Pinaceae—Pine family

Abies P. Mill.

fir

D. George W. Edwards

Dr. Edwards retired from the Canadian Forest Service's Pacific Forestry Centre

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.** *A. argentea* DC.; *A. candicans* Fisch. *A. nobilis* A. Dietr.; *A. Pardei* Gauss *A. pectinata* DC.; *A. picea* Lindl. *A. taxifolia* Desfont.; *A. vulgaris* 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** *A. grandis* A. Murr. *A. grandis* var. *densiflora* Engelm.	**Pacific silver fir,** lovely fir, amabilis fir, Cascades fir, white fir, silver fir, *sapin gracieux*	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.** *A. aromatica* Rafn. *A. balsamifera* Mich. *A. minor* 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.** *A. venusta* (Dougl.) K. Koch	**bristlecone fir,** Santa Lucia fir, silver fir, fringed spruce	Santa Lucia Mtns, Monterey Co., California (37°–36°N)
***A. cephalonica* Loudon** *A. panachaica* Heildr.; *A. lusombiana* Loudon *A. peloponesica* 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** *A. selinusia* Carrière	**Cilician fir**	Turkey (Cilicia), N Syria, & Lebanon
***A. concolor* var. *concolor* (Gord. & Glend.) Lindl. ex Hildebr.** *A. lowiana* (Gord.) A. Murr. *A. grandis* var. *lowiana* (Gord.) Hoopes *A. concolor* var. *lowiana* (Gord.) Lemm.	**white fir,** white balsam, balsam fir, Rocky Mountain white fir, Colorado white fir, *piño real blanco,* 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** *A. lowiana* (Gord.) A. Murr. *A. concolor* (Gord. & Glend.) *A. concolor* var. *lasiocarpa* Engelm. & Sarg. *A. grandis* var. *lowiana* 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.** *A. bifida* Sieb. & Zucc.; *A. momi* Sieb.	**Japanese fir,** *momi, momi* fir, Japanese silver fir	Mtns of central & S Honshu, Shikoku, & Kyushu, Japan (39°–30°N)
***A. fraseri* (Pursh) Poir.** ``*humilis* 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.** *A. amabilis* A. Murr.; *A. excelsior* (Franco) *A. gordoniana* Carr. *A. lasiocarpa* Lindl. & Gord.	**grand fir,** lowland white fir, white fir, balsam fir, great silver fir, Oregon fir, western white fir, western balsam, *sapin grandissime, sapin du Vancouver*	W Montana & N Idaho to S British Columbia, Vancouver Island, S to Sonoma Co. in coastal California & E Oregon
***A. guatemalensis* Rehd.** *A. tacanensis* Lund. *A. guatemalensis* var. *tacanensis* (Lund.) Mart. *A. guatemalensis* var. *jaliscans* Mart.	**Guatemalan fir,** Guatemala fir, *paxaque, pinabete, romerillo*	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
A. holophylla **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)
A. homolepis **Sieb. & Zucc.** *A. brachyphylla* Maxim.	**Nikko fir,** *urajiro-momi, Dake-momi, Nikko-momi*	Mtns of central Honshu & Shikoku, Japan (37°–33°30'N)
A. koreana **E.H. Wilson** *A. nephrolepis* Nakai	**Korean fir**	Confined to the volcanic island of Cheju & the Chiri-san Mtns, South Korea
A. lasiocarpa **(Hook.) Nutt.** *A. bifolia* A. Murr.; *A. sub-alpina* Engelm. *A. sub-alpina* var. *fallax* Engelm.	**subalpine fir,** alpine fir, balsam fir, white fir, *piño real blanco de la sierras, sapin concolore*	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)
A. lasiocarpa **var. *arizonica* (Merriam) Lemmon** *A. bifolia* (A. Murr.); *A. subalpina* 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
A. magnifica **A. Murr.** *A. campylocarpa* A. Murr. *A. nobilis* var. *magnifica* 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
A. mariesii **Mast.** *A. mayriana* Miyabe & Kudo	**Maries fir**, *Toddomatsu* fir, *Aomori-todo-matsu, O-shirabiso*	Mtns of N & central Honshu, Japan (41°–35°N)
A. nebrodensis **(Lojac.) Mattei** *A. pectinata* Gilibert var. *nebrodensis* Lojac. *A. alba* Mill. var. *nebrodensis* (Lojac.) Svob.	**Sicilian fir,** *Abete delle Nebrodi*	Monte Cervo, Polizzo; Monti Nebrodi & Monte Scalane, Sicily
A. nephrolepis **(Trautv. ex Maxim.) Maxim.** *A. sibirica* var. *nephrolepis* Trautv. *A. gracilis* 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)
A. nordmanniana **(Steven) Spach** *A. leioclada* (Stev.) Gord. *A. pectinata* var. *leioclada* (Stev. ex Endl.) Carr.	**Nordmann fir**, Caucasian fir, Crimean fir	W Caucasus & mtns connecting Caucasus with Armenian Highlands (44°–40°N & 46°–38°E)
A. nordmanniana **ssp. *equi-trojani* (Asch. & Sint. ex Boiss.) Coode & Cullen** *A. bornmuelleriana Mattf.*	**Turkey fir**	Mt. Olympus, Bithynia (NW Turkey) to Paphlagonia (N Turkey), Asia Minor (~39°–42°N & 26°–38°W)
A. numidica **de Lannoy ex Carrière** *A. pinsapo* var, *baborensis* Coss. *A. baborensis* Letourn.	**Algerian fir,** Algerian silver fir,	Kabylie Range, near summits of Mt Babor & Mt. Thabador, Kabylie. NE Algeria
A. pindrow **(D. Don) Royle** *A. webbiana* Brandis	**west Himalayan fir,** west Himalayan silver fir, Pindrow fir	W Himalayas, India & Pakistan, N Afghanistan to Nepal & Tibet
A. pinsapo **Boiss.** *A. hispanica* De Chamb.	**Spanish fir,** Spanish silver fir	Mtns of Malaga & Granada provinces, S Spain; Morocco (var. *marocana*)
A. procera **Rehd.** *A. nobilis* (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)
A. recurvata **Mast.** *A. ernestii* Rehd.; *A. beissberiana* Rehd. & Wilson	**Min fir**, *Min-kiang* 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) Schltdl. & Cham.** *A. glaucascens* Roezl; *A. hirtella* Lindl. *A. lindleyana* Roezl	**sacred fir**, sacred Mexican silver fir, Mexican silver fir, *oyamel, pinabete*	Mtns of central & S Mexico, C. Michoacan to Veracruz & N & W Guatemala (~24°–15°N)
A. sachalinensis **(Fr. Schm.) var.** ***sachalinensis*** **Mast.** *A. akatodo* Miyabe *A. veitchii* var. *sachalinensis* Fr. Schm.	**Sakhalin** [or Sachalin] **fir**, Japanese fir, *todo-matsu, akatodo*	Sakhalin & Kurile Islands, Kamchatka, Russia; Hokkaido, Japan (53°34'–41°30'N)
A. sachalinesis **(Fr. Schm.) Mast. var.** ***mayriana*** **Miyabe & Kudo** *A. mayriana* Miyabe & Kudo	**Mayr Sakhalin fir**, *Ao-todomatsu, todomatsu, aotodo*	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** *A. shastensis* (Lemmon) Lemmon *A. nobilis* var. *robusta* Mast. *A. magnifica* var. *shastensis* 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.** *A. hetrophylla* K. Koch; *A. pichta* Forbes *A. semenovii* 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,** *linpi lengshan*	High Mtns SW China, SE Xizang, W Sichuan, S Gansu & S Qinghay Provinces (26°–34°N & 98°30'–104°E)
A. veitchii **Lindl.** *A. eichleri* Lauche; *A. sikokiana* Nakai	**Veitch fir**, Veitch silver fir, *shirabe, shirabiso,* 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. Rushf. & Nar.; *A. durangensis* Mart. (Durango fir); *A. flinckii* sp. nov. Rushf.; *A. hickelii* Flous et Gauss. (Hickel fir); *A. hidalgensis* sp. nov. Debr., Rácz & Guíz.; *A. neodurangensis* sp. nov. Debr., Rácz & Salaz.; *A. zapotekensis* sp. nov. Debr., Rácz & Ramír.; *A. vejarii* Mart. (Vejar fir).

EAST ASIA: *A. beshanzuensis* Wu (Baishan fir); *A. chengii* Rushf. (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 has it 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 *oyamel*s 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 *Keteleéria;* species of this genus have upright, cylindrical cones that resemble those of firs, but *Keteleéria* 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 American 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 build 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 *Pseudotorreya* 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 include*s 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. balsame*a) in subsection Laterales; this separation is based on whether bract scales are exserted 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
Abies P. Mill.	—	***Abies alba*** (type) *A. cephalonica, A. cilicica*[1], *A. nebrodensis, A. nordmanniana* [2], *Abies x borisii-regis*
Piceaster Spach emended Farjon & Rushforth	—	***Abies pinsapo*** (type) [3] *A. numidica*
Bracteata Engelmann emended Sargent	—	***Abies bracteata*** (type)
Momi Franco emended Farjon & Rushforth (type: *Abies firma*)	***Homolepides*** (Franco) Farjon & Rushworth	***Abies homolepis*** (type) [4] *A. recurvata* (includes *A. recurvata* var. *ernestii*)
	Firmae (Franco) Farjon & Rushforth	***Abies firma*** (type) ***A. beshanzuensis***
	Holophyllae Farjon & Rushforth	***Abies holophylla*** (type) *A. chensiensis* [5], *A. pindrow* [6], *A. ziyuanensis*
Amabilis (Matzenko) Farjon & Rushforth	—	***Abies amabilis*** (type) *A. mariesii*
Pseudopicea Hickel emended Farjon & Rushworth (type: *Abies spectabilis*)	***Delavayianae*** Farjon & Rushforth	***Abies delavayi*** (type) [7] *A. chengii, A. densa, A. fabri* [8], *A. fargesii* [9], *A. forestii* [10], *A. fanjingshanensis, A. spectablis, A. yuanbaoshanensis*
	Squamatae E. Murray	***Abies squamata*** (type)
Balsameae Engelmann emended Farjon & Rushforth (type: *Abies balsamea*)	***Laterales*** Patschke emended Farjon & Rushforth	***Abies kawakamii*** (type) *A. balsamea, A. bifolia, A. lasiocarpa, A. sibirica* (includes var. *semenovii*)
	Medianae Patschke emended Farjon & Rushforth	***Abies sachalinensis*** (type) (includes var. *mayriana* = *A. mayriana*) *A. fraseri, A. koreana, A. nephrolepis, A. veitchii* (includes var. *sikokiana*)
Grandes Engelmann emended Farjon & Rushforth	—	***Abies grandis*** (type) *A. concolor* (includes var. *concolor* & var. *lowiana*), *A. durangensis* [11], *A. flinckii* (= *guatemalensis* var. *jaliscans*), *A. guatemalensis*
Oiamel Franco (type: *Abies religiosa*)	***Religiosae*** (Matzenko) Farjon & Rushforth	***Abies religiosa*** (type) *A. colimensis, A. mexicana* [12], *A. vejarii*
	Hickelianae Farjon & Rushforth	***Abies hickelii*** (type) [13]
Nobiles Engelmann	—	***A. procera*** (type) *A. magnifica* (includes var. *shastensis*)

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. *salouenensis*, 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
A. grandis	Coastal lowlands of southern British Columbia, Washington, Oregon, and California, including lower elevations on the western slopes of the Cascade Range
A. grandis	Eastern slopes and higher elevations in the Cascade Range north of about 44° to 45°N latitude
A. grandis	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
*A. concolor**	Sierra Nevada, California
A. concolor	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 (Lester1968; 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 x Fraser fir and reciprocals, Fraser x bracted balsam fir and reciprocals, and bracted balsam x 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 x 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 interor—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 horticultural 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 (megasporangiate) 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. Microsporophyls 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)
A. alba	Europe	May–mid-June	Mid-Sept–mid-Oct	Mid-Sept–mid-Oct	25–45	25–30	2–3†
A. amabilis	W Washington & Oregon (150–400)	Late Apr–May	Late Aug	Late Aug–Sept	35–65	30	3–6
	Vancouver Is., British Columbia (500)	Mid-May–June	Mid-Sept		—		
	Lewis Co., Washington (1,600)	June	—	Mid-Sept			
A. balsamea	—	Mid–late-May	Late Aug–early Sept	Mid-Sept	10–20	20–30	2–4
	Minnesota	Late Apr–early June	—	Early Oct	—	—	—
A. bracteata	Sta. Lucia Mtns, Monterey Co., California	Late Apr–early May	Late Aug	Mid-Sept	10–35	—	3–5
A. concolor	—	May–June	Sept–Oct	Sept–Oct	25–60	40	3–9
var. *lowiana*	Stanislaus NF, California (2,000)	Late May	—	Late Sept–late Oct	—	—	—
	Fremont NF, Oregon (1,600)	Mid-May–early June	—	—	—	—	—
A. firma	Japan	Late Apr–mid-May	Mid–late Oct	Late Oct–early Nov	30–45	—	4–6
A. fraseri	Roan Mtn, North Carolina	Mid-May–early June	Sept–mid-Oct	Sept–early Nov	10–25	15	3
A. grandis	Northern Idaho (750–1,100)	Mid-June	Aug	Early Sept	35–65	20	2–3
	W Washington & Oregon (100–400)	Mid-April–mid-May	—	Late Aug–mid-Sept	—	—	—
	Linn Co., Oregon (1,600)	Early–mid-June	—	Early Oct	—	—	—
	Mendocino Co., California (65)	Late March–early Apr	—	—	—	—	—
A. guatemalensis	Guatemala, S Mexico, Honduras, & El Salvador	—	Oct–mid-Dec	Nov–mid-Dec	20–30	—	2–3‡
A. homolepis	Japan	Mid-May–mid-June	Mid–late Sept	Mid–late Sept	20–30	—	5–7
A. lasiocarpa	San Francisco Peaks, Coconino Co., Arizona	Late June	Mid-Sept–early Oct	Late Sept–early Oct	10–35	50	2–3
	Northern Idaho (950)	Late June–early July	Mid-Aug	Mid-Sept	10–35	20	2–4
	Eastern Montana (2,100)	Early–mid-July	Late Aug	Early Sept	—	—	—
	Linn County, Oregon (1,750)	Late May–early July	—	Early Oct	—	—	—
A. magnifica							
	—	Late May–early June	Aug	Sept–Oct	30–55	35–45	2–3
A. mariesii	Japan	Mid–late June	Mid–late Sept	Late Sept–early Oct	10–25	—	5–7
A. nordmanniana	—	—	May	Sept–Oct	40–60	30–40	2–3
	Russian Georgia	—	After Oct 1	—	—	—	—
A. pindrow §	Himalayas	Late Apr–mid-May	Sept–early Oct	Oct–Nov	—	30–40	2–4
A. pinsapo	Czech Republic & Soslovakia	—	—	—	—	50	—
A. procera	Benton & Linn Cos., Oregon (1,350–1,550)	June	Mid–late Sept	Early Oct	45–80	12–15	3–6
	Lewis Co., Washington (1,600)	June–early July	Late Sept	Early Oct	—	—	—
A sachalinensis	Hokkaido, Japan	May–June	Sept–Oct	Oct	—	—	2–4
A. × shastensis	SW Oregon (1,850–2,000)	Mid–late June	Late Sept	Late Sept–mid-Oct	30–55	30–40	2–3
	N. California coast ranges (2,000)	—	Late Sept	Early–mid-Oct	—	—	—
	Shasta Co., California (1,700–2,000)	—	—	Mid-Oct	—	—	—
A. sibirica	W Siberia	—	—	—	—	—	2–8
A. veitchii	Japan	June	Sept–early Oct	Sept–Oct	20–25	30	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), Løfting (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).

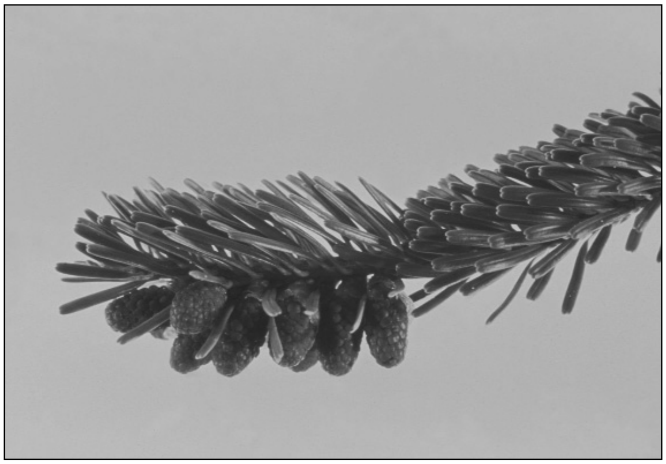
Thinning promoted fruiting in 150- to 170-year-old stands of Siberian fir in Siberia (Zelenin 1991), and best Sakhalin fir seeds occurred after heavy thinning (Sato 1940). In contrast, after a commercial thinning in a younger Siberian fir stand, the remaining trees produced such small amounts of pollen 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 (Itoo 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 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).

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).



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**).

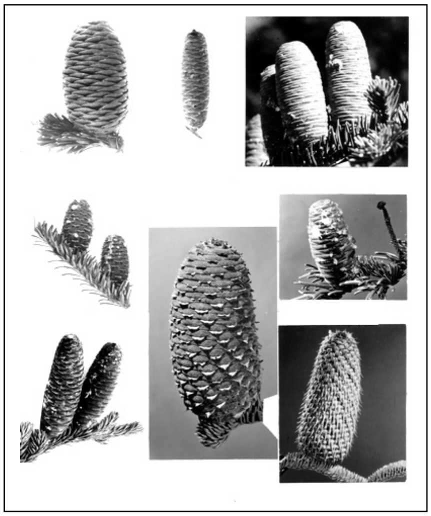
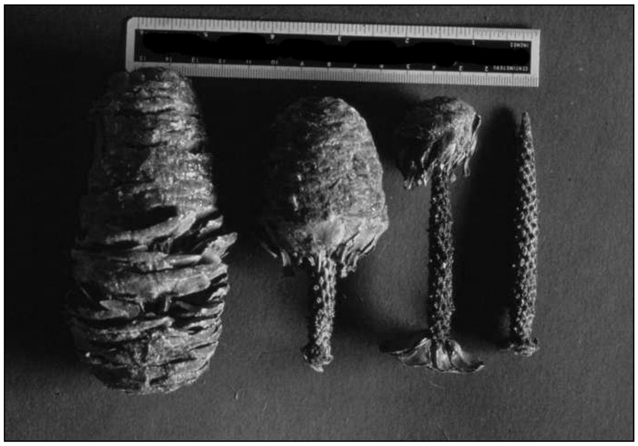


Figure 4—*Abies grandis*, grand fir: four stages in the abscision of ovuliferous scales from the cone axis (courtesy of D. Pigott)



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; Savcenko 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 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 (Kitzmiller 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**).

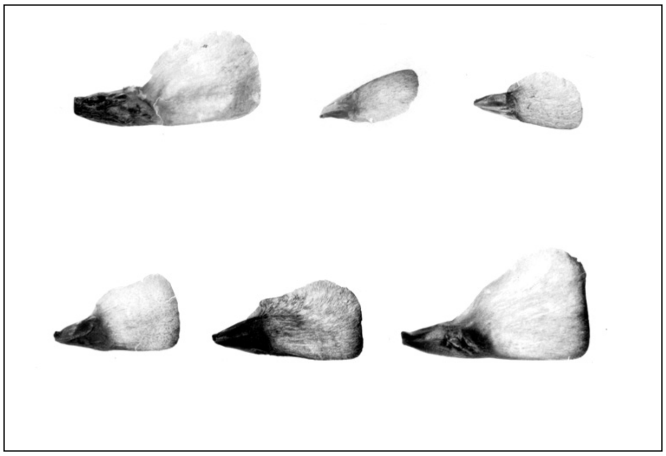
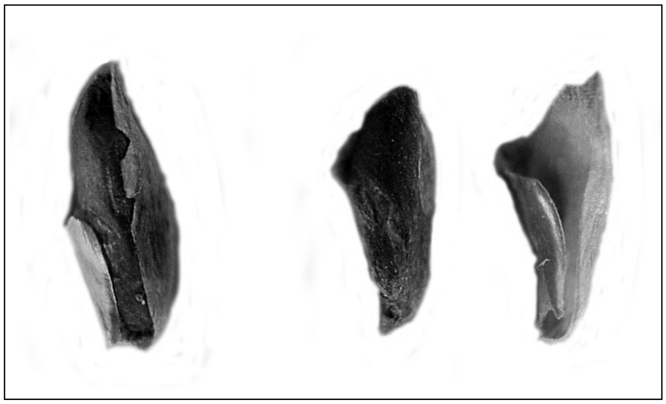


Figure 6—*Abies procera,* noble fir*:* abaxial view of seed showing (**left**) a seed with wing, but with integument still attached (indicated by the prominent flaps wrapping around the long margins) and which would be regarded as a "pure seed" commercially; a naked seed (**center**) without wing or 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 leakage 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).

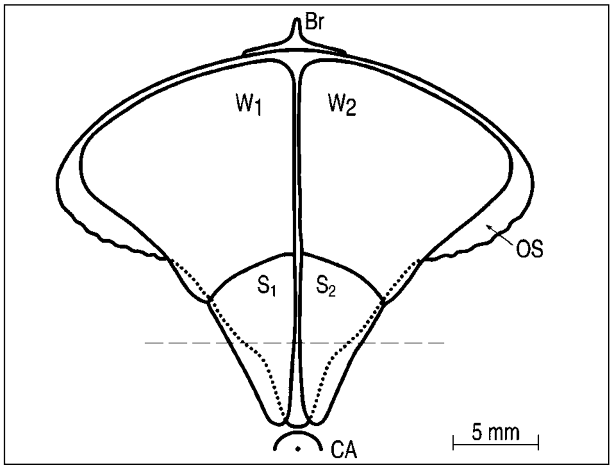


Figure 8—*Abies alba*, European silver fir: diagrammatic cross section of a seed (**S1** in figure 7). **OS** = ovuliferous scale; **Br** = bract; **W** = wing; **m** = median plane of the ovuliferous scale; **e** = embryo; **meg** = megagametophyte ("endosperm"). **A, B, D,** and **E** indicate individual resin vesicles located on the adaxial (**ad**) or abaxial (**ab**) surfaces, and medial (**med**) and marginal (**marg**) edges of the seed (after Cermak 1987).

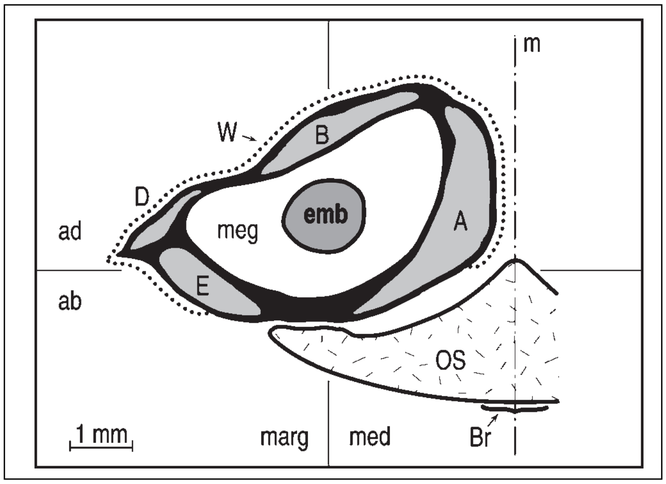


Figure 9—*Abies alba* European silver fir: digrammatic view of the abaxial surface of 1 seed. **W** = wing; **m** = median plane of the ovuliferous scale. Resin vesicles appear on the medial (**A**) or marginal (**E**) sides of the seeds, and at both ends (**C** and **F**) (after Cermak 1987).

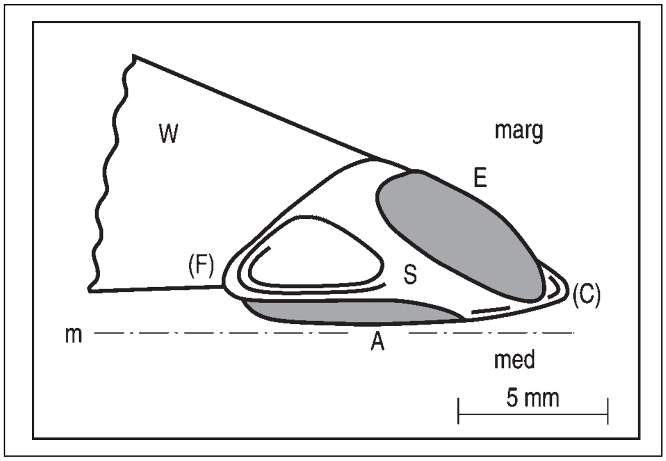
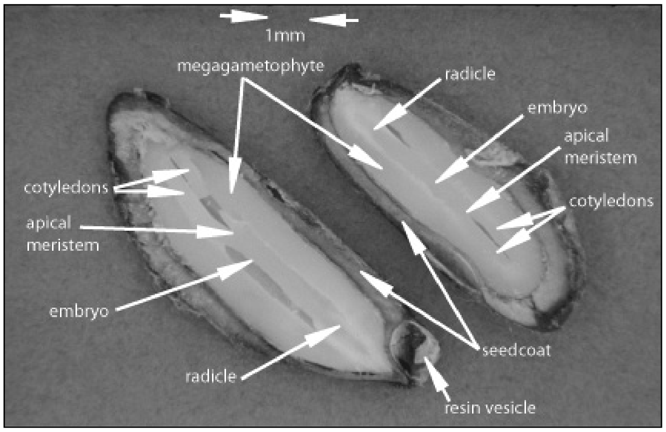


Figure 10—*Abies grandis*, grand fir: longitudinally sectioned mature seeds showing embryos (**e**) occupying 90+% of the corrosion cavity in the megagmetophytes (meg) ("endosperm." **C** = cotyledons; **AP** = apical meristem; **R** = radicle; **H**= hypocotyl/shoot axis: **V** = resin vesicle; **SC**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



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 maturation (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 subalpine 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 number 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 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 *bracteatana* (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 (Kolomiec 1950). Damage generally is

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

Figure 12—*Abies, Fir: seed chalcid.*

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

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

Sources: Androic (1960, 1976), Annila (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), Jesperson and Lomholdt (1983), Kailidis and Georgevits (1970, 1972), Kayacik (1964), Keen (1968), Koerber (1963), Kolomiec (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 (Annila 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 (*Clethrionomy*s *gapperi*, *Peromyscus maniculatus, P. leucopus*, and *Microtus pennsylvannicus*) 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 seedcrop 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
Alternaria spp.	*Abies* spp.*
Aspergillus spp.	*Abies* spp.
Botrytis cinerea Pers.: Fr.	*A. amabilis*
Caloscypha fulgens (Pers.) Boud.	*A. grandis*
Cephalosporium spp.	*Abies* spp.
Ciboria rufo-fusca (O.Weberb.) Sacc.	*A. alba, nordmanniana*
Cladosporium spp.	*A. grandis, magnifica,* × *shastensis*
Cylindrocarpon spp.	*A. amabilis, sibirica, Abies* spp.
Fusarium culmorum (Wm.G. Sm.) Sacc.	*Abies* spp.
Fusarium moniliforme J. Sheld.	*A. grandis, nordmanniana*
Fusarium oxysporum Schlechtend.: Fr.	*A. grandis, procera*
Fusarium roseum Link: Fr.	*A. grandis, procera*
Fusarium semitectum Berk.& Ravenel var. *majus* (Wollenweb.)	*A. amabilis*
Fusarium spp.	*Abies* spp.
Geniculodendron pyriforme G.A. Salt	*A. amabilis, grandis*
Heterobasidion annosum (Fr.:Fr.) Bref.	*Abies* spp.
Lirula macrospora (R. Hartig) Darker	*Abies* spp.
Melanospora zamiae Corda	*Abies* spp.
Mucor spp.	*Abies* spp.
Papulospora spp.	*A. amabilis, grandis*
Penicillium spp.	*A. amabilis, grandis, magnifica,* × *shastensis, procera*
Phoma spp.	*Abies* spp.
Rhacodium therryanum Theum.	*A. sachalinensis*
Rhizoctonia solani Kühn	*A. balsamea, fraseri, grandis*
Sclerotium spp.	*A. mariesii, Abies* spp.
Trichoderma spp.	*A. amabilis, grandis, Abies* spp.
Tricothecium roseum (Pers.:Fr.) Link	*A. grandis*
Truncatella hartigii (Tub.) Steyaert	*Abies* spp.
Virus-like particles	*A. alba, homolepis*

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—*Abies,* fir: cone and seed maturity indices identifying earliest collection date

Species	Cones	Seeds
A. amabilis	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*
A. balsamea	Turning purple; moisture content < 60%	—
A. concolor	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
A. firma	Turning yellow-brown, losing luster	—
A. fraseri	Blue-green turning brown	Distinct seedcoat color visible
A. grandis	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
A. guatemalensis	Turning dark green or purple; resin droplets visible on exterior	Wings yellow
A. homolepis	Turning yellow-brown & losing luster	—
A. lasiocarpa	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
A. magnifica	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
A. mariesii	Turning brown & losing luster.	—
A. procera	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 †
A. sachalinensis	Turning brown & losing luster	—
A. veitchii	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 15%, damage through seedcoat abrasion is reduced and makes the seed wings become more brittle and easier to break off (Rooke 1997).

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

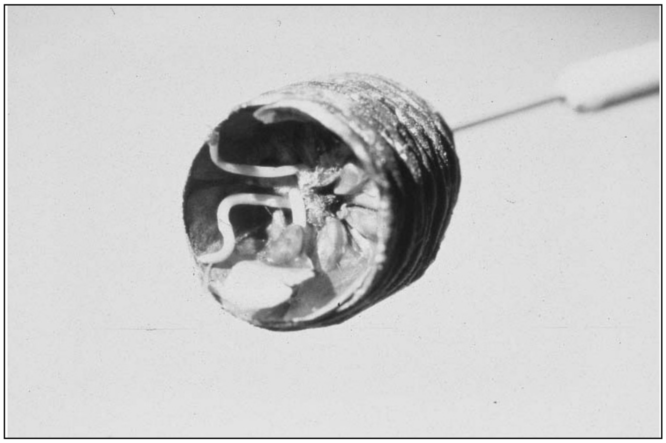


Figure 17—*Abies lasiocarpa*, subalpine fir: viviparous germination, with seeds germinating while still attached to the ovuliferous scales (courtesy of D. Pigott).

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)	Kiln-drying period Temp (°C)
A. amabilis	60–180	6–14 †	30–38
A. balsamea	20–30	0	—
A. concolor	7–14	0	—
A. firma	14	(†)	48
A. fraseri	30–45	0	—
A. grandis	60–180	6–14 †	30–38
A. guatemalensis	< 60§	0	—
A. homolepis	14	(‡)	48
A. lasiocarpa	60–180	6–14†	30–38
A. magnifica	8–21	0	—
A. mariesii	14	(‡)	48
A. procera	60–180	6–14 †	30–38
A. sachalinensis	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 or +20 °C; (c) maintained viability at 6 to 9% moisture when stored at –18 and +5 °C; and (d) maintained viability at 4% moisture when stored at –18, +5, and +20 °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/ cone wt		Seed wt/ cone vol		Seeds/	Seeds/wt				
										Range		Average		
	kg/hl	lb/bu	/hl	/bu	g/kg	oz/100lb	kg/hl	oz/bu	cone	/kg	/lb	/kg	/lb	Samples
A. alba	36	28	—	—	55	89	2	25	—	17,400–41,000	7,900–18,600	22,500	10,200	>72
A. amabilis	—	—	—	—	—	—	3.7	48	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
A. balsamea	45	35	2,700–5,500	1,000–2,000	—	—	2.9–3.6	37–46	134	66,150–208,400	30,000–94,500	131,400	59,600	42
A. concolor	39–45	30–35	—	—	32	51	1.3–2.5	17–32	185	18,950–39,100	8,600–17,720	24,500	11,100	46
A. firma	—	—	—	—	—	—	—	—	—	20,500–30.900	9,300–14,000	25,150	11,400	>12
A. fraseri	—	—	2,500–2,700	900–1,000	—	—	2.5–3.7	32–48	—	117,950–173,650	53,500–78,750	134,050	60,800	10
A. grandis	—	—	700	250	—	—	1.9–2.5	24–32	115	26,250–63,500	11,900–28,800	40,600	18,400	144
	—	—	—	—	—	—	—	—	—	—	—	44,550*	20,200*	12
A. guatemalensis	—	—	—	—	—	—	—	—	—	30,000–43,000	13,600–19,500	36,500	16,500	>2
A. homolepis	54–64	42–50	800	300	—	—	—	—	67–89	32,200–49,000	14,600–22,200	43,650	19,800	19
A. lasiocarpa	—	—	—	—	—	—	1.7	22	—	52,700–108,700	23,900–49,300	76,750	34,800	19
	—	—	—	—	—	—	—	—	—	—	—	47,600*	21,600*	4
var. *arizonica*	—	—	—	—	—	—	1.2–1.9	16–24	—	38,800–56,200	17,600–25,500	49,200	22,300	8
A. magnifica	32–39	25–30	—	—	40	64	1.4	18		8,800–19,600	4,000–8,900	14,100	6,400	36
A. mariesii	33–41	26–32	850	312	—	—	—	—	52–65	42,100–65,050	19,100–29,500	50,700	23,000	>6
A. nordmanniana	40–50	31–39	—	—	125	196	4.8–5.8	62–75	—	11,550–19,000	5,700–8,600	15,650	7,100	>24
A. procera	—	—	200	80	—	—	1.7–3.6	22–46	500	20,300–42,100	9,200–19,100	29,800*	13,500*	>36
A. sachalinensis	—	—	—	—	—	—	—	—	—	65,050–118,000	29,500–53,5000	97,000	44,000	>29
A. x *shastensis*	—	—	—	—	—	—	—	—	—	11,250–24,700	5,100–11,200	16,100*	7,300*	36
A. veitchii	—	—	—	—	—	—	—	—	—	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), Soljanik (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)
A. alba	5–7	–3 to 7	2–6
	5–8	**–10 to –17**	**15**
	< 9	–15	4–5
A. amabilis	**6–8**	**–17**	**> 5**
A. balsamea	5–8	+0.5 to +4	5
	6–8	**–17**	**13**
A. cephalonica	9–11	+ 4	1–2
A. concolor	**5–8**	**0 to –18**	**7**
	6–10	–18	3
A. firma	—	–2 to –4	> 6
A. fraseri	10–15	–12	—
A. grandis	5–8	–7	> 2
	7–10	–4 to –10	3
	11	–4	10 +
	9–11	+4	1–2
	< 9	**–15**	**> 5**
A. guatemalensis	6-8	+3 to +4	<1
A. homolepis	—	–2 to +4	> 6
A. lasiocarpa	**5–8**	**–17**	**> 5**
A. magnifica	9–11	+5	5
A. mariesii	—	–2 to +4	> 6
A. nordmanniana	9–11	+4	2
	< 9	**–15**	**> 5**
A. procera	6–9	0 to –18	7
	6–9	**–4**	**> 10**
A. sachalinensis	—	–2 to +4	> 6
A. × *shastensis*	11	–4	> 10

Sources: Allen (1957), Edwards (1982a), Franklin (1974b), Gradi (1966), Heit (1941, 1968b), Hofman and Vackova (1966), Holmes and Buszewicz (1962), Issleib (1956), Jones (1962), Loffler (1985), Machanicek (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	Bareroot production						Container production	
			Seedling density		Sowing depth		Mulch^{a}	Stock type	Container type^{b}	Stock type
			/m^{2}	/ft^{2}	cm	in				
A. alba	0	Fall	270–430	25–40	2^{c}	$^{3}/_{4}{}^{c}$	Pine needles	—	—	—
	30^{d}–80	Mid-Mar–mid-Apr	—	—	—	—	—	—	Styro 2, 5	1+0
A. amabilis	28^{f}	Mar–Apr	270–540	25–50	0.5–1	$^{1}/_{4}$–$^{1}/_{2}$	Straw^{g}	3+0, 3+1	—	—
	—	—	—	—	—	—	None	1+0, 2+0, 3+0	—	—
	—	Late Apr–early May	330/row	100/row	—	—	—	3+0, 3+1	—	—
	30^{d}–120^{h}	Early Jan (1+0) for fall/winter lift	—	—	—	—	—	—	313B, 410A	1+0
	30^{d}–120^{h}	Jan–Mar (1+0)	—	—	—	—	—	—	313A&B, 410A, PCT410, 412A, 415B&D, 615A	1+0, P+1^{3}
	30^{d}–120^{h}	Early Mar–early April	—	—	—	—	—	—	313A, Styro 2, 5,& 7	1+0, 2+0, P+1
	30^{d}–120^{h}	Apr–early May (2+0) outdoors	—	—	—	—	—	—	415B,D, 412A	2+0
A. balsamea	0	Fall	220–54	20–50	—	—	—	—	—	—
	28–60^{h}	Late Mar–early Apr	—	—	—	—	—	—	Styro 2, 5, 7	1+0, 2+0, P+1
A. bracteata	0	Fall	—	—	0.5	$^{1}/_{4}$	—	2+0	—	—
	14–28	Feb-Mar	—	—	—	—	—	—	313A, 415B, D, 615A	1+0, 2+0, 2+1, P+1
A. concolor	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	1+0, 2+0, 2+1, P+1
	—	Apr–early May (2+0) outdoors	—	—	—	—	—	—	415B, 412A	2+0
A. firma^{i}	3 0–60	Apr–early May	—	—	—	—	—	2+2	—	—
A. fraseri	0	Fall	220–540	20–50	0.3–0.5	$^{1}/_{8}$–$^{1}/_{4}$	Sawdust	3+0, 4+0	—	—
	28–60	Late Mar–early Apr	270	25	—	—	—	—	—	—
	28^{d}–60^{h}	Early Jan (1+0) for fall/winter lift	—	—	—	—	—	—	313B, 410A	1+0
	40—60	Mid-March–early May	330	100	—	—	—	—	—	—
	28^{d}–60^{h}	Jan (1+0)	—	—	—	—	—	—	415B, D, 615D	1+0
	28^{d}–60^{h}	Feb–early Apr	—	—	—	—	—	—	313A, 415B,D, 615D, Styro 2, 5, 7	1+0, 2+0, P+1
	28^{d}–60^{h}	Apr–early May (2+0) outdoors	—	—	—	—	—	—	415B, 412A	2+0
A. grandis	0	Fall	270–430	25–40	2^{c}	$^{3}/_{4}{}^{c}$	None, sawdust	2+0, 2+1, 3+0	—	—
	0^{j}–$42^{f,g}$	Spring (early Apr–early May)	215–270	20–25	0.5–2	$^{1}/_{4}$–$^{3}/_{4}$	pine needles	1+0, 2+0, 3+0, P+1	—	—
	28^{d}–120^{h}	Early Jan (1+0) for fall/winter lift	—	—	—	—	—	—	313B, 410A	1+0
	28^{d}–120^{h}	Jan–early Feb (1+0)	—	—	—	—	—	—	313A, 410A, 415B,D, 615A	1+0
	28^{d}–120^{h}	Early Feb–Apr	—	—	—	—	—	—	313A, 410A, 415B,D, 412A, 615A, Leach 1,2, Styro 2,5,7	1+0, 2+0, 2+1, P+1
	28^{d}–120^{h}	Early Mar (greenhouse)–early May (2+0) (incl outdoors)	—	—	—	—	—	—	412A	2+0, P+1
A. homolepis	30–60	Spring	—	—	—	—	—	2+2	—	—
	60–80	Mid-Mar–mid-Apr	—	—	—	—	—	—	Styro 2,5	1+0
A. koreana	60–80	Mid-Mar–mid-Apr	—	—	—	—	—	—	Styro 2,5	1+0
A. lasiocarpa var. *arizonica*	0	Fall	—	—	0.3	$^{1}/_{8}$	Leaf mold	—	—	—
	30^{d}–80^{h}	Mid-Mar–mid-Apr	—	—	—	—	—	—	Styro 2,5	1+0, 2+0

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

			Bareroot production						Container production	
			Seedling density		Sowing depth					
Species	Stratification time (days)	Sowing season	/m^{2}	/ft^{2}	cm	in	Mulch^{a}	Stock type	Container type^{b}	Stock type
A. lasiocarpa	30^{d}–120	Early Jan (1+0) for fall/winter lift	—	—	—	—	—	—	313B, 410A	1+0
var. *lasiocarpa*	30^{d}–120	Jan–to early Feb (1+0)	—	—	—	—	—	—	313B, 410A, 415B,D, 615A	1+0
		Jan–Mar	—	—	—	—	—	—	313A,B, 410A, PCT410,	1+0, 2+0, 2+1, P+1
	30^{d}–120	Early Mar–late May (2+0)	—	—	—	—	—	—	410A, 412A, 415B,D,415B, 615A	1+0, 2+0, 2+1, P+1
	30^{d}–120	(incl outdoors)								
A. magnifica var. *magnifica*	30–42^{f}	Mid-Mar–early May	215–430 (330/row)	20–40 (100/row)	0.5–1.5	$^{1}/_{4}$–$^{1}/_{2}$	None	1+0, 2+0, 2+2 P+1	—	—
	30^{d}–60^{h}	Jan	—	—	—	—	—	—	415B,D, 615A	1+0
	—	Late Mar–early Apr	—	—	—	—	—	—	Styro 2,5,7	1+0, 2+0, P+1
A. nordmanniana	0	Fall	220–540	20–50	2^{c}	$3/4^{c}$	Pine needles, none	—	—	—
	50–70^{f}	Spring	540	50	1–2.5	3/8–1	Peat moss	3+0	—	—
	14^{d}–80^{h}	Mid-Mar–mid-Apr	—	—	—	—	—	—	Styro 2,5,7	1+0, 2+0
A. pindrow	30^{d}–80	Mid-Mar–mid-Apr	—	—	—	—	—	—	Styro 2,5	1+0
A. procera	0	Fall	220–540	20–50	2^{c}	$^{3}/_{4}{}^{c}$	Pine needles, none	1+0, 2+0, 3+0	—	—
	0^{j}–42^{f}	Spring	320–430	30–40	0.5–1.5	$^{1}/_{4}$–$^{1}/_{2}$	None	2+0, 3+0, 2+0	—	—
	28^{d}–120^{h}	Early Mar–early May	220–380	20–35	0.5–1.5	$^{1}/_{4}$–$^{1}/_{2}$	None	2+0, 3+0, 2+0	—	—
	28^{d}–120^{h}	Early Jan (1+0) for fall/winter lift	—	—	—	—	—	—	313B, 410A	1+0
	28^{d}–120^{h}	Jan–early Feb (1+0)	—	—	—	—	—	—	313B, 410A, 415B,D, 615A	1+0
	28^{d}–120^{h}	Feb–Apr	—	—	—	—	—	—	313B, 415B,D, 410A, 615A, Styro 2,5, Leach 1,2	1+0, 2+0, 2+1, P+1
	28^{d}–120^{h}	Early Mar (greenhouse)	—	—	—	—	—	—	313A	2+0, P+1
	28^{d}–120^{h}	Apr–early May (2+0) (incl outdoors)	—	—	—	—	—	—	415B,D, 412A	2+0
A. sachalinensis	30–60^{k}	Spring	—	—	—	—	—	2+2	—	—
A. x *shastensis*	0^{j}–42^{f}	Spring	220–430	20–40	1–1.5	$^{3}/_{8}$–$^{1}/_{2}$	None	1+0, 2+0, 2+1, 3+0	—	—
	30^{d}–45^{h}	Late Feb–Apr	—	—	—	—	—	—	410A, 412A, Styro 5, Leach 1,2	1+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), Heit (1964, 1967, 1968b), Heit and Eliason (1940), Helson (1997), Henry and Blazich (1990), Holmsgaard and Kjaer (1951), ISTA (1993), Kusisto (1997), Lehar (1997), Leloup (1956), MacDonald (1998), Moore (1997), Nagao and Asakawa (1963), NBV (1946), Pelton (1997), Rafn (1915), Rafn and Son (nd), Riskin (1997), Rutar (1991), Snyder (1997), Speers 1962, Stubley 1998, Thompson 1997, Toumey and Stevens (1928), Triebwasser (1997), Trimble (1997), Tulstrup (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 (_–_ in); pine needles, 3–4.5 cm (1_–1_ in); sawdust, 0.5 cm (_ 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 in^{3}); 313B, 65 ml (3.9 in^{3}); 410A & PCT 410, 80 ml (4.9 in^{3}); 415B, 93 ml (6.3 in^{3}); 412A, 126 ml (7.7 in^{3}); 415D, 172 ml (10.5 in^{3}); 615A, 336 ml (20.0 in^{3}); Styro 2, 39 ml (2.3 in^{3}); Styro 5, 77 ml (4.7in^{3}); Stryo 7, 121 ml (7.4in^{3}); Leach 1, 50 ml (3 in^{3}), Leach 2, 164 ml (10 in^{3}).

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

d For 28–30 days only if intending to strat-redry.

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 papr 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 (Kozlowski 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).

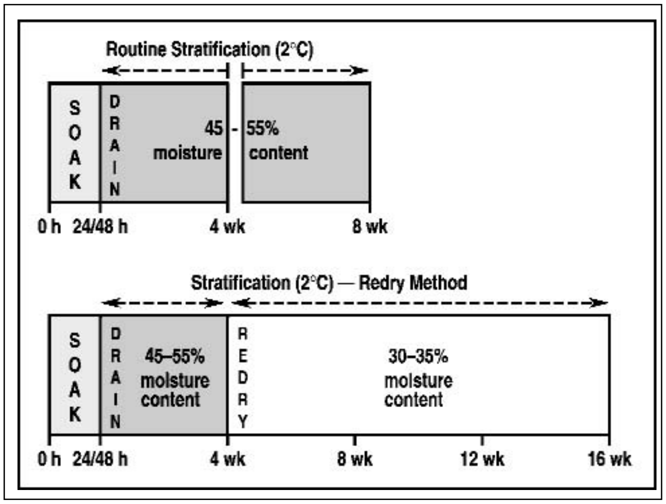
As described above, seeds air-dried to 25% moisture content can be "stored" in the refrigerator for up to a year without losing the beneficial effect of the initial stratification, that is, they remain in a ready-to-germinate state. Stratified seeds of noble and Pacific silver firs have been dried to 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 GA_3 worked well for Guatemalan fir seeds (Salazar 1991). Use of gibberellin GA_{4+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).

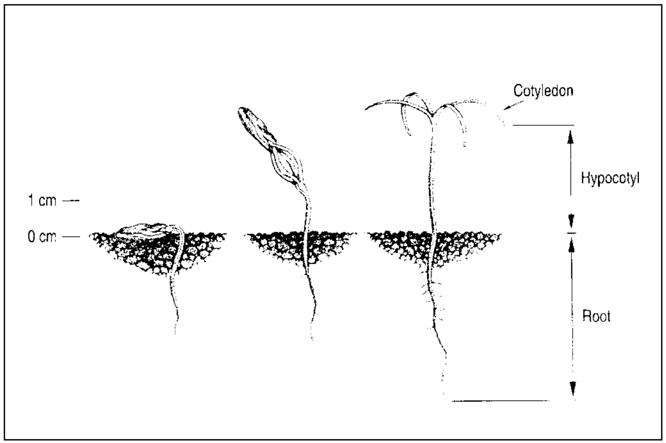
By the time newly harvested fir seeds have been processed, there is often insufficient time to complete standard germination tests that require a minimum of 3 weeks for completion, and more than twice this duration if the seeds must be stratified, before they are required for sowing the following spring. 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 an 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 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).

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).

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/m^2 (25 to 30/ft^2) (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/m^2 or 260 to 300/linear m of seed bed (20 to 23/ft^2 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 $1^{1}/_{2}$ 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).

References

Abbott HG. 1962. Tree seed preferences of mice and voles in the Northeast. Journal of Forestry 60: 97–99.

