peat moss, pine needles, sawdust, and straw beneficial, especially during the first winter (table 10). Protection of 1+0 seedlings can be accomplished also by sowing seeds between rows of transplants (Anon. 1977). Germination and seedling survival of west Himalayan fir was improved by sowing the seeds 15 to 20 mm ($1/2$ to $3/4$ in) deep (Singh and Singh 1984), then covering the beds with 10 to 15 cm (4 to 6 in) of humus (Singh and Singh 1990); other aspects of nursery culture of this species have been reviewed (Sharma and others 1987).

Vegetative propagation of Fraser fir, which is easy to graft and air-layer and readily produces roots on stem cuttings, is transforming the production of this species for the all-important (4 to 5 million trees annually) eastern North America Christmas tree market (Blazich and Hinesley 1994, 1995). A genetically improved balsam fir Christmas tree, with increased foliage density and higher frost resistance, has been field tested (Girardin 1997b).

Micropropagation techniques have been applied to selected firs, and regeneration of somatic embryos using seed explants of European silver fir (Gebhart 1990; Hartmann and others 1992), and Pacific silver fir (Kulchetscki and others 1995) have been obtained. However, the problems encountered with Fraser and balsam firs make cloning of these 2 species by micropropagation a future development (Blazich and Hinesley 1994).

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