Abbott HG, Hart AC. 1960. Mice and voles prefer spruce seeds. Sta. Pap. 153. Upper Darby, PA: USDA Forest Service, Northeastern Forest Experiment Station. 12 p.

Adkins CR. 1984. Role of stratification, temperature and light in Fraser fir seed germination. Combined Proceedings of the International Plant Propagators' Society 33: 504–515.

Adkins CR, Hinesley LE, Blazich FA. 1984. Role of stratification, temperature, and light in Fraser fir germination. Canadian Journal of Forest Research 14: 88–93.

Agee JK. 1982. True fir management for wilderness, water, recreation and wildlife values. In: Oliver CD, Kenady RM, eds. Proceedings, Symposium on Biology and Management of True Fir in the Pacific Northwest; 1981; Seattle/Tacoma, WA. Contrib. 45. Seattle: University of Washington, Institute of Forest Resources: 227–237.

Aguirre-Planter E, Furnier GR, Eguiarte LE. 2000. Low levels of genetic variation within and high levels of genetic differentiation among populations of species of *Abies* from southern Mexico and Guatemala. American Journal of Botany 87: 362–371.

Ahlgren CE. 1957. Phenological observations of nineteen native tree species in northeastern Minnesota. Ecology 38: 622–628.

Alexander RR, Shearer RC, Shepperd WD. 1990. *Abies lasiocarpa* (Hook.) Nutt., subalpine fir. In: Burns RM, Honkala BA, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 60–70.

Allen GS. 1957. Storage behavior of conifer seeds in sealed containers held at 0° F., 32° F., and room temperature. Journal of Forestry 55: 278–281.

Allen GS. 1958. Factors affecting the viability and germination behavior of coniferous seed: 3. Commercial processing and treatments similar to processing *Pseudotsuga menziesii* (Mirb.) Franco, and other species. Forestry Chronicle 34: 283–298.

Allen GS. 1960. Factors affecting the viability and germination behaviour of coniferous seed. Part 4. Stratification period and incubation temperature, *Pseudotsuga menziesii* (Mirb.) Franco. Forestry Chronicle 36: 18–29.

Allen GS, Bientjes W. 1954. Studies on coniferous tree seed at the University of British Columbia. Forestry Chronicle 30: 183–196.

Allison CJ. 1980. X-ray determination of horticultural seed quality. Combined Proceedings of the International Plant Propagators' Society 30: 78–89.

Anderson RL. 1985. Checklist of micro-organisms associated with tree seeds in the world, 1985. Gen. Tech. Rep. SE-39. Asheville, NC: USDA Forest Service, Southeastern, Forest Experiment Station. 34 p.

Androic M. 1960. *A. fundella*—a pest of *Abies alba* needles—the cause of dieback of *A. alba* in Gorski Kotar. Sumarski List 84: 203–215.

Androic M. 1976. Population dynamics of *Argyresthia fundella* and their effects on Croatian fir stands. Proceedings, IUFRO Division II, Forest Plants and Forest Protection. 16th IUFRO World Congress, Oslo, Norway: 362–466.

Annila E. 1982. Diapause and population fluctuations in *Megastigmus specularis* Walley and *Megastigmus spermotrophus* Wachtl. (Hymenoptera, Torymidae). Annales Entomologici Fennici 48: 33–36.

Anonymous. 1950a. Effective pollination distances. Ann. Rep. 1949. Upper Darby, PA: USDA Forest Service, Northeastern Forest Experiment Station: 12–13.

Anonymous. 1950b. Silvicultural studies: Report of the Forest Service 1949. Victoria: British Columbia Department of Lands and Forests: 25–28.

Anonymous. 1951. Natural regeneration [seed fall studies]. Ann. Rep. 1950. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station: 13.

Anonymous. 1969. Record of the First Session of the FAO Panel of Experts on Forest Gene Resources, 1968. Rome: FAO: 21–25.

Anonymous. 1970. Cone harvesting by mechanical shaker, report on Forest Research 1969/1970, Forestry Commission. London: Her Majesty's Stationery Office: 112–113.

Anonymous. 1977. Sowing between rows in the nursery. Allgemeine Forstzeitschrift 32: 39.

Anonymous. 1986. Databook on endangered tree and shrub species and provenances. For. Pap. 77. Rome: FAO. 524 p.

Anonymous 1998. *Abies guatemalensis* Rehder. Nota técnica sobre manejo de semillas forestales #55. Costa Rica: Centro Agronómico Tropical de Investigación y Enseñanza (CATIE). 2 p.

AOSA [Association of Official Seed Analysts]. 1983. Seed vigor testing handbook. Contrib. 23 to the Handbook on seed testing. Lincoln, NE: Association of Official Seed Anaylsts. 93 p.

AOSA [Association of Official Seed Analysts]. 1998. Rules for testing seeds (revised 1998). Lincoln, NE: Association of Official Seed Analysts. 123 p.

Arbez M. 1967. *Abies nordmanniana* (Spach), *Abies bornmuelleriana* Mattfeld. [First results of a provenance trial in the nursery]. Annales des Sciences Forestiere 24: 121–156.

Arbez M. 1969a. *Abies nordmanniana* in northern Turkey. Revue Forestiere Francaise 21: 189–95.

Arbez M. 1969b. Réparation, écologie et variabilité des sapins de Turquie du nord: *Abies nordmanniana* (Spach), *Abies bornmuelleriana* Mattfeld, *Abies equi-trojani* Ascherson et Sintenis. Annales des Sciences Forestiere 26: 257–284.

Arena M. 1959a. The ecological characters of the juvenile vegetative organs of *A. nebrodensis* deduced from their structure. Atti dell'Accademia Nazionale dei Lincei, Roma (ser. 8) 26: 252–258.

Arena M. 1959b. The biological behaviour of *A. nebrodensis*. Nuovo Giornale Botanico Italiano (n.s.) 66: 451–456.

Arena M. 1960. The germinative capacity of the seed, and the survival of seedlings, of *A. nebrodensis.* Italia Forestale e Montana 15: 247–50.

Arista M, Talavera S. 1994a. Pollen dispersal capacity and pollen viability of *Abies pinsapo* Boiss. Silvae Genetica 43: 155–158.

Arista M, Talavera S. 1994b. Phenology and anatomy of the reproductive phase of *Abies pinsapo* Boiss. (Pinaceae). Botanical Journal of the Linnean Society 116: 223–234.

Arista M, Talavera S. 1995. Cone production and cone crop pattern in *Abies pinsapo* Boiss. Anales del Jardin Botanico de Madrid 53: 5–12.

Arista M, Talavera S, Herrera J. 1992. Viability and germination of the seeds of *Abies pinsapo* Boiss. Acta Botanica Malacitana 17: 223–228.

Arno SF, Hammerly RP. 1977. Northwest trees. Seattle, WA: The Mountaineers. 222 p.

Arnold RJ, Jett JB, Allen HL. 1992. Identification of nutritional influences on cone production in Fraser fir. Soil Science Society of America Journal 56: 586–591.

Arnott JT, Matthews RG. 1982. Nursery production of true firs in British Columbia. In: Oliver CD, Kenady RM, eds. Proceedings, Symposium on Biology and Management of True Fir in the Pacific Northwest; 1981; Seattle/Tacoma, WA. Contrib. 45. Seattle: University of Washington, Institute of Forest Resources: 195–201.

Arya SR, Bhagat S, Singh V, Singh O. 1994. Seed fertility in relation to tree size of *Abies pindrow* and *Picea smithiana*. Indian Forester 120(8): 677–681.

Asakawa S. 1959. Germination behaviour of several coniferous seeds. Journal of the Japanese Forestry Society 41: 430–435.

Asakawa S. 1968. Some proposals to amend the International Rules for Seed Testing, with special references to forest tree seeds. Proceedings, 15th International Seed Testing Congress. Reprint 101. 6 p.

Atimetov MA. 1968. Fruiting of *Abies sibirica* and *Picea schrenkiana* in the Dzhungarian Alatau range [S. Kazakhstan]. Trudy Kazanskogo Sel'skokhozyaistvennogo Instituta 11: 211–218.

Aussenac G. 1966. Seed dispersal in *Abies grandis*. Revue Forestiere Francaise 18:431–434.

Bakuzis EV, Hansen HL. 1965. Balsam fir, *Abies balsamea* (Linnaeus) Miller: a monographic review. Minneapolis: University of Minnesota Press. 445 p.

Bang C. 1979. Various lopping methods and intensities for the production of decoration greenery of *Abies procera*. Forstlige Forsφgsvaesen i Danmark 37: 1–22.

Barbour MG. 1988. Californian upland forests and woodlands. In: Barbour MG, Billings WD, eds. North American terrestrial vegetation. Cambridge: Cambridge University Press: 131–164.

Baron FJ. 1969. Ten years of forest seed crops in California. Journal of Forestry 67: 490–492.

Barton LV. 1930. Hastening the germination of some coniferous seeds. American Journal of Botany 17: 88–115.

Barton LV. 1953. Seed storage and viability. Contributions of the Boyce Thompson Institute 17: 87–103.

Barton L.V. 1961. Seed preservation and longevity. London: Leonard Hill Books. 216 p.

Bauer Z, Tichy J. 1960. Effect of *Parus ater* (L.) on silver fir in E. Slovakia. Sbornik Československe Akademie Zemedelskych ved (Lesnictvi) 6: 395–408.

Beck DE. 1990. *Abies fraseri* (Pursh) Poir., Fraser fir. In: Burns RM, Honkala BA, tech.coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 47–51.

Bennett E. 1966. Partial chemical composition of four species of coniferous seeds. Forest Science 12: 316–318.

Benzie JW. 1960. Viability of balsam fir seed depends on age of tree. Tech. Note 591. St. Paul: USDA Forest Service, Lake States Forest Experiment Station. 2 p.

Bergsten U. 1993. Removal of dead-filled seeds and invigoration of viable seeds: a review of a seed conditioning concept used on conifers in Sweden. In: Edwards DGW, comp. & ed. Dormancy and barriers to germination. Proceedings, Internatational Symposium, IUFRO Project Group P2.04-00 (Seed Problems); 1991; Victoria, BC. Victoria, BC: Forestry Canada, Pacific Forestry Centre: 7–15.

Beskok TE. 1970. Seed maturation period in *Pinus brutia, Picea orientalis* and *Abies börnmulleriana*. Teknik Bülten 42. Ankara: Ormancilik Arastirma Enstitüsü. 64 p.

Bess HA. 1946. Staminate flowers and spruce budworm abundance. Bi-monthly Progress Report 2. [Ottawa, Dominion Department of Agriculture, Science Service, Division of Entomology. Forest Insect Investigations]: 3–4.

Blais JR. 1952. The relationship of the spruce budworm to the flowering condition of balsam fir. Canadian Journal of Zoology 30: 1–29.

Blazich FA, Hinesley LE. 1984. Low temperature germination of Fraser fir seed. Canadian Journal of Forest Research 14: 948–949.

Blazich FA, Hinesley LE. 1994. Propagation of Fraser fir. Journal of Environmental Horticulture 12: 112–117.

Blazich FA, Hinesley LE. 1995. Fraser fir. American Nurseryman 181(5): 54–58, 60–67.

Bloomberg WJ. 1969. Diseases of Douglas-fir seeds during cone storage. Forest Science 15: 176–181.

Boivin B. 1959. *Abies balsamea* (Linné) Miller et ses variations. Le Naturaliste Canadien 86: 219–223.

Bongio D. 1997. Correspondence, Sept. 1997. Trinidad, CA: Louisiana-Pacific Corp., Western Division, Big Lagoon Woods.

Bouvarel P, Lemoine M. 1958. Notes sur le reboisement: la conservation par le froid des graines de resineux. Revue Forestiere Francaise (Nancy) 10: 493–497.

Bradley L, Ebel BH. Summerville KO. 1981. *Leptoglossus* spp. observed on eastern whitepine and Fraser fir cones. Res. Note SE-310. Asheville, NC: USDA Forest Service, Southeastern Forest Experiment Station. 3 p.

Bryant DG, Hudak J. 1968. Aphid impact on forest stands. Report of the Newfoundland Forest Protection Association 1968: 60–61.

Buchwald NF, Klinge AB, Toft K. 1961. *Ciboria rufo-fusca* on *Abies alba* and *A. nordmanniana* in Denmark. Friesia, Kobenhavn 6: 321–34.

Buszewicz G, Holmes GD. 1957. Seven years seed testing experience with the tetrazolium viability test for conifer seeds. Report on Forest Research 1956/1957, Forestry Commision. London: Her Majesty's Stationery Office: 142–51.

Campbell SJ, Landis TD. 1990. Managing seedborne diseases in western forest nurseries. Tree Planters' Notes 41(4): 3–7.

Camenzind WG. 1990. A guide to aerial cone collection equipment and techniques in British Columbia. Victoria: British Columbia Ministry of Forests. 30 p.

Canakcioglu H. 1969. Insect damage on cones and seeds of forest trees in Turkey. Istanbul Üniversitesi Orman Fakültesi Dergisi 19A: 2, 82–88.

Carkin RE, Franklin JF, Booth J, Smith CE. 1978. Seeding habits of upper-slope tree species: 4. Seed flight of noble fir and Pacific silver fir. Res. Note PNW-312. Corvallis, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 10 p.

Carman RS. 1953. How tree seed is procured: the collecting, extracting, processing and storing of tree seed with particular reference to heredity and provenance. Pulp Paper Magazine of Canada 54: 100–107.

Carrillo A, Garcia AA, Perez MC. 1994. Influence of time and temperature on the composition of seed oil from 5 species of commercial timber. Phyton (Buenos Aires) 56: 51–58.

Carrillo SA, Patino VF, Talavera AI. 1980. Moisture content of stored seed of 7 *Pinus* species and *Abies religiosa* and its relation to percentage germination. Ciencia Forestal 5: 39–48.

Cermak J. 1987. Monoterpene hydrocarbon contents of the resin from seeds of silver fir (*Abies alba* Mill.). Trees: Structure and Function 1: 94–101.

Cermak J, Penka M. 1979. An attempt to estimate potential production of volatile terpenes from the logging by-products of silver fir (Abies *alba* Mill.). Planta Medica 36: 3, 252.

Chiasson LP. 1967. Interspecific hybridisation in *Abies*. In: Proceedings, 14th Northeastern Forest Tree Improvment Conference; 1966; Toronto, ON. Upper Darby, PA: USDA Forest Service, Northeastern Forest Experiment Station: 20–23.

Cheng WC, Fu KL. 1987. Flora Republicae Popularis Sinicae. Tomus 7: Gymnospermae. Beijing, China: Kexue Chubanshe [in Chinese; English version available as: Flora of China. Beijing: Science Press/St. Louis: Missouri Botanical Garden. *Abies* is found in Volume 4: 44 ff; also available at: http://hua.huh.harvard.edu].

Ching TM. 1960. Seed production from individual cones of grand fir (*Abies grandis* Lindl.). Journal of Forestry 58: 959–961.

Ching TM, Parker MC. 1958. Hydrogen peroxide for rapid viability tests of some coniferous tree seeds. Forest Science 4: 128–134.

Clarkson RB, Fairbrothers DE. 1970. A serological and electrophoretic investigation of eastern North American *Abies* (Pinaceae). Taxon 19: 720–727.

Cooper SV, Neiman KE, Steele R, Roberts DW. 1987. Forest habitat types of northern Idaho: a second approximation. Gen. Tech. Rep. INT-236. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 135 p.

Cope EA [auth.], King BS [illus]. 1993. Native and cultivated conifers of northeastern North America: a guide. Ithaca, NY: Cornell University Press/London: Comstock Publishing Associates. 231 p.

Crawford PD, Oliver CD. 1990. *Abies amabilis* Dougl. ex Forbes., Pacific silver fir. In: Burns RM, Honkala BA, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 17–25.

Critchfield WB. 1988. Hybridization of the California firs. Forest Science 34: 139–151.

Curtis K. 1997. Correspondence, Sept. 1997. Olympia: Washington State Department of Natural Resources, Webster Forest Nursery.

Czernik Z. 1993. Studies of geometrical properties of silver fir seeds. Sylvan 137: 57–64.

Dallimore W, Jackson AB. 1967. A handbook of Coniferae including Ginkgoaceae. 4th ed. [rev. by Harrison SG]. New York: St. Martin's Press: 107–175.

Dalskov F. 1960. Handling seed of *Abies* spp. Dansk Skovforenings Tidsskrift 45: 331–338.

Daniels JD. 1969. Variation and intergradation in the grand fir–white fir complex [PhD thesis]. Moscow, ID: University of Idaho. 235 p.

Danielson HR, Grabe DF. 1973. Storage of noble fir seeds. Proceedings of the Association of Official Seed Analysts 63: 161–165.

Davidson R. 1993. Variation in germination parameters within and among populations of Pacific silver fir (*Abies amabilis*) on Vancouver Island. In: Edwards DGW, comp. & ed. Dormancy and barriers to germination. Proceedings, International Symposium, IUFRO Project Group P2.04-00 (Seed Problems); 1991; Victoria, BC. Victoria, BC: Forestry Canada, Pacific Forestry Centre: 23–30.

Davidson RH, Edwards DGW, Sziklai O. 1984. Treatment and temperature effects on the germination of Pacific silver fir. Missoula, MT: Northwest Scientific Association Meeting. 12 p.

Davidson RH, Edwards DGW, Sziklai O, El-Kassaby YA. 1996. Genetic variation in germination parameters among populations of Pacific silver fir. Silvae Genetica 45: 165–171.

Dässler H-G, Zentsch W. 1959. Über die Keimungshemmende Wirkung von Bestandteilen des Tannenzapfenöls [Germination-inhibiting components of the oil from silver fir cones]. Pharmazie (Berlin) 14: 111–112.

Debreczy Y, Racz I. 1995. New species and varieties of conifers from Mexico. Phytologia 78: 217–243.

Diebel KE, Feret, PP. 1991. Isozyme variation within the Fraser fir (*Abies fraseri* (Pursh) Poir.) population on Mount Rogers, Virginia: lack of microgeographic differentiation. Silvae Genetica 40: 79–85.

Dietrichson J. 1971. Genetic variation in subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). Meddelelser fra det Norske Skogforsoeksvesen 29(1): 1–19.

Dobbs RC, Edwards DGW, Konishi J, Wallinger D. 1976. Guideline to collecting cones of B.C. conifers. Joint Rep. 3. Victoria: British Columbia Forest Service/Canadian Forestry Service. 98 p.

Doikov G. 1973. Determination of phenotype forms in *Abies alba*. Gorskostopanska Nauka 9: 20–25.

Donahue JK, Dvorak WS, Gutierrez EA, Kane MB. 1985. *Abies guatemalensis* : a two year status report. Bull. Trop. For. 3. Raleigh: North Carolina State University, Central America and Mexico Resources Cooperative. 17 p.

Douglass BS. 1969. Collecting forest seed cones in the Pacific Northwest 1969. Portland, OR: USDA Forest Service, Pacific Northwest Region. 16 p.

Douglass BS. 1975. Floral greenery from Pacific Northwest forests. Portland, OR: USDA Forest Service, Pacific Northwest Region. 35 p.

Ducci F, Paci M. 1986. Evaluation of the viability of ungerminated seeds at the end of germination tests: comparison of three evaluation methods for silver fir. Annali dell'Istituto Sperimentale per la Selvicoltura 17: 237–254.

Durzan DJ. 1979. Nutritional relations between the spruce budworm and seed cones. In: Bonner F, ed. Proceedings, IUFRO/USFS/Mississippi State University International Symposium on Flowering and Seed Development in Trees; 1978; Starkville, MS. New Orleans: USDA Forest Service, Southern Forest Experiment Station: 358 p.

Dvorak WS. 1997. Personal communication. Director, Central America and Mexico Coniferous Resources (CAMCORE) Cooperative. Raleigh: North Carolina State University, College of Forest Resources.

Earle CJ. 1999. Gymnosperm database [online]. Available at: http://www.geocities.com/~earlecj/pi/ab/index.htm [1999 March 28] or http://www.biologie.uni-hamburg. de/b-online/earle/pi/ab/index.htm [2000 March 16].

Ebell LF, Schmidt RL. 1964. Meteorological factors affecting conifer pollen dispersal on Vancouver Island. Pub. 1036. Ottawa: Canada Department of Forestry. 28 p.

Eden CJ. 1965. Use of X-ray technique for determining sound seed. Tree Planters' Notes 72: 25–28.

Edwards DGW. 1969. Investigations on the delayed germination of noble fir [PhD thesis]. Seattle: University of Washington. 231 p. [Dissertation Abstracts International 1969 30B: 2484].

Edwards, DGW. 1971. The kinetics of water absorption in stratifying and nonstratifying noble fir (*Abies procera* Rehd.) seeds. Canadian Journal of Forest Research 1: 235–240.

Edwards DGW. 1978. Tree Seed Research, Pacific Forest Research Centre, B.C. Proceedings, 16th Meeting of the Canadian Tree Improvement Association, Part 1. Winnipeg, MB. 1977: 209–216.

Edwards DGW. 1979. An improved air seed-sorter for laboratory use. Rep. BC-X-188. Victoria, BC: Environment Canada, Forestry Service. 11 p.

Edwards DGW. 1980a. Maturity and seed quality, a state-of-the-art review. In: Bonner F, ed. Proceedings, IUFRO/USFS/Mississippi State University International Symposium on flowering and seed development in trees; 1978; Starkville, MS. New Orleans: USDA Forest Service, Southern Forest Experiment Station: 233–263.

Edwards DGW. 1980b. Tree seed research, Pacific Forest Research Centre, BC, 1977–1979. In: Proceedings, 17th Meeting of the Canadian Tree Improvement Association, Part 1; 1979; Gander, NF; 1979: 231–236.

Edwards DGW. 1981. A new prechilling method for true fir seeds. Proceedings, Joint Meeting of the Intermountain Nurseryman's Association and Western Forest Nursery Association; 1980; Boise, ID. Gen. Tech. Rep. INT-109. Boise, ID: USDA Forest Service, Intermountain Forest and Range Experiment Station: 58–66.

Edwards DGW. 1982a. Collection, processing, testing and storage of true fir seeds: a review. In: Oliver CD, Kenady RM, eds. Proceedings, Symposium on the Biology and Management of True Fir in the Pacific Northwest; 1981; Seattle/Tacoma, WA. Contrib. 45. Seattle: University of Washington, Institute of Forest Resources: 113–137.

Edwards DGW. 1982b. Improving seed germination in *Abies*. Combined Proceedings of the International Plant Propagators' Society 31: 69–78.

Edwards DGW. 1982c. Storage of prechilled *Abies* seeds. In: Wang BSP, Pitel JA, eds. Petawawa National Forestry Institute: Proceedings, IUFRO WP S2.01.06 International Symposium on Forest Tree Seed Storage; 1980; Chalk River, ON. Chalk River, ON: Environment Canada, Canadian Forestry Service: 195–203.

Edwards DGW. 1986a. Cone prediction, collection and processing. In: Shearer RC, comp. Proceedings, Symposium on Conifer Tree Seed in the Inland Mountain West; 1985; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 78–102.

Edwards DGW. 1986b. Special prechilling techniques for tree seeds. Journal of Seed Technology 10: 151–171.

Edwards DGW. 1987. Methods and procedures for testing tree seeds in Canada. For. Tech. Rep. 36. Ottawa: Canadian Forestry Service. 31 p.

Edwards DGW. 1997. The stratification–redry technique with special reference to true fir seeds. In: Landis TD, South DB, tech. coords. Proceedings, Western Forest and Conservation Nursery Association Meeting; 1996; Salem, OR. Gen. Tech. Rep. PNW-GTR-389. Portland, OR: USDA Forest Service, Pacific Northwest Research Station: 172–182.

Edwards DWG, 2002. Seed-to-wing attachments in important members of the Pinaceae, with additional observation on members of the Cupressaceae. In: Thanos CA, Beardmore T, Connor K. Tolentino I, eds. Tree Seeds 2002; Proceedings, International Symposium, IUFRO Research Group 2.09.00 (Seed Physiology and Technology; 2002 Sept. 11–15; Chania, Crete. Athens: University of Athens, MAICh, Hellenistic Ministry of Agriculture, Interational Society for Seed Science: 59-69.

Edwards DGW, Sutherland JR. 1979. Hydrogen peroxide treatment of *Abies* seeds. Bi-Monthly Research Notes 35. [Ottawa: Environment Canada, Canadian Forestry Service]: 3–4.

Edwards G. 1962. The germination requirements of *Abies* species. Report of the Forest Seeds Committee, Part 2. Proceedings, International Seed Testing Association 27: 142–180.

Edwards IK. 1986. Review of literature on fertilization and conifer seed production. Forest Management Note 40. Edmonton, AB: Canadian Forest Service, Northern Forestry Centre. 7 p.

Eis S. 1970. Reproduction and reproductive irregularities of *Abies lasiocarpa* and *A. grandis*. Canadian Journal of Botany 48: 141–143.

Eis S. 1973. Cone production of Douglas-fir and grand fir and its climatic requirements. Canadian Journal of Forest Research 3: 61–70.

Eis S, Garman EH, Ebell LF. 1965. Relation between cone production and diameter increment of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), grand fir (*Abies grandis* (Dougl.) Lindl.), and western white pine (*Pinus monticola* (Dougl.). Canadian Journal of Botany 43: 1553–1559.

Enescu V. 1960. Seed production by *Abies alba* in the Stalin Forest District. Revista Padurilor 75: 724–726.

Enescu V. 1968. The use of tetrazolium salts for determining the germinative capacity of seed. Revista Padurilor 83: 587–589.

Eremko RD, Edwards DGW, Wallinger D. 1989. A guide to collecting cones of British Columbia conifers. FRDA Rep. 055. Victoria: Canada/British Columbia Forest Resources Development Agreement. 114 p.

Fady B, Arbez M, Ferrandès P. 1991. Variability of juvenile Greek firs (*Abies cephalonica* Loud.) and stability of characteristics with age. Silvae Genetica 40: 91–100.

Fady B, Arbez M, Marpeau A. 1992. Geographic variability of terpene composition in *Abies cephalonica* and *Abies* species around the Aegean: hypotheses for their possible phylogeny from the Miocene. Trees 6: 162–171.

Fady B, Conkle MT. 1992. Segregation and linkage of allozymes in seed tissues of the hybrid Greek fir *Abies borisii regis* Mattfeld. Silvae Genetica 41: 273–278.

Fady B, Conkle MT. 1993. Allozyme variation and possible phylogenetic implications in *Abies cephalonica* Loudon and some related eastern Mediterranean firs. Silvae Genetica 42: 351–359.

Fang SY, Roques A, Sun JH. 1988. Report on the survey of cone and seed insects in conifer forest in Northeast China. Journal of the Northeast Forestry University, China 16: 91–98.

Fang SY, Roques A, Sun JH. 1989. Results of a survey of cone and seed insects in some conifer forests of northeast China. In: Miller GE, comp. Proceedings, IUFRO WP S2.07-01 3rd Cone and Seed Insects Working Party Conference; 1988; Victoria, BC. Victoria, BC: Forestry Canada, Pacific Forestry Centre: 2–11.

Farjon A. 1990. Pinaceae: drawings and descriptions of the genera *Abies, Cedrus, Pseudolarix, Keteleeria, Nothotsuga, Tsuga, Cathaya, Pseudotsuga, Larix* and *Picea*. Regnum Vegetabile 121. Königstein, Germany: Koeltz Scientific Books. 330 p.

Farjon A, Rushforth KD. 1989. A classification of *Abies* Miller (Pinaceae). Notes of the Royal Botanical Gardens Edinburgh 46: 59–79.

Farr DF, Bills GF, Chamuris GP, Rossman AY. 1989. Fungi on plants and plant products in the United States. St. Paul: American Phytopathological Society. 1252 p.

Farrar JL. 1995. Trees in Canada. Markham, ON: Fitzhenry & Whiteside Ltd./Natural Resources Canada, Canadian Forestry Service: 81–94.

Farris MA, Mitton JB. 1985. Effects of cone color dimorphism on reproductive output of white fir growing along elevational gradients. American Journal of Botany 72: 1719–1725.

Faulkner R, Aldhous JR. 1959. Nursery investigations. Report on Forest Research 1957/1958. London: Her Majesty's Stationery Office: 20–37.

Fedde GF. 1973a. Cone production in Fraser firs infested by the balsam woolly aphid, *Adelges piceae* (Homoptera: Phylloxeridae). Journal of the Georgia Entomological Society 8: 127–130.

Fedde GF. 1973b. Impact of the balsam woolly aphid (Homoptera: Phylloxeridae) on cones and seed produced by infested Fraser fir. Canadian Entomologist 105: 673–680.

FEIS [Fire Effects Information System]. 1996. Prescribed fire and fire effects research work unit, Rocky Mountain Research Station (producer) [online]. Available at: http://www.fs.fed.us/database/feis/ [1998 March 12].

Fenimore M. 1997. Correspondence, Sept. 1997. Puyallup, WA: Fir Run Nursery.

Fernald ML. 1909. A new variety of *Abies balsamea*. Rhodora 11: 201–203.

Firenzuoli AM, Vanni P, Mastronuzzi E, Zanobini A, Baccari V. 1968. Enzymes of glyoxylate in conifers. Plant Physiology 43: 1125–1128.

Flachmann M, Lesemann DE, Frenzel B, Koenig R. 1990. Isometric virus-like particles in *Abies alba* Mill. and other *Abies* species: partial purification and improved detection by means of immunoelectron microscopy. Journal of Phytopathology 129: 193–202.

Flemion F, Poole H. 1948. Seed viability tests with 2,3,5-triphenyltetrazolium chloride. Contributions of the Boyce Thompson Institute 15: 243–258.

Foiles MW, Graham RT, Olson DF Jr. 1990. *Abies grandis* (Dougl. ex D. Don) Lindl., grand fir. In: Burns RM, Honkala BA, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 52–59.

Fowells HA. 1965. Silvics of forest trees of the United States. Agric. Handbk. 271. Washington, DC: USDA Forest Service. 762 p.

Fowells HA, Schubert GH. 1956. Seed crops of forest trees in the pine region of California. Tech. Bull. 1150. Washington, DC: USDA Forest Service. 48 p.

Franco J-do-A. 1950. *Abetos*. Anais do Instituto de Agronomia Lisbon 17: vii + 260 p.

Frank RM. 1990. *Abies balsamea* (L.) Mill., balsam fir. In: Burns RM, Honkala BA, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 26–35.

Franklin JF. 1964. Douglas' squirrels cut Pacific silver fir cones in the Washington Cascades. Res. Note PNW-15. Corvallis, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 3 p.

Franklin JF. 1965. An exploratory study of cone maturity in noble fir. Res. Note PNW-21. Corvallis, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 12 p.

Franklin JF. 1968. Cone production by upper-slope conifers. Res. Pap. PNW-60. Corvallis, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 21 p.

Franklin JF. 1974a. Seeding habits of upper-slope tree species: 1. A 12-year record of cone production. Res. Note PNW-213. Corvallis, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 12 p.

Franklin JF. 1974b. *Abies* Mill., fir. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 168–183.

Franklin JF. 1979. Vegetation of the Douglas-fir region. In: Heilman PE, Anderson HW, Baumgartner DM, eds. Forest soils of the Douglas-fir region. Pullman: Washington State University, Cooperative Extension Service: 93–112.

Franklin JF. 1982a. The true fir resource. In: Oliver CD, Kenady RM, eds. Proceedings, Symposium on Biology and Management of True Fir in the Pacific Northwest; 1981; Seattle/Tacoma, WA. Contrib. 45. Seattle: University of Washington, Institute of Natural Resources: 1–6.

Franklin JF. 1982b. Ecology of noble fir. In: Oliver CD, Kenady RM, eds. Proceedings, Symposium on Biology and Management of True Fir in the Pacific Northwest; 1981; Seattle/Tacoma, WA. Contrib. 45. Seattle: University of Washington, Institute of Natural Resources: 59–69.

Franklin JF. 1990. *Abies procera* Rehd., noble fir. In: Burns RM, Honkala BA, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 80–87.

Franklin JF, Dyrness CT. 1973. Natural vegetation of Oregon and Washington. Gen. Tech. Rep. PNW-8. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 417 p.

Franklin JF, Greathouse TE. 1968a. Seed origin studies, noble–California red fir species complex. In: Western reforestation. Proceedings, Meeting of the Western Forest Nursery Council; Placerville, CA: 11–16.

Franklin JF, Greathouse TE. 1968b. Identifying noble fir source from the seed itself. Proceedings, Annual Meeting of the Western Reforestation Coordinating Committee; 1968; San Francisco, CA. Portland, OR: Western Forestry and Conservation Association: 13–16.

Franklin JF, Krueger KW. 1968. Germination of true fir and mountain hemlock seed on snow. Journal of Foresty 66: 416–417.

Franklin JF, Ritchie GA. 1970. Phenology of cone and shoot development of noble fir and some associated true firs. Forest Science 16: 356–364.

Franklin JF, Sorensen FC, Campbell RK. 1978. Summarization of the ecology and genetics of the noble and California red fir complex. Proceedings, IUFRO joint meeting of working parties. Vancouver, BC: Vol. 1. 1978; Victoria: British Columbia Ministry of Forests, Information Service Branch: 133–139.

Furnier GR, Nava YG, Keiman A, Aguirre A, Espinosa F, Eguiarte LE. 1996. Genetic variation in the Mexican *Abies*. In: Forest management impacts on ecosystem processes; Proceedings, 14th. North American Forest Biology Workshop; 1996; Université Laval, Quebec City, Canada: 100.

Fye RE, Wylie WD. 1968. Notes on insects attacking spruce and fir cones at Black Sturgeon Lake, Ontario, 1963–4. Bi-Monthly Research Notes 24 [Canada Department of Fisheries and Forestry]: 47–48.

Gagov V. 1973. Variation in the seeds of the silver fir *Abies alba* Mill. from different populations in Bulgaria. Nauchni Trudove, Vissh Lesotekhnicheski Institut, Sofia, Seriya Gorsko Stopanstvo 19: 57–60.

Gagov V. 1976. Use of the x-ray (seed examination) method. Gorsko Stopanstvo. 32: 27–30.

Gambi G, Stradajoli G. 1971. Chemical analyses of forest tree seed and their possible applications. Annali dell'Istituto Sperimentale per la Selvicoltura, Arezzo 2: 199–215.

Gara RI. 1982. Insect pests of true firs in the Pacific Northwest. In: Oliver CD, Kenady RM, eds. Proceedings, Symposium on Biology and Management of True Fir in the Pacific Northwest; 1981; Seattle/Tacoma, WA. Contrib. 45. Seattle: University of Washington, Institute Forest Resources: 157–159.

Garren T. 1997. Correspondence, Sept. 1997. Salem, OR: USDI Bureau of Land Management.

Gates W. 1994. *Abies* seedling production. In: Konishi J, Barber B, comps. & eds. Proceedings, *Abies* spp. Workshop: Problems and Solutions; 1994; Parksville, BC. Victoria: British Columbia Ministry of Forests: 20 p.

Gates W. 1997. Correspondence, Sept. 1997. Bradner, BC: Pacific Regeneration Technologies, Nursery Extension.

Gaussen H. 1964. Les gymnospermes actuelles et fossiles. Fascicle VII, Genres *Pinus* (suite), *Cedrus* et *Abies*. Travaux Laboratoire Forestiere de Toulouse, Tome II, sect. 1, vol. 1, part 2: 273–480.

Gebhart K. 1990. *In vitro* culture of forest trees: studies in *in vitro* techniques for breeding and raising forest trees. Schriften des Forschungsinstitutes für Schnellwachsende Baumarten 6: 1–57.

Ghent AW. 1958. Studies of regeneration in forest stands devastated by the spruce budworm: 2. Age, height growth, and related studies of balsam fir seedlings. Forest Science 4: 135–146.

Giami G. 1970. The fall of seed and litter of silver fir and beech. Annali Accademia Italiana di Scienze Forestali 19: 41–81.

Giannini R, Marinelli E. 1977. Further tests on seeds and seedlings of *Abies alba* Mill. of different provenances. Italia Forestale e Montana 32: 105–125.

Giannini R, Murazio S. 1972. Further investigations on the long-term storage of silver fir seed. Italia Forestale e Montana 27: 76–80.

Giannini R, Parducci L, Rossi P, Villani F. 1994. Genetic structure and mating system of silver fir in the Campolino reserve (North Apennines, Italy). Journal of Genetics and Breeding 48: 335–338.

Girardin R. 1997a. On the farm. Exotic News [semi-annual newsletter, Girardin R, ed. Sandborton, NH] 7(1): 1.

Girardin R. 1997b. Biotech company provides superiority of new Christmas trees. Exotic News [semi-annual newsletter, Girardin R, ed. Sandborton, NH] 7(1): 3.

Godwin JH. 1997. *Abies nordmanniana*. Exotic News [semi-annual newsletter, Girardin R, ed. Sandborton, NH] 7(1): 2–3.

Gogala N. Vardjan M. 1989. The location of the cause of dormancy, viability and seed decay in the silver fir *Abies alba* Mill. Bioloski Vestnik 37: 33–42.

Gordon DT. 1962. Trial of a photographic technique to count cones. Journal of Forestry 60: 546–547.

Gordon DT. 1970. Natural regeneration of white and red fir. Res. Pap. PSW-58. Corvallis, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 32 p.

Gordon DT. 1978. California red fir literature: some corrections and comments. Forest Science 24: 52–56.

Gosling PG, Parratt M, Peace A. 1999. Identifying the optimum pretreatment duration and germination temperature for *Abies nordmanniana* ([Steven] Spach) seed, and assessing the effect of moisture content and storage temperature on seed longevity. Seed Science and Technology 27: 951–961.

Grabe DF. 1976. Measurement of seed vigor. Journal of Seed Technology 1: 18–32.

Gradi A. 1966. The commercial storage of *Abies alba* seed. Monti e Boschi 17: 41–47.

Graham A. 1999. The tertiary history of the northern temperate element in the northern Latin American biota. American Journal of Botany: 86 32-38.

Gramuglio G. 1962. Sexual awakening of *Abies nebrodensis*. Giornale Botanico Italiano 69 (1/3): 207–210.

Greenbank DO. 1963. Staminate flowers and the spruce budworm. In: Morris RF, ed. The dynamics of epidemic budworm populations. Memoirs of the Entomological Society of Canada 31: 202–218.

Grittanuguya N. 1962. The effects of temperatures, stratification, and locality on the germination of several Rocky Mountain coniferous species [Master's thesis]. Logan: Utah State University. 64 p.

Gunia S, Simak M. 1967. Die anwendung von H_2O_2 bei der keimzungsprüfung der samen von weisstanne (*Abies alba* Mill.). Proceedings, International Scientific Conference, Zvolen, Czechoslovakia, B-4: 27–36.

Gunia S, Simak M. 1970. Effect of damaging resin vesicles in the seed coat on the germination of silver fir (*Abies alba* Mill.) seeds. In: Bialokok S, Suszka B, eds. Proceedings, International Symposium on Seed Physiology of Woody Plants; 1968; Kornik, Poland: 79–83.

Guo Y, Wang HD, Wang YJ, Li XB. 1984. Analysis of unusual fatty acids in seed-oils from plants of Pinaceae indigenous to northeast of China. Acta Botanica Sinica 26: 290–293.

Gvozdikov AI. 1980. Yield of normal fir and larch seedlings of different provenance in the Rudnyi Altai. Kazakstan Auyl Saruasylyk Gylymynyn Habarsysy 9: 74–76.

Gyimah A. 1977. Effect of hydrogen peroxide on the germination of grand fir, lodgepole pine and Douglas fir seeds. Tech. Bull. 1. Accra, Ghana: Forest Products Research Institute: 28–32.

Haig IT, Davis KP, Weidman RH. 1941. Natural regeneration in the western white pine type. Tech. Bull. 767. Washington, DC: USDA Forest Service. 99 p.

Hall JP. 1981. Seed procurement in Newfoundland: review and outlook. Information Report N-X-204. St. John's: Canadian Forestry Service, Newfoundland Forest Research Centre. 25 p.

Hall O, Olson E. 1986. Effect of stratification, drying, and cold storage on noble fir and Pacific silver fir. Journal of Seed Technology 10: 58–61.

Halvorson CH. 1986. Influence of vertebrates on conifer seed production. In: Shearer RC, comp. Proceedings, Symposium on Conifer Tree Seed in the Inland Mountain West; 1985; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 201–222.

Hamrick JL III. 1966. Geographic variation in white fir [Master's thesis]. Berkeley: University of California. 64 p.

Hamrick JL, Libby WJ. 1972. Variation and selection in western U.S. montane species. 1. White fir. Silvae Genetica 21: 29–35.

Handley DL. 1982. True fir management in Europe. In: Oliver CD, Kenady RM, eds. Proceedings, Symposium on Biology and Management of True Fir in the Pacific Northwest; 1981; Seattle/Tacoma, WA. Contrib. 45. Seattle: University of Washington, Institute of Forest Resources: 243–246.

Hansen OB, Leivsson TG. 1990. Germination and seedling growth in *A. lasiocarpa* (Hook.) Nutt. as affected by provenance, seed pretreatment, and temperature regime. Scandinavian Journal of Forest Research 5: 337–345.

Hanson D. 1997. Correspondence, Oct. 1997. Courtenay, BC: Arbordale Nurseries Ltd.

Haq RU. 1992. Effect of seed production, distribution, viability, losses and germination on the natural regeneration of silver fir (*Abies pindrow*) in moist temperate forests of Pakistan. Pakistan Journal of Forestry 42: 102–111.

Harris AS. 1965. Subalpine fir [*Abies lasiocarpa* (Hook.) Nutt.] on Harris Ridge near Hollis, Prince of Wales Island, Alaska. Northwest Science 39: 123–128.

Hart J. 1976. Montana: native plants and early peoples. Helena: Montana Historical Society. 75 p.

Hartmann S, Lang H, Reuther G. 1992. Differentiation of somatic embryos from protoplasts isolated from embryogenic suspension cultures of *Abies alba* L. Plant Cell Reports 11: 554–557.

Hasegawa S, Kaneko N, Hirose Y. 1987. Triterpenes from the seed of *Abies firma*. Phytochemistry 26: 1095–1099.

Hawksworth FG. 1978. Biological factors of dwarf mistletoe in relation to control. In: Scharpf RF, Parmeter JR Jr., tech. coords. Proceedings of the Symposium on dwarf mistletoe control through forest management; 1978; Berkeley, CA. Gen. Tech. Rep. PSW-31. Berkeley: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station: 5–15.

Hawksworth FG, Wiens D. 1965. *Arceuthobium* in Mexico. Brittonia 17: 213–238.

Hawley GJ, DeHayes DH. 1985a. Hybridization among several North American firs: 1. Crossability. Canadian Journal of Forest Research 15: 42–49.

Hawley GJ, DeHayes DH. 1985b. Hybridization among several North American firs: 2. Hybrid verification. Canadian Journal of Forest Research 15: 50–55.

Hayashi K, Endo K. 1975. Effect of soil fungi and drought on the germination of Todo fir seed. Bull. 274. Meguro, Tokyo: Government Forest Experiment Station: 1–22.

Hedlin AF. 1966. Cone and seed insects of grand fir, *Abies grandis* (Dougl.) Lindl. Bi-Monthly Research Notes 22 [Ottawa: Canada Department of Forestry and Rural Development]: 3.

Hedlin AF. 1974. Cone and seed insects of British Columbia. Info. Rep. BC-X-90. [Victoria]: Environment Canada, Canadian Forestry Service. 63 p.

Hedlin AF, Ruth DS. 1974. *Barbara colfaxiana siskiyouana* (Kft.), a pest in cones of *Abies grandis*. Journal of the Entomological Society of British Columbia 71: 13.

Hedlin AF, Yates HO III, Tovar DC, Ebel DH, Koerber TW, Merkel EP. 1980. Cone and seed insects of North American conifers. Canadian Forestry Service/USDA Forest Service/Secretariá de Agricultura y Recursos Hidráulicos, México. Ottawa: Environment Canada, Canadian Forestry Service: 122 p.

Heit CE. 1941. Storage of conifer seed. New York Nursery Notes 10: 2–3.

Heit CE. 1964. The importance of quality, germinative characteristics, and source for successful seed propagation and plant production. Proceedings of the International Plant Propagators' Society 14: 74–85.

Heit CE. 1967. Propagation from seed: 9. Fall sowing of conifer seeds. American Nurseryman 126(6): 10–11, 56, 60, 62, 64–69.

Heit CE. 1968a. Propagation from seed: 14. Testing and growing less common and exotic fir species. American Nurseryman 127(10): 10–11, 34–36, 38, 40, 42, 44–45, 48–51.

Heit CE. 1968b. Thirty-five years' testing of tree and shrub seed. Journal of Forestry 66: 632–634.

Heit CE, Eliason EJ. 1940. Coniferous tree seed testing and factors affecting germination and seed quality. Tech. Bull. 255. Geneva, NY: New York Agricultural Experiment Station. 45 p.

Heit CE, Natti JJ. 1969. Accurate germination of *Abies balsamea* and *Abies fraseri* in laboratory tests by control of *Rhizoctonia solani* and other fungi with PCNB. Proceedings of the Association of Official Seed Analysts 59: 148–153.

Helson T. 1997. Correspondence, Sept. 1997. Prince George, BC: Northwood Forest Centre.

Henderson JA. 1982. Ecology of subalpine fir. In: Oliver CD, Kenady RM, eds. Proceedings, Symposium on the Biology and Management of True Fir in the Pacific Northwest; 1981; Seattle/Tacoma, WA. Contrib. 45. Seattle: University of Washington, Institute of Forest Resources: 53–58.

Henry PH, Blazich FA. 1988. Influence of gibberellins 4+7 on germination of Fraser fir. Journal of Environmental Horticulture 6: 93–96.

Henry PH, Blazich FA. 1990. Seed germination of Fraser fir: timing of irradiation and involvement of phytochrome. Journal of the American Society of Horticultural Science 115: 231–234.

Hetherington JC. 1965. The dissemination, germination, and survival of seed on the west coast of Vancouver Island from western hemlock and associated species. Res. Note 39. Victoria: British Columbia Forest Service. 22 p.

Heusser CJ. 1954. Alpine fir at Taku glacier, Alaska, with notes on its post glacial migration to the territory. Bulletin of the Torrey Botanical Club 81: 83–86.

Hofman J. 1966. Pretreatment of *Abies grandis* seed. Les, Bratislava 22: 402–405.

Hofman J, Vackova M. 1966. Storage of *Abies grandis* seed. Lesnicka Prace 45: 373–374.

Hofmann JV. 1911. Natural reproduction from seed stored in the forest floor. Journal of Agricultural Research 11: 1–26.

Holmes GD, Buszewicz G. 1958. The storage of seed of temperate forest tree species. Forestry Abstracts 19: 313–322, 455–476.

Holmes GD, Buszewicz GM. 1962. Forest tree seed: seed storage. Report on Forest Research 1960/1961, Forestry Commission. London: Her Majesty's Stationery Office: 18.

Holmsgaard E, Kjaer A. 1951. Undersøgelse over spiring i laboratorium og planteskole af 4 *Abies* og 2 *Picea*-arter. Dansk Skovforenings Tidsskrift 36: 203–226.

Holstener-Jorgensen H, Johansen V. 1975. Irrigation of decoration greenery stands of *Abies nobilis*. Forstlige Forsøgsvaesen I Danmark 34: 307–316.

Holubcik M. 1969. Need for plant collection for research. In: 2nd FAO/IUFRO World Consultation on Forest Tree Breeding; 1969; FO-FTB-69-8/2, 8 p.

Hopkins WE. 1979. Plant associations of south Chiloquin and Klamath Ranger Districts: Winema National Forest. Rep. R6-Ecol-79-005. Portland, OR: USDA Forest Service, Pacific Northwest Region. 96 p.

Hopkins WE. 1982. Ecology of white fir. In: Oliver CD, Kenady RM, eds. Proceedings, Biology and Management of True Fir in the Pacific Northwest; 1981; Seattle/Tacoma, WA. Contrib. 45. Seattle: University of Washington, Institute of Forest Resources: 35–41.

Hosie RC. 1969. Native trees of Canada. Don Mills, ON: Fitzhenry & Whiteside [for Canadian Forestry Service, Environment Canada]: 86–95.

Houle G. 1992. The reproductive ecology of *Abies balsamea, Acer saccharum* and *Betula alleghaniensis* in the Tantare Ecological Reserve, Quebec. Journal of Ecology 80: 611–623.

Houle G. 1995. Seed dispersal and seedling recruitment: the missing link(s). Ecoscience 2: 238–244.

Houle G, Payette S. 1991. Seed dynamics of *Abies balsamea* and *Acer saccharum* in a deciduous forest of northeastern North America. American Journal of Botany 78: 895–905.

Huchler (no initials). 1956. N fertilizer trials in mature silver fir stands. Allgemeine Forstzeitschrift 11: 157–158.

Hughes EL. 1967. Studies in stand and seedbed treatment to obtain spruce and fir reproduction in the mixedwood slope type of northwestern Ontario. Depart. Pub. 1189. Ottawa: Forestry Branch, Department of Forestry and Rural Development. 138 p.

Hunt RS. 1993. *Abies*. In: FNA Editorial Committee, eds. Flora of North America, north of Mexico. Volume 2, Pteridophytes and Gymnosperms. New York: Oxford University Press: 354–362.

Hunt RS, von Rudloff E. 1974. Chemosystematic studies in the genus *Abies*: 1. Leaf and twig oil analysis of alpine and balsam firs. Canadian Journal of Botany 52: 477–487.

Hunt RS, von Rudloff E. 1979. Chemosystematic studies in the genus *Abies*: 4. Introgression in *Abies lasiocarpa* and *Abies bifolia*. Taxon 28: 297–305.

Hunt RS, von Rudloff E. 1983. Further clarification on the *Abies balsamea–A. bifolia–A. lasiocarpa* complex with reference to the Parker and others publication. Taxon 32: 444–447.

Hupp BM. 1984. Importance of seed selection for Christmas tree production. Combined Proceedings of the International Plant Propagators' Society 33: 68–71.

Hussey NW. 1954. Revised descriptions of three *Megastigmus* species (Hym. Torymidae) associated with seeds of silver fir. Entomologists' Monthly Magazine 90 (1085): 223–225.

Hussey NW. 1957. *Megastigmus* species (Hym. Torymidae) associated with seeds of silver fir and cedar. Entomologists' Monthly Magazine 93 (1121): 252.

Hussey NW. 1960. Two new species of *Mesopolobus* Westwood (Hym. Pteromalidae) with notes on other parasites of *Megastigmus* Dalman (Hym. Torymidae). Entomologists' Monthly Magazine 95 (1145): 237–239.

Hussey NW, Klinger J. 1954. Variation in *Megastigmus pinus* Parfitt (Hym., Chalcidoidea, Torymidae). Entomologists' Monthly Magazine 90 (1084): 198–201.

Imai S, Takei T, Ishikawa T. 1955. Studies on the control of damping-off of coniferous seeds [*Abies mayriana*] in Hokkaido [reproduced from jubilee publication, in commemoration of 60th birthdays of Prof. Tochinai and Prof. Fukushi, Tokyo]: 145–52.

Irmak A. 1961. The seed-fall of firs and their germination in the snow. Istanbul Üniversitesi Orman Fakültesi Dergisi, Ser. A 11(1): 1–6.

Isaac LA. 1930a. Cold storage prolongs life of noble fir seed. Journal of Forestry 28: 571.

Isaac LA. 1930b. Seed flight in the Douglas-fir. Journal of Forestry 28: 492–499.

Isaac LA. 1934. Cold storage prolongs the life of noble fir seed and apparently increases germinative power. Ecology 15: 216–217.

Issleib [no initials]. 1956. Extraction and winter storage of seeds of *Abies alba*. Allgemeine Forstzeitschrift 11: 553–556.

ISTA [International Seed Testing Association]. 1993. International rules for seed testing. Seed Science and Technology 21 (Suppl.): 1–288.

ISTA [International Seed Testing Association]. 1995. Handbook of vigour test methods. 3rd. ed. In: Hampton JG, TeKrony DM, eds. Zurich [now Bassersdorf]: International Seed Testing Association. 117 p.

Itoo M. 1975. Flowering and pollen-dispersal in a seed orchard of *Abies homolepis*. Journal of Japanese Forestry Society 57: 121–124.

Iwai M, Nishioka I. 1945. Properties of the seed oil of Korean fir tree. Journal of the Society of Chemical Industry, Japan: 48 [Chemical Abstracts 42(16): 6140].

Jacobs BF, Werth CR, Guttman SI. 1984. Genetic relationships in *Abies* (fir) of eastern United States: an electrophoretic study. Canadian Journal of Botany 62: 609–616.

Jain KK. 1976. Introgressive hybridization in the west Himalayan silver firs. Silvae Genetica 25: 107–109.

Jain PP, Dobhal NP, Rajendra P, Ayyar KS. 1988. Chemical studies on oil-seeds of forest origin. Indian Forester 114: 158–162.

Jakimova TV. 1965. Effect of stratification on the germination of seeds of subtropical plants. Byulleten Glavnogo Botanicheskogo Sada 57: 94–97.

Jensen M. 1997. Moisture content controls the effectiveness of dormancy breakage in *Abies nordmanniana* (Steven) Spach seeds. In: Ellis RH, Black M, Murdoch AJ, Hong TD, eds. Basic and applied aspects of seed biology; Proceedings, 5th International Workshop on Seeds; 1995; Reading, UK. Current Plant Science and Biotechnology in Agriculture 30. Dordrecht, The Netherlands: Kluwer Academic Publishers: 181–190.

Jespersen C, Lomholdt O. 1983. The Danish seed wasps, *Megastigmus* Dalmann, 1820 (Hymenoptera, Chalcidoidea, Torymidae). Entomologiske Meddelelser 50: 111–118.

Johnson CJS. 1984. Conifer seed sources, testing, stratification, and sowing for the Industrial Forestry Association. Combined Proceedings of the International Plant Propagators' Society 33: 64–66.

Jones L. 1962. Recommendations for successful storage of tree seed. Tree Planters' Notes 55: 9–20.

Jones SK, Samuel YK, Gosling PG. 1991. The effect of soaking and prechilling on the germination of noble fir seeds. Seed Science and Technology 19: 287–294.

Jorgensen J. 1990. Conservation of valuable gene resources by cryopreservation in some forest tree species. Journal of Plant Physiology 136: 373–376.

Kailidis DS, Georgevits RP. 1970. Outbreak of insect pests attacking cones and seeds on fir at Parnis. Kentron Dasikon Ereunon Boreiou Hellados, Thessalonike 34: 1–36.

Kailidis DS, Georgevits RP. 1972. Forest insects of Greece: fir insects. Anzeiger für Schädlingskunde und Pflanzenschutz 45: 25–28.

Kandya AK, Ogino K. 1986. Reserve dry weight of seed: a significant factor governing the germination potential of seeds in some conifers. Journal of Tropical Forestry 2: 21–26.

Kaneko N, Hasegawa S, Hirose Y. 1985. Terpenoids from seeds of *Abies firma*. Phytochemistry 24: 185–186.

Kantor J, Chira E. 1965. Variability of pollen size in some species of *Abies*. Sbornik Vysoke Skoly Zemedelskych, Brno (Rada C) 3: 165–178.

Kantor J, Chira E. 1971. On the possibility of crossing certain species of the genus *Abies*. Acta Universitatis Agriculturae, Brno (Facultas Silviculturae) 40: 15–27.

Kantor J, Chira E. 1972. Results of some intraspecific and interspecific crossings of individuals within the genus *Abies*. Lesnictvi 18: 487–499.

Karrfalt RP. 1997. Upgrading seeds with IDS: a review of successes and failures. In: Landis TD, South DB, tech. coords. Proceedings, Western Forest Conservation Nursery Association Meeting; 1996; Salem, OR. Gen. Tech. Rep. PNW-GTR-389. Portland, OR: USDA Forest Service: 183–186.

Katsuta M, Saito M, Yamamoto C, Kaneko T, Itoo M. 1981. Effect of gibberellins on the promotion of strobilus production in *Larix leptolepis* Gord. and *Abies homolepis* Sieb. et Zucc. Bulletin of the Forestry and Forest Products Research Institute, Ibaraki, Japan 313: 37–45.

Kawamuro K, Kinoshita I, Suyama Y, Takahara H. 1995. Inspection of DNA in fossil pollen of *Abies* spp. from Late Pleistocene peat. Journal of the Japanese Forestry Society 77: 272–274.

Kayacik H. 1964. Deformations on the cone scales and seed wings of *Abies cilicica* Carr. and their cause. Istanbul Üniversitesi Orman Fakültesi Dergisi, 14A: 15–20.

Khattak GM, Ahmad A. 1980. Germination tests of silver fir (*Abies pindrow*) seed. Pakistan Journal of Forestry 30: 78–80.

Keen FP. 1968. Cone and seed insects of western forest trees. Tech. Bull. 1169. Washington, DC: USDA Forest Service. 168 p.

Khutortsov II. 1987. Seed-bearing of *Abies nordmanniana* in the Caucasus Reserve. Lesovedenie 2: 81–86.

Kirgizov NYa, Mosin VI. 1980. Intraspecific variation and seed production in *Abies sibirica* in eastern Kazakhstan. Trudy Kazakhskogo NII les. Khozyaistva Agrolesomelior 11: 99–104.

Kitzmiller JM, Battigin JM, Helms JA. 1973. Effect of resin vesicle damage on germination of stored *Abies concolor* seed. Internal Rep. 1. Berkeley: University of California, School of Forestry and Conservation, True Fir Management Cooperative: 16 p.

Kitzmiller JM, Helms JA, Stover P. 1975. Influence of seed treatment on germination of *Abies concolor* and *Abies magnifica*. Internal Rep. 3. Berkeley: University of California, School of Forestry and Conservation, Industry/University True Fir Management Cooperative: 39 p.

Klaehn FU, Winieski JA. 1962. Interspecific hybridization in the genus *Abies*. Silvae Genetica 11: 130–142.

Knierim M, Leist N. 1988. Methodological improvement in the tetrazolium testing of viability of *Abies* seed. Seed Science and Technology 16: 227–237.

Kociova M. 1974a. Heritability of cone characters in *Abies alba* in Slovakia. Casopis Slezskeho Muzea, C 23: 171–179.

Kociova M. 1974b. Cone inheritance in silver fir (*Abies alba* Mill.) in Slovakia. Acta Facultatis Rerum Naturalium, Universitatis Comenianae, Genetica 5: 113–123.

Koerber TW. 1963. *Leptoglossus occidentalis* (Hemiptera, Coreidae), a newly discovered pest of coniferous seed. Annals of the Entomological Society of America 56: 229–234.

Koedam A. 1981. Composition of the volatile leaf oil from Greek fir (*Abies cephalonica* Loud.). Fitoterapia 52: 25-30.

Kolomiec NG. 1950. Damage (to Siberian fir seed) by *Evetria margarotana*. Lesnoe Khozyaistvo 3:80.

Kolotelo D. 1993. Operational density separation processing (DSP) at the BCFS Tree Seed Centre (TSC)—1993. In: Proceedings, Joint Meeting of the BC Tree Seed Dealers' Association and the Western Forest Range Seed Council; 1993; Vernon, BC. Victoria: Forestry Canada/British Columbia Ministry of Forests: 25–35.

Kolotelo D. 1994. *Abies* seed testing (pre-treatment) and storage. In: Konishi J, Barber B, comps. and eds. Proceedings, *Abies* spp. Workshop: Problems and Solutions; 1994; Parksville, BC. Victoria: British Columbia Ministry of Forests: 15–19.

Kolotelo D. 1997. Anatomy and morphology of conifer tree seed. For. Nurs. Tech. Ser. 1.1. Victoria: British Columbia Ministry of Forests, Nursery and Seed Operations Branch. 60 p.

Konnert M. 1991. Attempt at determining provenances in silver fir stands with the aid of isozyme analysis. Allgemeine Forstzeitschrift 46: 884–885.

Konnert M, Bergmann F. 1995. The geographical distribution of genetic variation of silver fir (*Abies alba*, Pinaceae) in relation to its migration history. Plant Systematics and Evolution 196: 1–2, 19–30.

Kormutak A. 1988. Isoenzyme and serological variation of selected fir (*Abies*) species. Lesnictvi 34: 721–730.

Kormutak A. 1991. Utilization of introduced species of firs (*Abies* spp.) in artificial hybridization. Thaiszia 1: 113–118.

Kormutak A. 1997. Cytological aspects of interspecific hybridization in true firs (*Abies* species). In: Borzan Z, Schlarbaum SE, eds. Proceedings, First IUFRO Cytogenetics Working Party S2.04-08 Symposium; 1993; Brijuni National Park, Croatia: 303–310.

Kormutak A, Bencat F, Rudin D, Sezyedyazdani R. 1982. Isozyme variation in the four slovakian populations of *Abies alba* Mill. Biologia (Bratislava) 37: 433-440.

Kormutak A, Szmidt AE, Wang X-R. 1993. Restriction fragment length polymorphism of chloroplast DNAs in some species of fir (*Abies* spp.). Biologia Plantarum 35: 113–119.

Korpel S, Paule L, Laffers A. 1982. Genetics and breeding of the silver fir (*Abies alba* Mill.). Annales Forestales Anali za Sumarstvo 9/5, Zagreb: 151–184.

Köstler JN. 1957. Firs between Scylla and Charybdis. Monti e Boschi 8: 38, 42–43.

Kovac M, Wrischer M. 1989. Ultrastructural changes in silver fir (*Abies alba*) seeds during germination. Bioloski Vestnik 37: 43–56.

Kozlowski TT. 1960. Effect of moist stratification and storage in polyethylene bags on germination of forest tree seed. For. Res. Note 59. Wisconsin College of Agriculture. 3 p.

Kravchenko L, Trukhanovkii DS, Chastii VP. 1974. Conditions for the preservation of fir (*Abies*) pollen. Vesti Akademiia Navuk Belaruskai SSR, Ser. Biyalagichnykh Navuk 5: 114–116.

Kulchetscki L, Harry IS, Yeung EC, Thorpe TA. 1995. *In vitro* regeneration of Pacific silver fir (*Abies amabilis*) plantlets and histological analysis of shoot formation. Tree Physiology 15: 727–738.

Kulhavy DL, Schenk JA. 1976. Cone and seed insect damage and prediction of cone production in grand fir in Potlatch area of Northern Idaho. Sta. Note 23. Moscow, ID: University of Idaho, College of Forestry, Wildlife, and Range Sciences. 6 p.

Kulhavy DL, Schenk JA, Hudson TJ. 1976. Cone and seed insects of subalpine fir during a year of low cone production in northern Idaho. Journal of the Entomological Society of British Columbia 73: 25–28.

Kusisto J. 1997. Correspondence, Sept. 1997. Tappen: British Columbia Ministry of Forests, Skimikin Nursery.

Laacke RJ. 1990a. *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr., white fir. In: Burns RM, Honkala BA, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 36–46.

Laacke RJ. 1990b. *Abies magnifica* A. Murr., California red fir. In: Burns RM, Honkala BA, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 71–79.

Laacke RJ, Fiske JN. 1983. Red fir and white fir. In: Burns RM, tech. comp. Silvicultural systems for the major forest types of the United States. Agric. Handbk. 44. Washington, DC: USDA Forest Service: 41–43.

Lacaze JF. 1967. Compte rendu d'une experimentation sur les provenances d'*Abies grandis*. Premiéres conclusions sur le stade pépinière. Doc. 67/4: Paris: Institut National de la Recherche Agronomique. 35 p. [limited distribution].

Laffers A. 1979. Evaluation of seed weight in fir of Czechoslovakian and foreign provenance in relation to modified geographical latitude, to geographical longitude and to particular mountain ranges of Europe. Lesnicky Casopis 25: 111–125.

Lalu I. 1993. Seed yield of silver fir in the Carpathians for the period 1984–91. Revista Padurilor 108: 7–9.

Landis TD, Tinus RW, McDonald SE, Barnett JP. 1989. The container tree nursery manual. Volume 4, Seedling nutrition and irrigation. Agric. Handbk. 674. Washington, DC: USDA For. Serv. 119 p.

Landis TD, Tinus RW, McDonald SE, Barnett JP. 1990a. The container tree nursery manual. Volume 2, Containers and growing media. Agric. Handbk. 674. Washington, DC: USDA For. Serv. 87 p.

Landis TD, Tinus RW, McDonald SE, Barnett JP. 1990b. The container tree nursery manual. Volume 5, The biological component: nursery pests and mycorrhizae. Agric. Handbk. 674. Washington, DC: USDA For. Serv. 171 p.

Landis TD, Tinus RW, McDonald SE, Barnett JP. 1992. The container tree nursery manual. Volume 3, Atmospheric environment. Agric. Handbk. 674. Washington, DC: USDA For. Serv. 145 p.

Landis TD, Tinus RW, McDonald SE, Barnett JP. 1995. The container tree nursery manual. Volume 1, Nursery planning, development and management. Agric. Handbk. 674. Washington, DC: USDA For. Serv. 188 p.

Lanner RM. 1983. Trees of the Great Basin: a natural history. Reno: University of Nevada Press. 215 p.

Lanquist KB. 1946. Tests of seven principal forest tree seeds in northern California. Journal of Forestry 44: 1063–1066.

Lanz AJ. 1942. Some data on the *Megastigmus* species damaging conifer seed in Holland. Nederlands Bosbouwtijdschrift 15: 329–336.

Lanz AJ. 1943. *Megastigmus* attack on conifer seed in 1942–43. Nederlands Bosbouwtijdschrift 16: 410–411.

Larsen JA. 1922. Some characteristics of seeds of coniferous trees from the Pacific Northwest. National Nurseryman 30: 246–249.

Lavender DP. 1979. Current nursery management regimes for *Abies* spp. Proceedings [limited distribution], True Fir Management Cooperative Symposium, Regeneration and Management of Young True Fir Stands. 1979; Redding, CA. 4 p.

Leach HR, Hiele JL. 1956. Food habits of the Tehama deer herd. California Fish and Game 43: 161–178.

Leadem CL. 1982. Seed viability of *Abies, Picea* and *Tsuga* after storage in the cones. In: Wang BSP, Pitel JA, eds. Petawawa National Forestry Institute: Proceedings, IUFRO WP S2.01.06 International Symposium on Forest Tree Seed Storage; 1980; Chalk River, ON. Chalk River, ON: Environment Canada, Canadian Forestry Service: 57–67.

Leadem CL. 1984. Quick tests for tree seed viability. Land Management Rep. 18. Victoria: British Columbia Ministry of Forests. 45 p.

Leadem CL. 1986. Stratification of *Abies amabilis* seeds. Canadian Journal of Forest Research 16: 755–760.

Leadem CL. 1988a. Dormancy and vigour of tree seeds. In: Landis TD, ed. Proceedings, Combined Meeting of the Western Forest Nursery Association/Western Forest Nursery Council/Forest Nursery Association/British Columbia and Intermountain Forest Nursery Association, Vernon, BC. Gen. Tech. Rep. RM-167. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: 4–9.

Leadem CL. 1988b. Improving dormancy release and vigour of *Abies lasiocarpa*: FRDA Project No. 2.41. FRDA Res. Memo 40. Victoria: Forestry Canada/British Columbia Development Agreement. 2 p.

Leadem CL. 1989. Stratification and quality assessment of *Abies lasiocarpa* seeds. FRDA Rep. 095. Victoria, BC: Forestry Canada/British Columbia Development Agreement. 23 p.

Leadem CL. 1993. Respiration of tree seeds. In: Edwards DGW, comp. & ed. Proceedings, International Symposium, Dormancy and Barriers to Germination, IUFRO Proj. Group P2.04-00 (Seed problems); 1991; Victoria, BC. Victoria: Forestry Canada, Pacific Forestry Centre: 57–66.

Leadem CL, Eremko RD, Davis IH. 1990. Seed biology, collection and post-harvesting handling. In: Lavender DP, Parish R, Montgomery G, Vyse A, Willis RA, Winston D, eds. Regenerating British Columbia's forests. Vancouver: Canada/British Columbia Forest Resource Development Agreement Vancouver: University of British Columbia Press: 193–205.

Lebrun C. 1967. Separation of [full and empty] seeds by specific-gravity measurement through immersion in liquids. Revue Forestiere Francaise 19: 786–789.

Legg K. 1953. Bristlecone fir makes its last stand. Nature Magazine 46: 521–522.

Lehar G. 1997. Correspondence, Sept. 1997. Korbel, CA: Simpson Timber Company, Korbel Forest Nursery.

Leloup M. 1956. Tree planting practices in temperate Asia: Japan. For. Dev. Pap. 10. FAO. Rome. 156 p.

Lester DT. 1968. Variation in cone morphology of balsam fir, *Abies balsamea*. Rhodora 70: 83–94.

Li XJ, Burton PJ, Leadem CL. 1994. Interactive effects of light and stratification on the germination of some British Columbia conifers. Canadian Journal of Botany 72: 1635–1646.

Libby WJ. 1982. Biology of the true firs: genetic factors, problems, and opportunities. In: Oliver CD, Kenady RM, eds. Proceedings, Symposium on Biology and Management of True Fir in the Pacific Northwest; 1981; Seattle/Tacoma, WA. Contrib. 45. Seattle: University of Washington, Institute Forest Resources: 15–18.

Littke WR, Browning JE. 1991. Assaying for seed-borne fungi of Douglas-fir and true fir species. Info. Rep. BC-X-331. Victoria, BC: Canadian Forest Service, Pacific Forestry Centre: 253–258.

Little EL Jr. 1953. Checklist of native and naturalized trees of the United States (including Alaska). Agric. Handbk. 41. Washington, DC: USDA Forest Service. 472 p.

Little EL Jr. 1975. Rare and local conifers in the United States. Cons. Res. Rep. 19. Washington, DC: USDA Forest Service. 25 p.

Little EL Jr. 1979. Checklist of United States trees (native and naturalized). Agric. Handbk. 541. Washington, DC: USDA Forest Service. 375 p.

Little EL Jr, DeLisle AL. 1962. Time periods in development: forest trees, North America. In: Altman PL, Dittmer DS, eds. Biological handbook on growth. Washington, DC: Federation of American Societies for Experimental Biology: table 104.

Liu T-S. 1971. A monograph of the genus *Abies*. Taipei: National Taiwan University, Department of Forestry, College of Agriculture. 608 p.

Loffler J. 1985. The present situation and developments relating to storage of forest tree seed in Europe. Allgemeine Forstzeitschrift 24: 611–615.

Loffler J. 1988. Do air pollutants threaten the regeneration potential of West German forests? Allgemeine Forstzeitschrift 33: 916–918.

Løfting ECL. 1961. *Abies nordmanniana* i Kaukasus. Dansk Skovforenings Tidsskrift 46: 426–455.

Løfting ECL. 1966. *Abies magnifica* med varieteten *Abies magnifica* var. *shastensis* ogdennes overgangsformer til *Abies procera*. Dansk Skovforenings Tidsskrift 51: 445–461.

Løfting ECL. 1967. *Abies magnifica*, with the variety *shastensis* and the intermediate forms between the latter and *Abies procera*. Meddelelser fra det Norske Skogforsoeksvesen 23(85): 32–39.

Lowe WJ. 1974. Effect of storage upon balsam fir pollen viability and seed development. In: Schreiner EJ. ed. Proceedings, 21st Northeastern Forest Tree Improvement Conference, University of Maine, Orono. Upper Darby, PA: Northeastern Forest Experiment Station: 71–84.

Luebke W. 1994-2000. Pine needle oil (*Abies sibirica* Ledeb.) Siberia. Oak Creek, WI: The Good Scents Co. [online]. Available at: http://www.execpc.com/~goodscnt/data/es1005151.html [2000 January 30].

MacDonald A. 1998. Correspondence, Feb. 1998. Victoria: British Columbia Ministry of Forests.

MacDonald J, Wood RF, Edwards MV, Aldhous JR, eds. 1957. Exotic forest trees in Great Britain. Bull. 30. London: Forestry Commission. London, Her Majesty's Stationery Office. 167 p.

MacGillivray H.G. 1955. Germination of spruce and fir seed following different stratification periods. Forest Chronicle 31: 365.

Machanicek J. 1965. Long-term storage of fir and beech seed. Prace Vyzkumneho Ustavu Lesniho Hospodarstvi a Myslivosti (Zbraslav-Strnady) 31: 69–100.

MacKay MR. 1949. White fir cone maggot (*Earomyia* spp.). Annual Report of the Forest Insect Survey 1948 [Ottawa: Department of Agriculture, Canada Division of Entomology, Science Service, Forest Insect Investigations]: 117.

MacLean DW. 1960. Some aspects of the aspen–birch–spruce–fir type in Ontario. Tech. Note 94. Ottawa: Canada Department of Forestry, Forest Branch, Forest Research Division. 24 p.

Magini E. 1953. Influence of age of mother tree on seed quality in *Abies alba*. Italia Forestale e Montana 8: 287–292.

Magini E. 1962. Forest seed handling, equipment and procedures: 2. Seed treatments, storage, testing and transport. Unasylva 16(1): 20–35.

Magini E, Cappelli M. 1964a. Experiments on the storage of silver fir seed, *Abies alba*. Collana Verde Ministero dell'Agricoltura Forestale, Roma 19: 1716–1792.

Magini E, Cappelli M. 1964b. Cold storage of *Abies alba* seed. Italia Forestale e Montana 19: 189–98.

Martinez M. 1948. Los *Abies* mexicanos. Anales del Instituto de Biología de México 19: 11–104.

Matic S. 1972. Natural regeneration in silver fir stands infested by *Argyresthia fundella*. Sumarski List 96: 11–12, 432–441.

Matsuura T. 1963. Deduction of cone production and method of predicting the abundance or failure of cones in the Todo fir seed production areas. 1962 Annual Report of the Forestry Experiment Station, Hokkaido, Japan: 21–30.

Maze J, Parker WH. 1983. A study of population differentiation and variation in *Abies procera*. Canadian Journal of Botany 61: 1094–1104.

McDonald PM. 1980. Seed dissemination in small clearcuttings in north-central California. Res. Pap. PSW-150. Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. 7 p.

McDonald PM. 1992. Estimating seed crops of conifer and hardwood species. Canadian Journal of Forest Research 22: 832–838.

McKeever S. 1964. Food habits of the pine squirrel in northeastern California. Journal of Wildlife Management 28: 402–404.

Mergen F, Burley J, Simpson BA. 1965. Artificial hybridization in *Abies*. Züchter 34: 242–251.

Mergen F, Gregoire TG. 1988. Growth of hybrid fir trees in Connecticut. Silvae Genetica 37: 118–124.

Messeri A, Salvi F. 1964. The ecology of *Abies alba* : a study of germination of *A. alba* seed of several Apennine provenances. Annali Accademia Italiana di Scienze Forestali 13: 129–172.

Miller GE. 1986. Insects and conifer seed production in the Inland Mountain West. In: Shearer RC, comp. Proceedings, Symposium on Conifer Tree Seed in the Inland Mountain West; 1985; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 225–237.

Miller GE, Ruth DS. 1989. The relative importance of cone and seed insect species on commercially important conifers in British Columbia. In: Miller GE, comp. Proceedings, IUFRO WP S2.07-01 3rd Cone and Seed Insects Working Party Conference; 1988; Victoria, BC. Victoria, BC: Forestry Canada, Pacific Forestry Centre: 25–34.

Miller JT, Knowles FB. 1989. Introduced forest trees in New Zealand: recognition, role, and seed source: 7. The silver firs: *Abies* spp. New Zealand Forestry Research Institute Bulletin 124 (7): 1–20.

Miller LK. 1983. Controlled pollination techniques for Fraser fir. Tree Planters' Notes 34(3): 3–8.

Mitsopoulos DJ, Pantesos CP. 1987. Origin of variation in fir forests in Greece. Silvae Genetica 36: 1-15.

Moller K. 1986. Genetic studies in silver fir using enzyme gene markers. Allgemeine Forstzeitung 97: 60–61.

Moody BH, comp. 1988. Forest insect and disease conditions in Canada 1987. Forestry Canada, Forest Insect and Disease Survey 1988: 3–92.

Moore R. 1997. Correspondence, Aug. 1997. Woodland, WA: Lewis River Reforestation, Inc.

Mormann [no initials]. 1956. Experiences with the raising of exotics [in German]. Allgemeine Forstzeitschrift 11(8/9): 116–118.

Morris RF. 1951. The effects of flowering on the foliage production and growth of balsam fir. Forestry Chronicle 27: 40–57.

Moss EH. 1955. The vegetation of Alberta. Botanical Review 21: 493–567.

Moulalis D. 1986. Self-incompatibility and inbreeding of silver fir (*Abies alba*). Forstwissenschaftliches Centralblatt 105: 487–494.

Muller C. 1971. After-ripening of seeds of *Abies nordmanniana*. Revue Forestiere Francaise 23: 436–439.

Muller C. 1977. Conservation des graines de sapins. Bilan des recherches menées de 1966 à 1975. Pub. 77-29. Seichamps, France: Centre National de Recherches Forestieres, Station d'Amèlioration des Arbres Forestiers. 48 p. [also Interne Doc. 77/5, limited distribution].

Muller C. 1980. Long term storage of fir seeds and its influence on the behaviour of seed in the nursery. Seed Science and Technology 8: 103–118.

Muller KM. 1935. *Abies grandis* und ihre Klimarassen. Teil I. Deutsche Dendrologische Gesellschaft Mitteilungen 47: 54–123.

Muller KM. 1936. *Abies grandis* und ihre Klimarassen. Teil II. Deutsche Dendrologische Gesellschaft Mitteilungen 48: 82–127.

Munz PA, Keck DD. 1959. A California flora. Berkeley: University of California Press. 1681 p.

Murray MD, Crawford PD. 1982. Timber and boughs: compatible crops from a noble fir plantation. In: Oliver CD, Kenady RM, eds. Proceedings, Symposium on the Biology and Management of True Fir in the Pacific Northwest; 1981; Seattle/Tacoma, WA. Contrib. 45. Seattle: University of Washington, Institute of Forest Resources: 215–219.

Myers O Jr, Bormann FH. 1963. Phenotypic variation in *Abies balsamea* in response to altitudinal and geographic gradients. Ecology 44: 429–436.

Nagao A, Asakawa S. 1963. Light-sensitivity in the germination of *Abies* seeds. Journal of the Japanese Forestry Society 45: 375–377.

Nanu N. 1979a. The biometry of fir-tree cones and seeds (*Abies alba* Mill.) of Romania. In: Bonner F, ed. Proceedings, IUFRO/USFS/Mississippi State University International Symposium on Flowering and Seed Development in Trees; 1978; Starkville, MS. New Orleans: USDA Southern Forest Experiment Station: 361.

Nanu N. 1979b. The destroying insects of fir-tree (*Abies alba* Mill.) cone and seed: biology and ecology. In: Bonner F, ed. Proceedings, IUFRO/USFS/ Mississippi State University International Symposium on Flowering and Seed Development in Trees; 1978; Starkville, MS. New Orleans: USDA Southern Forest Experiment Station: 363.

Nanu N. 1980. *Resseliella piceae* Seitner (Dipt., Cecidomyiidae) as a pest of fir (*Abies alba*) seeds in Romania. Buletinul Informativ al Academiei Stiinte Agricole si Silvice 10: 151–162.

Nanu N, Lacatusu M, Tudor C. 1986. The balance factor in the conifer merocenes in Romania. In: Roques A, ed. Proceedings, 2nd Conference IUFRO Cone and Seed Working Party S2.07-01; 1986; Briancon, France. Institut National de la Recherche Agronomique, Olivet, France. Ardon, France: Station de Zoologie Forestière: 91–99.

NBV [Nederlandsche Boschbouw Vereeniging]. 1946. Boomzaden: handleiding inzake het oogsten, behandelen, bewaren en witzaaien van boomzaden. Wageningen, The Netherlands: Ponsen & Looijen. 171 p.

Neale DB, Adams WT. 1981. Inheritance of isozyme variants in seed tissues of balsam fir (*Abies balsamea*). Canadian Journal of Botany 59: 1285–1291.

Neale DB, Adams WT. 1985. Allozyme and mating system variation in balsam fir (*Abies balsamea*) across a continuous elevational transect. Canadian Journal of Botany 63: 2448–2453.

Nekrasova P. 1974. Losses of cone and seed crops in coniferous species. Lesovedenie 4: 3–8.

Nekrasova TP. 1978a. Parthenospermy and parthenocony in *Abies sibirica*. Izvestiya Sibirskogo Otdeleniya Akademii Nauk SSSR, Seriya Biologicheskikh Nauka 10: 100–103.

Nekrasova TP. 1978b. Losses of cones and seeds and the potential seed yield of *Abies sibirica*. Lesovedenie 2: 8–45.

Nekrasova TP, Ryabinikov AP. 1978. Variation in fruiting of *Abies sibirica*. Referativnyi Zhurnal 36: 367.

Neubacher F. 1959. Sowing silver fir in winter in a forest worker's hut for transplanting after the thaw. Allgemeine Forstzeitung 70 (1/2): 13–14.

Neuhoferova P. 1994. Cryopreservation of seed of European beech, sessile oak and silver fir, and embryos and axillary buds of sessile oak. Lesnictvi–Forestry 40: 519–522.

Nyholm I. 1956. Germination tests on *A. alba*. Dansk Skovforenings Tidsskrift 41: 150–159.

O'Connor JP, O'Connor MA. 1984. The fir seed chalcid, *Megastigmus pinus* Parfitt (Hym., Torymidae), new to Ireland. Entomologists' Monthly Magazine 120: 1440–1443.

Okada S. 1966. Investigation of the provenance character of Todomatsu (*Abies sachalinensis*) seedlings: 1. The variation and the difference of the cotyledon number among the provenances and mother trees. Journal of the Forestry Society 48:331–333.

Okada S. 1983. On the variation in Sakhalin fir (*Abies sachalinensis* Mast.) from different areas in Hokkaido. Bulletin of the Forest Tree Breeding Institute, Japan 1: 15–92.

Okishev BF, Pugachev AN. 1983. The fruiting of thin trees of spruce and fir on the Ufa plateau. Lesnoe Khozyaistvo 2: 36–38.

Oliver WW. 1974. Seed maturity in white fir and red fir. Res. Pap. PSW-99. Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. 12 p.

Ono K. 1974. Studies on 'Ezo-raigan' disease, *Sclerotium* germination loss, of Todo-Fir seeds. Bull. 268. Meguro, Tokyo: Government Forest Experiment Station: 49–80.

Ouden P den, Boom BK. 1965. Manual of cultivated conifers. The Hague: Martinus Nijhoff. 526 p.

Overhulser DL, Tanaka Y. 1983. Insect damage to noble fir seed and the feasibility of protecting cone crops in natural stands. Forest Science 29: 112–116.

Owens JN. 1984. Bud development in grand fir. Canadian Journal of Forest Research 14: 575–588.

Owens JN, Molder M. 1974. Bud development in western hemlock: 2. Initiation and early development of pollen cones and seed cones. Canadian Journal of Botany 52: 283–294.

Owens JN, Molder M. 1977a. Vegetative bud development and cone differentiation in *Abies amabilis*. Canadian Journal of Botany 55: 992–1008.

Owens JN, Molder M. 1977b. Sexual reproduction of *Abies amabilis*. Canadian Journal of Botany 55: 2653–2667.

Owens JN, Molder M. 1985. The reproductive cycles of the true firs. Victoria, BC: British Columbia Ministry of Forests, Forestry Branch, Research Division. 32 p.

Owens JN, Morris SJ. 1998. Factors affecting seed production in amabilis fir (*Abies amabilis* (L.) Mill.). Canadian Journal of Forest Research 28: 1146–1163.

Owston PW. 1979. Production of container-grown true firs in Pacific Coast greenhouse facilities. Proceedings [limited distribution], True Fir Management Cooperative Symposium, Regeneration and Management of Young True Fir Stands. Redding, California, 1979: 1 p.

Owston PW, Kozlowski TT. 1981. Growth and cold-hardiness of container-grown Douglas-fir, noble fir, and Sitka spruce seedlings in simulated greenhouse regimes. Canadian Journal of Forest Research 11: 465–474.

Packee EC, Oliver CD, Crawford PD. 1982. Ecology of Pacific silver fir. In: Oliver CD, Kenady RM, eds. Proceedings, Biology and Management of True Fir in the Pacific Northwest Symposium; 1981; Seattle/Tacoma, WA. Contrib. 45. Seattle: University of Washington, Institute of Forest Resources: 20–34.

Paiero P, Piussi P. 1964. Tests of pre-treatment of seed for use in forest nurseries. Italia Forestale e Montana 19: 67–72.

Panetsos CP. 1975. Monograph of *Abies cephalonica* Loudon. Annales Forestales Anali za Sumarstvo 7/1, Zagreb: 1–22.

Panov A. 1949. Physiological maturity and periodicity of seed years in forest tree species. Sumarski List 73: 334–345, 407–413.

Parducci L, Szmidt AE. 1997. Genetic variation among nine Mediterranean *Abies* species based on PCR-RFLP analysis of chloroplast DNA. Proceedings, International Conference on Biodiversity and Bioresources: Conservation and Utilization; 1997; Phuket, Thailand: 87.

Parducci L, Szmidt AE. 1998. PCR-RFLP analysis of cpDNA in the genus *Abies*. Proceedings, 18th International Congress of Genetics; 1998; Beijing: 110.

Parducci L, Szmidt AE. 1999. Genetic variation of the chloroplast genome in ten *Abies* species based on PCR-RFLP analysis. Theoretical and Applied Genetics 98: 802–808.

Parducci L, Szmidt AE, Anzidei M, Madaghiele A, Vendramin GG. 1999. Family structure in *Abies nebrodensis* (Lojac.) Mattei and differentiation from related *Abies* species using allozymes and chloroplast microsatellites. In: Fontdevila A, ed. Proceedings, VII International Congress of the European Society for Evolutionary Biology (ESEB); 1999; Barcelona: 225.

Parducci L, Szmidt AE, Madaghiele A, Anzidei M, Vendramin GG. 2000. Genetic variation at chloroplast microsatellites (cpSSR) in *Abies nebrodensis* (Lojac.) Mattei and in three neighbouring *Abies* species. Theoretical and Applied Genetics 102: 733–740.

Parducci L, Szmidt AE, Villani F, Wang X-R, Cherubini M. 1996. Genetic variation of *Abies alba* (Mill.) in Italy. Hereditas 125: 11–18.

Parducci L, Villani, F, Cherubini M, Szmidt AE. 1993. Genetic variation of Italian *Abies alba* Mill. populations. Proceedings, Fourth Congress of the European Society for Evolutionary Biology (ESEB); 1993; Montpellier, France: 336.

Parker WH, Maze J. 1984. Intraspecific variation in *Abies lasiocarpa* from British Columbia and Washington. American Journal of Botany 71: 1051–1059.

Parker WH, Maze J, Bradfield GE. 1981. Implications of morphological and anatomical variation in *Abies balsamea* and *A. lasiocarpa* (Pinaceae) from western Canada. American Journal of Botany 68: 843–854.

Parmete JR Jr, Scharpf RF. 1963. Dwarfmistletoe on red fir and white fir in California. Journal of Forestry 61: 371–374.

Pascual L, Garcia FJ, Perfectti F. 1993. Inheritance of isozyme variations in seed tissues of *Abies pinsapo* Boiss. Silvae Genetica 42: 335–340.

Pavlenko IA. 1972. Preparation of seeds of *Abies holophylla* for sowing in the Maritime Province. Lesnoi Zhurnal 15: 160–161.

Pearson GA. 1931. Forest types in the Southwest as determined by climate and soil. Tech. Bull. 247. Washington, DC: USDA. 144 p.

Pedro White JL, White MD. 1986. Squirrel behaviour influences quality of cones and seeds collected from squirrel caches: field observations. In: Shearer RC, comp. Proceedings, Symposium on Conifer Tree Seed in the Inland Mountain West; 1985; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 223–224.

Peek JM. 1974. Initial response of moose to a forest fire in northeastern Minnesota. American Midland Naturalist 91: 435–438.

Pelton S. 1997. Correspondence, Oct. 1997. Maple Ridge, BC: Pelton Reforestation Ltd.

Penka M, Cermak J, Tesarik K. 1977. Chromatographic determination of monoterpene hydrocarbons and alcohols contained in the resin from *Abies alba* Mill. seeds. Acta Universitatis Agriculturae, Brno, Ser. C (Facultas Silviculturae) 46: 147–169.

Pfister RD. 1966. Artificial ripening of grand fir cones. Northwest Science 40: 103–112.

Pfister RD. 1967. Maturity indices for grand fir cones. Res. Note INT-58. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 7 p.

Pfister RD, Woolwine PC. 1963. Insect damage in grand fir cones. Res. Note INT-8. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 3 p.

Pigott D. 1994. Collection methods of *Abies* sp. In: Konishi J, Barber B, comps. and eds. Proceedings, *Abies* spp. Workshop: Problems and Solutions; 1994; Parksville, BC. Victoria, BC: British Columbia Ministry of Forests: 9–11.

Pojar J, MacKinnon A. 1994. Plants of coastal British Columbia. Vancouver, BC: Lone Pine Publishing. 527 p.

Pollock BM, Roos EE. 1972. Seed and seedling vigor. In: Kozlowski TT, ed. Seed biology. New York: Academic Press: 313–387.

Portlock FT, comp. 1996. A field guide to collecting cones of British Columbia conifers. British Columbia Tree Seed Dealers' Association. Canada/British Columbia Forest Resource Development. Victoria: Canadian Forestry Service/British Columbia Ministry of Forests: FRDA II. 91 p.

Poulsen KM. 1996. Prolonged cold, moist pretreatment of conifer seeds at controlled moisture content. Seed Science and Technology 24: 75–87.

Powell GR. 1970. Post-dormancy development and growth of microsporangiate and megagasporangiate strobili of *Abies balsamea*. Canadian Journal of Botany 48:419–428.

Powell GR. 1972. Some observations on the transition from female bearing to male bearing in balsam fir. In: Schreiner EJ, ed. Proceedings, 19th Northeastern Forest Tree Improvement Conference. 1971; University of Maine, Orono. Upper Darby, PA: Northeastern Forest Experiment Station: 18–26.

Powell GR. 1973. The spruce budworm and megasporangiate strobili of balsam fir. Canadian Journal of Forest Research 3: 424–429.

Powell GR. 1977. Biennial strobilus production in balsam fir (*Abies balsamea*): a review of its morphogenesis and a discussion of its apparent physiological basis. Canadian Journal of Forest Research 7: 547–555.

Powell GR. 1979. Influence of position in the crown on cone size and seed yields of *Abies balsamea*. In: Bonner FT, ed. Proceedings, IUFRO/USFS/Mississippi State University International Symposium on Flowering and Seed Development in Trees; 1978; Starkville, MS. New Orleans: USDA Southern Forest Experiment Station: 122–137.

Pribylova MV. 1975. *Diptera* as dangerous pests of *Abies nordmanniana* seeds. Lesovedenie 6: 51–57.

Prisyazhnyuk AA. 1960. Fungal diseases of seed and cones of conifers. Lesnoi Zhurnal 3: 31–37.

Puri GS, Gupta RK. 1968. Ecology of silver firs in western Himalayas. Tropical Ecology (Varanasi) 9: 1–16.

Pyle RS. 1992. Handbook for butterfly watchers. Boston: Houghton Mifflin Co. 280 p.

Pyle RS. 1999. Chasing monarchs: migrating with the butterflies of passage. Boston: Houghton Mifflin Co. 307 p.

Radulescu S. 1968. Establishing a method of storing *Abies alba* seed in winter. Studii si Cercetari Institutului de Cercetari Forestiera Bucuresti (Silvicoltura) 26: 71–84.

Rafn J. 1915. The testing of forest seeds during 25 years, 1887–1912. Copenhagen: Langjaers Bogtrykkeri. 91 p.

Rafn J and Son. [no date, ca. 1928]. Skovfrökontoret's Fröanalyser gennem 40 Aar, 1887–1927. Udfört paa Statsfrökontrollen i Köbenhavn. 5 p.

Rahman W, Chaudhry MI. 1986. Assessment of damage to silver fir seed caused by cone-borer, *Dioryctria abietella* Schiff. Pakistan Journal of Forestry 36: 89.

Rediske JH. 1961. Maturation of Douglas-fir seed: a biochemical study. Forest Science 7: 204–213.

Rediske JH. 1967. Cone collection, seed processing and storage: newest developments. In: Western reforestation. Proceedings, Annual Meeting Western Forest and Conservation Association, Portland, OR. Seattle, WA: Western Reforestation Coordinating Committee: 18–20.

Rediske JH, Nicholson DC. 1965. Maturation of noble fir seed: a biochemical study. For. Pap. 2. Centralia, WA: Weyerhaeuser Co. 15 p.

Rehder A. 1958. Manual of cultivated trees and shrubs hardy in North America exclusive of the subtropical and warmer temperate regions. Second ed. New York: Macmillan. 920 p.

Ripple WJ, Johnson DH, Hershey KT, Meslow EC. 1991. Old-growth and mature forests near spotted owl nests in western Oregon. Journal of Wildlife Management 55: 316–318.

Riskin K. 1997. Correspondence, Aug. 1997. Eddyville, OR: Qualitree Inc.

Robinson JF, Thor E. 1969. Natural variation in *Abies* of the southern Appalachians. Forest Science 15(3): 238–245.

Roe EI. 1946. Extended periods of seedfall of white spruce and balsam fir. Tech. Note 261. St. Paul: USDA Forest Service, Lake States Forest Experiment Station. 1 p.

Roe EI. 1948a. Early seed production by balsam fir and white spruce. Journal of Forestry 46: 529.

Roe El. 1948b. Balsam fir seed: its characteristics and germination. Res. Pap. 11. St. Paul: USDA Forest Service, Lake States Forest Experiment Station. 13 p.

Rohmeder E. 1951. Beitrage zur Keimungsphysiologie der Forstpflanzen [Contributions to the physiology of germination of forest plants]. Munich: Bayerischer Landswirtschafts. 140 p.

Rohmeder E. 1953. Long storage of *Abies alba* seed. Allgemeine Forstzeitschrift 8: 117–119.

Rohmeder E. 1960a. Bastardierung der Gattung *Abies* [Hybridization in the genus *Abies*; abstract]. Silvae Genetica 9: 136–137.

Rohmeder E. 1960b. Guteuntersuchungen am Saatgut der *Abies* grandis [Testing the seed quality of *Abies grandis*]. Allgemeine Forstzeitschrift 15: 105–106.

Rohmeder E, Eisenhut G. 1961. Bastardierungsversuche an der Gattung *Abies* [Studies on hybridization in the genus *Abies*]. Allgemeine Forstzeitschrift 16: 495–497.

Rohmeder E, Schönbach H. 1959. Genetik und Züchtung der Waldbäume. Berlin: Paul Parey. 338 p.

Roller KJ. 1967. Preliminary report on the possible occurrence of hybrid firs in north-central Alberta. Bi-Monthly Research Notes 23. [Ottawa: Canada Department of Forestry and Rural Development, Forestry Branch]: 10.

Rooke H. 1994. *Abies* spp. cone and seed processing. In: Konishi J, Barber B, comps. and eds. Proceedings, *Abies* spp. Workshop: Problems and Solutions; 1994; Parksville, BC. Victoria: British Columbia Ministry of Forests: 12–14.

Rooke H. 1997. Personal communication. Surrey: British Columbia Ministry of Forests, Tree Seeds Centre.

Rudolf PO. 1940. When are pine cones ripe? Proceedings of the Minnesota Academy of Science 8: 31–38.

Rudolf PO. 1950. Cold soaking: a short-cut substitute for stratification? Journal of Forestry 48: 31–32.

Rudolf PO. 1952. Low temperature seed storage for western conifers. Misc. Rep. 20. St. Paul, MN: USDA Forest Service, Lake States Forest Experiment Station. 8 p.

Rushforth KD. 1983. *Abies chengii*, a previously overlooked Chinese silver fir. Notes of the Royal Botanical Gardens Edinburgh 41: 333–338.

Rushforth KD. 1984. Notes on Chinese silver firs 2. Notes of the Royal Botanical Gardens Edinburgh 41: 535–540.

Rushforth KD. 1986. Notes on Chinese silver firs 3. Notes of the Royal Botanical Gardens Edinburgh 43: 269–275.

Rushforth KD. 1987. Conifers. New York: Facts on File Publications. 232 p.

Rushforth KD. 1989. Two new species of *Abies* (Pinaceae) from western Mexico. Notes of the Royal Botanical Gardens Edinburgh 46: 101–109.

Rutar R. 1991. Determination of seed viability of fir (*Abies alba*). Sjemenarstvo 8: 3–6, 145–148.

Rutar V, Kovac M, Lahajnar G. 1989. Nondestructive study of liquids in single fir seeds using nuclear magnetic resonance and magic angle sample spinning. Journal of the American Oil Chemists' Society 66: 961–965.

Salazar ME. 1991. Development of treatments to improve seed germination, and effect of nitrogen on seedling growth of *Abies guatemalensis* Rehder. [MS thesis]. Raleigh, NC: North Carolina State University, College of Forest Research. 118 p.

Sanftleben H. 1989. Isoproturon: an active compound for nurseries? Deutsche Baumschule 41: 534–535.

Saralidze GM, Homeriki GK. 1964. Machines for extracting tree seeds. Lesnoe Khozyaistvo 17: 72–73.

Sato K. 1962. Studies on the control of damping off of forest tree seedlings by seed treatment with fungicides. Bull. 139. Meguro, Tokyo: Government Forest Experiment Station: 163–175.

Sato Y. 1940. On seed fall in mixed stands of *Abies sachalinensis* and *Picea jezoensis*. Res. Bull. 11. Hokkaido, Japan: Hokkaido University, College of Experimental Forestry: 1–18.

Savcenko AM. 1966. Seed-dispersal distance of *Abies sibirica* in plains forests. Trudy Sibirskogo Nauchno Issledovatel'skogo Institut Lesnoj Promyhslennosti 14: 3–5.

Sawyer JO, Thornburgh DA. 1977. Montane and subalpine vegetation of the Klamath Mountains. In: Barbour MG, Major J, eds. Terrestrial vegetation of California. New York: John Wiley & Sons: 699–732.

Scerbakova MA. 1964. Determining conifer seed quality by radiography. Lesnoe Khozyaistvo 17: 52–56.

Schmidt WC, Lotan JE. 1980. Phenology of common forest flora of the northern Rockies—1928 to 1937. Res. Paper INT-259. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 20 p.

Schooley HO. 1975. Cone production of balsam fir damaged by balsam woolly aphid. Forestry Chronicle 51: 105–107.

Schooley HO. 1976. Effect of balsam woolly aphid on cone and seed production by balsam fir. Forestry Chronicle 52: 237–239.

Schooley HO. 1978. Effect of spruce budworm on cone production of balsam fir. Forestry Chronicle 54: 298–301.

Schroeder S. 1989a. Outcrossing rates and seed characteristics in damaged natural populations of *Abies alba* Mill. Silvae Genetica 38: 185–189.

Schroeder S. 1989b. Silver fir in south Germany: genetic variation, clines, correlations. Allgemeine Forst- und Jagdzeitung 160: 100–104.

Schroeder S. 1989c. Isozyme polymorphisms in silver fir (*Abies alba* Mill.). Silvae Genetica 38: 130–133.

Schubert GH. 1954. Viability of various coniferous seeds after cold storage. Journal of Forestry 52: 446–447.

Schutt P. 1991. The species of fir of Europe and Asia Minor. Basel: Birkhauser Verlag. 132 p.

Schwenke HJ. 1956. Raising *A. nobilis* (= *procera*) in the nursery. Forschungsberichte des Landes Nordrhein–Westfalen 2: 116–127.

Schwenke HJ. 1961. Raising *Abies procera* Rehd. Forst- und Holzwirt 16: 263–264.

Scurlock JH, Mitchell RG, Ching KK. 1982. Insects and other factors affecting noble fir seed production at two sites in Oregon. Northwest Science 56: 101–107.

Seal DT, Matthews JD, Wheeler RT. 1965. Collection of cones from standing trees. For. Rec. 39. London: Her Majesty's Stationery Office. 47 p.

Seiler JR, Kreh RE. 1987. The effect of chilling and seed source on the growth of containerized seedlings of Fraser fir (*Abies fraseri* [Pursh] Poir.). Tree Planters' Notes 38(2): 19–21.

Sharma HP, Sharma KC, Singh O. 1987. Nursery technology of silver fir (*Abies pindrow* Spach). Indian Journal of Forestry 10: 80–82.

Shea PJ. 1989a. Interactions among phytophagous insect species colonizing cones of white fir (*Abies concolor*). Oecologia (Berlin) 81: 104–110.

Shea PJ. 1989b. Phytophagous insect complex associated with cones of white fir, *Abies concolor* (Gord. and Glend.) Lindl., and its impact on seed production. Canadian Entomologist 121: 699–708.

Shearer RC, Tackle D. 1960. Effect of hydrogen peroxide on germination in three western conifers. Res. Note 80. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 4 p.

Sheedy G. 1974. Effets comparés de divers fertilisants sur la production de semences du sapin baumier. Note 3. Ste.-Foy, QC: Gouvernment de Quebec, Ministère des Terres et Forêts, Direction Générale des Forêts, Service de la Recherche. 11 p.

Sheedy G. 1978. Effets de sept traitments de fertilization sur la production des cones et de graines d'un peuplement de sapin baumier age de 60 ans. Note 8. Ste.-Foy, QC: Gouvernment de Quebec, Ministère des Terres et Forêts, Direction Générale des Forêts, Service de la Recherche. 10 p.

Sidhu SS, Staniforth RJ. 1986. Effects of atmospheric fluorides on foliage, and cone and seed production in balsam fir, black spruce, and larch. Canadian Journal of Botany 64: 923–931.

Silen RR, Critchfield WB, Franklin JF. 1965. Early verification of a hybrid between noble and California red firs. Forest Science 11: 460–462.

Simak M. 1970. Germination analyses of *Abies alba* seed. Proceedings of the International Seed Testing Association 35: 361–367.

Simak M. 1973. Separation of forest seed through flotation. In: Simak M, Kamra SK, eds. Proceedings, IUFRO WP S2.01.06 International Symposium on Seed Processing. Bergen, Norway; 1973; Volume 1, Paper 16. Stockholm: Royal College of Forestry. 10 p.

Simak M. 1984. A method for removal of filled-dead seeds from a sample of *Pinus contorta*. Seed Science and Technology 12: 767–775.

Singh H, Owens JN. 1981. Sexual reproduction in subalpine fir (*Abies lasiocarpa*). Canadian Journal of Botany 59: 2650–2666.

Singh H. Owens JN. 1982. Sexual reproduction in grand fir (*Abies grandis*). Canadian Journal of Botany 60: 2197–2214.

Singh O, Bhagat S. 1989. Effect of soil fumigation on the incidence of damping off in silver fir nurseries. Van Vigyan 27: 207–209.

Singh O, Singh V. 1990. Germination and growth of spruce and silver fir in relation to covering media. Indian Forester 116: 278–282.

Singh RV, Singh V. 1981. Preliminary studies on the quality of spruce and silver fir seed as affected by its source. Indian Forester 107: 571–577.

Singh RV, Singh V. 1984. Germination of silver fir (*Abies pindrow* Spach) as affected by depth of sowing. Indian Journal of Forestry 7: 328–329.

Singh V, Singh RV. 1984a. Seed dispersal, seed germination and seedling establishment in natural forests of silver fir and spruce: 1. Seed dispersal pattern. Indian Forester 110: 529–539.

Singh V, Singh RV. 1984b. Seed dispersal, seed germination and seedling establishment in natural forests of silver fir and spruce: 2. Seed germination and seedling establishment. Indian Forester 110: 632–639.

Singh V, Singh O, Sharma HP. 1986. Germination of silver fir (*Abies pindrow*) seed as affected by moisture stress. Indian Journal of Forestry 9: 293–295.

Singh V, Sah VK, Bana OPS, Singh V. 1991. Effect of cone diameter on seed yield, moisture content and germination in silver fir (*Abies pindrow* Spach). Van Vigyan 29: 218–222.

Sjoberg NE. 1974. The Styroblock container system. In: Tinus RW, Stein WI, Balmer WE, eds. Proceedings, North American Containerized Forest Tree Seedling Symposium; Denver, CO. Pub. 68. Lincoln, NB: Great Plains Agricultural Council: 217–228.

Skrzypczynska M. 1982. Pests of cones and seeds of *Abies alba* at selected sites in the Sadecki Beskids in 1976–80. Acta Agraria et Silvestria, Series Silvestris 21: 79–97.

Skrzypczynska M. 1984. Preliminary studies on entomofauna of cones of *Abies alba* in Ojcowski and Tatrzanski National Parks in Poland. Zeitschrift für Angewandte Entomologie 98: 375–379.

Skrzypczynska M. 1985. Gall-midge (Cecidomyiidae, Diptera) pests in seeds and cones of coniferous trees in Poland. Zeitschrift für Angewandte Entomologie 100: 448–450.

Skrzypczynska M. 1989a. *Megastigmus suspectus* Borr. (Hymenoptera Torymidae) and *Resseliella piceae* Seitn. (Diptera, Cecidomyiidae) within fir (*Abies alba* Mill.) stands in Poland in 1986. Acta Agraria et Silvestria, Series Silvestris 28: 3–16.

Skrzypczynska M. 1989b. Review of insects found in cones of *Abies alba* Mill. in Poland. In: Miller GE, comp. Proceedings, IUFRO WP S2.07-01 3rd Cone and Seed Insects Working Party Conference; 1988; Victoria, BC. Victoria, BC: Forestry Canada, Pacific Forestry Centre: 42–49.

Skrzypczynska M, Krolik R, Piatek H, Lokacijewski G, Kurzeja M. 1990. Cone entomofauna of fir (*Abies alba* Mill.) of Beskid Sadecki Mts. in Poland in 1986–1988. Journal of Applied Entomology 110: 82–91.

Skrzypczynska M, Sikora Z, Guzek R. 1995. Cono- and seminiphagous insects of fir *Abies alba* Mill. in the Babia Gora National Park and its surroundings in southern Poland. Anzeiger für Schaedlingskunde, Pflanzen- und Umweltschutz 68: 34–36.

Skrzypczynska M, Wisniowski B, Dembinska F, Koziol M. 1988. Insect pests of *Abies alba* cones and seeds in selected parts of Roztocze National Park (Poland) in 1982–86. Acta Agraria et Silvestria, Series Silvestris 27: 3–16.

Smirnov AA. 1991. Dynamics of seed dispersal in *Abies mayriana*. Lesovedenie 4: 96–99.

Smith CC. 1968. The adaptive nature of social organization in the genus of tree squirrels *Tamiasciurus*. Ecological Monographs 38: 31–63.

Smith JP, Berg K. 1988. Inventory of rare and endangered vascular plants of California. 4th. ed. Spec. Pub. 1. Sacramento: California Native Plant Society. 168 p.

Smith R. 1982. Utilization of true firs. In: Oliver CD, Kenady RM, eds. Proceedings, Biology and Management of True Fir in the Pacific Northwest Symposium; 1981; Seattle/Tacoma, WA. Contrib. 45. Seattle: University of Washington, Institute of Forest Resources: 239–242.

Snyder J. 1997. Correspondence, Aug. 1997. Parkdale, OR: Lava Nursery.

Snyder JL. 1976. Maturation of noble fir (*Abies procera*) and grand fir (*Abies grandis*) seed [MS thesis]. Corvallis: Oregon State University. 92 p.

Soljanik I. 1950. Planning for sowing of forest seed in nurseries and at site. Sumarski List 74: 341–346.

Sorensen FC, Campbell RK, Franklin JF. 1990. Geographic variation in growth and phenology of seedlings of the *Abies procera/A. magnifica* complex. Forest Ecology and Management 36: 205–232.

Sorensen FC, Franklin JF. 1977. Influence of year of cone collection on cotyledon number in *Abies procera*. Silvae Genetica 26: 41–43.

Sorensen FC, Franklin JF, Wollard R. 1976. Self-pollination effects on seed and seedling traits in noble fir. Forest Science 22: 155–159.

Souleres G. 1965. Variation in seed production and germinative capacity of *Abies alba*. Revue Forestiere Francaise 17: 219–30.

Speers CF. 1962. Fraser fir seed collection, stratification, and germination. Tree Planters' Notes 53: 7–8.

Speers CF. 1967. Insect infestation distorts Fraser fir seed tests. Tree Planters' Notes 18(1): 19–21.

Speers CF. 1968. Balsam fir chalcid causes loss of Fraser fir seed. Tree Planters' Notes 19(2): 18–20.

Speers CF. 1969. *Megastigmus specularis* Walley infests fir seed from Canada to North Carolina. Tree Planters' Notes 20(2): 28–29.

Speers CF. 1974a. Pine seed chalcid transcontinental in range. Tree Planters' Notes 25(2): 24.

Speers CF. 1974b. Fraser fir seed storage and germination: some new data. Tree Planters' Notes 25(3): 19.

Stanwood PC, Bass LN. 1978. Ultracold preservation of seed germplasm. In: Li PH, Sakai A, eds. Plant cold hardiness and freezing stress: mechanisms and crop implications. New York, Academic Press: 361–371.

St.-Clair JB, Critchfield WB. 1988. Hybridization of a Rocky Mountain fir (*Abies concolor*) and a Mexican fir (*Abies religiosa*). Canadian Journal of Forest Research 18: 640–643.

Steele R, Pfister RD, Ryker RA, Kittams JA. 1981. Forest habitat types of central Idaho. Gen. Tech. Rep. INT-114. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 138 p.

Stein WI. 1951. Germination of noble and silver fir seed on snow. Journal of Forestry 49: 448–449.

Stein WI. 1967. Laboratory seed tests: are they doing the job? In: Western reforestation. Proceedings, Annual Meeting Western Forest and Conservation Association, Portland, OR. Seattle: Western Reforestation Coordinating Committee: 20–23.

Stein WI, Slabaugh PE, Plummer AP. 1974. Harvesting, processing, and storage of fruits and seeds. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 98–125.

Steinhoff RJ. 1978. Distribution, ecology, silvicultural characteristics, and genetics of *Abies grandis–Abies concolor* complex. In: Proceedings, Joint Meeting of Working Parties S2.02-05 Douglas fir provenances, S2.02-06 lodgepole pine provenances, S2.02-12 Sitka spruce provenances and S2.02-14 *Abies* provenances. Vancouver, BC: Volume 1. Victoria: British Columbia Ministry of Forests: 123–132.

Stilinovic S, Tucovic A. 1971. Preliminary study on seed of *Abies concolor* from the seed stand at Avala [Yugoslavia]. Glasnik Sumarskog Fakulteta, Univerzitet u Beogradu 39: 95–102.

Stoeckeler JH, Jones GW. 1957. Forest nursery practice in the Lake States. Agric. Handbk. 110. Washington, DC: USDA Forest Service: 1–124.

Stubley D. 1998. Correspondence, February 1998. Surrey: British Columbia Ministry of Forests, Tree Seed Centre.

Sutherland JR. 1979. The pathogenic fungus *Caloscypha fulgens* in stored conifer seeds in British Columbia and relation of its incidence to ground and squirrel-cache collected cones. Canadian Journal of Forest Research 9: 129–132.

Suyama Y, Kawamuro K, Kinoshita I, Yoshimura K, Tsumura Y, Takahara H. 1996. DNA sequence from a fossil pollen of *Abies* spp. from Pleistocene peat. Genes and Genetic System 71: 145–149.

Suyama Y, Tsumura Y, Ohba K. 1992. Inheritance of isozyme variants and allozyme diversity of *Abies mariesii* in three isolated natural populations. Journal of the Japanese Forestry Society 74: 65–73.

Suyama Y, Tsumura Y, Ohba K. 1997. A cline of allozyme variation in *Abies mariesii*. Journal of Plant Research 110: 219–226.

Sweeney JD, El-Kassaby YA, Taylor DW, Edwards DGW, Miller GE. 1991. Applying the IDS method to remove seeds infested with the seed chalcid *Megastigmus spermotrophus* Wachtl, in Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco. New Forests 5: 327–334.

Talley SN. 1974. The ecology of Santa Lucia fir (*Abies bracteata*), a narrow endemic of California [PhD thesis]. Durham, NC: Duke University. 209 p. [Dissertation Abstracts International B 35: 3767–3768].

Tanaka Y. 1982. Biology of *Abies* seed production. In: Oliver CD, Kenady RM, eds. Proceedings, Biology and Management of True Fir in the Pacific Northwest Symposium; 1981; Seattle/Tacoma, WA. Contrib. 45. Seattle: University of Washington, Institute of Forest Resources: 103–111.

Tanaka Y, Edwards DGW. 1986. An improved and more versatile method for prechilling *Abies procera* Rehd. seeds. Seed Science and Technology 14: 457–464.

Thanos CV. 2003a. Mt. Ida in mythology and classical antiquity: a plant scientist's approach. Proceedings, 1st National Symposium on the Past, Present, and Future of the Kasdaglari Mountains; 2001; Ankara: Engineers, Turkish Chamber of Forest, 14 p.

Thanos CV. 2003b. The geography of Theophrastus' life and of his botanical writings. In: Karamanos A, Thanos CA, eds. Proceedings, Theophrastus 2000—Biodiversity and Natural Heritage in the Aegean; 2000; Ererssos-Sigri, Lesbos, Greece. Athens. 13 p.

Thompson M. 1997. Correspondence, Sept. 1997. Sublimity, OR: Silver Mountain Christmas Trees.

Tillisch ET. 1952. *Abies grandis*: its possibilities in Danish forestry. Dansk Skovforening Tidsskrift 37: 139–205.

Tocci AV. 1966. Preparation and storage of silver fir seed. Monti e Boschi 17: 39–53.

Tokarz Z. 1974. Trials in storing seed of silver fir, beech and oak over one growing season. Sylwan 118: 53–56.

Toth J. 1973. The damage caused by the *Megastigmus* pest of cedar in France. Revue Forestiere Francaise 25: 576.

Toumey JW, Stevens CL. 1928. The testing of coniferous tree seeds at the School of Forestry, Yale University, 1906–1926. Bull. 21. New Haven, CT: Yale University School of Forestry. 46 p.

Triebwasser M. 1997. Correspondence, Sept. 1997. Aurora, OR: Weyerhaeuser Company, Aurora Forest Nursery.

Trimble P. 1997. Correspondence, Sept. 1997. Camino, CA: USDA Forest Service, Placerville Nursery.

Tsumura Y, Suyama Y. 1998. Differentiation of mitochondrial DNA polymorphisms in populations of five Japanese *Abies*. Evolution 52: 1031–1042.

Tsumura Y, Taguchi H, Suyama Y, Ohba K. 1994. Geographical decline of chloroplast DNA variation in *Abies mariesii*. Theoretical and Applied Genetics 89: 922–926.

Tulstrup NP. 1952. Skovfrø: nogle praktiske oplysninger. Dansk Skovforenings Frøudvalg [Springforbi]. 70 p.

Tumbarello G. 1960. The storage of *Abies alba* seed. Italia Forestale e Montana 15: 176–182.

Turner NJ. 1998. Plant technology of First Peoples in British Columbia. Vancouver: University of British Columbia Press. 256 p.

Turpin P. 1963. An inexpensive installation for extracting the seed of firs. Revue Forestiere Francaise 15: 922–930.

Ujiie M, Katayose T, Kudoh H. 1991. Seasonal changes of chemical components in the cones from various clones of *Abies sachalinensis* in a seed orchard and germination test of the mature seeds. Res. Bull. 48. Hokkaido, Japan: Hokkaido University, College of Experimental Forestry: 157–182.

USDA FS [Forest Service}. 1948. Woody-plant seed manual. Misc. Pub. 654. Washington, DC: USDA Forest Service. 416 p.

USDA FS [Forest Service]. 1992. Every species counts: research on threatened, endangered, and sensitive plants and animals. Prog. Aid 1481. Washington, DC: USDA Forest Service. 20 p.

Vabre-Durrieu A. 1956. Le froid et les graines de quelques Abiétacées [The reaction to cold of some species of Abietineae]. Travaux du Laboratoire Forestier de Toulouse 1(5) Art. 29: 1–6.

Vacowicz P. 1997. Correspondence, Sept. 1997. Oliver, BC: K & C Silvicultural Farms.

Veblen, TT. 1978. Guatemalan conifers. Unasylva 29 (118): 25–30.

Vetrova VP. 1992. Variation of seed and cover scales in *Abies sibirica.* Lesovedenie 1(2):67–71.

Vidakovic M. [Soljan M, trans.] 1991. Conifers: morphology and variation. Croatia: Graficki Zavod Hrvatske. 754 p.

Vilmorin R de. 1944. Note on the conservation of the germinative capacity of the seed of *Abies pectinata*. Compte Rendu des Seances de l'Académie d'Agriculture de France 17: 509–512.

Vladyshevskii DV, Shtarker VV. 1982. Utilization of *Abies sibirica* seeds by vertebrates. Lesovedenie 4: 26–30.

Vlase I. 1960. Factors favourable to the maintenance of germinability in seed of *Abies alba*. Revista Padurilor 75: 476–80.

Vlase I, Iesan T. 1959. Raising *Abies alba* in the nursery. Revista Padurilor 74: 697–700.

Von Rudloff E. 1976. Chemosystematic studies in the genus *Abies*: 2. Leaf and twig oil analysis of grand fir. Canadian Journal of Botany 54: 1926–1931.

Von Rudloff E, Hunt RS. 1977. Chemosystematic studies in the genus *Abies*: 3. Leaf and twig oil analysis of amabilis fir. Canadian Journal of Botany 55: 3087–3092.

Voroshilova GI. 1983. Formation of the wing in conifer seeds. Biologijos Mosklai 8. Mokslas, Vilnius; Lietuvos TSR Mokslu Akademijos Darbai, C serija: 81–84.

Wallinger DP. 1986. Aerial cone collection in British Columbia. In: Shearer RC, comp. Proceedings, Symposium on Conifer Tree Seed in the Inland Mountain West; 1985; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 133–139.

Wang BSP. 1960. The effects of stratification and incubation temperatures on the germination of grand fir (*Abies grandis* (Dougl.) Lindl.) seed [Master's thesis]. Vancouver: University of British Columbia. 110 p.

Wang BSP. 1974. Tree seed storage. Pub. 1335: Ottawa: Canada Department of Environment, Canadian Forestry Service. 32 p.

Wappes L. 1932. Wald und Holz ein Nachschlagebuch für die Praxis der Forstwirte, Holzhändler und Holzindustriellen. Volume 1. Berlin: J. Neumann. 872 p.

Weber WA. 1987. Colorado flora: western slope. Niwot: University Press of Colorado. 530 p.

Wedman I. 1997. Correspondence, Aug. 1997. Black Creek, BC: Sylvan Vale Nursery Ltd.

Welch HJ. 1991. The conifer manual. Vol. 1. Kluwer Academic Publishers. Boston: 436 p.

WFTSC [Western Forest Tree Seed Council]. 1966. Sampling and service testing western conifer seeds. In: Stein WI, ed. Portland, OR: Western Forest Tree Seed Council/Western Forest and Conservation Association. 36 p.

Weyerhaeuser Timber Company. 1957. Annual report for 1956. Centralia, WA: Weyerhaeuser Forest Research Center. 39 p.

Weyerhaeuser Timber Company. 1958. Annual report for 1957. Centralia, WA: Weyerhaeuser Forest Research Center. 51 p.

Wolfenbarger DO. 1946. Dispersion of small organisms: Distance dispersion rates of bacteria, spores, seeds, pollen and insects: incidence rates of diseases and injuries. American Midland Naturalist 35: 1–152.

Wong J. 1997. Correspondence, Oct. 1997. Telkwa, BC: Woodmere Nursery Ltd.

Woodwell GM. 1961. The influence of the spruce budworm and DDT on the reproductive potential of balsam fir [Abstract]. Bulletin of the Ecological Society of America 42: 104.

Wright JW. 1950. Summary of tree-breeding experiments by the Northeastern Forest Experiment Station, 1947-1950. Sta. Pap. 56. Upper Darby, PA: USDA Forest Service, Northeastern Forest Experiment Station. 47 p.

Yanagisawa T. 1965. Effect of cone maturity on the viability and longevity of coniferous seed. Bull. 172. Meguro, Tokyo: Government Forest Experiment Station: 45–94.

Yoshida S. 1960. Biochemistry of germination and low-temperature stratification of *Abies sachalinensis* Fr. Schm. seeds: 1. On the change of auxin and inhibitor in the seeds during low-temperature stratification. Journal of the Japanese Forestry Society 42: 259–262.

Young JA, Young CG. 1992. Seeds of woody plants of North America. Portland, OR: Dioscorides Press: 1–8.

Zavarin E, Critchfield WB, Snajberk K. 1978. Geographic differentiation of monoterpenes from *Abies procera* and *Abies magnifica*. Biochemical Systematics and Ecology 6: 267–278.

Zavarin E, Snajberk K, Senter P. 1979. Analysis of terpenoids from seedcoats as a means of identifying seed origin. Forest Science 25: 20–24.

Zelenin NP. 1991. Silvicultural and economic assessment of thinnings for fruiting in *Pinus sibirica* stands in the Altai mountains. Lesnoe Khozyaistvo 10: 38–41.

Zemanek G. 1997. Correspondence, Sept. 1997. Canim Lake, BC: Roserim Forest Nursery.

Zentsch W. 1960. Untersuchungen zur Erhöhung des Keim.–bezm. Pflanzenprozentes bei der Tanne (*Abies pectinata*) [Experiments to improve germination or plant percents in *A. pectinata* (= *alba*)]. Forst und Jagd 10: 36–38.

Zentsch W, Jahnel H. 1960. Tests with stratified seed at Rovershagen State Forest Estate. Forst und Jagd 10: 81–83.

Zhang SM. 1982. Study on the cone seed pests of different needleleaved forest types in natural forest. Journal of the Northeast Forestry Institute, China 3: 21–27.

Zon R. 1914. Balsam fir. Bull. 55. Washington, DC: USDA Forest Service. 68 p.

Fabaceae—Pea family

Acacia L.

acacia

John K. Francis and Craig D. Whitesell

Dr. Francis retired from the USDA Forest Service's International Institute of Tropical Forestry;
Dr. Whitesell retired from the USDA Forest Service's Pacific Southwest
Forest and Range Experiment Station

Growth habit, occurrence, and use. The acacias include about 1,200 species of deciduous or evergreen trees and shrubs widely distributed in the tropics and warmer temperate areas (Guinet and Vassal 1978). Nearly 300 species are found in Australia and about 70 in the United States. Some 75 species are of known economic value, and about 50 of these are cultivated. Certain species of acacias—Cootamundra wattle (*A. baileyana* F. Muell.), Karoo thorn (*A. karroo* Hayne), golden wattle (*A. pycnantha* Benth.), and others—rank among the most beautiful of all flowering trees, and many have been planted in the warmer regions of the United States (LHBH 1976; Menninger 1962, 1964; Neal 1965). Acacias produce many benefits: collectively they yield lumber, face veneer, furniture wood, fuelwood, and tannin; and such products as gum arabic, resins, medicine, fibers, perfumes, and dyes; some are useful for reclamation of sand dunes and mine spoils, and for shelterbelts, agroforestry hedgerows, and forage; and some serve as a host for the valuable lac insect (ACTI 1980; Prasad and Dhuria 1989; Turnbull 1986). They are valuable not only to the forest but also to pastures and agricultural crops for the nitrogen that is fixed in their root nodules (Hansen and others 1988).

Green wattle, introduced to Hawaii about 1890, has been declared noxious for state land leases (Haselwood and Motter 1966). A fast-growing tree of no local value, it spreads rapidly by seeds and root suckers, crowding out other plants. More than 90 years ago, Maiden (1908) commented on the pestiferous nature of several varieties of this species in Australia. Only acacia species that do not spread by suckering should be selected for planting. Also to be avoided under most circumstances are the thorny acacias—such as sweet acacia and gum arabic tree—which are widely dispersed rangeland pests. These 2 species are know to exert allelopathic effects on plants growing near them (Hampton and Singh 1979; Singh and Lakshminarayana 1992). Reliable seed data are available on 8 species (table 1), all of which grow naturally or are widely planted in the United States or associated territories.

Flowering and fruiting. Acacia flowers are perfect or polygamous; most of them are yellow, some are white. They usually appear in the spring or summer. The fruit is a 2-valved or indehiscent legume (pod) that opens in the late summer. The 1 or more kidney-shaped seeds (figure 1) that develop per fruit are usually released by the splitting of the legume. The seeds contain no endosperm (figure 2). Acacias begin bearing seeds between 2 to 4 years of age (Atchison 1948; Turnbull 1986). There are good seedcrops nearly every year and seed production can be quite high. Individual trees in a mangium plantation were reported to produce 1 kg (2.2 lbs) of seeds (about 100,000 seeds) annually (ACTI 1983). Seeding habits of 8 acacias are listed in table 2.

Collection, cleaning, and storage. Ripe acacia legumes are usually brown. They can be picked from the trees, or fallen legumes and seeds can be collected from underneath the trees. Collections from the ground may include legumes more than a year old. Seeds can be extracted by hammermilling, trampling, or placing the

Figure 1—*Acacia,* acacia: seeds (3 to 12 cm): *A. melanoxylon*, blackwood (**top**); *A. decurrens*, green wattle (**left**); *A. koa*, koa (**right**).

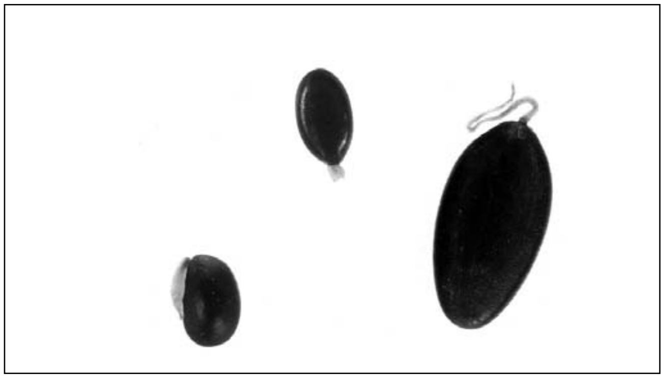
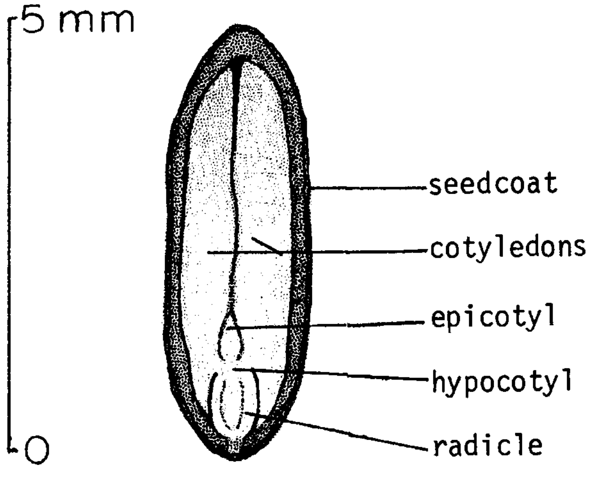


Table 1—*Acacia,* acacia: nomenclature, occurrence, and height

Scientific name & synonym(s)	Common names	Occurrence: Native	Occurrence: US	Height at maturity (m)
***A. auriculiformis* A. Cunningham ex Benth.**	**earleaf acacia**	Australia	Florida & Puerto Rico	12–30
***A. decurrens* Willd.** *A. decurrens* var. *normalis* Benth.	**green wattle**, black wattle, Sidney black wattle	Australia	California & Hawaii	8–18
***A. farnesiana* (L.) Willd.** *Vachellia farnesiana* (L.) Wright & Arn.	**sweet acacia**, *huisache*, aroma	France & Italy	S US, Puerto Rico, & Virgin Islands	3–5
***A. koa* Gray**	**koa**	Hawaii	Hawaii	24–34
***A. mangium* Willd.** *Mangium montanum* Rumph.	**mangium**	Indonesia, New Guinea, & Australia	Hawaii & Puerto Rico	12–30
***A. mearnsii* de Wildeman** *A. decurrens* var. *mollis* Lindl.	**black wattle,** green wattle, black wattle	Australia	California & Hawaii	15
***A. melanoxylon* R. Br. ex Ait. f.**	**blackwood,** Australian black wood, Tasmanian blackwood, black acacia, Sally wattle	Australia	California & Hawaii	24–36
***A. nilotica* (L.) Willd. ex Delile** *A. arabica* (Lam.) Willd. *Mimosa nilotica* L	**gum arabic tree,** Egyptian thorn, red heat	Asia & Africa	Puerto Rico & Virgin Islands	3–20

Source: Anderson (1968), Barrett (1958), Fagg (1992), Munoz (1959), Parrotta (1992), Turnbull (1987), Whitesell (1974).

Figure 2—*Acacia melanoxylon*, blackwood: longitudinal section through a seed.



legumes in a cloth bag and flailing it against the floor. Seeds are sometimes separated by feeding the legumes to cattle and collecting the seeds from the manure (NFTA 1992). Blowers and shakers will remove legume fragments and debris satisfactorily for most species. The weights of cleaned seeds for 8 species are listed in table 3 (Goor and Barney 1968; Letourneux 1957; Mangini and Tulstrup 1955; Salazar 1989; Turnbull 1986; Whitesell 1964, 1974). Seeds of blackwood collected and cleaned in Uruguay had a purity of 93% (Whitesell 1974).

Acacia seeds are among the most durable of forest seeds and need not be kept in sealed containers, although it is still advisable to do so. If kept in a cool, dry place, the seeds of most acacia species will germinate after many years of storage. For example, 63% of green wattle seeds germinated after 17 years in storage (Atchinson 1948). Seeds of blackwood, which were air-dried to a constant weight and then stored in sealed containers, retained viability unimpaired for at least 3 months; seeds stored in the open still retained 12% viability after 51 years (Whitesell 1974). Koa seeds lying on the ground are known to have retained their ability to germinate for as long as 25 years (Judd 1920).

Pre-germination treatments. The seeds of most species have hard coats that cause poor germination unless they are first scarified by briefly treating them with sulfuric acid or soaking in hot water (Gunn 1990; Kumar and Purkayastha 1972; Natarajan and Rai 1988; Rana and Nautiyal 1989). Hot water treatment is the most practical. The seeds are placed in hot or boiling water, the source of heat removed, and the seeds allowed to soak for 3 minutes to 24 hours (Clemens and others 1977). Blackwood seeds subjected to 90 to 100 °C water for 3 minutes and than stratified at 4 °C for 4 to 6 weeks germinated at a rate of

Table 2— *Acacia,* acacia: phenology of flowering, fruit ripening, and seed dispersal

Species	Location	Flowering	Fruit ripening	Dispersal
A. auriculiformis	Florida	Mar–Apr	Jun–Jul	Aug–Dec
A. decurrens	California	Feb–Mar		
A. farnesiana	Puerto Rico	Nov–Feb	Mar–Sep	Mar–Dec
A. koa	Hawaii	Jan–Jul	Jun-Jul	Feb; Jun–Nov
A. mangium	Puerto Rico	Mar–Apr		May–Aug
A. mearnsii	California	Jun & later	Jun–Oct	Jun–Oct
A. melanoxylon	California	Feb–Jun	Jul–Nov	Jul–Dec or later
	Hawaii	May–Jun		
A. nilotica	Puerto Rico	Almost continuously	All year	All year

Sources: Parrotta (1992), Turnbull (1986), Whitesell (1974).

Table 3—*Acacia,* acacia: legume (pod) and seed data

	Legume size (cm)		Cleaned seeds/wt	
Species	**Length**	**Width**	**/kg**	**/lb**
A. auriculiformis	5–10	1.3	30,000–158,000	14,000–72,000
A. decurrens	10	—	53,000–88,000	26,000–40,000
A. farnesiana	4–7	2.0	7,600–13,000	3,000–6,000
A. koa	3–6	1.5–2.5	5,300–16,300	2,000–7,000
A. mangium	3–12	1.3	80,000–110,000	36,000–50,000
A. mearnsii	5–8	—	33,000–74,000	15,000–34,000
A. melanoxylon	4–13	1.0	44,000–88,000	20,000–40,000
A. nilotica	5–15	0.8–1.6	5,000–16,000	2,000–7,000

Sources: ACTI (1983), Fagg (1992), Goor (1968), Letourneux (1957), Magini and Tulstrup (1955), NFTA (1987a,b), Salazar (1989), Turnbull (1986), Whitesell (1974).

over 98% and grew 25% faster than control seedlings in the first 3 months (De Zwaan 1978). Some species also appear to require 2 to 4 months of "after-ripening" in dry storage before good germination may be obtained (Whitesell 1974). Germination is epigeal.

Germination testing. Prescriptions for official testing for acacias call for clipping, nicking, or filing through the seedcoats and soaking in water for 3 hours, or soaking seeds in concentrated sulfuric acid for 1 hour, then rinsing thoroughly (ISTA 1993). Germination should then be tested on moist blotter paper at alternating 20/30 °C or constant 20 °C for 21 days. Germination tests of acacias can also be made in flats with sand or soil. Results of tests for 8 species of acacias are given in table 4**.**

Nursery and field practice. After proper pretreatment, the small-seeded acacias should be covered with 6 to 12 mm (1/4 to 1/2 in) of soil. Optimum sowing depth for sweet acacia seeds was found to be 2 cm (3/4 in) (Scifres 1974). A 2:1 mixture of soil and sand proved to be a better germination medium for gum arabic tree than other mixtures of soil, sand, and manure (Bahuguna and Pyare 1990). The use of sawdust in germination mixtures was found to inhibit the germination of mangium (Newman 1989b). Sowing is done in spring in the warm temperate zone of the United States mainland and year-round in tropical areas, except during dry periods. Earleaf acacia can be grown from cuttings treated with indole acetic acid (IAA) with a high degree of success (Huang 1989). Seedlings of mangium and earleaf acacia inoculated with Bradyrhizobium and Rhizobium bacterial strains nodulated, but only the Bradyrhizobium strains fixed nitrogen (Galiana and others 1990). Blackwood is preferably outplanted as small 1.25-cm ($^{6}/_{10}$-in) stumps lifted from a seedbed 1 year after planting (Parry 1956) or as transplanted seedling 20 to 25 cm (7.8 to 9.8 in) high (Streets 1962). The best survival for koa planted in Hawaii is obtained with potted seedlings. Mangium is usually planted as potted (plastic nursery bags, or polybags) seedlings but may be planted bareroot (Webb and others 1984). Container seedlings 20 cm (7.8 in) high were recommended for earleaf acacia (Wiersum and Ramlan 1982).

Table 4—*Acacia,* accacia: pregermination treatments, germination test conditions, and results

			Germination test conditions			
Species	**Seed source**	**Pretreatment**	**Medium**	**Temp (°C)**	**Duration (days)**	**Germination (%)**
A. auriculiformis	Puerto Rico	None	Soil	—	21	56
	Puerto Rico	Hot water	Soil	—	14	30
	Java	Warm water	Soil	—	85	—
A. decurrens	—	—	—	—	—	74
A. farnesiana	Puerto Rico	Abrasion	Paper	79	30	56
A. koa	Hawaii	Hot water	Soil	—	30	18
A. mangium	Australia	Hot water	—	—	10	80
A. mearnsii	—	—	Soil	60	14	72
A. melanoxylon	Tasmania	Hot water	Paper	77	60	70
	Tasmania	Hot water	Paper	77	30	74
	Victoria	Hot water	Paper	77	90	93
	Uruguay	None	—	—	30	4
	Uruguay	H_2SO_4	—	68	21	48
	Uruguay	Abrasion	—	68	28	26
	—	—	Soil	—	15	52
A. nilotica	—	Hot water	—	75	85	—
	—	Hot water	Soil	—	30	74

Sources: ACTI (1983), Francis and Rodriguez (1993), Newman (1989a), Parrotta (1992), Webb and others (1984), (1986), Whitesell (1974).

Plantable seedlings of gum arabic tree were produced in India by planting pretreated seeds in May in polybags containing a nursery mixture in full sun and fertilizing them twice (Kumar and Gupta 1990). The use of straw mulch increased the emergence of direct-seeded sweet acacia in old fields (Vora and others 1988).

References

ACTI [Advisory Committee on Technology Innovation]. 1980. Firewood crops, shrub and tree species for energy production. Washington, DC: National Academy of Sciences. 236 p.

ACTI [Advisory Committee on Technology Innovation]. 1983. Mangium and other fast-growing acacias for the humid tropics. Washington, DC: National Academy of Sciences. 62 p.

Anderson RH. 1968. The trees of New South Wales, 4th ed. Sydney, Australia: Department of Agriculture. 510 p.

Atchison E. 1948. Studies on the Leguminosae: 2. Cytogeography of *Acacia* (Tourn.). American Journal of Botany 35(10): 651–655.

Bahuguna VK, Pyare L. 1990. To study the effects of environment and different soil mixture on germination of *Acacia nilotica* seed at nursery stage. Journal of Tropical Forestry 5(1): 51–56.

Barrett MF. 1956. Common exotic trees of south Florida (Dictyledons). Gainesville: University of Florida Press. 414 p.

Clemens J, Jones PG, Gilbert NH. 1977. Effect of seed treatments on germination of *Acacia*. Australian Journal of Botany 25(3): 269–276.

De Zwaan JG. 1978. The effects of hot-water-treatment and scarification on germination of blackwood (*Acacia melanoxylon*) seed. South African Forestry Journal 105: 40–42.

Fagg CW. 1992. *Acacia nilotica*: pioneer for dry lands. NFTA 92-04. Paia, HI: Nitrogen Fixing Tree Association. 2 p.

Francis JK, Rodríguez, A. 1993. Seeds of Puerto Rican trees and shrubs: second installment, Res. Note SO-374. New Orleans: USDA Forest Service, Southern Forest Research Station. 5 p.

Galiana A, Chaumont J, Diem HG, Dommergues 1990. Nitrogen-fixing potential of *Acacia mangium* and *Acacia auriculiformis* seedlings inoculated with *Bradyrhizobium* and *Rhizobium* spp. Biology and Fertility of Soils 68(4): 263–272.

Goor AY, Barney CW. 1968. Forest tree planting in arid zones. New York: Ronald Press. 498 p.

Guinet P, Vassal J. 1978. Hypothesis on the differentiation of the major groups in the genus *Acacia* (Leguminosae). Kew Bulletin 32(3): 509–527.

Gunn BV. 1990. Germination pretreatments for selected acacia species from the Pilbara region of Western Australia. ACIAR Proceedings Series (Australia) 28: 46–50.

Hampton CO, Singh SP. 1979. The presence of growth and germination inhibitors in the seeds of certain desert plants. Transactions of the Kansas Academy of Science 82(2): 87.

Hansen AP, Stoneman G, Bell DT. 1988. Potential inputs of nitrogen by seeder legumes to the Jarrah forest ecosystem. Australian Forestry 51(4): 226–231.

Haselwood EL, Motter GG, eds. 1966. Handbook of Hawaiian woods. Honolulu: Hawaiian Sugar Planters' Association. 479 p.

Huang LS. 1989. Study on the introduction and cultural techniques of *Acacia auriculiformis*. Forest Science and Technology (China) 5: 10–11.

ISTA [International Seed Testing Association]. 1993. Rules for testing seeds: rules 1993. Seed Science and Technology 21 (Suppl.): 1–259.

Judd CS. 1920. The koa tree. Hawaiian Forestry and Agriculture 17(2): 30–35.

Kumar A, Gupta BB. 1990. Production of field plantable seedlings of *Acacia nilotica* in fifty days. Indian Forester 116(4): 306–322.

Kumar P, Purkayastha BK. 1972. Note on germination of the seeds of lac hosts. Indian Journal of Agricultural Sciences 42(5): 430–431.

Letourneux C. 1957. Tree planting practices in tropical Asia. For. Dev. Pap. 11. Rome: FAO: 109–111.

LHBH [Liberty Hyde Bailey Hortorium]. 1976. Hortus third: a concise dictionary of plants cultivated in the United States and Canada. New York: Macmillan: 4–7.

Mangini E, Tulstrup NP. 1955. Tree seed notes. For. Dev. Pap. 5. Rome: FAO. 354 p.

Maiden JH. 1908. The forest flora of New South Wales. Volume 3. Sydney, Australia: W.A. Gullick, Government Printer. 180 p.

Menninger EA. 1962. Flowering trees of the world. New York: Hearthside Press. 336 p.

Menninger EA. 1964. Seaside plants of the world. New York: Hearthside Press. 303 p.

Munz PA. 1959. A California flora. Berkeley: University of California Press. 1861 p.

Natarajan N, Rai RSV. 1988. Studies to maximization of germination in *Acacia auriculiformis*. Indian Journal of Forestry 11(4): 304–306.

Neal MC. 1965. In gardens of Hawaii. Spec. Pub. 50. Honolulu: Bishop Museum Press. 924 p.

Newman V. 1989a. Effects of pretreatments on germination of *Acacia mangium* (Willd.) in Sabah. FRC publication 3/89. Sandakan, Sabah: Forest Research Centre. 21 p.

Newman V. 1989b. Results of media trials using sawdust on germination of *Acacia mangium* (Willd.) FRC Publication 53. Sandakan, Sabah: Forest Research Centre. 17 p.

NFTA [Nitrogen Fixing Tree Association]. 1987. *Acacia auriculiformis*: the adaptable tropical wattle. NFTA 87-03. Waimanalo, HI: NFTA. 2 p.

NFTA [Nitrogen Fixing Tree Association]. 1987. *Acacia mangium*: a fast-growing tree for the humid tropics. NFTA 87-04. Waimanalo, HI: NFTA. 2 p.

NFTA [Nitrogen Fixing Tree Association]. 1992. *Acacia nilotica*: pioneer for dry lands. NFTA 92-04. Waimanalo, HI: NFTA. 2 p.

Parrotta JA. 1992. *Acacia farnesiana* (L.) Willd., aroma, huisache. Res. Note SO-ITF-SM-49. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 6 p.

Parrotta JA. 1994. Personal communication. Río Piedras, PR: USDA Forest Service, International Institute of Tropical Forestry.

Parry MS. 1956. Tree planting practices in tropical Africa. FAO For. Dev. Pap. 8. Rome: FAO. 302 p.

Prasad R, Dhuria SS. 1989. Reclamation of iron-ore mined-out areas: biomass production efficiency of species. Journal of Tropical Forestry 5(1): 51–56.

Rana U, Nautiyal AR. 1989. Coat imposed dormancy of *Acacia farnesiana* seeds. Seed Research 17(2): 122–127.

Salazar R. 1989. Genetic variation of 16 provenances of *Acacia mangium* at nursery level in Turrialba, Costa Rica. Commonwealth Forestry Review 68(4): 263–272.

Scifres DJ. 1974. Salient aspects of huisache seed germination. Southwestern Naturalist 18(4): 383–392.

Singh J, Lakshminarayana K. 1992. Effect of allelopathic rhizobium of *Acacia nilotica* on *Azotobacter chrococcum* and *Rhizobium* cowpea. In: Tauro P, Narwal SS, eds. Allelopathy in agroecosystems. Hisar, India: Haryana Agricultural University. 146 p.

Streets RJ. 1962. Exotic trees in the British Commonwealth. Oxford: Clarendon Press. 765 p.

Turnbull JW. 1986. Multipurpose Australian trees and shrubs. Canberra, Australia: Australian Centre for International Agriculture Research. 316 p.

Turnbull JW. 1987. *Acacia auriculiformis*: the adaptable tropical wattle. NFTA Highlights 87-03. Waimanalo, HI: Nitrogen Fixing Tree Association. 2 p.

Vora, RS, Schumacher RW, Labus Z. 1988. Planting seeds of four South Texas native species under mulch cover. Texas Journal of Science 40(2): 122–127.

Webb DB, Wood PJ, Smith JP, Henman GS. 1984. A guide to species selection for tropical and subtropical plantations. Trop. For. Pap. 15. Oxford: Commonwealth Forestry Institute. 256 p.

Whitesell CD. 1964. Silvical characteristics of koa (*Acacia koa* Gray). Res. Pap. PSW-16. Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. 12 p.

Whitesell CD. 1974. *Acacia*, acacia. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 184–186.

Wiersum KF, Ramlan A. 1982. Cultivation of *Acacia auriculiformis* on Java, Indonesia. Commonwealth Forestry Review 61(2): 135–144.

Aceraceae—Maple family

Acer L.

maple

John C. Zasada and Terry F. Strong

Dr. Zasada retired from the USDA Forest Service's North Central Research Station; Mr. Strong is a research silviculturalist at the USDA Forest Service's North Central Research Station, Rhinelander, Wisconsin

Growth habit, occurrence, and use. Maples—members of the genus *Acer*—are deciduous (rarely evergreen) trees; there are 148 species (de Jong 1976; Van Gelderen and others 1994). The majority of species originate in central and eastern Asia, China, and Japan (de Jong 1976; Van Gelderen and others 1994; Vertrees 1987). There are several taxonomic treatments available for the genus. Vertrees (1987) and Van Gelderen and others (1994) should be consulted for a discussion and comparison of the different classifications. Van Gelderen and others (1994) recognize 16 sections, some of which are further divided into 2 to 3 series. The publications by De Jong (1976), Van Gelderen and others (1994), and Vertrees (1987) are filled with interesting information and are wonderful reference books for the genus *Acer*.

Based on the classification of Van Gelderen and others (1994), there are 9 species in the United States and Canada (tables 1 and 2). In addition, there are 8 taxa closely related to sugar maple—these include black maple, Florida maple, bigtooth maple, and whitebark maple—as well as a number of subspecies for others. Van Gelderen and others (1994)

Table 1—*Acer,* maple: nomenclature, occurrence, and uses

Scientific name & synonym(s)	Common name(s)	Occurrence
A. circinatum **Pursh**	**vine maple,** mountain maple	SW British Columbia to N California E side of Cascades W to Pacific Coast
A. ginnala **Maxim.**	**Amur maple,** Siberian maple	NE Asia; introduced to N & central Great Plains
A. glabrum **var.** ***glabrum*** **Torr.**	**Rocky Mountain maple,** dwarf maple, mountain maple	SE Alaska, S to S California, E to S New Mexico, N to Black Hills, South Dakota
A. grandidentatum **Nutt.**	**bigtooth maple**, sugar maple	SE Idaho, S to SE Arizona, E to S New Mexico & northern Mexico, N to W Wyoming
A. griseum **(Franch.) Pax**	**paperbark maple**	Central China & Japan
A. macrophyllum **Pursh**	**bigleaf maple,** broadleaf maple, Oregon maple	Pacific Coast from W British Columbia S to S California
A. negundo **L.** *Negundo aceroides* (L.) Moench.	**boxelder,** ashleaf maple, California boxelder	Throughout most of US & prairie provinces of Canada*
A. palmatum **Thunb.**	**Japanese maple**	Japan, China, & Korea
A. pensylvanicum **L.** *A. striatum* DuRoi.	**striped maple,** moosewood	Nova Scotia, W to Michigan S to Ohio, E to S New England, mtns of N Georgia
A. platanoides **L.**	**Norway maple**	Europe & the Caucasus; introduced to central & E US
A. pseudoplatanus **L.**	**planetree maple,** sycamore maple	Europe & W Asia; introduced to central & E US
A. rubrum **L.** *A. carolinianum* Walt.	**red maple,** soft maple, swamp maple	Throughout E US & southern Canada from SE Manitoba & E Texas to Atlantic Coast
A. saccharinum **L.** *A. dasycarpum* Ehrh.	**silver maple,** river maple, soft maple	New Brunswick, S to NE Florida NW to E Oklahoma, N to central Minnesota
A. saccharum **Marsh.** *A. saccharophorum* K. Koch	**sugar maple,** rock maple, hard maple	New Brunswick, S to central Georgia, W to E Texas, N to SE Manitoba
A. spicatum **Lam.**	**mountain maple**	Newfoundland, S to New Jersey, W to Iowa, N to Saskatchewan, S in Appalachian Mtns to N Georgia

Sources: De Jong (1976), Dirr (1990), Fischer (1990), Olson and Gabriel (1974), Rehder (1940), Van Gelderen and others (1994), Vertrees (1987), Viereck and Little (1972).

* Introduced into subarctic interior Alaska, where it forms a small tree and produces viable seeds (Viereck 1996).

Table 2—*Acer,* maple: height, seed-bearing age, and seedcrop frequency

Species	Height (m) at maturity	Year first cultivated	Minimum seed-bearing age (yrs)	Years between large seedcrops
A. circinatum	9	1826	—	1–2
A. ginnala	6	1860	5	1
A. glabrum var. *glabrum*	9	1882	—	1–3
A. griseum	8	1901	—	—
A. macrophyllum	35	1812	10	1
A. negundo	23	1688	—	1
A. palmatum	6	1820	—	—
A. pensylvanicum	11	1755	—	—
A. platanoides	31	Long ago	—	1
A. pseudoplatanus	31	Long ago	—	1
A. rubrum	28	1656	4	1
A. saccharinum	28	1725	11	1
A. saccharum	31	Long ago	22	3–7
A. spicatum	9	1750	—	—

Sources: Burns and Honkala (1990), Dirr (1990), De Jong (1976), Olson and Gabriel (1974), Vertrees (1987).
Note: *A. rubrum, A. negundo, A. pensylvanicum,* and *A. saccharinum* are dioecious to varying degrees. The other species are monoecious, but male and female flowers may occur in different parts of the tree.

actually classify the 4 species mentioned above as subspecies of sugar maple. Eight of the 16 sections of the genus are represented in North America (Van Gelderen 1994). Additionally, a number of species (table 1) have been introduced for use as ornamentals (Burns and Honkala 1990; Dirr 1990; Dirr and Heuser 1987; Fischer 1990; Van Gelderen and others 1994; Vertrees 1987). The native species range in size from trees that dominate forest canopies to medium to tall understory shrubs or small trees (table 2). Boxelder has been introduced into Alaska, where it survives and reproduces; however, it does dieback periodically under extreme winter temperatures (Viereck 1997).

The native maples all regenerate vegetatively by basal sprouting, but the ability to do so varies among species and with plant age (Burns and Honkala 1990; Fischer 1990). Vine, Rocky Mountain, striped, and mountain maples frequently layer, giving them the potential to develop relatively complex clones of varying size and morphology (Hibbs and Fischer 1979; O'Dea and others 1995; Post 1969; Zasada and others 1992).

Some species of maple are important sources of firewood, pulpwood, high-quality lumber, and veneer (Alden 1995; Burns and Honkala 1990). Four species have been used to produce maple sugar and syrup—sugar, black, red (Jones 1832; USDA FS 1982), and bigleaf maple. Sugar maple is the most important of these species because it has the highest sugar content. In the western United States, bigleaf maple produces adequate quantities of sap, but its sugar content is low compared to the sap of sugar and red maples, and the flow is erratic (Burns and Honkala 1990).

Maples are very important for wildlife, providing browse and cover for a variety of mammals, important sites for cavity-nesting birds, and food for seed-eating mammals and birds (Burns and Honkala 1990). Maples are also important substrates for various lichens and mosses. Their occurrence on mountain slopes makes them useful in the protection of watersheds. Boxelder is an important species for shelterbelt planting.

Many of the maples have ornamental value because of their attractive foliage or interesting crown shape, flowers, or fruit; native and introduced maple varieties with desirable features such as a particular foliage color or attractive bark have been propagated specifically for ornamental use (Dirr 1990). For an interesting discussion of variation in form and leaf morphology in Japanese maples, see the wonderfully written and illustrated book by Vertrees (1987).

Flowering and fruiting. There is substantial variation within the genus in terms of gender of trees. Some species—for example sugar, black, and bigleaf maples—are monoecious with flowers that appear perfect but are functionally either male or female. In the monoecious species, the functionally male and female flowers often occur in different parts of the crown (Burns and Honkala 1990; De Jong 1976).

Other species—for example boxelder and red, striped, silver, and bigtooth maples—are primarily dioecious, but some individual trees are monoecious to varying degrees. In natural populations of red maple, the sex ratio tends to be male-biased. The ratio may vary somewhat between geographic areas within the species range. Sex ratio was also found to be highly skewed to males in red maples just beginning to flower. Change of sexual expression does occur in these dioecious species but only in a small percentage of the population. Variation in sex expression was related to site conditions in boxelder (Freeman and others 1976), but the relationship of gender to site has not been well-established for all species. There do not appear to be consistent differences in growth rate between males and females. Sakai and Oden (1983) reported that monoecious silver maples were larger than dioecious trees and exhibited a different size distribution pattern. Male boxelder trees showed no growth advantage over females despite the increased amount of carbon needed for fruit production (Willson 1986). However, it was observed that female trees that were previously male had a higher mortality rate than trees that were consistently male or trees that were previously female (Barker and others 1982; De Jong 1976; Hibbs and Fischer 1979; Primack and McCall 1986; Sakai 1990b; Sakai and Oden 1983; Townsend and others 1982).

Flowering and pollination occur in spring and early summer (table 3). Dichogamy (male and female parts in the same flower or different flowers on the same tree mature at different times) is common in maples and has been described for sugar maple and other species (De Jong 1976; Gabriel 1968). Insect and wind pollination both occur, but the relative importance of each differs among species (De Jong 1976; Gabriel 1968; Gabriel and Garrett 1984).

The fruit is composed of 2 fused samaras (a term used interchangeably with seeds here), which eventually separate on shedding, leaving a small, persistent pedicel on the tree. The fused samaras may be roughly identical in appearance or differ in physical size; both samaras may or may not contain viable embryos (Abbott 1974; Greene and Johnson 1992). Parthenocarpic development occurs but differs in the strength of expression among species; this phenomena may explain size differences in paired samaras (De Jong 1976). Samara pairs may occur singly or in clusters of 10 or more. The fruits of the maples vary widely in shape, length of wings, and angle of divergence of the fused samaras (figure 1) (Carl and Snow 1971; De Jong 1976; Greene and

Figure 1—*Acer*, maple: samaras of *A. platanoides*, Norway maple (**top left**); *A. circinatum*, vine maple (**top right**); *A. saccharum*, sugar maple (**second row left**); *A. grandidentatum*, bigtooth maple (**second row center**); *A. spicatum*, mountain maple (**second row right**); *A. saccharinum*, silver maple (**third row left**); *A. macrophyllum*, bigleaf maple (**third row center**); *A. negundo*, boxelder, (**third row right**); *A. glabrum* var. *glabrum*, Rocky Mountain maple (**bottom left**); *A. rubrum*, red maple (**bottom center**); *A. pensylvanicum* (**bottom right**).

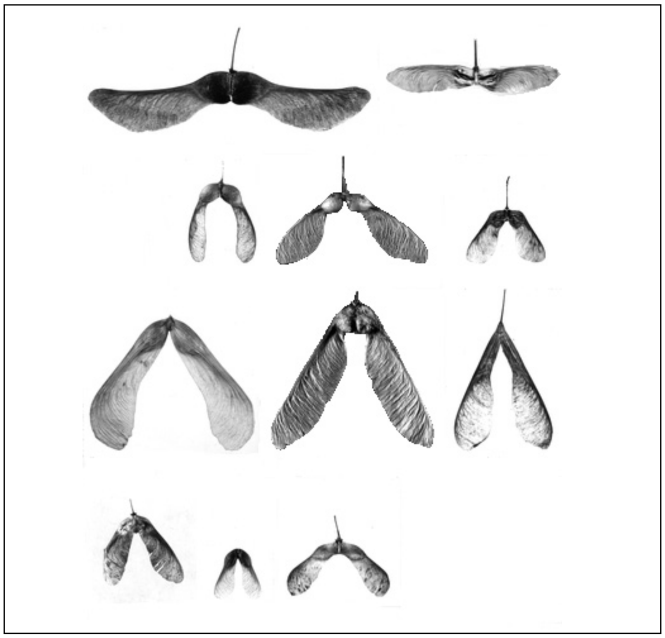


Table 3—*Acer,* maple: phenology of flowering and fruiting

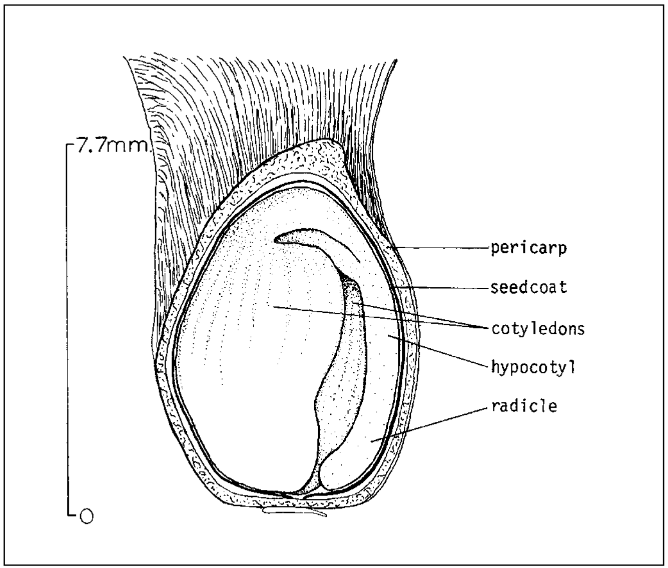
Species	Flowering	Fruit ripening	Seed dispersal
A. circinatum	Mar–June	Sept–Oct	Oct–Nov
A. ginnala	Apr–June	Aug–Sept	Sept–Jan
A. glabrum var. *glabrum*	Apr–June	Aug–Oct	Sept–Feb
A. macrophyllum	Apr–May	Sept–Oct	Oct–Mar
A. negundo	Mar–May	Aug–Oct	Sept–Mar
A. palmatum	May–June	Aug–Sept	Sept–Oct
A. pensylvanicum	May–June	Sept–Oct	Oct–Feb
A. platanoides	Apr–June	Sept–Oct	Oct–Nov
A. pseudoplatanus	Apr–June	Aug–Oct	Sept–Nov
A. rubrum	Mar–May	Apr–June	Apr–July
A. saccharinum	Feb–May	Apr–June	Apr–June
A. saccharum	Mar–May	Sept–Oct	Oct–Dec
A. spicatum	May–June	Sept–Oct	Oct–Dec

Sources: Dirr (1990), Burns and Honkala (1990), Olson and Gabriel (1974).

Johnson 1992; Sipe and Linnerooth 1995). Each filled samara typically contains a single seed without endosperm (figure 2). However, polyembryony has been observed in sugar and bigleaf maples (Carl and Yawney 1972; Zasada 1996). Maple seeds turn from green or rose to yellowish or reddish brown when ripe; the color of mature samaras can vary among species. Pericarps have a dry, wrinkled appearance when fully mature (Al'benskii and Nikitin 1956; Anon. 1960; Carl and Snow 1971; Harris 1976; Rehder 1940; Sargent 1965; Vertrees 1987).

The embryo with associated seedcoats is contained within the pericarp (figure 2). The surface of the pericarp is usually glabrous (except that of bigleaf maple, which has dense, reddish brown pubescence). The pericarp can be extremely hard (particularly when it has dried out) and difficult to cut open. Development of the samara in black maple has been described in detail by Peck and Lersten (1991). Both the pericarp and seedcoat have been identified as causes of dormancy. The cavity (locule) in which the embryo occurs may have concave or convex walls. There are 2 types of embryo folding: (a) incumbent folding, in which the hypocotyl is against the back of one cotyledon, and (b) accumbent folding, in which the hypocotyl is against the edges of the folded cotyledons. Of the native maples, vine and sugar maples are classified as incumbent and the others (except bigtooth maple, which was not classified) are accumbent. The cotyledons may be green while still in the pericarp (Carl and Yawney 1972; De Jong 1976; Dirr and Heuser 1987; Olson and Gabriel 1974; Peck and Lersten 1991; Vertrees 1987).

Figure 2—*Acer circinatum*, vine maple: longitudinal section of a seed showing bent embryo. On drying the seed shrinks, leaving space between the seedcoat and the pericarp.



During the maturation process, the pericarp and wing change color as seed biochemistry, anatomy, and moisture content change (Carl and Yawney 1966; Peck and Lersten 1991; Vertrees 1987). Both anatomical and physiological studies indicate that green samaras photosynthesize, thus contributing to the carbon balance and growth of the fruit (Bazzaz and others 1979; Peck and Lersten 1991).

The native species can be divided into 2 groups based on timing of seed dispersal (table 3) (Burns and Honkala 1990). Silver and red maples release samaras in late spring and early summer, whereas the other species disperse theirs in late summer and fall. The summer-dispersing species appear to release seeds over a period of about 1 month (Bjorkbom 1979). The fall-dispersing species release samaras in a more protracted manner, usually over 2 months or more (Bjorkbom 1979; Garrett and Graber 1995; Graber and Leak 1992). In sugar maples, seedfall has been observed in every month of the year, but seeds dispersed during the summer months are usually empty (Garrett and Graber 1995). Bigleaf maples in western Oregon and Washington may retain seeds through March.

The mechanics of samara flight following release from the tree have been studied in considerable detail (Green 1980; Greene and Johnson 1990, 1992; Guries and Nordheim 1984; Matlack 1987; McCutchen 1977; Norberg 1973; Peroni 1994; Sipe and Linnerooth 1995). The remainder of this paragraph briefly summarizes the main points of these papers. Maple seeds spin when they fall. There are 2 components to flight—the initial free-fall before spinning and the spinning itself. Depending on species, the initial phase covers a distance of 0.4 to 0.8 m. The terminal velocity attained during spinning varies from 0.8 to 1.3 m/sec and is related to the size of the seeds. Within an individual species, descent rate of individual samaras varied from 0.6 to 1.7 m/sec, depending on seed size and shape. These are the main factors determining how far seeds will fly during primary dispersal under different wind conditions. In relatively strong winds, the free-fall phase may not occur. Wind conditions for early summer dispersal of red and silver maples may differ substantially from those of fall dispersal of seeds because the fully developed canopy can affect within-stand wind conditions. Secondary dispersal after flying may occur over a fairly long distance if seeds fall into moving water or a short distance if seeds are cached by rodents or moved by rainwater or snowmelt.

The maximum dispersal distance for maple seeds is reported to be at least 100 m under open conditions as might occur in a large gap or clearcut (Burns and Honkala 1990). Dispersal distance and patterns of seed rain will vary within stands due to tree distribution and stand microclimate. For example, seed rain around an individual red maple within a hemlock–hardwood forest dropped from 340 seeds/m^2 (range, 200 to 450/m^2) at the base of the tree to about 50/m^2 (range, 0 to 100/m^2) at 10 m from the base (Ferrari 1993). The large variation in seed rain at each distance indicates that microclimate, location of seeds within the tree crown, and other factors create a relatively heterogeneous pattern of seed deposition.

The weight of maple seeds varies substantially among species (table 4) (Green 1980; Guries and Nordheim 1984). Some examples of within-species variation in seed weight are given below. The average dry weight of sugar maple seeds varied from 0.09 to 0.03 g in a collection from across the eastern United States; the heaviest seeds were from New England area and the lightest from the southern part of the range (Gabriel 1978). In the central Oregon coastal range, the dry weight of bigleaf maple samaras varied from 0.25 to 0.65 g; embryo dry weight accounted for 30 to 40% of total samara weight (Zasada 1996). Sipe and Linnerooth (1995) found that average weight of silver maple seeds varied from 0.10 to 0.16 g. Peroni (1994) found that the dry weight of red maple samaras from 10 North Carolina seed sources varied from 0.013 to 0.016 g. Townsend (1972) reported a 2- to 3-fold variation in red maple fruit weight for seeds collected throughout the species' range.

Seed production can vary significantly among years for a single stand or between stands in a given year in quantity, quality, biomass, and seed weight as a percentage of total litterfall (Bjorkbom 1979; Bjorkbom and others 1979; Burns and Honkala 1990; Chandler 1938; Curtis 1959; Garrett and Graber 1995; Godman and Mattson 1976; Graber and Leak 1992; Grisez 1975; Pregitzer and Burton 1991; Sakai 1990). Although separated geographically and conducted in stands differing in composition, seed production studies over 11 to 12 years in Wisconsin and New Hampshire reported similar results. In Wisconsin, the quantity of sugar maple seedfall in a pure stand of sugar maple varied from 0.1 to 13 million seeds/ha and percentage of filled seeds from 3 to 50% during a 12-year period. Seed production exceeded 2.5 million seeds/ha in 5 of 12 years (Curtis 1959). In a mixed hardwood stand in New Hampshire in which sugar maple made up 69% of the basal area, production varied from 0.2 to 11.9 million seeds/ha; viability was generally related to size of the seed crop and ranged from 0 to 48%. Seed production exceeded 2.5 million seeds/ha in 6 of 11 years (Graber and Leak 1992). In northern Wisconsin, good or better seed years occurred every other year in red maples over a 21-year period and every third year for sugar maples over a 26-year period (Godman and Mattson 1976). In a gradient study of sugar maple stands from southern Michigan to the Upper Peninsula, production of reproductive litter (seeds and flower parts) varied by a factor of 2 and 4 for 2 seed years. The southern stands were more productive one year, whereas the northern stands were more productive the other year (Pregitzer and Burton 1991). Flower and seedcrops in red and sugar maples were related and the former could be used to predict seedcrops (Bjorkbom 1979; Grisez 1975). Fertilization has been shown to alter seed production in maples (Bjorkbom 1979; Chandler 1938). Long and others (1997) reported that liming affected seedcrop size but not periodicity in sugar maple in Allegheny hardwood forests. They also reported that good sugar maple seedcrops occurred the year after a June–July period with a relatively severe drought index (that is, when plants were subjected to a high level of moisture stress).

Table 4—*Acer,* maple: seed yield data

	Cleaned seeds/weight			
	Range		Average	
Species	**/kg**	**/lb**	**/kg**	**/lb**
A. circinatum	7,710–12,220	3,490–5,530	10,210	4,620
A. ginnala	22,980–44,640	10,400–20,200	37,570	17,000
A. glabrum var. *glabrum*	17,280–44,860	7,820–20,300	29,680	13,430
A. macrophyllum	5,970–8,840	2,700–4,000	7,180	3,250
A. negundo	18,120–45,080	8,200–20,400	29,610	13,400
A. pensylvanicum	21,430–34,400	9,700–15,600	24,530	11,100
A. platanoides	2,810–10,300	1,270–4,660	6,320	2,860
A. pseudoplatanus	6,480–15,910	2,930–7,200	11,290	5,110
A. rubrum	28,070–84,420	12,700–38,200	50,520	22,860
A. saccharinum	1,990–7,070	900–3,200	3,930	1,780
A. saccharum	7,070–20,110	3,200–9,100	15,540	7,030
A. spicatum	33,810–60,330	15,300–27,800	48,910	22,130

Source: Olson and Gabriel (1974).

Most studies of seed production are conducted in pure stands or those with a majority of the stems of the desired species. However the availability of seeds when species make up only a minor component of the stand is of interest when estimating seeds available for further colonization. An example of this is provided for a New Hampshire sugar maple–yellow birch–beech stand (Graber and Leak 1992). In this study covering 11 years, the total production of red and striped maples, both minor components, was 0.6 (0% viability) and 0.5 million seeds/ha (40% viability), respectively (Graber and Leak 1992). Seed quality of species present in low number may be limited by pollination. Ferrari (1993) provided information on production and dispersal of seeds from an isolated red maple in a hemlock–hardwood forest in upper Michigan.

Abbott (1974) and Grisez (1975) found that seed production in red and sugar maples was related to dbh. The following listing provides some indication of this relationship for red maple (Abbott 1974):

Tree dbh (cm)	Seeds/tree (thousands)
5	11.9
12	54.3
20	91.4
31	955.8

Reductions in the potential seedcrop can result from biotic and abiotic factors. The strong summer winds and rain associated with thunderstorms in the northern hardwood forests often litter the forest floor with immature seeds and flower parts. Post-zygotic abortion occurring soon after fertilization was the primary cause of empty seeds; in addition, insects affected the quality of more than 10% of seedfall (Graber and Leak 1992). Furuta (1990) found that aphid infestations had an adverse effect on seed production in the Japanese maple *A. palmatum* subsp. *amoenum* (Carr.) H. Hara. Carl and Snow (1971) suggest that heavy aphid infestations affect seed production in sugar maple. Experimental defoliation reduced seed production in striped maples during the year of defoliation but not in the following year (Marquis 1988). Once seeds have been dispersed, seed predation by small mammals can greatly reduce the seed pool before germination (Fried and others 1988; Graber and Leak 1992; Myster and Pickett 1993; Tappeiner and Zasada 1993; Von Althen 1974).

Collection of fruits. Minimum seed-bearing age differs among species. Intervals between mast years vary by species, but some seeds are usually produced every year (table 3) (Burns and Honkala 1990). Seeds may be picked from standing trees or collected by shaking or whipping the trees and collecting the samaras on sheets of canvas or plastic spread on the ground. Samaras may also be collected from trees recently felled in logging operations. Samaras from species such as boxelder and vine, sugar, bigleaf, silver, and Norway maples can be gathered from lawns and pavements and from the surface of water in pools and streams. After collection, leaves and other debris can be removed by hand, screening, or fanning. The following weights were reported (Olson and Gabriel 1974) for samaras:

	Weight/volume of samaras	
Species	kg/hl	lb/bu
vine maple	15.3	11.9
bigleaf maple	5.9	4.6
sugar maple	13.1	10.2

Seed collection for most species occurs when the samaras are fully ripened and the wing and pericarp have turned tan or brown in color (Carl 1982a; Carl and Yawney 1966). However, for maples that are difficult to germinate—such as vine maple, striped maple, and the Japanese maples—it is recommended that seeds be collected before they have dried completely, when the wing has turned brown but the pericarp is still green (Dirr and Heuser 1987; Vertrees 1975, 1987).

Although the seeds of most maples are glabrous, those of bigleaf maple are often densely pubescent. The pubescence may irritate the skin and cause some respiratory tract congestion when airborne. Individuals who might be sensitive to this material should use rubber gloves and a face mask.

Extraction and storage of seeds. Maple seeds are generally not extracted from the fruits (samaras) after collection, except when seeds are used in research on seed dormancy or lots of particularly valuable seeds that are difficult to germinate. De-winging reduces weight—wings account for about 15 to 20% of samara weight (Greene and Johnson 1992; Sipe and Linnerooth 1995)—and bulk for storage. The separation of filled and empty samaras for sugar maple can be accomplished on small lots by floating the samaras in n-pentane (filled seeds sink). This practice had no apparent effect on long-term seed viability (Carl 1976, 1982a; Carl and Yawney 1966). Removal of empty samaras, which can be done readily on a gravity table, improves seed handling, storage, sowing, and control of seedbed density.

After dispersal, maple seeds (with the exception of silver maple seeds and some red maple seeds) lie dormant in the forest floor for at least 3 to 5 months before germinating (Fried and others 1988; Houle and Payette 1991; Marquis 1975; Sakai 1990b; Tappeiner and Zasada 1993; Wilson and others 1979). Sugar and bigleaf maples usually germinate fully in the spring and summer after dispersal. Seeds of vine, striped, red, and mountain maples and the Japanese maples may lie dormant for 1 to 2 or more growing seasons before germinating (Marquis 1975; Peroni 1995; Sakai 1990b; Tappeiner and Zasada 1993; Vertrees 1987; Wilson and others 1979). In the southern United States, however, one test has indicated that seeds of red maple will maintain viability only for a few months when buried in the litter (Bonner 1996). Thus, with the exception of silver maple and possibly red maple seeds in some areas, seeds of all maples are "stored" naturally in the forest floor for varying lengths of time.

The critical factors in seed storage are temperature and seed moisture content. The moisture content of samaras depends on the stage of seed development and species. Beginning in late August, the moisture content of sugar maple seeds declined from about 160% (dry weight basis) to between 30 to 40% at dispersal (Carl and Snow 1971). The moisture content of sycamore maple seeds decreased from 750% (100 days after flowering) to 125% (200 days after flowering). Moisture content at dispersal for other species has been reported to be 7 to 50% for bigleaf maples (Zasada and others 1990); 80 to 100% for silver maples (Becwar and others 1983; Pukacka 1989), 30 to 35% for Norway maples (Hong and Ellis 1990), and 125 to 130% for sycamore maple (Hong and Ellis 1990).

Moisture content for seed storage defines into 2 groups—seeds that can be stored at relatively low moisture contents (orthodox seeds) and those that must be stored at relatively high moisture contents (recalcitrant seeds). Silver and sycamore maple are clearly recalcitrant (Becwar and others 1982, 1983; Bonner 1996; Dickie and others 1991; Hong and Ellis 1990; Pukacka 1989). Seeds of these species can be stored for about a year (Bonner 1996), and seed moisture content should be maintained at about 80% (dry weight) (Dickie and others 1991; Pukacka 1989).

Orthodox seeds can be stored for longer times and at lower moisture contents than recalcitrant seeds. Viability of sugar maple seeds did not decrease over a 54-month storage period when seeds were stored in sealed containers at a moisture content of 10% (dry weight) and a temperature range of –10 to 7 °C. Similarly, viability did not decrease significantly at 17% moisture content and –10 °C. Seeds stored in open containers at the same temperature lost viability more rapidly than those in sealed containers (Yawney and Carl 1974). Sugar maple seed moisture content can be reduced slowly from 100% (dry weight basis) at the time of collection to 20% with little effect on viability (Carl and Yawney 1966). Under stress conditions (seeds maintained at 52 °C), longevity of Norway maple seeds increased linearly as seed moisture content declined from 23 to 7% (fresh weight); seeds died when dried to moisture contents of 4 and 2.5% (Dickie and others 1991). Viability of bigleaf maple seeds declined from 73 to 62% when they were stored for 1 year in sealed containers at 1 °C and at a moisture content of 16% (dry weight); viability was reduced from 73 to 12% when seeds were stored at –10 °C (Zasada and others 1990).

It was previously believed that bigleaf maple seeds could not be stored for even short periods (Olson and Gabriel 1974). Based on recent work by Zasada and co-workers (Zasada 1992, 1996; Zasada and others 1990) in the central Oregon coastal range, an important consideration in storing these seeds seems to be collecting them before autumn rains begin, when the seeds are at their lowest water content. When collected at this time, some seedlots have moisture contents of 7 to 15% (dry weight basis), whereas seeds collected at other times have moisture contents of 25 to 35%. Once autumn rains begin, seeds attached to the tree increase in moisture content and, if they stay on the tree, can germinate under the right conditions. Although more work is required to determine the optimum storage conditions, the limited data suggest that seeds collected at the lowest moisture content behave more like orthodox seeds whereas those collected after autumn rains have increased moisture contents and some characteristics similar to recalcitrant seeds. The pubescent pericarp may play an important role in the moisture content of samaras.

For the other native maples, the fact that they remain viable for 1 year or more in the forest floor or nursery bed suggests that they could be stored for extended periods. Temperatures of 1 to 3 °C and seed moisture contents when dispersed should retain viability for several years.

Pregermination treatment and germination. Germination is epigeal for most species (figure 3), but silver maple and *A. tataricum* L. exhibit hypogeal germination (Burns and Honkala 1990; De Jong 1976; Harris 1976).

Under field conditions, maple germination falls into 3 general types, with red maple exhibiting a combination of 2 types. The first general pattern includes the 2 late spring/early summer seed dispersers (table 3)—red and silver maples—which is the best example. All seeds of this species must germinate before they dry below a moisture content of about 30% (fresh weight) or they die (Pukacka 1989). In red

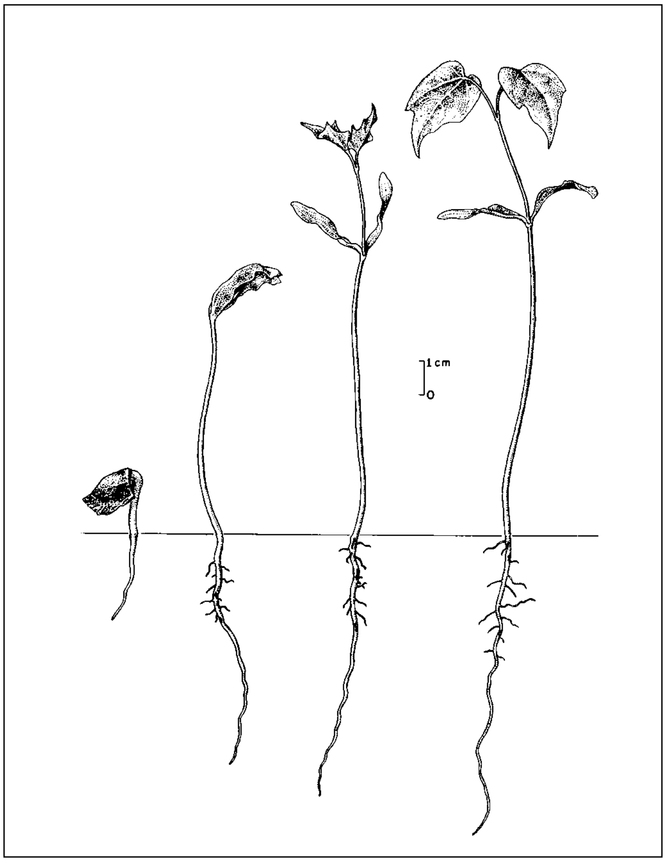


Figure 3—*Acer platanoides*, Norway maple: seedling development at 1, 3, 7, and 19 days after germination.

maples, the percentage of non-dormant seeds varies with the seed source and among trees in a given geographic area; indeed, this species shares some characteristics with the second type of germination (Abbott 1974; Farmer and Cunningham 1981; Farmer and Goelz 1984; Marquis 1975; Peroni 1995; Wang and Haddon 1978).

The second pattern is typified by sugar and bigleaf maples. Seeds are dispersed in the fall and early winter, stratify during winter and spring, and germinate as soon as temperature thresholds are reached. Both can germinate at constant temperatures just above freezing. In the relatively mild climate of western Oregon, bigleaf maple germinants begin to appear in late January. Bigleaf maple seeds that remain on the tree until late February or March can germinate on the tree (Zasada 1992; Zasada and others 1990). Sugar maple seeds have been observed to germinate under the snow in the spring (Godman and others 1990).

The third pattern has been observed in vine and striped maples (Tappeiner and Zasada 1993; Wilson and others 1979) and may occur in Rocky Mountain and mountain maples. Japanese and paperbark maples and other maples from Asia also exhibit this pattern (Dirr and Heuser 1987; Vertrees 1987). Seeds are dispersed as in the second pattern, but germination occurs over several years. In Massachusetts, less than 1 and 25% of striped maple seeds germinated, respectively, in the first and second years after sowing at the time of natural seedfall (Wilson and others 1979); in coastal Oregon 70 to 80% of vine maple seeds germinated in the second growing season after fall-sowing, with the remainder germinating in the first and third growing seasons (Tappeiner and Zasada 1993). Delayed germination of vine maple has also been observed in nursery beds (Vertrees 1975; Zasada 1996). Vertrees (1987) observed that Japanese maple germinants appeared over a 5-year period after a single sowing.

Methods for testing germination and pre-sowing treatments in nurseries are related in general to the germination patterns described above (tables 5 and 6). Silver maple seeds are not dormant (Pukacka 1989). Some red maple seeds may germinate without stratification, but stratification is necessary for seeds from some populations (Abbott 1974; Farmer and Cunningham 1981; Farmer and Goelz 1984; Peroni 1995; Wang and Haddon 1978). The group represented by sugar and bigleaf maples requires 30 to 90 days of stratification. Germination paper, sand, perlite, and sphagnum moss were all suitable stratification media for sugar maple seeds (Carl and Yawney 1966). Seeds will germinate completely at stratification temperatures. To assure that seeds have been stratified long enough, it may be advisable to wait until the first germinants appear before moving them to warmer temperatures to increase germination rate or sowing in the nursery. The optimum temperature for stratification in general is 0 to 3 °C, but some species will germinate well after stratification at temperatures up to 10 °C (Nikolaeva 1967).

The species that exhibit delayed germination are, under field conditions, exposed to warm and cold conditions and thus a warm period of incubation followed by cold stratification may stimulate germination. These species may also germinate better after a treatment that physically breaks the seed pericarp and testae (tables 5 and 6). Soaking seeds in warm water for 1 to 2 days is often recommended when they are completely dried out and the seedcoat has become very hard (Browse 1990; Dirr and Heuser 1987; Vertrees 1987). Seed testing rules recommend tetrazolium testing and excised embryo tests for the more difficult to germinate species (ISTA 1993).

Table 5—*Acer,* maple: warm and cold stratification treatments for internal dormancy

	Warm period		Cold period	
Species	**Temp (°C)**	**Days**	**Temp (°C)**	**Days**
*A. circinatum**	20–30†	30–60	3	90–180
*A. ginnala**	20–30†	30–60	5	90–150
A. glabrum	20–30†	180	3–5	180
A. macrophyllum	—	—	1–5	40–60
*A. negundo**	—	—	5	60–90
A. palmatum (dry seeds)	Warm water‡	1–2	1–8	60–120
A. palmatum (fresh seeds)	—	—	1–8	60–120
A. pensylvanicum	—	—	5	90–120
A. platanoides	—	—	5	90–120
A. pseudoplatanus	—	—	1–5	40–90
A. rubrum§	—	—	3	60–90
A. saccharinum	—	—	—	0
A. saccharum	—	—	1–5	40–90
A. spicatum	—	—	5	90–120

Sources: Browse (1990), Dirr and Heuser (1987), Harris (1976), Olson and Gabriel (1974), Vertrees (1987).

Note: Even after standard pretreatment, seedlots of *A. griseum* may require 2 to 3 years for complete germination.

* Mechanical rupture of the pericarp may improve germination. This is necessary in *A. negundo* when seeds are very dry; a warm soak as for *A. palmatum* may suffice.

† The benefit of warm incubation prior to stratification is not well-documented. Seeds may go through at least 1 warm/cold cycle before germinating under field conditions.

‡ Water temperature at start of incubation is 40 to 50 °C and allowed to cool gradually. Some recommend a 21 °C incubation period following warm water treatment and a 90-day stratification period.

§ Requirement for stratification is highly variable. In all seedlots, some seeds will germinate without stratification.

Optimum temperatures for germination are not clearly defined. Although most species have their best germination at higher temperatures within the optimum range (table 6), this is not always the case. Studies with red and striped maples have shown that, for seeds from some sources, germination is faster at lower than at higher temperatures (Farmer and Cunningham 1981; Farmer and Goelz 1984; Wilson and others 1979).

Germination occurs on a wide variety of substrates and a full range of light conditions (Burns and Honkala 1990; Fischer 1990; Olson and Gabriel 1974). Under field conditions, germination often occurs in association with leaf litter and other organic substrates on relatively undisturbed seedbeds. Germination paper, sand, perlite, and sphagnum moss support good germination in controlled environments. Red maple was shown to be more sensitive to the acidity of a substrate than sugar maple (Raynal and others 1982).

The morphological and physiological basis for seed dormancy in maples varies among species and includes pericarp-and-seed-coat-imposed dormancy and embryo dormancy (Farmer 1996; Young and Young 1992). The type of dormancy may change as seeds mature. There may be little relationship between dormancy of the mature seed and that of a seed with a fully developed embryo that is not yet mature in a biochemical sense (Thomas and others 1973). Thus for some species it may be best to collect and sow immature seeds as suggested by Vertrees (1975, 1987) for vine and Japanese maples and more generally by Dirr and Heuser (1987) for species with the third germination pattern mentioned above. The type of dormancy imposed by the pericarp and seedcoat (such as that in vine and striped maples) may be released by removing the pericarp and all or part of the testae (figure 2) or by physically breaking the pericarp without actually removing the embryo (table 5) (Wilson and others 1979). Some of the delayed field germination described above is caused by the impenetrability of the seedcoat after embryo dormancy has been released (Dirr and Heuser 1987; Wilson and others 1979).

Nursery practice. Maple seedlings can be produced as container stock or as bareroot seedlings. Bareroot seedlings seem to be the most common when all species of maples are considered. Pre-sowing treatment and sowing time are based on the characteristics of the seeds being sown, convenience, and experience. Cutting tests or x-radiography to determine the presence of embryos are advised for some of the introduced species because poor seed quality is common (Dirr and Heuser 1987; Hutchinson 1971; Vertrees 1987). The information reviewed above on dormancy and germination pattern suggest a number of options for sowing. The least amount of seed handling is required when seeds are sown immediately after collection and allowed to stratify "naturally" before germination. Silver and red maple

Table 6—*Acer,* maple: germination test conditions and results for stratified seeds

	Germination test conditions			Germination rate		
	Temp (°C)			Amount	Time	Total
Species	**Day**	**Night**	**Days**	**(%)**	**(days)**	**germination (%)**
A. circinatum	30	20	38	12	10	19
A. ginnala	30	20	38	50	10	52
A. glabrum	10–16	10–16	—	40	30	—
*A. macrophyllum**						
Source 1	2–3	2–3	120	15–66	60–90	100
Source 2	2–3	2–3	120	0–13	60–90	100
Source 3	2–3	2–3	120	8–92	60–90	100
A. negundo	—	—	24–60	14–67	14–48	24–96
A. pensylvanicum†	5	5	90	—	—	82
	23	23	60	—	—	76
A. platanoides	4–10	4–10	—	—	—	30–81
A. pseudoplatanus	—	—	—	24–37	20–97	50–71
A. rubrum‡						
Low elevation (U)	15	5	—	—	—	55
Low elevation (S)	15	5	—	—	—	89
High elevation (U)	15	5	—	—	—	13
High elevation (S)	15	5	—	—	—	54
A. saccharinum	30	30	5–18	72–91	3–13	94–97
A. saccharum	2–3	2–3	90	80	75	95
A. spicatum	—	—	—	32	31	34

Sources: Olson and Gabriel (1974), Farmer and Goelz (1984), Farmer and Cunningham (1981), Vertrees (1987).

Notes: Germination rate indicates the number of seeds germinating in the time specified and total germination all of the seeds germinating in the test. The length of germination tests are not same for all species.

Seeds of *A. griseum* and *A. palmatum* are very difficult to germinate and seed quality is usually poor. Cutting tests are recommended to determine potential viability. Tetrazolium tests could be used to determine if seeds are alive; knowing this one can sow and wait several years for seeds to germinate. Because the delay in germination appears related to a very hard pericarp, removing the pericarp can improve germination.

* Seed sources from central Oregon coastal range. Germination rate greatly increased when seeds moved to 20 to 25 °C when germination in stratification begins (Zasada 1996).

† Germination of seeds with testa removed over radicles. Seeds with testae did not germinate at 23 °C even after 5 months of stratification, whereas seeds kept at 5 °C germinated completely after 6 months (Wilson and others 1979).

‡ Seed sources from Tennessee, total germination at higher temperatures was lower than shown here (Farmer and Cunningham 1981). Similar trends were observed with red maple from Ontario (Farmer and Goelz 1984). U = stratified seeds, S = unstratified seeds.

seeds are sown after collection in late spring, whereas seeds of other maples are sown in the fall when they are mature and the nursery beds mulched (Harris 1976; Olson and Gabriel 1974; Yawney 1968). If stratification requirements are not satisfied with this method or if secondary dormancy is imposed, there may be a substantial number of seeds that do not germinate in the first growing season. Treatment of seeds may result in more uniform germination. For example, Webb (1974) proposed soaking sugar maple seeds for 24 hours before stratification to promote more uniform germination.

For difficult species such as vine and striped maples, which germinate over a several-year period, it has been recommended that seedcoats be either physically broken to promote more uniform germination or soaked in warm water, or given both treatments to reduce the number of seeds not germinating during the first growing season (Browse 1990; Olson and Gabriel 1974; Vertrees 1975, 1987). Vertrees (1987) describes several sowing methods for Japanese maples. The choice of a method depends on degree of maturity, length of time seeds have been stored, and the time desired for sowing. It is also recommended that nurserybeds in which these seeds are sown be maintained for several years so that late-germinating seeds are not destroyed; this is particularly true when seed supplies are limited.

Maple seeds are usually sown 0.6 to 2.5 cm ($^1/_4$ to 1 in) deep, either broadcast or using drills. Seedbed densities from 158 to 1,520/m^2 (15 to 144/ft^2) have been recommended (Carl 1982b; Olson and Gabriel 1974; Vertrees 1987; Yawney 1968). Densities in the range of 158 to 320/m^2 (15 to 30/ft^2) appear most satisfactory for the production of vigorous seedlings. In some instances, seedbeds require treatment with repellents against birds and mice and treatment with fungicides to prevent damping off (Olson and Gabriel 1974; Vertrees 1987). Shade is recommended during the period of seedling establishment (Olson and Gabriel 1974).

Sometimes maple seedlings are large enough to plant as 1+0 stock, but frequently 2+0 or even 2+2 stock is needed to ensure satisfactory results. In general, the larger the planting stock, the better the survival.

Container seedling production is less common than bareroot production, but is used by some producers (Tinus 1978). Container seedlings grown in a greenhouse will usually be larger than those grown outdoors in containers or in a nursery bed (Wood and Hancock 1981). Container production would probably be best achieved with stratified seeds that are just beginning to germinate; this can be easily achieved for species like bigleaf and sugar maples that germinate during stratification. Various sizes and types of containers can be used. One grower uses a container that is 4 cm (1.6 in) in diameter and 15 cm (6 in) deep to produce 30- to 40-cm-high (12- to 16-in-high) stock in 1 growing cycle. These seedlings can be outplanted or transplanted to nursery beds or larger containers for production of larger stock for ornamental purposes.

Artificial sowing in field situations is an alternative to planting seedlings. Successful germination and early growth have been demonstrated for bigleaf maple and vine maple under a variety of forest conditions (Fried and others 1988; Tappeiner and Zasada 1993) and red maple (Brown and others 1983). One drawback to sowing under forested conditions is heavy seed predation by various small mammals.

Desirable maple genotypes can also be propagated vegetatively by rooting stem cuttings and various types of layering (Dirr 1990; Dirr and Heuser 1987; O'Dea and others 1995; Post 1969; Vertrees 1987; Yawney 1984; Yawney and Donnelly 1981, 1982). Methods for rooting and overwintering cuttings before outplanting are available for sugar maple (Yawney and Donnelly 1982) and Japanese maples (Dirr and Heuser 1987; Vertrees 1987).

References

Abbott HG. 1974. Some characteristics of fruitfulness and seed germination in red maple. Tree Planters' Notes 25(2): 25–27.

Alden HA. 1995. Hardwoods of North America. Gen. Tech. Rep. FPL-83. Madison, WI: USDA Forest Service, Forest Products Laboratory. 136 p.

Al'benskii AV, Nikitin PD. 1956. Agrolesomeliortsiya, 3rd ed. Moscow: Gosundarstvennoye Izdatel'stvo Sel'skohozyaystvennoy Litrtsyury [Handbook of afforestation and soil amelioration. Transl. TT 66-51098, 1967. Springfield, VA: USDC National Technical Information Service. 516 p.].

Anonymous. 1960. Collection and storage of ash, sycamore, and maple seed. For. Comm. Leafl. 33. [London]: Her Majesty's Stationery Office. 11 p.

Barker PA, Freeman DC, Harper KT. 1982. Variation in the breeding system of *Acer grandidentatum*. Forest Science 28(3): 563–572.

Bazzaz FA, Carlson RW, Harper JL. 1979. Contribution to reproductive effort by photosynthesis of flowers and fruits. Nature 279 (5713): 554–555.

Becwar MR, Stanwood PC, Roos EE. 1982. Dehydration effects on imbibitional leakage from desiccation-sensitive seeds. Plant Physiology 69: 1132–1135.

Becwar MR, Stanwood PC, Leonhardt KW. 1983. Dehydration effects on freezing characteristics and survival in liquid nitrogen of desiccation-tolerant and desiccation-sensitive seeds. Journal of the American Society of Horticultural Science 108(4): 613–618.

Bjorkbom JC. 1979. Seed production and advance regeneration in Allegheny hardwood forests. Res. Pap. NE-435. Broomall, PA: USDA Forest Service, Northeastern Forest Experiment Station. 10 p.

Bjorkbom JC, Auchmoody LR, Dorn DE. 1979. Influence of fertilizer on seed production in Allegheny hardwood stands. Res. Pap. NE-439. Broomall, PA: USDA Forest Service, Northeastern Forest Experiment Station. 5 p.

Bonner F. 1996. Personal communication. Starkville, MS: USDA Forest Service, Southern Research Station, Forestry Sciences Laboratory.

Brown JE, Maddox JB, Splittstoesser WE. 1983. Performance of trees, shrubs, and forbs seeded directly in the fall on minespoil and silt loam soil. Journal of Environmental Quality 12(4): 523–525.

Browse PM. 1990. Seed stratification: an individual exercise. Plantsman 11(4): 241–243.

Burns RM, Honkala BH, tech. coords. 1990. Silvics of North America. Volume 2, Hardwoods. Agric. Handbk. 654. Washington, DC: USDA Forest Service. 877 p.

Carl CM Jr. 1976. Effect of separation in N-pentane on storability of sugar maple seeds. Res. Note NE-218. Upper Darby, PA: USDA Forest Service, Northeastern Forest Experiment Station. 3 p.

Carl CM Jr. 1982a. The propagation and planting of sugar maples: seed collection and handling. In: Sugar maple research: sap production, processing, and marketing of maple syrup. Gen. Tech Rep. NE-72. Upper Darby, PA: USDA Forest Service, Northeastern Forest Experiment Station: 42–46.

Carl CM Jr. 1982b. The propagation and planting of sugar maples: nursery practices. In: Sugar maple research: sap production, processing, and marketing of maple syrup. Gen. Tech. Rep. NE-72. Upper Darby, PA: USDA Forest Service, Northeastern Forest Experiment Station: 47–52.

Carl CM Jr, Yawney HW. 1966. Four stratification media equally effective in conditioning sugar maple seed for germination. Tree Planters' Notes 77: 24–28.

Carl CM Jr, Snow AG. 1971. Maturation of sugar maple seed. Res. Pap. NE-217. Upper Darby, PA: USDA Forest Service, Northeastern Forest Experiment Station. 9 p.

Carl CM Jr, Yawney HW. 1969. The use of pentane to separate filled and empty sugar maple samaras. Tree Planters' Notes 20(3): 24–27.

Carl CM Jr, Yawney HW. 1972. Multiple seedlings in *Acer saccharum*. Bulletin of the Torrey Botanical Club 99: 142–144.

Chandler RF Jr. 1938. The influence of nitrogenous fertilizer applications upon seed production of certain deciduous forest trees. Journal of Forestry 36: 761–766.

Curtis JT. 1959. The vegetation of Wisconsin: the ordination of plant communities. Madison: University of Wisconsin Press. 657 p.

De Jong PC. 1976. Flowering and sex expression in *Acer* L.: a biosystematic study. Wageningen, the Netherlands: H. Veenman and Zonen. 191 p.

Dickie JB, May K, Morris SVA, Titley SE. 1991. The effects of desiccation on seed survival in *Acer platanoides* L. and *Acer pseudoplatanus* L. Seed Science Research 1: 149–162.

Dirr MA. 1990. Manual of woody landscape plants: their identification, ornamental characteristics, culture, propagation and uses. Champaign, IL: Stipes Publishing. 1007 p.

Dirr MA, Heuser CW Jr. 1987. The reference manual of woody plant propagation: from seed to tissue culture. Athens, GA: Varsity Press. 239 p.

Farmer RE. 1996. Seed ecophysiology of temperate and boreal zone forest trees. Del Ray, FL: St. Lucie Press. 340 p.

Farmer RE, Cunningham M. 1981. Seed dormancy of red maple in east Tennessee. Forest Science 27(3): 446–448.

Farmer RE, Goelz J. 1984. Germination characteristics of red maple in northwestern Ontario. Forest Science 30: 670–672.

Ferrari JB. 1993. Spatial patterns of litterfall, nitrogen cycling, and understory vegetation in a hemlock–hardwood forest [PhD thesis]. St. Paul: University of Minnesota. 180 p.

Fischer WC, comp. 1990. The Fire Effects Information System [database]. Missoula, MT: USDA Forest Service, Intermountain Research Station, Intermountain Fire Sciences Laboratory [contains literature reviews of 8 maple species].

Freeman DC, Klikoff LG, Harper KT. 1976. Differential resource utilization by the sexes of dioecious plants. Science 193: 597–599.

Fried JS, Tappeiner JC, Hibbs DE. 1988. Bigleaf maple seedling establishment and early growth in Douglas-fir forests. Canadian Journal of Forest Research 18 (10): 1226–1233.

Furuta K. 1990. Seedling behavior of *Acer amoenum* and the effect of the infestation of aphids. Bulletin of the Tokyo University Forests 82: 147–156.

Gabriel WJ. 1967. Reproductive behavior in sugar maple: self-compatibility, cross-compatibility, agamospermy, and agamocarpy. Silvae Genetica 16: 165–168.

Gabriel WJ. 1968. Dichogamy in *Acer saccharum*. Botanical Gazette 129(4): 334–338.

Gabriel WJ. 1978. Genetic variation in seed and fruit characters in sugar maple. Res. Pap. NE-404. Broomall, PA: USDA Forest Service, Northeastern Forest Experiment Station. 4 p.

Gabriel WJ, Garrett PW. 1984. Pollen vectors in sugar maple (*Acer saccharum*). Canadian Journal of Botany 62: 2889–2890.

Garrett PW, Graber RE. 1995. Sugar maple seed production in northern New Hampshire. Res. Pap. NE-697. Radnor, PA: USDA Forest Service, Northeastern Forest Experiment Station. 6 p.

Godman RM, Mattson GA. 1976. Seed crops and regeneration problems of 19 species in northeastern Wisconsin. Res. Pap. NC-123. St. Paul: USDA Forest Service, North Central Forest Experiment Station. 5 p.

Godman RM, Yawney HW, Tubbs CH. 1990. *Acer saccharum* Marsh., sugar maple. In: Burns RM, Honkala BH, Tech. coords. Silvics of North America. Volume 2, Hardwoods. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 78–91.

Graber RE, Leak WB. 1992. Seedfall in an old-growth northern hardwood forest. Res. Pap. NE-663. Broomall, PA: USDA Forest Service, Northeastern Forest Experiment Station. 11 p.

Green DS. 1980. The terminal velocity and dispersal of spinning samaras. American Journal of Botany 67(8): 1218–1224.

Greene DF, Johnson EA. 1990. The dispersal of winged fruits and seeds differing in autorotative behavior. Canadian Journal of Botany 68: 2693–2697.

Greene DF, Johnson EA. 1992. Fruit abscission in *Acer saccharinum* with reference to seed dispersal. Canadian Journal of Botany 70: 2277–2283.

Grisez TJ. 1975. Flowering and seed production in seven hardwood species. Res. Pap. NE-315. Upper Darby, PA: USDA Forest Service, Northeastern forest Experiment Station. 8 p.

Guries RP, Nordheim EV. 1984. Flight characteristics and dispersal potential of maple samaras. Forest Science 30: 434–440.

Harris G. 1976. Growing maples from seed. Garden 101: 503–506.

Hibbs DE, Fischer BC. 1979. Sexual and vegetative reproduction of striped maple (*Acer pensylvanicum* L.). Bulletin of the Torrey Botanical Club 106(3): 222–226.

Hong TD, Ellis RH. 1990. A comparison of maturation drying, germination, and desiccation tolerance between developing seeds of *Acer pseudoplatanus* L. and *Acer platanoides* L. New Phytologist 116: 589–596.

Houle G, Payette S. 1991. Seed dynamics of *Abies balsamea* and *Acer saccharum* in a deciduous forest of northeastern North America. American Journal of Botany 78(7): 895–905.

Hutchinson PA. 1971. Propagation of *Acers* from seed. Proceedings of the Plant Propagators' Society 2: 233–235.

ISTA [International Seed Testing Association]. 1993. International rules for seed testing. Proceedings of the International Seed Testing Association 31(1): 1–152.

Jones E. 1832. Review of facts and observations made by naturalists, botanists, historians, and travelers on the properties and productions of the sugar maple tree; process of extracting its sap, converting it into sugar, &c. &c. London: E. Colyer.

Long RP, Horsley SB, Lilja PR. 1997. Impact of forest liming on growth and crown vigor of sugar maple and associated hardwoods. Canadian Journal of Forest Research 27: 1560–1573.

Marquis DA. 1975. Seed storage and germination under northern hardwood forests. Canadian Journal of Forest Research 5: 478–484.

Marquis RJ. 1988. Intra-crown variation in leaf herbivory and seed production in striped maple, *Acer pensylvanicum* L. (Aceraceae). Oecologia 77: 51–55.

Matlack GR. 1987. Diaspore size, shape, and fall behavior: wind-dispersed plant species. American Journal of Botany 74(8): 1150–1160.

Myster RW, Pickett STA. 1993. Effects of litter, distance, density and vegetation patch type on postdispersal tree seed predation in old fields. Oikos 66: 381–388.

McCutchen CW. 1977. The spinning rotation of ash and tulip tree samaras. Science 197: 691–692.

Nikolaeva MG. 1967. Fiziologiya glubokogo pokoya semyan. Komarovskie Chteniya Botanicheskogo Instituta Akademii Nauk SSR Akad. Nauk SSSR [Physiology of deep dormancy in seeds. Transl. TT68-50463. Springfield, VA: USDC National Technical Information Service. 1969. 220 p.].

Norberg RA. 1973. Autorotation, self-stability, and structure of single-winged fruits and seeds (samaras) with comparative remarks on animal flight. Biological Review 48: 561–596.

O'Dea M, Zasada J, Tappeiner J. 1995. Vine maple clone growth and reproduction in managed and unmanaged coastal Oregon Douglas-fir forests. Ecological Application 51: 63–73.

Olson DF, Gabriel WJ. 1974. *Acer* L., maple. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 187–194.

Peck CJ, Lersten NR. 1991. Samara development of black maple (*Acer saccharum* ssp. *nigrum*) with emphasis on the wing. Canadian Journal of Botany 69: 1349–1360.

Peroni PA. 1994. Seed size and dispersal potential of *Acer rubrum* (Aceraceae) samaras produced by populations in early and late successional environments. American Journal of Botany 81(11): 1428–1434.

Peroni PA. 1995. Field and laboratory investigations of seed dormancy in red maple (*Acer rubrum* L.) from the North Carolina piedmont. Forest Science 41: 378–386.

Post LJ. 1969. Vegetative reproduction and the control of mountain maple. Pulp and Paper of Canada 70: 115–117.

Pregitzer KS, Burton AJ. 1991. Sugar maple seed production and nitrogen in litterfall. Canadian Journal of Forest Research 21: 1148–1153.

Primack RB, McCall C. 1986. Gender variation in a red maple population (*Acer rubrum*; Aceraceae). American Journal of Botany 73: 1239–1248.

Pukacka S. 1989. The effect of desiccation on viability and phospholipid composition of *Acer saccharinum* L. seeds. Trees: Structure and Function 3: 144–148.

Raynal DJ, Roman JR, Eichenlaub WM. 1982. Response of tree seedlings to acid precipitation. I. effect of substrate acidity on seed germination. Environmental and Experimental Botany 22 (3): 377–383.

Rehder A. 1940. Manual of cultivated trees and shrubs. New York: Macmillan. 996 p.

Sakai AK. 1990a. Sex ratios of red maple (*Acer rubrum*) populations in northern lower Michigan. Ecology 71(2): 571–580.

Sakai AK. 1990b. Sexual reproduction of red maple (*Acer rubrum*) in northern lower Michigan. American Midland Naturalist 123: 309–318.

Sakai AK, Oden NL. 1983. Spatial pattern of sex expression in silver maple (*Acer saccharinum* L.): Moritita's index and spatial autocorrelation. American Naturalist 122(4): 489–508.

Sargent CS. 1965. Manual of the trees of North America (exclusive of Mexico). New York: Dover Publishing. 934 p.

Sipe TW, Linnerooth AR. 1995. Intraspecific variation in samara morphology and flight behavior in *Acer saccharinum* (Aceraceae). American Journal of Botany 82(11): 1412–1419.

Stoeckeler JH, Jones GW. 1957. Forestry nursery practices in the Lake States. Agric. Handbk. 110. Washington, DC: USDA Forest Service. 124 p.

Sudworth GB. 1900. The forest nursery: collection of tree seeds and propagation of seedlings. Bull. 29. Washington, DC: USDA Division of Forestry. 63 p.

Sudworth GB. 1908. Forest trees of the Pacific slope. Washington, DC: US Government Printing Office. 441 p.

Tappeiner J, Zasada J. 1993. Establishment of salmonberry, salal, vine maple, and bigleaf maple seedlings in the coastal forests of Oregon. Canadian Journal of Forest Research 23: 1775–1780.

Thomas H, Webb DP, Wareing PF. 1973. Seed dormancy in *Acer*: maturation in relation to dormancy in *Acer pseudoplatanus* L. Journal of Experimental Botany 24: 958–967.

Tinus RW. 1978. Production of container-grown hardwoods. Tree Planters' Notes 29(4): 3–9.

Toumey JW, Korstian CF. 1942. Seeding and planting in the practice of forestry. New York: John Wiley and Sons. 520 p.

Townsend AM. 1972. Geographic variation in fruit characteristics of Acer rubrum. Bulletin of the Torrey Botanical Club 99: 122–127.

Townsend AM, Wright JW, Beineke WF, Guries RP, Mohn CA. 1982. Early patterns of flowering, winter injury, and flushing of red maple progenies grown in five locations. Canadian Journal of Forest Research 12: 814–821.

USDA FS [USDA Forest Service]. 1948. Woody plant seed manual. Misc. Pub. 654. Washington, DC: U.S. Department of Agriculture. 416 p.

USDA FS [USDA Forest Service]. 1982. Sugar maple research: sap production, processing, and marketing of maple syrup. Gen. Tech. Rep. NE-72. Radnor, PA: USDA Forest Service, Northeastern Forest Experiment Station.

Van Gelderen DM, De Jong PC, Oterdoom HJ, Van Hoey Smith JRP. 1994. Maples of the world. Portland OR: Timber Press. 512 p.

Vertrees JD. 1975. Observations on *Acer circinatum* Pursh. propagation. Plant Propagator 21(4): 11–12.

Vertrees JD. 1987. Japanese maples. Portland, OR: Timber Press. 332 p.

Viereck LA. 1997. Personal communication. Fairbanks, AK: USDA Forest Service, Pacific Northwest Research Station, Institute of Northern Forestry.

Viereck LA, Little EL Jr. 1972. Alaska trees and shrubs. Agric. Handbk. 410. Washington, DC: USDA Forest Service: 265 p.

Von Althen F. 1974. Successful establishment of sugar maple in a Scots pine plantation. Info. Rep. 0-X-208. Ottawa: Department of Environment, Canadian Forest Service. 6 p.

Wang BSP, Haddon BD. 1978. Germination of red maple seed. Seed Science and Technology 6: 785–790.

Webb DP. 1974. Germination control of stratified sugar maple seeds. Forestry Chronicle 50: 112–113.

Willson MF. 1986. On the costs of reproduction in plants: *Acer negundo*. American Midland Naturalist 115: 204–207.

Wilson BF, Hibbs DE, Fischer BC. 1979. Seed dormancy in stripped maple. Canadian Journal of Forest Research 9: 263–266.

Wood BW, Hancock JW. 1981. Early genetic differentiation of sugar maple by accelerating seedling growth. Canadian Journal of Forest Research 11: 287–290.

Yawney HW. 1968. Artificial regeneration. In: Proceedings, Sugar Maple Conference; 1968 August 20-22; Houghton, MI: 65–74.

Yawney HW. 1984. How to root and overwinter sugar maple cuttings. American Nurseryman 160 (8): 95–102.

Yawney HW, Carl CM Jr. 1974. Storage requirements for sugar maple seeds. Res. Pap. NE-298. Upper Darby, PA: USDA Forest Service, Northeastern Forest Experiment Station. 6 p.

Yawney HW, Donnelly JW. 1981. Clonal propagation of sugar maple by rooting cuttings. In: Proceedings, 27th Northeastern Forest Tree Improvement Conference; 1980 July 29–31; Burlington, VT. Burlington: University of Vermont, School of Natural Resources: 72–81.

Yawney HW, Donnelly JR. 1982. Rooting and overwintering sugar maple cuttings. In: Sugar maple research: sap production, processing, and marketing of maple syrup. Gen. Tech Rep. NE-72. Broomall, PA: USDA Forest Service. Northeastern Forest Experiment Station: 61–70.

Young JA, Young CG. 1992. Seeds of woody plants in North America: revised and enlarged edition. Portland, OR: Dioscorides Press.

Zasada J. 1992. Climbing trees to look for maple seedlings. COPE Report 5(1/2): 12–13.

Zasada J. 1996. Unpublished data. Rhinelander, WI: USDA Forest Service, North Central Forest Experiment Station, Forestry Sciences Laboratory.

Zasada J, Tappeiner J, Max T. 1990. Viability of maple seeds after storage. Western Journal of Applied Forestry 5(2): 52–55.

Zasada J, Tappeiner J, O'Dea M. 1992. Clone structure of salmonberry and vine maple in the Oregon Coast Range. In: Clary WP, McArthur ED, Bedunah D, Wambolt CL, comps. Proceedings, Symposium on Ecology and Management of Riparian Shrub Communities; 1991 May 29–31; Sun Valley, ID. Gen. Tech. Rep. INT-289. Odgen, UT: USDA Forest Service.

Fabaceae—Pea family

Adenanthera pavonina L.

peronías

J.A. Vozzo

Dr. Vozzo retired from the USDA Forest Service's Southern Research Station

Other common names. jumbie-bead

Occurrence and growth habit. Originally from tropical Asia, this genus has spread to parts of tropical Africa and America that have 1,300 to 2,100 mm of rainfall, soil pH 5.0 to 7.5, and nutrient-rich soils with moist but well-drained profiles. It maintains a common abundance relative to other competitors (Francis and Liogier 1991). *Peronías—Adenanthera pavonina* L.—has large bipinnate leaves, 30 to 60 cm in length, and narrow, erect flower clusters with shiny scarlet seeds. The medium-sized deciduous tree can be 13 m tall and 45 cm in trunk diameter, with brown, smooth bark (Little and Wadsworth 1964). Two other species—*A. microsperma* Teysm. & Binn. and *A. bicolor* Moon —are similar but smaller (Neal 1965). Only a small number of species are included in the genus. Gunn (1984) recognizes only the following 5 species—*A. abrosperma* F. v. *Mueller, A. bicolor, A. intermedia* Merrill, *A. pavonina* L. var. *microsperma,* and *A. pavonina* L. var. *pavonina*. Only *A. pavonina* var. *pavonina* is commonly found in the American tropics, where it has naturalized in Puerto Rico (Francis and Liogier 1991).

Use. The mature trees are good shade trees but not particularly ornamental (Neal 1965), although they are valued for their attractive feathery foliage and bright red seeds in Nyasaland (Streets 1962). Peronías is also planted as a hedge in Asia, where it is called peacock flower fence (Bailey 1941). Its sapwood is light brown and hard, and its heartwood is hard and red. The heavy, hard wood (specific gravity 0.6 to 0.8) makes durable, strong furniture. It is used locally for poles and firewood as well as a source of red dye (Little and Wadsworth 1964). It gets its Asian common name—red sandalwood—from its use as a substitute for sandalwood. The red seeds are known as "Circassian seeds" and used for bead work. An interesting (but questionable) use is as commercial weights for goldsmiths and silversmiths, who claim each seed weighs a uniform 4 grains (Neal 1965).

Flowering and fruiting. Flowers are borne on racemes (either lateral or terminal) on short stalks 3 mm long and may be pale yellow to white. The small, inconspicuous flowers have a sweet smell and form axillary clusters during the hot, humid season. The fruits mature in the dry season and remain on the tree several months as dark brown legumes (pods) that measure 10 to 20 mm wide and 15 to 20 cm long and are twisted. They readily split and show seeds (figures 1 and 2) attached to the smooth, yellow interior. There are about 3,500 seeds/kg (~1,580/lb) (Bailey 1941; Little and Wadsworth 1964; Neal 1965; Troup 1921). Seeds store well with no special techniques required (Francis 1994).

Germination. Although presoaking is helpful, seeds will germinate with no pre-germination treatment. Several reports do, however, suggest that germination is enhanced by hot-wire scarification (Sandiford 1988) and sulfuric acid exposure (Ahmed and others 1983; Xu and Gu 1985). Francis and Rodriguez (1993) report 86% germination of mechanically scarified seeds held for 6 days on blotter paper at ambient temperature (24 to 30 °C). Germination is epigeal (figure 3).

Figure 1—*Adenanthera pavonia*, peronías: seed.

Nursery practice. Although there are no printed reports of nursery practices, seeds readily germinate along moist roadsides. Peronías will readily propagate from cuttings planted during rainy periods (Troup 1921).

Figure 2—*Adenanthera pavonia,* peronías: cross section of a seed.

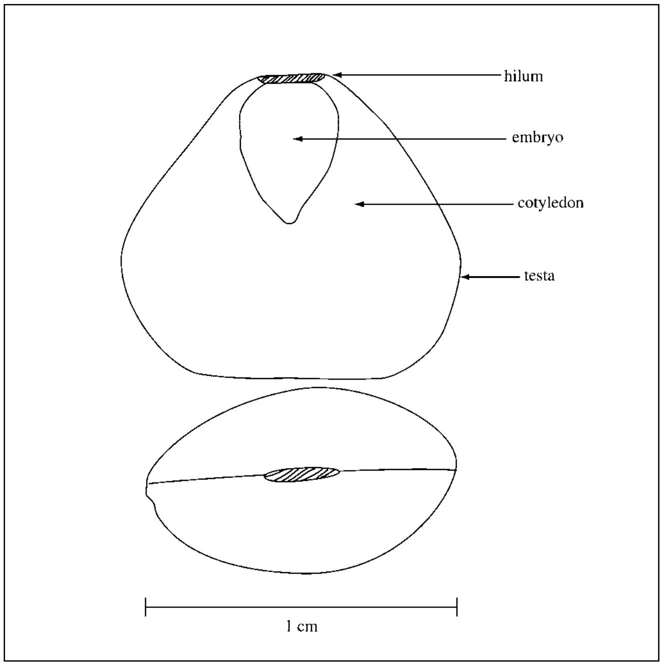
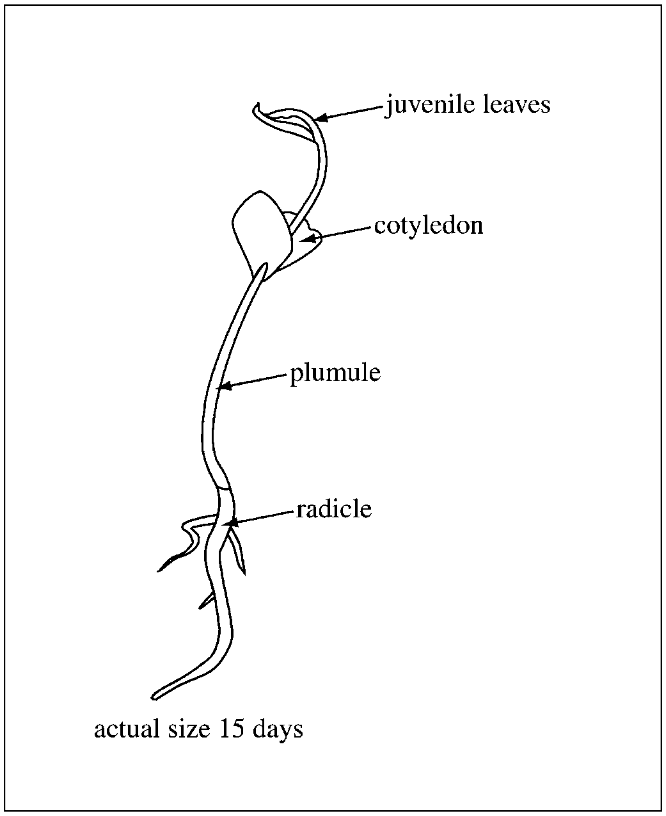


Figure 3—*Adenanthera pavonia*, peronías: seedling, 15 days.



References

Ahmed FU, Sharmila-Das, Hossain MA. 1983. Effect of seed treatment on the germination of Rakta Kambal seeds. Bano-Biggyan-Patrika 12(1/2): 62–65.

Bailey LH. 1941. Standard cyclopedia of horticulture. New York: Macmillan. 1200 p.

Francis JK. 1994. Personal communication. Río Piedras, PR: USDA Forest Service, International Institute of Tropical Forestry.

Francis JK, Liogier HA. 1991. Naturalized exotic tree species in Puerto Rico. Gen. Tech. Rep. SO-82. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 12 p.

Francis JK, Rodríguez A. 1993. Seeds of Puerto Rican trees and shrubs: second installment. Res. Note SO-374. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 5 p.

Gunn CR. 1984. Fruits and seeds of genera in the subfamily Mimosoidaceae (Fabaceae). Tech. Bull. 1681. Washington, DC: USDA Agricultural Research Service. 194 p.

Little EL Jr, Wadsworth FH. 1964. Common trees of Puerto Rico and the Virgin Islands. Agric. Handbk. 249. Washington, DC: USDA Forest Service. 548 p.

Neal MC. 1965. In gardens of Hawaii. Spec. Pub. 50. Honolulu: Bishop Museum Press. 924 p.

Sandiford M. 1988. Burnt offerings: an evaluation of the hot-wire seed scarifier. Commonwealth Forestry Review 67(3): 285–292.

Streets RJ. 1962. Exotic forest trees in the British Commonwealth. Oxford, UK: Clarendon Press. 750 p.

Troup RS. 1921. Silviculture of Indian trees. Volume 2, Leguminosae (Caesalpinieae) to Verbenaceae. Oxford, UK: Clarendon Press. 783 p.

Xu BM, Gu ZH. 1985. Effect of sulfuric acid treatment in breaking dormancy in hard seeds. [Beijing]: Plant Physiology Communications 2: 22–25.

Hippocastanaceae—Horsechestnut family

Aesculus L.

buckeye

Paul O. Rudolf and Jill R. Barbour

Dr. Rudolph (deceased) retired from the USDA Forest Service's North Central Forest Experiment Station;
Ms. Barbour is a germination specialist at the USDA Forest Service's National Seed Laboratory
Dry Branch, Georgia

Growth habit, occurrence, and use. The buckeyes—which occur in North America, southeastern Europe, and eastern and southeastern Asia—include about 25 species of deciduous trees and shrubs (Rehder 1940). They are cultivated for their dense shade or ornamental flowers, and the wood of some species is occasionally used for lumber and paper pulp. They also provide wildlife habitat. The shoots and seeds of some buckeyes are poisonous to livestock (Bailey 1939). Seven of the 9 species described (table 1) are native to the United States. The horsechestnut was introduced into this country from southern Europe, and the Himalayan horsechestnut occurs naturally in the Himalayas.

Seven of these 8 species are not used much in reforestation, but all are used for environmental forestry planting. Himalayan horsechestnut is used extensively for reforestation and the nuts are fed to sheep and goats (Maithani and others 1990). This is also true of horsechestnut, which has been widely planted as a shade tree in Europe and also in the eastern United States, where it sometimes escapes from cultivation (Bailey 1939). Ohio and yellow buckeyes are sometimes planted in Europe and the eastern United States, the former having been successfully introduced into Minnesota, western Kansas, and eastern Massachusetts. California buckeye is also occasionally planted in Europe and to a somewhat greater extent in the Pacific Coast states. A natural hybrid—*A.* × *bushii Schneid. (A. glabra* × *pavia),* called Arkansas buckeye—occurs in Mississippi and Arkansas (Little 1953). At least 5 other hybrids are known in cultivation (Little 1953).

Flowering and fruiting. Buckeye flowers are irregular in shape and white, red, or pale yellow in color; they are borne in terminal panicles that appear after the leaves. The

Table 1—*Aesculus,* buckeye: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
A. californica **(Spach) Nutt.** *A. octandra* Marsh	**California buckeye**	Dry gravelly soils; lower slopes of coastal range & Sierra Nevada in California
A. flava **Ait.**	**yellow buckeye,** sweet buckeye, big buckeye	Moist, rich soils; SW Pennsylvania, W to S Illinois, S to N Georgia, & N to West Virginia
A. glabra **Willd.**	**Ohio buckeye,** fetid buckeye, American horsechestnut	Moist, rich soils; W Pennsylvania to SE Nebraska, S to Oklahoma, then E to Tennessee
A. glabra **var.** ***arguta*** **(Buckl.) B.L. Robins.** *A. arguta* Buckl. *A. glabra* var. *buckleyi* Sarg. *A. buckleyi* (Sarg.) Bush	**Texas buckeye**	Limestone & granite soils; S Oklahoma, E & central Texas to Edwards Plateau
A. hippocastanum **L.**	**horsechestnut,** chestnut, bongay	Native to Balkan Peninsula of Europe; planted extensively in US
A. indica **(Wall. ex. Cambess) Hook.**	**Himalayan horsechestnut**	Himalayas between 1,524 to 3,050 m
A. parviflora **Walt.**	**bottlebrush buckeye**	SW Georgia & Alabama
A. pavia **L.**	**red buckeye,** scarlet buckeye, woolly buckeye, firecracker plant	Moist, rich soils; Virginia to Missouri, S to Texas & Florida
A. sylvatica **Bartr.** *A. neglecta* Lindl. *A. georgiana* Sarg. *A. neglecta* var. *georgiana* (Sarg.) Sarg.	**painted buckeye,** dwarf buckeye, Georgia buckeye	Coastal plain & outer piedmont, from SE Virginia to Georgia, Alabama, & NW Florida

Source: Rudolph (1974).

flower spikes are 15 to 20 cm tall by 5 to 7.5 cm wide (Browse and Leiser 1982). The flowers are polygamo-monoecious, bearing both bisexual and male flowers. Only those flowers near the base of the branches of the cluster are perfect and fertile; the others are staminate (Bailey 1939; Rehder 1940).

The fruit is a somewhat spiny or smooth, leathery, round or pear-shaped capsule with 3 cells (figure 1), each of which may bear a single seed. Sometimes only 1 cell develops and the remnants of the abortive cells and seeds are plainly visible at maturity. When only 1 cell develops, the large seed is round to flat in shape. The ripe seeds (figure 1) are dark chocolate to chestnut brown in color, with a smooth and shining surface and have a large, light-colored hilum resembling the pupil of an eye. They contain no endosperm, the cotyledons being very thick and fleshy (figure 2). When ripe in the fall, the capsules split and release the seeds. The times of flowering and fruiting for 7 species of buckeyes are given in table 2. Other fruiting characteristics are listed in table 3.

Normally, horsechestnut and Ohio buckeye will set viable seeds almost every year. Bottlebrush buckeye rarely sets seed except in very hot, dry, late summers (Browse 1982).

Collection of fruits; extraction and storage of seeds. The fruits may be collected by picking or shaking them from the trees as soon as the capsules turn yellowish and begin to split open or by gathering them from the ground soon after they have fallen. The fruits may be dried for a short time at room temperature to free the seeds from any parts of the capsules that may still adhere to them, but great care must be taken not to dry them too long. When this occurs, the seedcoats become dull and wrinkled and the seeds lose their viability. There is ample evidence that buckeyes are recalcitrant in nature (Bonner 1969; Pence 1992; Tompsett and Pritchard 1993). Moisture contents at the time of shedding have been reported as 49% for horsechestnut (Suszka 1966) and 56% for red buckeye (Bonner 1969). The seeds of this genus should be sown at once in the fall or stratified promptly for spring-sowing.

Figure 1—*Aesculus,* buckeye: capsules and seeds of *A. glabra*, Ohio buckeye (**topleft**); *A. pavia*, red buckeye (**top right**); *A.hippocastanum*, painted buckeye (**middle left**); *A. sylvatica*, horsechesnut (**middle right**); *A. california*, yellow buckeye (bottom).

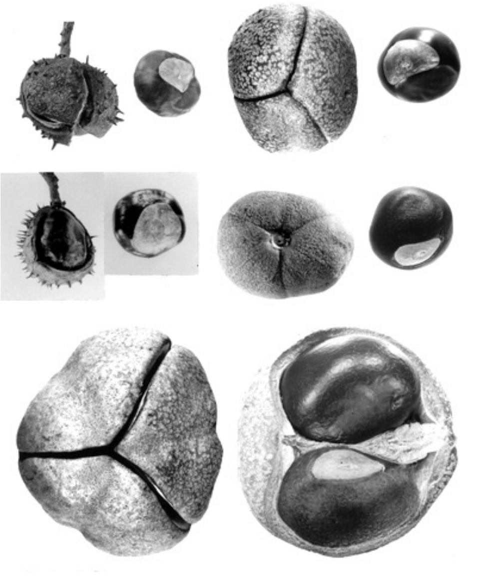
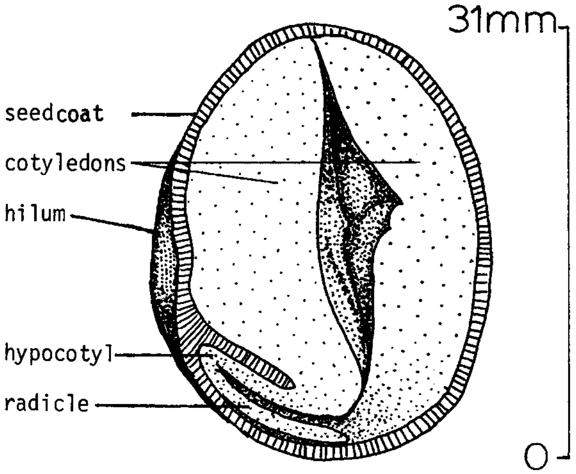


Figure 2—*Aesculus glabra*, Ohio buckeye: longitudinal section through a seed.



Buckeye seeds must be stored with moisture contents close to what they are shed with, but even then their viability cannot be maintained very long. Initial viability of fresh seeds of horsechestnut was maintained for 6 months when they were stored in polyethylene bags at 1 °C. This storage condition is the same as cold moist stratification because of the high moisture content of fresh seeds (Suszka 1966). When seeds were stored at –1 °C in sealed packages without added moisture for 13 months, germination dropped from 85% to 60%; after 15 months, however, germination was only 25% (Widmoyer and Moore 1968). Data on number of cleaned seeds per weight are listed for 7 species in table 4. Purity and soundness usually are close to 100% (Rudolf 1974). Nonviable seeds will float in water and can be discarded (Browse 1982).

Pregermination treatments. Seeds of Ohio, yellow, and painted buckeyes and horsechestnut require stratification or prechilling to induce prompt germination (Rudolf 1974). Stratification has been done in moist sand or sand-peat mix-

Table 2—*Aesculus,* buckeye: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal
A. californica	S California	Apr–Sept	Sept–Oct	Nov & Dec
A. flava	—	Apr–June	Sept	Sept
A. glabra	—	Mar–May	Sept–mid-Oct	Early Sept–late Oct
var. *arguta*	Texas	Mar–Apr	May–June	—
	Minnesota	May	Sept–Oct	Sept–Oct
A. hippocastanum	Europe & NE US	Late Apr–early June	Mid-Sept–early Oct	Mid-Sept–mid-Oct
A. parviflora	SW Georgia, Alabama	July-Aug	Oct–Nov	Oct–Nov
A. pavia	South part of range	Mar–Apr	Sept–Oct	Sept–Nov
	North part of range	May–June	Sept–Oct	Sept–Nov
A. sylvatica	—	Apr–May	July–Aug	July–Aug
	Minnesota	May	Sept–Oct	Sept–Oct

Sources: Brown and Kirkman (1990), Harrar and Harrar (1962), Little (1953), Loiseau (1945), NBV (1946), Radford and others (1964), Rehder (1940), Rudolf (1974), Sargent (1965), Sus (1925), Turner (1969), van Dersal (1938), Vines (1960), Wyman (1947).

Table 3—*Aesculus,* buckeye: height, year first cultivated, flower color, seed-bearing age, seed crop frequency, and fruit ripeness criteria

Species	Height at maturity (m)	Year 1st cultivated	Flower color	Min seed-bearing age (yr)	Years of large seedcrops	Fruit ripeness criteria	
						Preripe color	Ripe color
A. californica	4.5–12	1855	White to rose	5	1–2	—	Pale brown
A. flava	7.5–27	1764	Yellow	—	—	Yellowish	Yellowish
A. glabra	9–21	1809	Pale greenish yellow	8	—	Green	Yellowish
var. *arguta*	2–11	1909	Light yellowish green	8	1+	Yellow	Yellowish green
A. hippocastanum	7.5–24	1576	White tinged with red	—	1–2	Green	Yellowish brown
A. parviflora	4.5–6	—	White	—	—	—	—
A. pavia	2.5–8.5	1711	Bright red	—	—	—	Light brown
A. sylvatica	7.5–20	1826	Pale yellow, red veins towards base	8	1+	Yellow-green	Yellowish tan

Sources: Brown and Kirkland (1990), Rehder (1940), Rudolf (1974), Sargent (1965)

Table 4—*Aesculus,* buckeye: seed data

Species	Place collected	Cleaned seeds/weight*			
		Range		Average	
		/kg	/lb	/kg	/lb
A. californica	El Dorado & Contra Costa Cos., California	18–36	8–16	26	127
A. flava	Kentucky & North Carolina	60–66	27–30	62	28
A. glabra	—	106–148	48–67	128	58
var. *arguta*	Carver Co., Minnesota	71–104	32–47	88	40
A. hippocastanum	W Europe	51–75	23–34	64	29
A. parviflora	SW Georgia, Alabama	40–60	18–27	51	23
A. pavia	Oktibbeha Co., Mississippi	—	—	117	53
A. sylvatica	Greene Co., Georgia, & Carver Co., Minnesota	68–126	31–57	88	40

Sources: Browse (1982), NBV (1946), Rudolf (1974).

* This value varies not only with seed size but also with moisture content, which is initially rather high in *Aesculus* seeds. One sample of *A. flava* seeds showed a moisture content of 95% (dry-weight basis) after it had been kept at room temperature for 36 days after collection.

tures at 5 °C for about 120 days, and by storage in sealed containers at 1 °C for 100 days or longer (May 1963; Rudolf 1974; Suszka 1966). In contrast, fresh seeds of California and red buckeyes can germinate satisfactorily without pretreatment (Rudolf 1974). Red buckeye seeds requires no stratification even though germination is delayed until spring. Cool winter temperatures suppress the germination, thus preventing autumn emergence (Browse 1982).

Bottlebrush buckeye seeds exhibit a type of epicotyl dormancy in so far as the root system continues to develop, but the shoot becomes dormant after it has emerged (Browse 1982). Further development of the shoot system does not occur until the spring (Browse 1982).

Presowing treatments of horsechestnut seeds increased germination 3 to 15% over the control. The treatments yielded the following germination rates: exposure to 50 °C, 92% germination; soaking with slight drying, 92%; exposure to 35 °C, 87%; exposure to high pressure, 87%; soaking in cobalt nitrate, 85%; soaking in chlorocholine chloride, 80%; and control, 77% (Tarabrin and Teteneva 1980).

Stratification benefits Himalayan horsechestnut. There was a 5-fold increase in germination at 30 °C from 12% for the control to 60% following stratification for 15 days (Maithani and others 1990). Prolonging the stratification period to 30 days resulted in 79% germination (Maithani and others 1990).

Germination tests. Stratified buckeye seeds have been germinated in sand or on wet paper at diurnally alternating temperatures of 30 and 20 °C. Results are summarized in table 5. Official testing rules for red buckeye (AOSA 1998) call for germinating unstratified seeds for 28 days on the top of wet paper at the 30/20 °C regime. A recommendation for germinating seeds of horsechestnut without stratification is to soak them in water for 48 hours and cut off one-third of the seed at the scar end without removing the seedcoat. The portion with the scar should then be germinated in sand flats for for 21 days at the same 30/20 °C regime (ISTA 1993).

Nursery practice. Under natural conditions, seeds of most buckeye species germinate in the early spring. California buckeye, however, germinates just after winter rains have begun, usually in November. In the nursery, buckeye seeds usually are sown in the fall as soon after collection as possible to prevent drying and loss of viability. If desired, however, the seeds of species having embryo dormancy can be stratified or placed in cold, moist storage promptly and then sown in the spring (Rudolf 1974; Suszka 1966). Himalayan horsechestnut seeds without any treatment showed 80% germination after 133 days (Maithini and others 1990). Seeds sown after 30 days of cold stratification showed 68% germination in 78 days (Maithini and others 1990). The seeds should be sown about 5 cm (2 in) apart in rows 15 cm (6 in) apart (NBV 1946) and covered with 2.5 to 5 cm (1 to 2 in) of soil. The seeds should be sown with the scar underneath so that the radicle emerges in the correct position to produce a normal seedling (Browse and Leiser 1982). If the seeds are variable in size, it is better to grade them so that small sizes are discarded or sown separately, as these rarely make large 1-year seedlings (Browse 1982).

Germination is hypogeal (figure 3) and usually is complete 3 to 4 weeks after spring sowing (NBV 1946). A tree percentage of 70 has been obtained (Rudolf 1974). The beds should not be over-watered because the seeds rot rather easily (Rudolf 1974). Ordinarily, 1+0 stock is large enough for field planting.

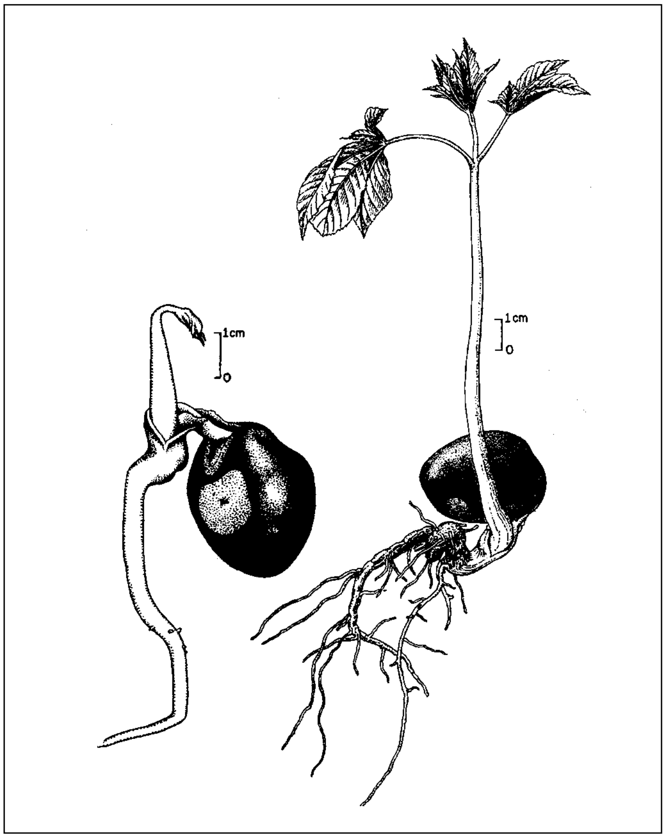
Table 5—*Aesculus,* buckeye: cold stratification periods, germination test conditions, and results

			Germination test conditions				Germinative energy		
				Temp (°C)					
Species	Cold stratification* (days)	Daily light (hrs)	Medium	Day	Night	Days	Amount (%)	Time (days)	Germinative (%)
A. californica	0	—	Sand	30	20	20	—	—	56
A. flava	120	—	Sand	30	20	40	62	27	76
A. glabra	120	—	Sand	30	20	40	—	—	59
var. *arguta*	120	8	Sand	24	17	30	—	—	76
A. hippocastanum	120	—	Sand	30	20	30	—	—	89
A. pavia	0	8	Kimpak	30	20	30	62	20	70
A. sylvatica	90	—	Sand	—	—	30	—	—	78

Sources: May (1963), NBV (1946), Rudolf (1974), Suszka (1966), Widmoyer and Moore (1968).

* Cold stratification temperatures ranged from – 0.5 to 5 °C.

Figure 3—*Aesculus californica*, California buckeye: seedling development at 2 and 4 days after germination.



References

AOSA [Association of Official Seed Analysts]. 1998. Rules for testing seeds. In: Proceedings of the Association of Official Seed Analysts: 1–123.

Bailey LH. 1939. The standard encyclopedia of horticulture. New York: Macmillan. 3639 p.

Bonner FT. 1969. Personnel communication. Starkville, MS: USDA Forest Service, Southern Forest Experiment Station.

Brown CL, Kirkman KL. 1990. Trees of Georgia and adjacent states. Portland, OR: Timber Press. 292 p.

Browse PM. 1982. The propagation of the hardy horse chestnuts and buckeyes. Plantsman 4(3): 150–164.

Browse PM, Leiser AT. 1982. The California buckeye. Plantsman 4(1): 54–57.

Harrar ES, Harrar JG. 1962. Guide to southern trees. 2nd ed. New York: Dover Publishing. 709 p.

ISTA [International Seed Testing Association]. 1993. Rules for testing seeds: rules 1993. Seed Science and Technology 21 (Suppl.): 1–259.

Little EL Jr. 1953. Checklist of native and naturalized trees of the United States (including Alaska). Agric. Handbk. 41. Washington, DC: USDA Forest Service. 472 p.

Loiseau J. 1945. Les arbres et la forêt. Paris. 204 p.

Maithani GP, Thapliyal RC, Bahuguna VK, Sood OP. 1990. Enhancement of seed germination and seedling growth of *Aesculus indica* by stratification. Indian Forester 116(7): 577–580.

May C. 1963. Note on storage of buckeye and horsechestnut seed. American Horticulture Magazine 42(4): 231–232.

NBV [Nederlandsche Boschbouw Vereeniging]. 1946. Boomzaden: handleiding inzake het oogsten, behandelen, bewaren en uitzaaien van boomzaden [Tree seed: handbook on the collection, extraction, storage, and sowing of tree seed]. Wageningen, The Netherlands: Ponsen and Looijen. 171 p.

Pence VC. 1992. Desiccation and the survival of *Aesculus, Castanea,* and *Quercus* embryo axes through cryopreservation. Cryobiology 29: 391–399 [Seed Abstracts 1994; 17(1): 21].

Radford AE, Ahles HE, Bell CR. 1964. Guide to the vascular flora of the Carolinas. Chapel Hill: University of North Carolina Book Exchange. 383 p.

Rehder A. 1940. Manual of cultivated trees and shrubs hardy in North America. 2nd ed. New York: Macmillan. 996 p.

Rudolf PO. 1974. *Aesculus* L., buckeye. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 195–200.

Sargent CS. 1965. Manual of the trees of North America (exclusive of Mexico). 2nd ed., corrected and reprinted. New York: Dover. 910 p.

Sus NI. 1925. Pitomnik [The forest nursery]. Moscow. 227 p.

Suszka B. 1966. Conditions for breaking of dormancy of germination of the seeds of *Aesculus hippocastanum* L. Arbor. Kórnicke. 11: 203–220.

Tarabrin VP, Teteneva TR. 1980. Presowing treatment of seeds and its effect on the resisitance of seedlings of woody plants against drought. Soviet Journal of Ecology 10 (3): 204–211.

Tompsett PB, Pritchard HW. 1993. Water status changes during development in relation to the germination and desiccation tolerance of *Aesculus hippocastanum* L. seeds. Annals of Botany 71: 107–116.

Turner BL. 1969. Personal communication. Austin: University of Texas.

Van Dersal WR. 1938. Native woody plants of the United States: their erosion control and wildlife values. Misc. Pub. 303. Washington, DC: USDA. 362 p.

Vines RA. 1960. Trees, shrubs, and woody vines of the Southwest. Austin: University of Texas Press. 1104 p.

Widmoyer FB, Moore A. 1968. The effect of storage period temperature and moisture on the germination of *Aesculus hippocastanum* seeds. Plant Propagator 14(1) : 14–15.

Wyman D. 1947. Seed collecting dates of woody plants. Arnoldia 7(9): 53–56.

Simaroubaceae—Quassia family

Ailanthus altissima (P. Mill.) Swingle

ailanthus

John C. Zasada and Silas P. Little

Dr. Zasada retired from the USDA Forest Service's North Central Research Station; Dr. Silas Little (deceased) retired from the USDA Forest Service's Northeastern Forest Experiment Station

Synonyms. *Toxicodendron altissimum* Mill., *Ailanthus glandulosa* Desf.

Other common names. Tree-of-heaven ailanthus, tree-of-heaven, copaltree.

Growth habit, occurrence, and use. Native to China, this 12.5- to 25-m-tall deciduous tree is described as "the most adaptable and pollution tolerant tree available" (Dirr 1990). Although it was originally considered a desirable ornamental tree, its desirability and usefulness are now questioned (Dirr 1990; Feret 1985) and many consider it an "invasive alien pest." It is sometimes planted for shelterbelts, for game food and cover, and, rarely, for timber as in New Zealand. Ailanthus was introduced into cultivation in England in 1751 (Feret 1985; Illick and Brouse 1926) and brought to America in 1784 (Little 1974). It has become naturalized in many parts of the United States—from Massachusetts to southern Ontario, Iowa, and Kansas, and south to Texas and Florida, as well as from the southern Rocky Mountains to the Pacific Coast (Feret and Bryant1974; Feret and others 1974; Little 1979). In some localities, ailanthus is so well-established that it appears to be a part of the native flora. Wood properties are summarized by Alden (1995) and silvics by Miller (1990). There are a number of other *Ailanthus* species grown in other parts of the world for various purposes (Alam and Anis 1987; Beniwal and Singh 1990; Feret 1985; Rai 1985; Ramikrishnan and others 1990).

Ailanthus is an aggressive, intolerant pioneer species with rapid juvenile growth of 1 to 1.5 m/year. It invades severely disturbed sites, harsh environments, and poor soils. It suckers from roots and can form dense stands, making it difficult for native species to colonize. Stands may be maintained by root suckering but it does not regenerate from seed under its own canopy (Bordeau and Laverick 1958; Miller 1990). One or more potent inhibitors of seed germination and seedling growth are produced in the bark, leaves, and seeds (Heisey 1990; Lawrence and others 1991). Heisey (1990) concluded that allelochemicals in ailanthus may have potential as naturally produced herbicides.

Flowering and Fruiting. The tree is mainly dioecious, with some monoecious individuals (Dirr 1990; Miller 1990). Flowers are usually unisexual, but perfect flowers do occur in some individuals (Feret 1973). Flowering has been observed in seedlings 6 weeks after germination (Feret 1973).

Commercial "seed" consists of the 1-celled, 1-seeded, oblong, thin, spirally twisted samaras. These samaras, with seeds near the middle, are 8 to 12 mm wide and 33 to 48 mm long (Feret and others 1974) and light reddish brown in color (figure 1). Flowering occurs from mid-April to July (Little 1974). Seeds ripen in large panicles in September to October of the same season and are dispersed from October to the following spring (Illick and Brouse 1926). Ailanthus is a prolific seeder: 15- to 20-year-old trees bear considerable quantities. Seeds have no endosperm (figure 2).

Collection of fruits; extraction and storage of seeds. Ailanthus seeds have been found in soil seedbanks in stands with no individuals present in the overstory. This suggests that seeds may be stored in the soil for some period of time after parent trees have disappeared from a site (Dobberpuhl 1980).

Figure 1—*Ailanthus altissima*, ailanthus: samara.

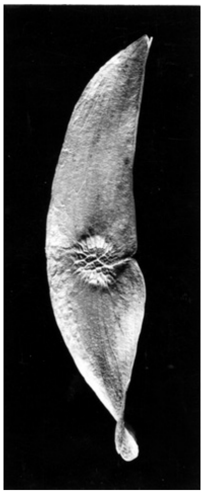
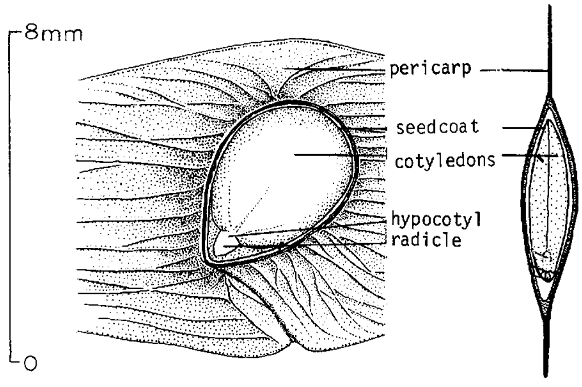


Figure 2—*Ailanthus altissima*, ailanthus: longitudinal section through a seed.



Ailanthus fruits are picked from standing trees by hand or flailed or stripped onto canvas at any time during the late fall and early winter. After collection, the fruits should be spread out to dry (to lose superficial moisture). They may then be run through a macerator and fanned to remove impurities, or they may be flailed or trampled in a burlap bag and run through a fanning mill (Little 1974).

Forty-five kilograms (100 lb) of fruit yields 13.6 to 40.9 kg (30 to 90 lb) of cleaned seeds (Little 1974). Seeds with wings attached weigh from 22,700 to 75,500/kg (10,300 to 34,300/lb), with an average of about 38,700/kg (17,500/lb) (Feret and others 1974; Little 1974). Cleaned seeds (without wings) weigh from 29,000 to 43,000/kg (13,200 to 19,500) with a mean of 37,200/kg (16,900/lb) (Al'benskii and Nikitin 1956). Germination capacity of seedlots is normally in the 75 to 96% range (Al'benskii and Nikitin 1956; Graves 1990; Little 1974).

Seeds should be stored with low moisture contents at temperatures of 1 to 3 °C, and in sealed containers (Heit 1967). However, seedlots stored in sacks for over a year at temperatures ranging from –6 to 40 °C still had germination of 75% (Little 1974). In Russia, seeds are stored in boxes at 0 to 4 °C, layers about 2.5 cm (about 1 in) thick being separated and topped by layers of dry sand half as thick (Shumiliana 1949). Although sensitive to moisture and fluctuating temperatures, seeds can be successfully stored for long periods in sealed containers at low moisture contents in a refrigerator (Heit 1967).

Germination. Stratification appears to improve germination in most cases, although varying amounts of germination occur in unstratified seeds (Bordeau and Laverick 1958; Dirr 1990; Graves 1990; Little 1974; Shumilina 1949). Graves (1990) found that although total germination was not affected by stratification, germination rate was greater in stratified seeds. Thirty to 60 days of stratification at 1 to 5 °C is usually recommended (Dirr 1990; Little 1974; Shumilina 1949); however, Graves reported 70, 77, and 96% germination after stratification at 5 °C for 0, 4, and 12 days, respectively. Seed testing rules recommend temperatures of 20 to 30 °C with no stratification (pericarp removal may increase germination rate); first evaluation at 7 days and a test duration of 21 days (ISTA 1993). Ailanthus seed germination was little affected by salt concentrations representative of roadside environments where salt is applied in winter; seeds of native oaks and birch were more sensitive (Bicknell and Smith 1975). Other *Ailanthus* spp. are more difficult to germinate than tree-of-heaven (Ramakrishnan and others 1990).

Nursery practice. Seeds can be sown immediately after collection if conditions permit or they can be stratified and sown in the spring with drills. Broadcast seeds should be covered with 1.3 cm ($^{1}/_{2}$ in) of soil. Fifteen to 25% of the viable seeds sown produce usable 1+0 seedlings (Little 1974). Thus, 0.45 kg (1 lb) of seeds may yield 3,000 usable plants (Van Dersal 1938). Greenhouse studies indicate that ailanthus could be grown in containers (Feret and Bryant 1974; Feret and others 1974; Heninger and White 1974). Maximum seedling growth occurs at a soil temperature of 19 °C (Heninger and White 1974). Ailanthus can be produced vegetatively from root cuttings (Dirr and Heuser 1987).

References

Alam MM, Anis M. 1987. Ethno-medicinal uses of plants growing in the Bulandshahr district of northern India. Journal of Ethnopharmacology 19(1): 85–88.

Al'benskii AV, Nikitin PD, eds. 1956. Agrolesomeliortsiya, 3rd ed. Moscow: Gosundarstvennoye Izdatel'stvo Sel'skohozyaystvennoy Litrtsyury [Handbook of afforestation and soil amelioration. Transl. TT 66-51098. 1967. Springfield, VA: USDC CFSTI. 516 p.].

Alden HA. 1995. Hardwoods of North America. Gen. Tech. Rep. FPL-83. Madison, WI: USDA Forest Service, Forest Products Laboratory. 136 p.

Beniwal BS, Singh NB. 1990. Genetic improvement of forest trees in Arunachal Pradesh. Indian Forester 116(1): 3–10.

Bicknell SH, Smith WH. 1975. Influence of soil salt, at levels characteristic of some roadside environments, on the germination of certain tree seeds. Plant and Soil 43(3): 719–722.

Bordeau PE, Laverick ML. 1958. Tolerance and photosynthetic adaptability to light intensity in white pine, red pine, hemlock, and ailanthus seedlings. Forest Science 4(3): 196–207.

Dirr MA. 1990. Manual of woody landscape plants: their identification, ornamental characteristics, culture propagation and uses. Champaign, IL: Stipes Publishing Co. 1007 p.

Dirr MA, Heuser CW Jr. 1987. The reference manual of woody plant propagation: from seed to tissue culture. Athens, GA: Varsity Press. 239 p.

Dobberpuhl J. 1980. Seed banks of forest soils in east Tennessee [MS thesis]. Knoxville: University of Tennessee. 219 p.

Feret PP. 1973. Early flowering in *Ailanthus*. Forest Science 19: 237–239.

Feret PP. 1985. *Ailanthus:* variation, cultivation, and frustration. Journal of Arboriculture 11(12): 361–368.

Feret PP, Bryant RL. 1974. Genetic differences between American and Chinese *Ailanthus* seedlings. Silvae Genetica 23(5): 144–148.

Feret PP, Bryant RL, Ramsey JA. 1974. Genetic variation among American seed sources of *Ailanthus altissima*. Scientia Horticulturae 2(4): 405–411.

Graves WR. 1990. Stratification not required for tree-of-heaven germination. Tree Planters' Notes 41 (2): 10–12.

Heisey RM. 1990. Allelopathic and herbicidal effects of extracts from the tree of heaven *Ailanthus altissima*. American Journal of Botany 77: 662–670.

Heit CE. 1967. Propagation from seed: 11. Storage of deciduous tree and shrub seeds. American Nurseryman 126(10): 12–13, 86–94.

Heninger RL, White DP. 1974. Tree seedling growth at different soil temperatures. Forest Science 20: 363–367.

Illick JS, Brouse, EF. 1926. The ailanthus tree in Pennsylvania. Pennsylvania Department of Forests and Waters Bulletin 38: 1–29.

ISTA [International Seed Testing Association]. 1993. International rules for seed testing: rules 1993. Seed Science & Technology 21 (Suppl.): 1–259.

Lawerence JG, Colwell A, Sexton OJ. 1991. The ecological impact of allelopathy in *Ailanthus altissima* (Simaroubaceae). American Journal of Botany 78(7): 948–958.

Little EL Jr. 1979. Checklist of United States trees (native and naturalized). Agric. Handbk. 541. Washington, DC: USDA, Forest Service. 375 p.

Little S. 1974. *Ailanthus altissima* (Mill.) Swingle, ailanthus. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 201–202.

Miller JH. 1990. *Ailanthus altissima* (Mill.) Swingle, ailanthus. In: Burns RM, Honkala BA, tech. coords. Silvics of North America. Volume 2, Hardwoods. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 101–104.

Rai SN. 1985. Notes on nursery and regeneration technique of some species occurring in southern tropical evergreen and semi-evergreen forests of Karnataka (India): 2. Indian Forester 111(8): 644–657.

Ramakrishnan HB, Jacqueline AS, Vinaya Rai RS. 1990. Studies on the ripeness index and presowing seed treatment in *Ailanthus excelsa* Roxb. Seed Science & Techology 18(3): 491–498.

Shumilina ZK. 1949. Podgotovka posevu semyan drevesnykh I kustarnikovykh porod. Vsesoyuznyy Nauchno-Issledovatel'skiy Institut Agrolesomelioratsii Goslesbumizdat Moscow [Preparation of tree and shrub seed for sowing. Transl. TT 67-51300. 1967. Springfield, VA: USDC CFSTI. 36 p.].

Van Dersal WR. 1938. Native woody plants of the United States: their erosion-control and wildlife values. Misc. Pub. 303. Washington, DC: USDA. 362 p.

Fabaceae—Pea family

Albizia Durazz.

albizia

John A. Parrotta, Herbert L. Wick, and Gerald A. Walters

Dr. Parrotta is a research program leader at the USDA Forest Service's Research and Development National Office, Arlington, Virginia; Drs. Wick and Walters retired from the USDA Forest Service's Pacific Southwest Forest and Range Experiment Station

Growth habit, occurrence, and use. The albizias include about 50 species of medium- to large-sized deciduous trees and climbers distributed throughout tropical and subtropical Asia, Africa, and Australia (Rock 1920). Many species have been introduced into the United States, and the 4 listed in table 1 are important. Silktree was introduced into the southern United States in 1745 and planted widely for ornamental purposes. Currently it is considered invasive. The species is also valuable for wildlife cover and browse (Wick and Walters 1974). Siris is planted in Hawaii for shade and ornament (Neal 1965) and was introduced into Puerto Rico during the Spanish colonial era. Its yellowish brown heartwood is moderately hard, coarse-grained, strong, and fairly durable and is used for a variety of purposes, including furniture-making, in its native Asian range (Parrotta 1987a). White siris is planted in Hawaii (Neal 1965) and was introduced into Puerto Rico in 1927 as an ornamental and fuelwood species. In Puerto Rico, white siris has become naturalized and is now common on severely disturbed sites and old fields. The light brown heartwood is moderately hard, straight-grained, strong, and durable and is used in the species' native range as an all-purpose timber (Parrotta 1987b). Raintree (formerly known as *Pithecellobium saman)* is valued for timber and wildlife habitat and as an ornamental. The wood is used for paneling, furniture, and specialty items. The tree was introduced into Florida and Hawaii (Little and Wadsworth 1964; Magini and Tulstrup 1955) and is now considered invasive.

Flowering and fruiting. The flowering and seeding dates of *Albizia* species are listed in table 2. Flowers of siris are greenish-yellow to whitish, those of silktree are light pink, and those of white siris are whitish (Little and Wadsworth 1964; Wick and Walters 1974). All species bear their flowers in clusters near the tips of branches. The fruits of all species are flat, linear, 6- to 12-seeded legumes (pods) (figure 1) and ripen within a year after the trees flower (Little and Wadsworth 1964; Rock 1920; Wick and Walters 1974). Silktree legumes are about 15 cm long; siris and white siris legumes are up to 20 cm long. When mature, the legumes of tall albizia are reddish brown, whereas those of

Table 1—*Albizia,* albizia: nomenclature, occurrence, and growth habit

Scientific name & synonym(s)	Common name(s)	Occurrence		Growth habit
		Native	US	
***A. julibrissin* Durz.** *Acacia julibrissin* (Durraz.) Willd. *A. nemu* Willd.	**silktree,** albizia, mimosa tree, powder-puff tree	Iran to Japan	Southern US	Deciduous ornamental
***A. lebbeck* (L.) Benth.** *Acacia lebbek* Willd. *Mimosa lebbek* L.	**siris,** woman's-tongue	Pakistan to Burma	Puerto Rico & Hawaii	Deciduous forest tree, ornamental
***A. procera* (Roxb.) Benth.** *Acacia procera* Willd. *Mimosa elata* Roxb. *M. procera* Roxb.	**white siris,** tall albizia	India to Melanesia & Hawaii	Puerto Rico	Deciduous forest tree
***A. saman* (Jacq.) F. Muell.** *Pithocellobium saman* (Jacq.) Benth. *Samanea saman* (Jacq.) Merr.	**raintree,** saman, monkey-pod	Central & South America & West Indies	S Florida & Hawaii	Evergreen tree (deciduous in Hawaii)

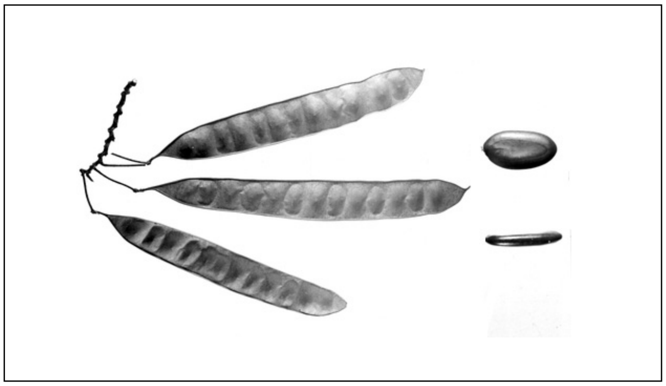
Sources: Walters and others (1974), Wick and Walters (1974).

Table 2—*Albizia,* albizia: phenology of flowering, fruit ripening, and seed dispersal

Species	Location	Flowering	Fruit ripening	Seed dispersal
A. julibrissin	S US	June–Aug	Sept–Nov	Sept–Nov
A. lebbeck	Puerto Rico	Apr–Sept	All year	All year
A. procera	Puerto Rico	Aug–Sept	Jan–June	All year
A. saman	—	Spring–fall	Fall–spring	All year

Sources: Little and Wadsworth (1964), Rock (1920), Wick and Walters (1974).

Figure 1—*Albizia julibrissin*, silktree: legumes and seeds.



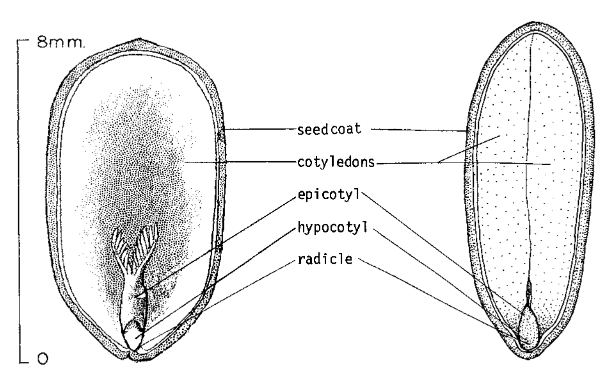
the other 2 species are straw-colored. The light brown seeds of all species are released from the dehiscent legumes from legumes that are still attached to the tree or from fallen legumes, which may travel considerable distances in high winds (Parrotta 1987a; Rock 1920; Wick and Walters 1974).

Collection, extraction, and storage. Collection of albizia seeds should begin as soon as the legumes mature. Siris seeds are particularly prone to predation by insect larvae, especially those of bruchid beetles (Parrotta 1987a). The legumes may be picked or shaken from the trees and collected on canvas. Seeds are readily extracted from the legumes by flailing or threshing. A seed cleaner or a fanning mill can be used to separate seeds from the remaining debris. Silktrees average about 24,000 clean seeds/kg (11,000/lb) (Wick and Walters 1974); siris, 7,000 to 11,000 seeds/kg (3,000 to 5,000/lb) (Parrotta 1987a); white siris, 17,000 to 25,000 seeds/kg (8,000 to 11,000/lb) (Francis and Rodríguez 1993; Parrotta 1987b); and raintrees, 4,400 to 7,720 seeds/kg (2,000 to 3,500/lb) (Walters and others 1974). Albizia seeds are orthodox in nature. Air-dried seeds of siris and white siris generally retain high germination rates for at least 1 to 2 years in storage at room temperature or under refrigeration (Parrotta 1987a). No definitive information is available on how long silktree seeds can be stored, although a small sample of seeds kept in loosely corked bottles in a laboratory for almost 5 years had a germination rate of almost 90% (Wick and Walters 1974).

Germination. Germination of albizia seeds is slow because of their impermeable seedcoats (figure 2). Dormancy can be broken either by mechanical scarification, sulfuric acid scarification, or soaking in water (Francis and Rodríguez 1993; Parrotta 1987a). The easiest, safest, and usually most effective means for breaking dormancy in siris and white siris is immersion of the seeds in boiling water for 1 to 3 minutes, soaking them in water at room temperature for 24 hours, then sowing the seeds immediately (Parrotta 1987a). Germination rates for scarified seeds range from 50 to 99% and germination begins within 2 to 4 days after sowing (Francis and Rodríguez 1993; Parrotta 1987a&b). Raintree seeds will often germinate without pretreatment, but a 10-minute soak in sulfuric acid will increase the percentage and rate of germination (Walters and others 1974). Germination as high as 92% has been reported for this species (Neal 1965; Rock 1920). Germination in albizias is epigeal (figure 3).

Nursery practice. Germination and seedling growth of albizia is favored by shallow sowing, up to 2.5 cm (1 in)

Figure 2—*Albizia julibrissin*, silktree: longitudinal section through a seed.



depth, in loose, moist soil under full sun (figure 3). Seedling growth is rapid; siris and white siris seedlings reach plantable size (20 cm in height) usually within 2 to 3 months after sowing under nursery conditions in Puerto Rico (Parrotta 1987a). Raintree seeds are sown in March in Hawaii for outplanting as $^{3}/_{4}$ + 0 stock the following winter. A sowing depth of 2.5 cm (1 in) and density of 160 to 215 seedlings/m^2 (15 to 20/ft^2) are recommended, with 75 to 85% shading of the beds (Walters and others 1974). Plantations can be established by direct sowing (for siris and white siris) or by using container seedlings (for all species). Stumped seedlings or stem, branch, and root cuttings can also be used to propagate siris and white siris (Parrotta 1987a).

References

Seeds of Puerto Rican trees and shrubs: second installment. Res. Note SO-374. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 5 p.

Little EL Jr, Wadsworth FH. 1964. Common trees of Puerto Rico and the Virgin Islands. Agric. Handbk. 249. Washington, DC: USDA Forest Service. 548 p.

Magini E, Tulstrup NP. 1955. Tree seed notes. For. Dev. Pap. 5. Rome: FAO. 354 p.

Neal MC. 1965. In gardens in Hawaii. Spec. Pub. 50. Honolulu: Bishop Museum Press. 924 p.

Parrotta JA. 1987a. *Albizia lebbek* (L.) Benth, siris. Res. Note SO-ITF-SM-7. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 5 p.

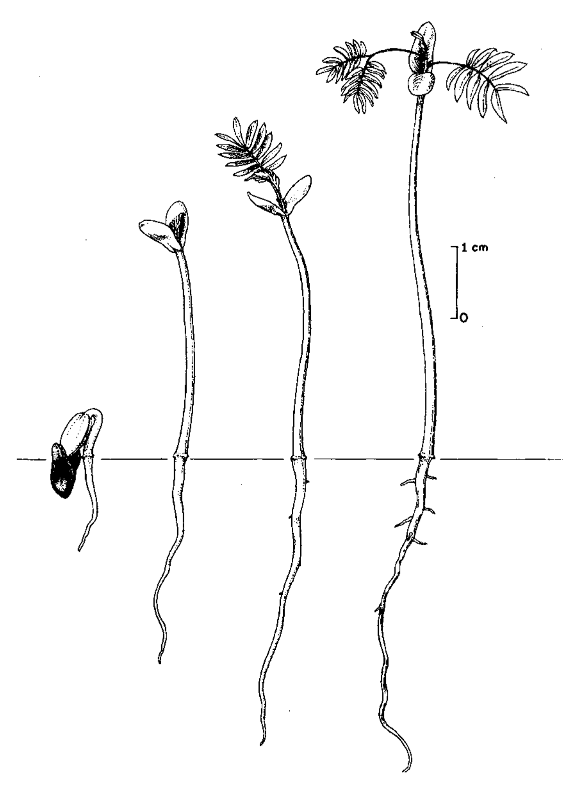
Parrotta JA. 1987b. *Albizia procera* (Roxb.) Benth., white siris, tall albizia. Res. Note SO-ITF-SM-6. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 4 p.

Rock JF. 1920. The leguminous plants of Hawaii. Honolulu: Hawaii Sugar Planters' Association. 234 p.

Walters GA, Bonner FT, Petteys EQP. 1974. *Pithecellobium* Mart., blackbead. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 639–640.

Wick HL, Walters GA. 1974. *Albizia*, albizzia. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 203–205.

Figure 3—*Albizia julibrissin*, silktree: seedling development at 1, 3, 5, and 8 days after germination.



Euphorbiaceae—Spurge family

Aleurites moluccana (L.) Willd.

Indian-walnut

Franklin T. Bonner

Dr. Bonner is a scientist emeritus at the USDA Forest Service's Southern Research Station, Mississippi State, Mississippi

Synonyms. *Aleurites javanica* Gand., *A. triloba* Forster & Forster f.

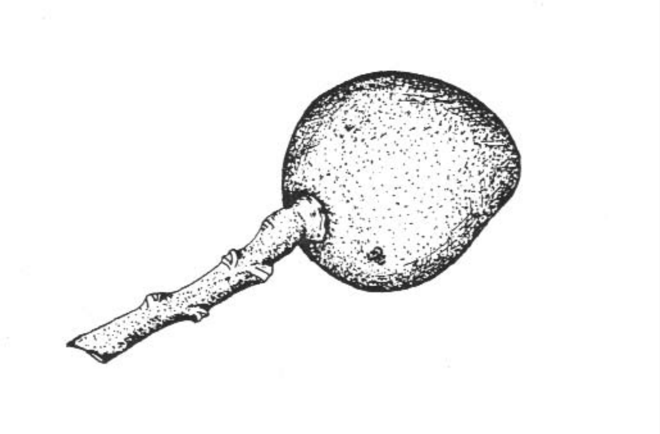
Other common names. Kukui, candlenut-tree, *tutui, nuez, nuez de India, lumbang, sakan, lama.*

Growth habit, occurrence, and uses. Indian-walnut is well-known as kukui, the state tree of Hawaii. On the Islands, it is a large, evergreen, spreading tree of moist lowland mountains up to an elevation of 671 m. It may grow to a height of 24 m and a bole diameter of 0.9 m (Little and Skolmen 1989). This species is a probable native of Malaysia, as its name suggests that it came from the Moluccan Islands. It can be found on islands throughout the Pacific region, and it has been introduced to other tropical areas, including Puerto Rico and the Virgin Islands (Little and Skolmen 1989).

The tree was introduced by early Hawaiians for its oily, nutlike seeds. Oil pressed from these seeds was once widely used for fuel in stone lamps, for paints and varnishes, and for medicines. In past years, as much as 37,850 liters (10,000 gal) of the oil was exported annually, but the industry has become unprofitable in Hawaii (Little and Skolmen 1989). The trees are still grown for production of the oil in the Philippines and other parts of the Pacific region (Eakle and Garcia 1977). In addition, the leftover oil cake can be used as fertilizer or cattle food. Local uses also included folk medicine and dyes, and a waterproofing substance can be made from the tree's sap and green fruits (Little and Skolmen 1989). Indian-walnuts have been utilized in shade, ornamental, and protection plantings in Hawaii (Little and Skolmen 1989).

Flowering and fruiting. Indian-walnut's flowers are borne in terminal cymes 9 to 15 cm long. The white individual flowers are about 10 mm long. Flowering is monoecious, with many more male flowers than female on the cymes (Little and Skolmen 1989). Fruits are round to ellipsoidal in shape, 5 to 6 cm long, and 5 to 7 cm wide, with fleshy to leathery husks (figure 1). There are 1 or 2 elliptical seeds per fruit. The seeds are 2.5 to 3.5 cm long, and the shells are hard, rough, and black (Dayan and Reaviles 1995; Little and Skolmen 1989). Flowering and fruiting occurs intermittently in Puerto Rico (Little and others 1974).

Figure 1—*Aleurites moluccana*, Indian-walnut: fruit (drawing from Little and others 1974).



Collection, extraction, and storage. Fruits may be collected from the ground after shedding or picked from the trees. In the Philippines, it is common practice to let the fruits decay for 3 to 5 days after collection and then remove the husks by hand under running water. The seeds are then dried in the sun for 3 or 4 days to a low moisture content; there are about 116/kg (53/lb) (Dayan and Reaviles 1995). Empty or deteriorated seeds can be removed by water flotation (Tamesis 1958; Eakle and Garcia 1977). There are no long-term storage data on Indian-walnut, but the seeds are apparently orthodox in storage characteristics. Dayan and Reaviles (1995) reported that seeds dried to 10 to 12% moisture can be successfully stored at room temperature for 7 months.

Germination. Indian-walnut germinates slowly, apparently due to dormancy imposed by the hard seedcoat (Eakle and Garcia 1977). Several pretreatments have been used to speed germination. In early tests in the Philippines, seeds were heated by burning grass over a layer of seeds or by planting imbibed seeds in drums of moist soil exposed to the sun (Tabat 1925; Tamesis 1958). The heat and moisture were thought to cause the seedcoats to crack. Sometimes, very good germination could be obtained by planting untreated nuts and keeping the seedbeds very moist; this method produced 86% germination 5 months after planting (Tabat 1925). Eakle and Garcia (1977) tested numerous acid scarification treatments with sulfuric, nitric, and hydrochloric acids, but none were successful. Dayan and Reaviles (1995) recommend manual cracking of the nuts, followed by an overnight soak in tap water.

Nursery practice. Seedborne fungi may be a problem for Indian-walnut, so treatment with a good fungicide prior to planting is recommended. For container production, a 1:1:1 ratio of sand, top soil, and dried organic matter should be used as a medium (Dayan and Reavile 1995). Direct seeding has also been successful in the Philippines. Seeds are allowed to start germination in a drum of moist soil heated by the sun, then removed for direct planting in the field when they start to crack open (Tamesis 1958).

References

Dayan MP, Reaviles RS. 1995. Seed technology manual of some reforestation species. Manila: National Forestation Development Office and Ecosystem Research and Development Bureau. 60 p.

Eakle TW, Garcia AS. 1977. Hastening the germination of lumbang [*Aleurites moluccana* (L.) Willd.] seeds. Sylvatrop 4: 291–295.

Little EL Jr, Skolmen RG. 1989. Common forest trees of Hawaii (native and introduced). Agric. Handbk. 679. Washington, DC: USDA Forest Service. 321 p.

Little EL Jr, Woodbury RO, Wadsworth FH. 1974. Trees of Puerto Rico and the Virgin Islands. Volume 2. Agric. Handbk. 449. Washington, DC: USDA Forest Service: 168–170.

Tabat E. 1925. An efficient method of germinating lumbang. Makiling Echo Philippines Bureau of Forestry, Division of Forest Investigation] 4(4): 19–22.

Tamesis F. 1958. Lumbang culture in Tungao, Butuan City. Forest Leaves [July 1958]: 7–9, 40.

Betulaceae—Birch family

Alnus P. Mill.

alder

Constance A. Harrington, Leslie Chandler Brodie, Dean S. DeBell, and C. S. Schopmeyer

Dr. Harrington and Ms. Brodie are foresters on the silviculture research team at the USDA Forest Service's Pacific Northwest Research Station, Olympia, Washington; Dr. DeBell retired from the USDA Forest Service's Pacific Northwest Research Station; Dr. Schopmeyer (deceased) was the technical coordinator of the previous manual

Growth habit and occurrence. Alder—the genus *Alnus*—includes about 30 species of deciduous trees and shrubs occurring in North America, Europe, and Asia and in the Andes Mountains of Peru and Bolivia. Most alders are tolerant of moist sites and thus are commonly found along streams, rivers, and lakes and on poorly drained soils; in addition, some species occur on steep slopes and at high elevations. The principal species found in North America are listed in table 1. Many changes in the taxonomy of alder have been made over the years; in this summary, species are referred to by their currently accepted names although in many cases the information was published originally under the synonyms (and alternative common names) listed in table 1.

Although some cultivated European alder is used commercially in the eastern United States, red alder is the largest native species. It is also the most extensively utilized of the native species. Management interest and research activity on red alders have increased dramatically during the past 2 decades, and the resulting information accounts for the majority of new information added to the previous summary on alder seeds prepared by Schopmeyer (1974).

Alders are pioneer species favored by high light levels and exposed mineral soils; in addition, their ability to fix atmospheric nitrogen facilitates establishment on geologically young or disturbed sites with low levels of soil nitrogen (Harrington and others 1994). Dense stands of naturally regenerated red alders established quickly on mudflows associated with the eruption of Mount St. Helens. The trees grew rapidly and soon overtopped other pioneer species such as poplars in the nitrogen-deficient soils (Heilman 1990). Sitka alder plays a similar role in primary succession following deglaciation in Alaska.

Use. Seedlings have been planted successfully for reforestation of coal mining spoil banks (Lowry and others 1962). Soil fertility is improved through fixation of atmospheric nitrogen by microorganisms in the root nodules (Tarrant and Trappe 1971). Alders also have been planted for wildlife food and cover (Liscinsky 1965) and for ornamental use. European and red alders have been considered for use in biomass plantings for energy (Gillespie and Pope 1994) and are considered excellent firewood. In recent years, harvest and utilization of red alder has expanded greatly on the Pacific Coast of North America, where the species is used for paper products, pallets, plywood, paneling, furniture, veneer, and cabinetry (Harrington 1984; Plank and Willits 1994). Red alder is also used as a fuel for smoking or curing salmon and other seafood and its bark is used to make a red or orange dye (Pojar and MacKinnon 1994). The soft, even-grained wood lacks odor or taste and has been traditionally been used by native peoples, and more recently other woodworkers, to make bowls, eating utensils, and other items (Pojar and MacKinnon 1994). In addition, alder exports have grown from almost nothing in 1990 to more than 153,000 m^3 (or 65 million board feet) of lumber annually (Tarrant and others 1994). Several options exist for managing alder in both mixed (Miller and Murray 1978) and pure stands (Tarrant and others 1983), and a summary of management principles and alternative strategies are available for red alder (Hibbs and DeBell 1994).

Geographic races and hybrids. Considerable geographic variation exists among populations of red (Ager and others 1993; Ager and Stettler 1994; Dang and others 1994; Hamann and others 1988; Lester and DeBell 1989), speckled (Bosquet and others 1988), American green (Bosquet and others 1987), and European alders (Funk 1990; Hall and Maynard 1979). Disjunct populations of red alder have been located in Idaho (Johnson 1968), and growth of such populations and those at the extremes of species' range differs markedly from that of most populations (Lester and DeBell 1989). Natural hybridization is common in alder, and zones of introgression between some species can occur where ranges overlap (Ager and Stettler 1994). Artificial hybridization has been conducted with numerous species, including

Table 1—*Alnus,* alder: nomenclature and occurrence

Scientific name(s) & synonyms	Common name(s)	Occurrence
A. glutinosa **(L.) Gaertn.** *A. alnus* (L.) Britt. *A. rotundifolia* Mill.; *A. vulgaris* Hill *Betula alnus* var. *glutinosa* L.	**European alder,** black alder, European black alder	Native of Europe, northern Africa, & Asia; naturalized locally in parts of E Canada & NE US, cultivated in E, central, & S US
A. incana **(L.) Moench** *Betula alnus* var. *incana* L.	**mountain alder,** European speckled alder, hoary alder, gray alder	Native of Europe & the Caucasus area; occurs in North America only under cultivation
A. incana **ssp.** ***rugosa*** **(Du Roi) Clausen** *A. incana* var. *americana* Reg. *A. glauca* Michx. *A. rugosa* (Du Roi) Spreng. var. *americana* (Reg.) Fern *A. rugosa* var. *tomophylla* (Fern.) Fern. *Betula alnus* var. *rugosa* Du Roi	**speckled alder,** tag alder, swamp alder, *aulne blanchâtre*	E & central Canada, N central US & in Appalachian Mtns to West Virginia & Maryland
A. incana **ssp.** ***tenuifolia*** **(Nutt.) Breitung** *A. incana* var. *occidentalis* (Dippel) Hitch. *A. incana* var. *virescens* S. Wats. *A. occidentalis* Dippel *A. rugosa* var. *occidentalis* (Dippel) Hitch. *A. tenuifolia* Nutt.	**thinleaf alder,** mountain alder	Yukon & Alaska S to W Montana & Oregon, in Sierra Nevada to central California, & E to Arizona & New Mexico
A. maritima **(Marsh.) Muhl. ex Nutt.** *A. maritima* ssp. *metoporina* (.Furlow) E. Murr *A. metoporina* Furlow *Betula-alnus maritima* Marsh.	**seaside alder,** brook alder	Widely disjunct populations in Delaware, Maryland, & Oklahoma
A. nepalensis **D. Don** *A. boshia* Buch.-Hamilt. ex D. Don *Clethropsis nepalensis* (D. Don) Spach.	**Nepal alder,** *utis, maibao*	Native of India & Burma; planted in Hawaii
A. oblongifolia **Torr.**	**Arizona alder,** New Mexican alder, *aliso* (Mexico)	Scattered populations in high mtns of Arizona, New Mexico, & Mexico
A. rhombifolia **Nutt.** *A. rhombifolia* var. *bernardina* Munz & Johnson	**white alder,** Sierra alder, California alder	Interior of S British Columbia, Washington, Oregon, & Idaho; Sierra Nevada & coastal ranges in California & N Baja California
A. rubra **Bong.** *A. oregona* Nutt. *A. oregona* var. *pinnatisecta* Starker	**red alder,** Oregon alder, western alder, Pacific Coast alder	Pacific Coast region from SE Alaska to S California
A. serrulata **(Ait.) Willd.** *A. incana* var. *serrulata* (Ait.) Boivin *A. novebroacensis* Britt. *A. rubra* (Marsh.) Tuckerman *A. rugosa* (Du Roi) Spreng. var. *serrulata* (Ait.) Winkler *A. serrulata* var. *subelliptica* Fern. *Betula serrulata* (Ait.)	**hazel alder,** smooth alder, black alder	SW Nova Scotia & central Maine W to Missouri & S to E Texas & Florida

hybrids of red alder with European or mountain alders (Chiba 1966; Hall and Maynard 1979; Ljunger 1959).

Flowering and fruiting. Species in the genus are typically monoecious, with clusters of separate male and female flowers in close proximity. Flower initiation probably occurs during late June or July for both red and European alders (Ager and others 1994; Brown 1986; McVean 1955). The male and female flowers develop into catkins that elongate in late winter or early spring and mature on the previous year's twigs (table 2). For red alders, peak pollen shedding precedes peak female receptivity by only 2 to 4 days (Stettler 1978). For a specific description of staminate and pistillate catkins, see Brayshaw (1976). The strobiles of most species are 10 to 15 mm long when mature (figure 1), but those of Nepal, red, and Sitka alders are larger, having lengths of 12 to 24 mm (Carlson and Bryan 1959; Funk 1990; Harrington 1990; Krstinic 1994; Townsend and Douglass 1994). They are produced in abundance before trees reach 10 years of age in at least 2 species. European alders can produce flowers by their second growing season, and individual red alder trees are sexually mature at 3 or 4 years. Most dominant trees in a red alder stand will produce seeds by age 6 to 8 years (Harrington and DeBell 1995; Stettler 1978). Although the majority of seeds produced are probably the result of outcrossing, both selfing and apomixis occur in red alder (Stettler 1978). Seed production resulting from selfing has been reported for European and mountain alders; however, in many cases self-fertilization results in

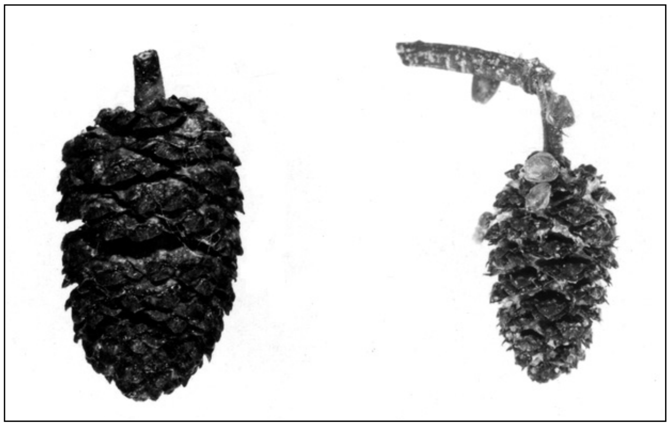
Table 1—*Alnus,* alder: nomenclature and occurrence (Continued)

Scientific name(s) & synonyms	Common name(s)	Occurrence
***A. viridis* (Vill.) Lam. & DC.** *A. ovata* (Schr.) Lodd. *Alnobetula* (Ehrh.) K. Koch *Betula viridis* Vill.	**Sitka alder**	S Arctic subarctic, and N mountainous regions of North America & Asia
***A. viridis* ssp. *crispa* (Ait.) Turrill** *A. crispa* (Ait.) Pursh *A. crispa* var. *elongata* Raup. *A. crispa* var. *harricanensiis* Lepage *A. crispa* var. *mollis* (Fern.) Fern. *A. crispa* var. *stragula* Fern. *A. mollis* Fern. *A. viridis* var. *crispa* (Michx.) House *A. alnobetula* var. *crispa* (Michx.) Winkler *Betula crispa* (Ait.)	**American green alder,** green alder, mountain alder	Labrador to Alberta, S to Minnesota & New England
A. viridis* ssp. *fruticosa* (Rupr.) Nyman *A. fruticosa* Rupr. *A. viridis* var. *fruticosa* (Rupr.) Reg.	**Siberian alder**	Alaska S to British Columbia & Alberta, disjunct populations in Washington, Oregon, & N California
***A. viridis* ssp. *sinuata* (Regel) A. Löve & D. Löve** *A. crispa* ssp. *sinuata* (Reg.) Hultén *A. sinuata* (Reg.) Rydb. *A. sitchensis* (Reg.) Sarg. *A. viridis* var. *sinuata* Reg.	**Sitka alder,** mountain alder, wavyleaf alder	Yukon & Alaska S to N California & W Montana; also in E Asia

Sources: Schopmeyer (1974), FNAEC (1997).

* In western North America, Siberian alder (*A. viridis* ssp. *fruticosa*) has long been mistaken for American green alder (*A. v.* ssp. *crispa*), which it closely resembles, or for Sitka alder (*A. v.* ssp. *sinuata*) (FNASEC 1997).

Figure 1—*Alnus*, alder: mature female catkins (strobiles) of *A. rhombifolia*, white alder (**left**); *A. serrulata*, hazel alder (**right**).



aborted ovules (Krstinic 1994). Information on the effects of management practices on reproductive processes is limited. In young red alder plantings in western Washington, flowering varied by half-sib family but overall was reduced in close spacings and by summer irrigation (Harrington and DeBell 1995). However, dry weather in spring reduced germination rates of European alder seeds, making irrigation early in the year desirable when precipitation is below normal (Hall and Nyong 1987).

Seed production varies from year to year, site to site, and tree to tree (Ager and others 1994; Brown 1985, 1986; Lewis 1985; Koski and Tallquist 1978; Krstinic 1994; McGee 1993), but good crops are borne at least once every 4 years (table 3). LaBastide and van Vredenburch (1970) reported that seed crops for European alder follow an annually alternating pattern. McVean (1955) concluded that seed crops of European alder could vary substantially from year to year, but that "boom-and-bust" patterns of seed production were not typical. Complete failure of a seedcrop is rare, but after a severe freeze in November 1955, almost no red alder seeds were produced in 1956 (Worthington 1965).

Seeds are small nuts ("nutlets") borne in pairs on the bracts of the strobiles. The nuts of red, Siberian, and Sitka alders have broad wings about as wide as or wider than the body of the nut. In the other species included here, the wings are reduced to a narrow border (figure 2) (Fernald 1950; Sargent 1965). Seeds are without endosperm and contain only small cotyledons (figure 3). For additional information on reproductive biology of red alders, see Ager and others (1994).

The factors regulating the timing of seed dispersal in alders have not been investigated, but they are probably similar to those regulating the release of seeds from the cones of conifers; that is, once strobiles are mature, disper-

Table 2—*Alnus,* alder: phenology of flowering and fruiting*

Species	Location	Flowering	Fruit ripening	Seed dispersal
A. glutinosa	E US	Mar–May	Sept	Sept or Oct–early spring
	S US & England	(can start Jan)	Feb–April	—
A. incana	Europe	Mar–May	Sept–Nov	Sept–Dec
ssp. *rugosa*	Canada, US	Mar-May	—	—
ssp. *tenuifolia*	Idaho, Montana, Oregon	Mar–Apr	Aug–Sept	—
A. nepalensis	Hawaii	—	Oct–Feb	Oct–Apr
A. rhombifolia	Oregon	Mar	Late Sept–early Oct	—
A. rubra	Washington, Oregon	Late winter–early spring	Aug–Oct	Sept–Dec
A. serrulata	—	Feb–May	Late Sept–early Oct	—
A. viridis				
ssp. *crispa*	E US, Alaska	Spring	Late Aug–mid-Oct	Soon after ripening
		Apr–June	Mid Sept–early Oct	Sept–early spring
ssp. *sinuata*	Alaska, W Canada, & NW US	Apr–June	Sept–Dec	—

Sources: Densmore (1979), Fernald (1950), Funk (1990), Harrington (1990), Hitchcock and others (1964), Lewis (1985), McDermott (1953), McGee (1988), McVean (1955), Schopmeyer (1974), White (1981).

* Flowering occurs during the period when leaves unfold.

Table 3—*Alnus,* alder: growth habit, height, seed-bearing age, and seedcrop frequency

Species	Growth habit	Height at maturity (m)	Year first cultivated	Minimum seed-bearing age (yrs)	Years between large seedcrops
A. glutinosa	Tree	to 35	1866	6–7	—
A. incana	Tree	to 20	—	under 25	1–4
ssp. *rugosa*	Tree or shrub	to 8	—	—	—
ssp. *tenuifolia*	Tree or shrub	1–9	1880	—	—
A. nepalensis (Hawaii)	Tree	15–30	1916	10	—
A. rhombifolia	Tree	20–25	1885	—	—
A. rubra	Tree	12–27	1884	3–4	3–5
A. serrulata	Tree or shrub	to 8	1769	—	—
A. viridis					
ssp. *crispa*	Shrub	to 3	1782	—	—
ssp. *sinuata*	Tree or shrub	to 12	1903	—	—

Sources: Carlson and Bryan (1959), Fernald (1950), Funk (1990), Harrington (1990), Sargent (1965), Schopmeyer (1974).

sal is determined by the occurrence of weather that dries them, thus opening scales and allowing the seeds to be released (Harrington and others 1994). In general, wet weather following dry weather closes the strobiles, thus terminating a dispersal event. Nonetheless, heavy seedfall can occur during wet weather under certain conditions (Lewis 1985), but dispersal will not occur if ice freezes the seeds in the strobile. Although most seed dispersal occurs from September or October through February to April (table 2), some red alder seedfall has been observed in all months (Lewis 1985). American green alder strobiles do not release many seeds if the weather is wet during the autumn; substantial seed dispersal onto snow can occur throughout the winter (Densmore 1979). Alder seeds are very light, and when released they are dispersed long distances by wind, and in some species by water. Seeds of European alder have remained viable after floating for 12 months in still water (McVean 1955). In Alaska, seeds of thinleaf alder have corky, thick wings and float for long periods of time, whereas seeds of American green alder have thinner wings and sink rapidly (Densmore 1979). Birds or other animals also act as dispersal agents when moving through alder crowns and when extracting seeds from the strobiles (Harrington and others 1994).

Information on damaging agents is limited. Fungal diseases of alder catkins—caused by *Taphrina occidentalis* Ray and *T. alni* (Berk. & Broome) Gjaerum—cause enlargements of the bracts of female catkins (Mix 1949) and thus prevent or hinder normal fertilization and seed development. Jumping plant lice—*Psylla alni* (L.)—lay eggs in alder catkins in western North America (Furniss and Carolin 1977). Alder seeds are an important source of food for some

Figure 2—Alnus, alder: nuts (seeds); *A. viridis ssp. crispa*, American green alder (**top left**); *A. glutinosa*, European alder (**top right**); *A. nepalensis*, Nepal alder (**middle left**); *A. rhombifolia*, white alder (**middle center**); *A. rubra*, red alder (**middle right**); *A. serrulata*, hazel alder (**bottom left**);

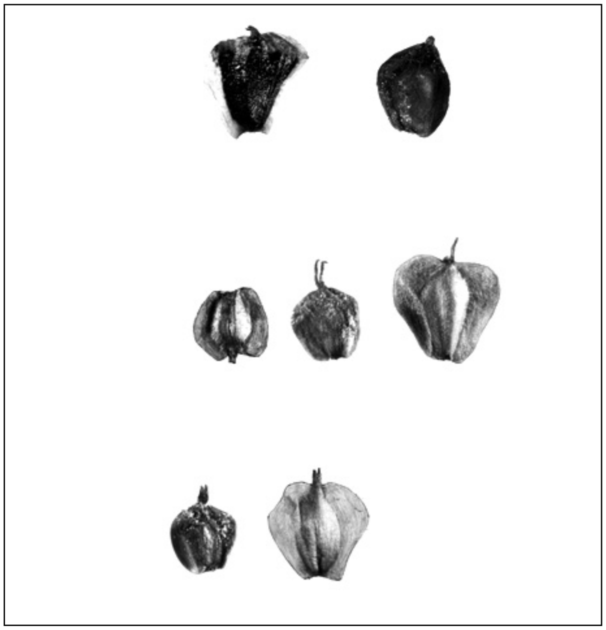
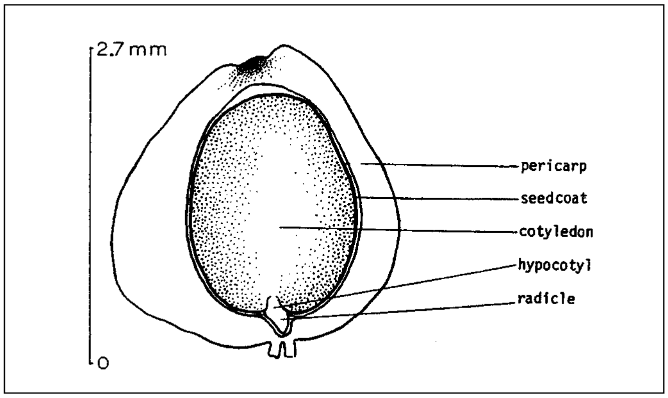


Figure 3—*Alnus rubra*, red alder: longitudinal section through a nut.



bird species (White and West 1977), and presumably seed predation by birds could have significant impacts when seedcrops are small.

Collection of fruits, extraction and cleaning, and storage of seeds. Seedcrops can be assessed in mid-summer by obtaining a count of mature strobiles and filled seeds (Ager and others 1994). Filled seed count should be determined from the upper third of the crown where viability is highest (Brown 1985). Seed quality can be assessed by cutting the strobile longitudinally and counting the filled seeds on one of the cut faces. Although the number of filled seeds on a cut face can vary from 0 to 20 or more in red alders, less than 3 or 4 seeds per cut face indicate a marginal crop (Ager and others 1994). Strobiles may be collected from standing or recently felled trees when the bracts (scales) start to separate on the most mature strobiles. In red alders, ripeness can be judged by twisting the cone along the long axis; if it twists easily and the scales part slightly, the seeds are sufficiently mature for collection (Hibbs and Ager 1989). Color is also a good indicator of maturity; immature cones are green whereas mature cones are mottled shades of green, yellow, gray, or brown (Hibbs and Ager 1989). Strobiles should be collected as soon as they are ripe, for the largest seeds with the best germinability are usually released first. Thus, both seed quality and seed yield are higher if collections are made in the fall rather than in the winter or spring (Lewis 1985; Krstinic 1994). Alder cones will open after being dried on screens or in fine mesh bags in a well-ventilated room for several weeks at ambient air temperature. They can be opened in a shorter time (2 to 7 days) by drying them in a kiln at 16 to 27 °C. Higher temperatures should not be used, as the strobiles will dry too quickly, harden and not open completely. Most of the seeds fall out of the strobiles during the drying process. The remainder, if needed, may be extracted by shaking or tumbling. Overall seed yields can be improved by either wetting cones again, placing them in a cooler for 24 hours, or spraying them with a fine water mist and then redrying (Ager and others 1994). Seeds may be cleaned by screening to remove large trash and further processing with an air column to remove small extraneous material.

Purity as high as 90% has been attained with European alder by fanning and screening seedlots. Quality, however, may be low because the light weight of alder seeds makes it difficult to separate and remove empty seeds (Ager and others 1994). Soundness in most cleaned seedlots has been between 30 and 70% (table 4). Number of seeds per weight ranges from 660,000 to 2,816,000/kg (or 300,000 to 1,277,000/lb) in lots of average quality (table 4). Except for seeds of American green alder, higher numbers may indicate a low percentage of filled seeds. Numbers ranging from 1,800,000 to 4,400,000 seeds/kg (800,000 to 2,000,000/lb) have been found in samples of Nepal, red, and thinleaf alders, but less than 5% of the seeds in these samples were full (Schopmeyer 1974). One red alder seedlot, however, was 70% sound and had 2,700,000 seeds/kg (1,224,000/lb). In a trial with red alder, the percentage of filled seeds determined by x-radiography was highly correlated ($r^2 = 0.91$)

Table 4—*Alnus*, alder: yield data and soundness

Species	Seed wt/vol of strobiles		Cleaned seeds/wt of strobiles		Cleaned seeds/vol of strobiles		Cleaned seeds (x1,000)/wt of strobiles				Soundness	
							Range		Average			
	kg/hl	lb/bu	kg/100 kg	lb/100 bu	kg/hl	lb/bu	/kg	/lb	/kg	/lb	Samples	(%)
A. glutinosa												
Pennsylvania	—	—	—	—	1.5	1.2	565–882	257–401	706	321	7	—
Europe	—	—	—	—	—	—	635–1,406	289–639	774	352	86	39
A. incana												
Europe	21–30	16–23	8–10	8–10	—	—	961–1,980	437–900	1,470	668	123	51
A. incana												
ssp. *rugosa*	—	—	—	—	4.8	3.7	—	—	660	299	—	30–60
ssp. *tenuifolia*												
(fresh)*	14	11	7	7	1.3	1.0	—	—	—	—	—	—
(air dry)*	8	6	13	13	1.0	0.8	—	—	1,485	673	1	—
A. rhombifolia												
(fresh)*	23	18	5	5	1.3	1.0	—	—	—	—	—	—
(air dry)*	9	7	13	13	1.3	1.3	1,349–1,511	613–687	1,430	650	2	71
A. rubra	9	7	1.4–15	1.4–15	0.1–1.4	0. 1–1.1	1,843–2,700	350–1,400	1,712	776	5	70
A. viridis												
ssp. *crispa*	—	—	—	—	—	—	1,530–4,101	694–1,860	2,816	1,277	2	42–93
ssp. *sinuata*	—	—	—	—	—	—	—	—	2,200	998	1	70

Sources: Hibbs and Ager (1989), Liscinsky (1965), Mirov and Kraebel (1939), Schopmeyer (1974), Niemic and others (1995), USDA data on file at Olympia Forestry Sciences Laboratory.

* Yield data were determined on clusters of strobiles including stems.

with the actual germination percentage (Ager and others 1994).

Air-dried seeds have been stored in sealed containers at < – 2 °C. Under these conditions, viability has been maintained for 2 years in seeds of European alder (Holmes and Buszewicz 1958) and for 10 years in speckled alder (Heit 1967). For long-term storage, however, further drying of seeds to moisture content of less than 10% has been recommended for red alder (Ager and others 1994). This can be accomplished by kiln-drying or placing seeds in a room at 27 °C with less than 25% relative humidity. Red alder seeds can then be placed in moisture-proof containers and stored at < –12 °C for 10 to 20 years without substantial losses in viability (Ager and others 1994).

Pregermination treatments and germination tests. The degree of dormancy appears to vary among alder species and among provenances (geographic origins) within species. Thus, percentage germination of fresh seeds of white and thinleaf alders was equally good for stratified and nonstratified seed (Schopmeyer 1974). Fresh seeds of European and mountain alders also germinated promptly without stratification; but dried seeds, at a moisture of content of 8 to 9%, were dormant (table 5) (Schalin 1967). Germination capacity of the dried seeds, after stratification for 180 days at 5 °C was higher than that of fresh seeds. Maximum germination capacity, however, was obtained only when the stratification period was followed by 3 days at –20 °C (table 5) (Schalin 1967). A more recent study found that fresh mountain alder seeds initially exhibited some dormancy (that is, only about half of the filled seeds germinated in the incubator), but no dormancy was observed after one winter in the soil (Granstrom 1987). Dormancy also has been encountered in occasional seedlots of speckled (Heit 1968) and American green alders (Schopmeyer 1974). Stratification for 30 to 60 days at 1 to 5 °C has been recommended for these dormant lots (Schopmeyer 1974). Stratification for 30 to 90 days also has been recommended for Sitka alder (Emery 1988).

Although physiological seed dormancy is not widespread in red alder, it can exist (Elliot and Taylor 1981). Stratification at low temperature (0 to 5 °C) has little or no effect on the rate or completeness of germination of red alder seeds when tested at warm germination temperatures (Elliot and Taylor 1981; Radwan and DeBell 1981; Tanaka and others 1991).

Table 5—*Alnus,* alder: stratification and germination testing data

Species	Cold stratification period* (days)	Germination test conditions: Temp (°C) Day	Germination test conditions: Temp (°C) Night	Germination test conditions: Days	Germination rate: Amount (%)	Germination rate: Days	Germination Avg (%)	Germination Samples	Soundness (%)
A. glutinosa (Pennsylvania)	0	30	21	28	—	—	52	7	—
A. glutinosa (Finland)									
fresh seed	0	25	25	21	21	5	28	1	43
dried seed	0	25	25	21	9	5	13	1	43
dried seed	180	25	25	21	27	5	35	1	43
dried seed	180+3†	25	25	21	35	5	46	1	43
A. incana (Europe)	0	21	21	30	—	—	45	100	—
A. incana (Finland)									
fresh seeds	0	25	25	21	21	5	29	1	45
dried seeds	0	25	25	21	12	5	16	1	45
dried seeds	180	25	25	21	25	5	34	1	45
dried seeds	180+3†	25	25	21	38	5	49	1	45
A. i. ssp. *tenuifolia*									
fresh seeds	0	30	20	26	4	13	4	1	6
A. rhombifolia									
fresh seeds	0	30	20	30	59	14	59	1	65
A. rubra	0	24	16	7	56	7	56	4	—
dried seeds	0–60‡	30§	20	28	18	7	71	6	—
fresh seeds	0	30	20	28	21	7	75	6	87
fresh seeds	14	30	20	28	42	7	72	6	87
fresh seeds	28	30	20	28	49	7	72	6	87
fresh seeds	0	15	5	56	0	21	16	6	87
fresh seeds	14	15	5	56	17	21	63	6	87
fresh seeds	28	15	5	56	54	21	80	6	87
A. serrulata	‖	27	23	10	27	2	36	1	—
A. viridis									
ssp. *crispa*	60	30	20	30–40	28	12	28	3	30–40
ssp. *sinuata*	14	30	20	21	5	7	14	1	—

Sources: ISTA (1993), McDermott (1953), Radwan and DeBell (1981), Schalin (1967), Schopmeyer (1974), Tanaka and others (1991), data on file at Olympia Forestry Sciences Laboratory.

Note: Day/night, 8 hrs/16 hours.

* Stratification, when used, was in a moist medium at 1 to 5 °C.

† 180 days at 5 °C, plus 3 days at 20 °C,

‡ No difference for 0, 30, or 60 days of stratification.

§ Light period was 10 housr/day at this temperature.

‖ Seeds were stratified for an unspecified period.

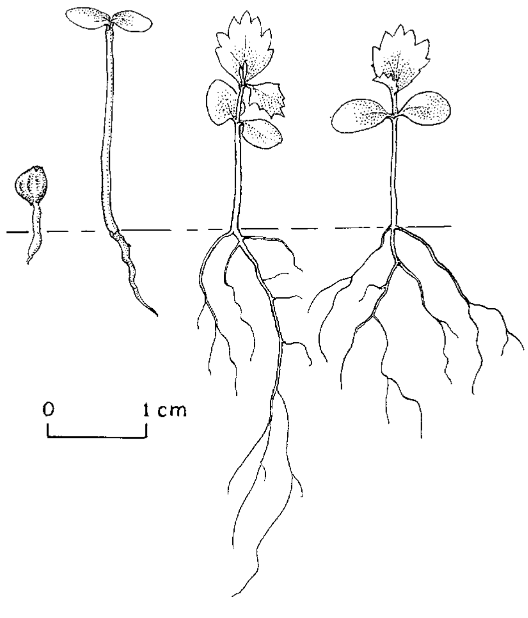
Under cool temperatures similar to those likely to prevail during outdoor sowings in early spring, however, 2 to 4 weeks of stratification substantially enhanced rate of germination and total germination (Tanaka and others 1991) and such a period is therefore recommended (Ager and others 1994). Thinleaf and American green alder seedlots collected near Fairbanks, Alaska, also germinated well without stratification at 25 °C but only germinated well at lower temperatures (10 to 15 °C) when combined with 72 days of stratification (Densmore 1979). Studies have also indicated the potential of 3 quick pregermination treatments for red alder seeds: gibberellin (Berry and Torrey 1985), 1% captan (Berry and Torrey 1985), and 30% hydrogen peroxide (Neal and others 1967). The results from these pregermination treatments, however, were obtained under warm germination conditions and need to be tested under the cooler conditions encountered in spring sowings. The captan and peroxide treatments may have a beneficial effect by reducing the amount of disease organisms present on seedcoats. Pretreatment with gibberellic acid improved greenhouse germination (21 °C day/13 °C night) of thinleaf alder seeds from 2 sources but did not affect germination of Arizona alder seeds from a single source (Dreesen and Harrington 1997).

For germination testing, both constant temperatures and diurnally alternating temperatures have been used (table 5). Official tests of the International Seed Testing Association (ISTA 1993) call for a 21-day test at alternating temperatures of 20/30 °C, with light during the 8 hours at 30 °C. Although seeds of European alder germinated as well in continuous darkness as under normal day length (McVean 1955), recent work indicates that seed germination of many alder species is markedly affected by light regime (Berry and Torrey 1985; Boojh and Ramakrishnan 1981; Bormann 1983; Densmore 1979; Khan and Tripathi 1989). Such effects in red alder are mediated by phytochrome: red light stimulates seed germination, far-red light inhibits it, and the effect of each light treatment can be reversed by the alternative treatment (Bormann 1983). Seeds of red alder are also sensitive to amount and quality of light under field conditions, and these factors—along with soil moisture—control germination success on disturbed sites (Haeussler and Tappeiner 1993; Haeussler and others 1995).

Nursery practice. Alder seedlings have been produced by bareroot nursery (open field or bedhouse) and container methods, as well as combinations thereof (Ahrens 1994; Ahrens and others 1992; Funk 1990; Radwan and others 1992). Successful stock types for red alder are grown in 1 year and include 1+0 open-bed bareroot, 1+0 bedhouse bareroot, 1+0 plug, and +0.5 (plug+transplant). Most nurseries sow in the spring when growing alder species (Ahrens and others 1992; Schopmeyer 1974), but fall-sowing is mentioned by Heit (1968). Spring-sowing is sometimes delayed until late spring to reduce seedling size. Sowing depths of 2 to 5 mm (.1 to .2 in) have been used for seeds of European alder and red alder (Schopmeyer 1974). In California, seeds of red alder have been mixed with 10 parts of vermiculite and drilled 1 cm (.4 in) deep (Schopmeyer 1974). In Oregon, seeds of red alder have also been sown on the soil surface and covered with peat. Seeds of Nepal alder have been mixed with sand and spread over the nursery beds. The number of plantable seedlings obtained from 1 kg (2.2 lb) of seed was 22,000 (10,000/lb) for European alder and 88,000 (40,000/lb) for hazel alder (Van Dersal 1938). Germination is epigeal (figure 4).

Alder seedlings, particularly those of red alder, grow rapidly and seedling densities should be lower than those used for conifers. Seedlings grown at open-bed densities of 60 to 180 seedlings/m^2 (5 to 15/ft^2) or in large containers result in much better outplanting performance than those grown at greater densities or in small Styroblocks® (Ahrens 1994). Inoculation of beds or container media with the nodulating actinomycete *Frankia* can improve establishment

Figure 4—*Alnus glutinosa*, European alder: seedling development at 1 and 7 days after germination (**left**); *Alnus incana* ssp. *tenuifolia*, thinleaf alder: 2 older seedlings (**right**).



and early growth in the nursery (Berry and Torrey 1985; Hilger and others 1991) and may enhance outplanting performance (McNeill and others 1990). Diluted suspensions of pure Frankia cultures and homogenates of crushed, fresh root nodules have been used for inoculation (Ahrens and others 1992; Perinet and others 1985). Detailed methods of preparation and application are available (Martin and others 1991; Molina and others 1994; Zasada and others 1991).

Development of nitrogen-fixing nodules is promoted by fertilization with low to moderate applications of nitrogen; phosphorus and lime are likely to be necessary for production of high-quality stock (Hughes and others 1968; Radwan 1987; Radwan and DeBell 1994). Although alder seedlings are produced operationally, optimum combinations of fertilizer source, amount, and timing of application have not been completely worked out; some combinations have had detrimental effects on alder seedlings or their root associates. Frequent irrigation may be necessary to prevent desiccation and heat damage of surface-sown seeds or germinants during germination and early establishment (Ahrens 1994).

Direct seeding in the field has been done successfully with 2 species. Speckled alder has been established in Pennsylvania by broadcast sowing on disked areas and on sod. Seeds collected in the fall were broadcast during the following February and March. Seeding rates were 0.28 liter/10 m^2 (or 0.5 pint/100 ft^2) on bare soil and 0.38 liter (0.7 pint) for the same area of sod (Liscinsky 1965). In England, better stocking was obtained on a shallow blanket bog with spot sowing of European alder than with broadcast sowing. About 15 viable seeds were sown in each spot and fertilized with about 60 g of rock phosphate (McVean 1959).

Seedling care. Information to guide lifting dates is very limited, even for red alder (Ahrens 1994; Ahrens and others 1992); current recommendations based on experience in southwest Washington are to lift seedlings in January. They are then stored at either +2 °C or –2 °C; the lower temperature is recommended because it prevents budbreak during storage (and possible *Botrytis* infection associated with budbreak during storage) and reduces the tendency for planted alders to break bud too soon after planting. Storage in sealed bags will prevent desiccation. Because alder stems are brittle and sensitive, seedlings must be handled carefully during storage, transport, and outplanting to avoid damage to stems, branches, and buds. At low elevations (< 300 m) in western Washington, it has been recommended that seedlings be planted between mid-March and mid-April. The spring planting period should begin when the probability of severe frost is low and end before there is appreciable soil drying (Dobkowski and others 1994).

References

Ager AA, Heilman PE, Stettler RF. 1993. Genetic variation in red alder (*Alnus rubra*) in relation to native climate and geography. Canadian Journal of Forest Research 23: 1930–1939.

Ager AA, Stettler RF. 1994. Genetics of red alder and its implications for future management. In: Hibbs DE, DeBell DS, Tarrant RF, eds. The biology and management of red alder. Corvallis: Oregon State University: 92–105.

Ager AA, Tanaka Y, McGrath J. 1994. Biology, ecology, and utilization of red alder seed. In: Hibbs DE, DeBell DS, Tarrant RF, eds. The biology and management of red alder. Corvallis: Oregon State University: 159–169.

Ahrens GR. 1994. Seedling quality and nursery practices for red alder. In: Hibbs DE, DeBell DS, Tarrant RF, eds. The biology and management of red alder. Corvallis: Oregon State University: 170–185.

Ahrens GR, Dobkowski A, Hibbs DE. 1992. Red alder: guidelines for successful regeneration. Spec. Pub. 24. Corvallis: Oregon State University, College of Forestry. 11 p.

Berry AM, Torrey JG. 1985. Seed germination, seedling inoculation and establishment of *Alnus* spp. in containers in greenhouse trials. Plant and Soil 87(1): 161–173.

Boojh R, Ramakrishnan PS. 1981. Germination of seeds of *Alnus nepalensis* Don. National Academy Science Letters 4(2): 53–56.

Bormann BT. 1983. Ecological implications of phytochrome mediated seed germination in red alder. Forest Science 29(4): 734–738.

Bousquet J, Cheliak WM, Lalonde M. 1987. Genetic differentiation among 22 mature populations of green alder *(Alnus crispa*). Canadian Journal of Forest Research 17: 219–227.

Bousquet J, Cheliak WM, Lalonde M. 1988. Allozyme variation within and among mature populations of speckled alder (*Alnus rugosa*) and relationships with green alder (*A. crispa*). American Journal of Botany 75: 1678–1686.

Brayshaw TC. 1976. Catkin bearing plants (Amentiferae) of British Columbia. Occ. Pap. 18. Victoria: British Columbia Provincial Museum: 127–135.

Brown SM. 1986. Sexual allocation patterns in red alder (*Alnus rubra* Bong.) along three elevational transects [MS thesis]. Seattle: University of Washington, College of Forest Resources. 241 p.

Brown SM. 1985. A study of reproductive biology of *Alnus rubra* along three elevational transects in Washington and Oregon. On file with: USDA Forest Service, Pacific Northwest Research Station, Olympia, WA. 48 p.

Carlson NK, Bryan LW. 1959. Hawaiian timber for the coming generations. Honolulu: Trustees for the Bernice P. Bishop Estate. 112 p.

Chapin FS III, Walker LR, Fastie CL, Sharman LC. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. Ecological Monographs, 64(2): 149–175.

Chiba S. 1966. Studies on the tree improvement by means of artificial hybridization and polyploidy in *Alnus* and *Populus* species. Bulletin of the Oji Institute for Forest Tree Improvement [Kuriyama, Japan: Aji Paper Co.] 1: 1–165.

Dang QL, Xie CY, Ying C, Guy RD. 1994. Genetic variation of ecophysiological traits in red alder (*Alnus rubra* Bong.). Canadian Journal of Forest Research 24: 2150–2156.

Densmore RVE. 1979. Aspects of the seed ecology of woody plants of the Alaskan taiga and tundra [PhD dissertation]. Durham, NC: Duke University, Department of Botany: 34–48.

Dobkowski A, Figueroa PF, Tanaka Y. 1994. Red alder plantation establishment. In: Hibbs DE, DeBell DS, Tarrant RF, eds. The biology and management of red alder. Corvallis: Oregon State University: 186–201.

Dreesen DR, Harrington JT. 1997. Propagation of native plants for restoration projects in the southwestern U.S.: preliminary investigations. In: Landis TD, Thompson JR, tech. coords. National Proceedings, Forest and Conservation Nursery Associations. Gen. Tech. Rep. PNW-419. Portland, OR: USDA Forest Service, Pacific Northwest Research Station: 77–88.

Elliot DM, Taylor IEP. 1981. Germination of red alder (*Alnus rubra*) seed from several locations in its natural range. Canadian Journal of Forest Research 11: 517–521.

Emery D. 1988. Seed propagation of native California plants. Santa Barbara, CA: Santa Barbara Botanic Garden. 115 p.

Fernald ML. 1950. Gray's manual of botany. 8th ed. New York: American Book Co. 1632 p.

FNAEC [Flora of North America Editorial Committee]. 1997. Flora of North America north of Mexico, Volume 3, Magnoliophyta: Magnoliidae and Hamamelidae. New York: Oxford University Press. 616 p.

Funk DT. 1990. *Alnus glutinosa* (L.) Gaertn., European alder. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 2, Hardwoods. Washington, DC: USDA Forest Service: 105–115.

Furniss R, Carolin VM. 1977. Western forest insects. Misc. Pub. 1339. Washington, DC: USDA Forest Service. 654 p.

Gillespie AR, Pope PE. 1994. Intensive culture of European black alder in central Indiana, U.S.A.: biomass yield and potential returns to farmers. Biomass and Bioenergy 6(6): 419–430.

Granstrom A. 1987. Seed viability of fourteen species during five years of storage in forest soil. Journal of Ecology 75(2): 321–331.

Haeussler S, Tappeiner JC II. 1993. Effect of the light environment on seed germination of red alder (*Alnus rubra*). Canadian Journal of Forest Research 23: 1487–1491.

Haeussler S, Tappeiner JC II, Greber BJ. 1995. Germination, survival, and early growth of red alder seedlings in the central coast range of Oregon. Candian Journal of Forest Research 25: 1639–1651.

Hall RB, Maynard CA. 1979. Considerations in the genetic improvement of alder. In: Gordon JC and others, eds. Symbiotic nitrogen fixation in the management of temperate forests. Corvallis: Oregon State University: 322–344.

Hall RB, Nyong RN. 1987. Design, establishment and management of a black alder (*Alnus glutinosa* L. Gaertn.) seed orchard. In: Proceedings, 19th Southern Forest Tree Improvement Conference. 1987 June 16–18; College Station, TX. Springfield, VA: USDC National Technical Information Service: 261–268.

Hamann A, El-Kassaby YA, Koshy MP, Namkoong G. 1998. Multivariate analysis of allozymic and quantitative trait variation in *Alnus rubra*: geographic patterns and evolutionary implications. Canadian Journal of Forest Research 28: 1557–1565.

Harrington CA. 1984. Red alder: an American wood. FS-215. Washington, DC: USDA Forest Service. 7 p.

Harrington CA. 1990. *Alnus rubra* Bong., red alder. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 2, Hardwoods. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 116–123.

Harrington CA, DeBell DS. 1995. Effects of irrigation, spacing and fertilization on flowering and growth in young *Alnus rubra*. Tree Physiology 15: 427–432.

Harrington CA, Zasada JC, Allen EA. 1994. Biology of red alder (*Alnus rubra* Bong.). In: Hibbs DE, DeBell DS, Tarrant RF, eds. The biology and management of red alder. Corvallis: Oregon State University: 3–22.

Heilman PE. 1990. Growth of Douglas-fir and red alder on coal spoils in western Washington. Soil Science Society of America Journal 54: 522–527.

Heit CE. 1967. Propagation from seed: 11. Storage of deciduous tree and shrub seeds. American Nurseryman 126(10): 12–13, 86–94.

Heit CE. 1968. Propagation from seed: 15. Fall planting of shrub seeds for successful seedling production. American Nurseryman 128(4): 8–10, 70–80.

Hibbs DE, Ager AA. 1989. Red alder: guidelines for seed collection, handling, and storage. Spec. Pub. 18. Corvallis: Oregon State University, Forest Research Laboratory. 6 p.

Hibbs DE, DeBell DS. 1994. Management of young red alder. In: Hibbs DE, DeBell DS, Tarrant RF, eds. The biology and management of red alder. Corvallis: Oregon State University: 202–215.

Hilger AB, Tanaka Y, Myrold DD. 1991. Inoculation of fumigated nursery soil increases nodulation and yield of bare-root red alder (*Alnus rubra* Bong.). New Forests 5: 35–42.

Hitchcock CL, Cronquist A, Ownbey M, Thompson JW. 1964. Vascular plants of the Pacific Northwest: Volume 2, Salicaceae to Saxifragaceae. Seattle: University of Washington Press: 72–76.

Holmes GD, Buszewicz G. 1958. The storage of seed of temperate forest tree species: 2. Forestry Abstracts 19: 455–476.

Hughes DR, Gessel SP, Walker RB. 1968. Red alder deficiency symptoms and fertilizer trials. In: Trappe JM, Franklin JF, Tarrant RF, Hansen GM, eds. Biology of alder. Proceedings, 40th Annual Meeting of the Northwest Science Association; 1967 April 14–15; Pullman, WA. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station: 225–237.

ISTA [International Seed Testing Association]. 1993. International rules for seed testing: rules 1993. Seed Science and Technology 21 (Suppl.): 1–259.

Johnson FD. 1968. Disjunct populations of red alder in Idaho. In: Trappe JM, Franklin JF, Tarrant RF, Hansen GM, eds. Biology of alder. Proceedings, 40th Annual Meeting of the Northwest Scientific Association; 1967 April 14–15; Pullman, WA. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station: 9–22.

Khan ML, Tripathi RS. 1989. Effect of soil moisture, soil texture and light intensity on emergence, survival and growth of seedlings of a few sub-tropical trees. Indian Journal of Forestry 12(3): 196–204.

Koski V, Tallquist R. 1978. Results of long-time measurements of the quantity of flowering and seed crop of forest trees. Folia Forestalia: 1–344.

Krstinic A. 1994. Genetics of black alder (*Alnus glutinosa* (L.) Gaertn.). Annales Forestales [Zagreb] 19(2): 33–72.

la Bastide JGA, van Vredenburch CLH. 1970. The influence of weather conditions on the seed production of some forest trees in the Netherlands. Stichting Bosbouwproefstation 'De Dorschkamp' Mededeling 102: 1–12.

Lester DT, DeBell DS. 1989. Geographic variation in red alder. Res. Pap. PNW-409. Portland: USDA Forest Service, Pacific Northwest Research Station. 8 p.

Lewis SJ. 1985. Seedfall, germination, and early survival of red alder [MS thesis]. Seattle: University of Washington, College of Forest Resources.

Liscinsky S. 1965. The American woodcock in Pennsylvania. Proj. W-50-R. Harrisburg: Pennsylvania Game Commission, Pittman Robertson (Federal Aid). 32 p.

Ljunger A. 1959. Al-och alföraäling. Skogen 46(5): 115–117.

Lowry GL, Brokow FC, Breeding CHJ. 1962. Alder for reforesting coal spoils in Ohio. Journal of Forestry 60: 196–199.

Martin KJ, Tanaka Y, Myrold DD. 1991. Peat carrier increases inoculation success with *Frankia* on red alder (*Alnus rubra* Bong.) in fumigated nursery beds. New Forests 5: 43–50.

McDermott RE. 1953. Light as a factor in the germination of some bottomland hardwood seeds. Journal of Forestry 51: 203–204.

McGee A, Feller MC. 1993. Seed banks of forested and disturbed soils in southwestern British Columbia. Canadian Journal of Botany 71(12): 1574–1583.

McNeill JD, Hollingsworth MK, Mason WL, Moffat AJ, Sheppard LJ, Wheeler CT. 1990. Inoculation of alder seedlings to improve seedling growth and field performance. Arbor. Res. Note 88. Washington, DC: USDoE, Arboricultural Advisory and Information Service. 3 p.

McVean DN. 1955. Ecology of *Alnus glutinosa* (L.) Gaertn.: 3. Seedling establishment. Journal of Ecology 44(1): 195–218.

McVean DN. 1959. Ecology of *Alnus glutinosa* (L.) Gaertn.: 4. Establishment of alder by direct seeding of shallow blanket bog. Journal of Ecology 47: 615–618.

Miller RE, Murray MD. 1978. The effects of red alder on Douglas-fir growth. In: Proceedings, Utilization and Management of Alder Symposium. Gen. Tech. Rep. PNW-70. Portland, OR: USDA Forest Service, Pacific Northwest Research Station: 283–306.

Mirov NT, Kraebel CG. 1939. Collecting and handling seeds of wild plants. For. Publ. 5. Washington, DC: USDA Forest Service, Civilian Conservation Corps. 42 p.

Mix AJA. 1949. A monograph of the genus *Taphrina*. University of Kansas Science Bulletin 33 (1): 3–167.

Molina R, Myrold D, Li CY. 1994. Root symbioses of red alder: technological opportunities for enhanced regeneration and soil improvement. In: Hibbs DE, DeBell DS, Tarrant RF, eds. The biology and management of red alder. Corvallis: Oregon State University: 23–46.

Neal JL Jr, Trappe JM, Lu KC, Bollen WB. 1967. Sterilization of red alder seedcoats with hydrogen peroxide. Forest Science 13: 104–105.

Niemic SS, Ahrens GR, Willits S, Hibbs DH. 1995. Hardwoods of the Pacific Northwest. Res. Contrib. 8. Corvallis: Oregon State University, Forestry Research Laboratory. 115 p.

Peeler KC, DeBell DS. 1987. Variation in damage from growing season frosts among open pollinated families of red alder. Res. Note. PNW-464. Portland OR: USDA Forest Service, Pacific Northwest Research Station. 8 p.

Perinet P, Brouillette JG, Fortin JA, LaLonde M. 1985. Large scale inoculation of actinorhizal plants with *Frankia*. Plant and Soil 87: 175–183.

Plank ME, Willits S. 1994. Wood quality, product yield, and economic potential. In: Hibbs DE, DeBell DS, Tarrant RF, eds. The biology and management of red alder. Corvallis: Oregon State University: 243–247.

Pojar J, MacKinnon A, comps. & eds. 1994. Plants of the Pacific Northwest Coast. Redmond, WA: Lone Pine Publishing: 44.

Radwan MA. 1987. Effects of fertilization on growth and foliar nutrients of red alder seedlings. Res. Pap. PNW-375. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 14 p.

Radwan MA, DeBell DS. 1981. Germination of red alder seed. Res. Note PNW-370. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 4 p.

Radwan MA, DeBell DS. 1994. Fertilization and nutrition of red alder. In: Hibbs DE, DeBell DS, Tarrant RF, eds. The biology and management of red alder. Corvallis: Oregon State University: 216–228.

Radwan MA, Tanaka Y, Dobkowski A, Fangen W. 1992. Production and assessment of red alder planting stock. Res. Pap. PNW-RP-450. Portland, OR: USDA Forest Service, Pacific Northwest Research Station.

Sargent CS. 1965. Manual of the trees of North America (exclusive of Mexico). 2nd ed., corrected and reprinted. New York: Dover Publications. 934 p.

Schalin I. 1967. Germination analysis of *Alnus incana* (L.) Moench and *Alnus glutinosa* (L.) Gaertn. seeds. Acta Oecologia Scandinavica 18: 253–260.

Schopmeyer CS. 1974. *Alnus* B. Ehrh., alder. In: Schopmeyer CS, ed. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 206–211.

Stettler RF. 1978. Biological aspects of red alder pertinent to potential breeding programs. In: Briggs DG, DeBell DS, Atkinson WA, eds. Utilization and management of alder. Gen. Tech. Rep. PNW-70. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station: 209–222.

Tanaka Y, Brotherton PJ, Dobkowski A, Cameron PC. 1991. Germination of stratified and non-stratified seeds of red alder at two germination temperatures. New Forests 5: 67–75.

Tarrant RF, Bormann BT, DeBell DS, Atkinson WA. 1983. Managing red alder in the Douglas-fir region: some possibilities. Journal of Forestry 81: 787–792.

Tarrant RF, Hibbs DE, DeBell DS. 1994. Introduction: red alder and the Pacific Northwest. In: Hibbs DE, DeBell DS, Tarrant RF, eds. The biology and management of red alder. Corvallis: Oregon State University: ix–xi.

Tarrant RF, Trappe JM. 1971. The role of *Alnus* in improving the forest environment. Plant and Soil (Spec. Vol. 1971): 335–348.

Van Dersal WR. 1938. Native woody plants of the United States: their erosion-control and wildlife values. Misc. Pub. 303. Washington, DC: USDA. 362 p.

White CM, West GC. 1977. The annual lipid cycle and feeding behavior of Alaskan redpolls. Oecologia 27: 227–238.

White G. 1981. Controlled pollination of European black alder. In: Franklin EC, ed. Pollen management handbook. Agric. Handbk. 587. Washington, DC: USDA Forest Service: 89–91.

Worthington NP. 1965. Red alder (*Alnus rubra* Bong.). In: Fowells HA, ed. Silvics of forest trees of the United States. Agric. Handbk. 271. Washington, DC: USDA Forest Service: 83–88.

Zasada J, Sharik T, Nygren M. 1991. The reproductive process in boreal forest trees. In: Shugart HH, Leemans R, Bonan GB, eds. A systems analysis of the global boreal forest. Cambridge, UK: Cambridge University Press: 85–125.

Asteraceae—Aster family

Ambrosia dumosa (Gray) Payne

bursage

Jane E. Rodgers and Carol Miller

Ms. Rodgers is at the Point Reyes National Seashore, Point Reyes Station, California; and Ms. Miller is former propagationist at USDI National Park Service's Joshua Tree National Park, Center for Arid Lands Restoration and Native Plants Nursery, Twentynine Palms, California

Synonyms. *Franseria dumosa* Gray

Other common names. white bursage, white burrobush, burrobush, burroweed, sandbur

Growth habit, occurrence, and use. Bursage is a low, intricately branched, rounded shrub abundant on well-drained soils through much of the Southwest. It is significant component in creosote bush scrub and Joshua tree woodland communities of the Mojave and Colorado Deserts of California, south and east to Utah, Arizona, Mexico, and lower California (Kay 1977). Bursage, like creosote, has a rhizomatous growth habit and is thus an extremely long-lived shrub (Muller 1953).

Flowering and fruiting. Bursage flowers are inconspicuous, with staminate and pistillate heads intermixed in the terminal and lateral spikes of the panicle (Bainbridge and Virginia 1989). Blooming occurs primarily from February to June, and occasionally during the fall or after rain (Kay 1977). Seeds resemble cockleburs (figure 1) and mature 3 to 4 months after flowering.

Collection, extraction, and storage. Seeds can be hand-stripped from the plants; collecting burs from the ground beneath the plants is impractical because the light burs are rapidly blown away (Bainbridge and Virginia 1989). Seed cleaning is difficult and rarely done due to the spiny burs. In long-term storage trials by Kay and others (1988), seeds were stored at room temperature, 4 °C, – 15 °C, and in warehouse conditions, with germination rates tested annually over a 14-year period. The results indicated that seed quality had been poor, even though seeds were collected numerous times. The sporadic germination under a variety of conditions reflected this. Kay recommended that seeding guidelines should specify seeding rates in seed weight of pure live seeds required for sowing an area (that is, kilograms per hectare or pounds per acre), and providing that extra seeds are planted to compensate for the low quality.

Pregermination treatments. After overnight leaching/soaking, seeds begin germinating during the first and second weeks in moist paper towels or directly in a 50% vermiculite–50% soil mixture (CALR 1995). Optimal germination temperatures appear to be between 15 to 25 °C (table 1), as colder temperatures tend to inhibit germination (Kay 1975).

Germination tests. Tests using activated carbon and scarification both resulted in a slightly improved early germination rate (Graves and others 1975). Germination conditions tested at Joshua Tree National Park (JTNP) Native Plants Nursery include: (1) direct sowing to blotter paper, (2) overnight cold water soaking, and (3) initial cold water soaking followed by overnight leaching. All of these methods had moderate success, indicating that no treatment is necessary when sowing directly to moist toweling; average gemination ranges from 30 to 50% (CALR 1995). Other tri-

Figure 1—*Ambrosia dumosa*, bursage: mature seed.

Table 1—*Ambrosia dumosa,* bursage: effect of temperature on germination

Temperature (°C)	2	5	10	15	20	25	30
Germination (%)	0	0	4	26	21	18	10

Source: Kay and others (1988).

als by Kay and others (1988) refer to initial germination of seeds using 4 replications of 100 seeds in damp paper toweling placed in a growth chamber at 15 °C. Test conditions were maintained for 28 days, with germination percentages recorded every 7 days; initial germination rate for bursage was 5%. Germination tests, conducted annually to test the effects of storage, were then averaged to a "best germination" of 9%. These annual tests consisted of 4 replications of 50 seeds using the same initial testing methods. Also tested were the effects of temperature on germination rates (table 1).

Nursery practice. Mature specimens have been transplanted with greater than 90% survival (Ruffner and others 1985). Graves (1976) transplanted 2-month-old stock in February 1973, with a survival rate 2 years later of 44 and 48% for 2 separate sites. Flowering occurred in 25% of the plants during first year's growth at one site, with no flowering or seed at other site. Initial mortality was due to cold transplanting temperatures. Spot-seeding, in comparison, was poor, with 18 burs/spot resulting in 16% germination and 0 to 4% stocking at the same sites. A one-time irrigation treatment did not improve results of either transplanting or spot-seeding. Seed germination may be induced from September–October rains (Went 1979).

At JTNP, 12-month-old plants grown from seed have been successfully outplanted using a 76-cm (30-in) tube "tall pot" with a 15-cm (6-in) diameter (CALR 1995). Other outplantings of bursage in the park include a restoration project at an abandoned surface mine. Three types of containers were used: 3.8-, 6.8-, and 9.2-liter (1-, 1.8-, and 2.6-gal) pots with an elongated design 35 to 43 cm (14 to 17 in) in height. Latest monitoring noted an overall survival rate of 80% (CALR 1995). Prior to outplanting, plants in smaller containers were between 4 and 5 months old and those in larger containers, between 6 and 7 months.

Seedling care. Seedlings grow quickly in greenhouse conditions, and new growth can be pruned back frequently to strengthen the sensitive root collar (CALR 1995). Both Graves (1976) and the JTNP Native Plants Nursery have noted seedling sensitivity to hardening-off in sub-freezing temperatures. Using plant bands, Graves (1976) recorded 80% mortality at 10 to –7 °C, with better survival after restarting and hardening-off at day-night temperatures of 14 and 4 °C. Stem pieces root easily from the field or greenhouse by dipping in rooting hormone powder and placing cuttings in vermiculite in a mist house until rooted (Wieland and others 1971).

References

Bainbridge DA, Virginia RA. 1989. Restoration in the Colorado Desert: species notes [Unpublished manuscript prepared for the California Department of Transportation].

CALR [Center for Arid Lands Restoration]. 1995. Seed test data filed 1989–1995. Twentynine Palms, CA: USDI National Park Service, Joshua Tree National Park. 24 p.

Graves WL. 1976. Revegetation of disturbed sites with native shrub species in the western Mojave Desert. In: Test seeds of Mojave Desert shrubs. Prog. Rep. BLM Contr. 53500-CT4-2(N): 11–35.

Graves WL, Kay BL, Williams WA. 1975. Seed treatment of desert shrubs. Agronomy Journal 67(Nov–Dec): 773–777.

Kay BL. 1975. Test of seeds of Mojave Desert shrubs: progress report. BLM Contract 53500-CT4-2(N). 24 p.

Kay BL, Graves WL, Young JA. 1988. Long-term storage of desert shrub seed. Mojave Reveg. Notes 23. Davis: University of California, Department of Agronomy and Range Science.

Kay BL, Ross CM, Graves WL. 1977. Burrobush. Mohave Reveg. Notes 1. Davis: University of California, Department of Agronomy and Range Science.

Ruffner GA, Fedock DA, Carothers SW. 1985. Transplanting native Sonoran Desert plants. Proceedings, 1st North American Riparian Conference, Riparian Ecosystems and Their Management: Reconciling Conflicting Uses; 1985 April 16–18; Tuscon, AZ.

Went FW. 1979. Germination and seeding behavior of desert plants. In: Arid land ecosystems: structure, functioning and management. Cambridge, UK: Cambridge University Press: 477–489.

Weiland PAT, Frolich EF, Wallace A. 1971. Vegetative propagation of woody shrub species from the northern Mojave and southern Great Basin Deserts. Madroño 21: 149–152.

Rosaceae—Rose family

Amelanchier Medik.

serviceberry

Kenneth A. Brinkman and Terry F. Strong

Dr. Brinkman retired from the USDA Forest Service's North Central Forest Experiment Station; Mr. Strong is a research forester at the USDA Forest Service's North Central Research Station, Rhinelander, Wisconsin

Growth habit, occurrence, and use. The serviceberries—the genus *Amelanchier*—include about 25 species of small deciduous trees and shrubs native to North America, Europe, and Asia. The distribution and chief uses of 6 species are listed in table 1. Most species provide browse and edible fruits for wildlife and many have attractive flowers. Saskatoon and common serviceberries have been used to a limited extent for shelterbelt and wildlife plantings and as a minor fruit crop, but other species also should be considered for these and other environmental uses. Native Americans have traditionally used most species of serviceberry for food and medicine (Meeker and others 1993; Moerman 1986). Common and Saskatoon serviceberries are tolerant of temperatures to –60 °C (Junttila and others 1983; Kaurin and others 1984; Lindstrom and Dirr 1989). Common serviceberry regenerates vegetatively and by seed after clearcutting and burning (Scheiner and others 1988). Geographic races of *Amelanchier* have not been identified, but they could occur in widely distributed species such as the Saskatoon and common serviceberries. Several natural hybrids are known (Campbell and others 1991; Cruise 1964; Flessner and others 1992).

Flowering and fruiting. The perfect white flowers of serviceberries appear in terminal and lateral clusters early in spring, before the leaves in some species (table 2). Fruits are berrylike pomes (figure 1) that turn dark purple or black when they ripen (table 3). Each fruit contains from 4 to 10 small seeds weighing from 1.1 to 6.9 mg, although some of these are usually abortive (St. Pierre and Steeves 1990). Gorchov (1985) reported that fruits containing more seeds develop quicker, suggesting asynchronous fruit development of the genus. Fertile seeds are dark brown with a leathery seedcoat (figure 2) and with the embryo filling the seed cavity (figure 3). Seeds are dispersed almost entirely by birds and animals; however, Turcek (1961) reported that seeds of some species are distributed by insects. Fruits usually are

Table 1—*Amelanchier,* serviceberry: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
A. alnifolia **(Nutt.) Nutt. ex M. Roemer** *Amelanchier carrii* Rydb. *Aronia alnifolia* Nutt.	**Saskatoon serviceberry,** juneberry, western shadbush	W Ontario to Yukon, S to Oregon & Utah, E to Utah, NW Iowa
A. alnifolia **var.** ***semiintegrifolia*** **(Hook.) C.L. Hitchc.** *A. florida* Lindl.	**Pacific serviceberry,** western serviceberry	Pacific Coast region from Alaska S through W British Columbia, Washington, & NW California
A. arborea **(Michx. f.) Fern.** *A. alabamensis* Britton *A. arborea* var. *alabamensis* (Britton) G. N. Jones	**common serviceberry,** downy serviceberry, shadblow, serviceberry	New Brunswick W to Ontario & Minnesota, S to Nebraska & Texas, E to Florida
A. canadensis **(L.) Medik.** *A. lucida* Fern. *A. canadensis* var. *subintegra* Fern.	**Canadian serviceberry,** thicket shadblow, shadbush, thicket serviceberry	Maine to Pennsylvania & Georgia
A. laevis **Wieg.** *A. arborea* var. *laevis* (Wieg.) Ahles	**Allegheny serviceberry,** juneberry, shadbush	Newfoundland & Quebec to Minnesota, S to Kansas, E to Ohio & Delaware, & in mtns to Georgia & Alabama
A. sanguinea **(Pursh) DC.**	**roundleaf serviceberry,** roundleaf juneberry, shore mtns. shadbush, Huron serviceberry	Maine & S Quebec to Minnesota, S to Iowa & E to New Jersey, mtns.of North Carolina

Table 2—*Amelanchier,* serviceberry: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening
A. alnifolia	—	May–June	July–Aug
var. *semiintegrifolia*	Oregon (520 m)	Apr	Aug
	Oregon (1,310 m)	May	—
		May	Aug
A. arborea	—	Mar–June	June–Aug
A. canadensis	Carolinas	Mar–April	May–June
		May	June
A. laevis	—	Mar–June	June–Aug
A. sanguinea	—	May–June	July–Sept

Sources: Fernald (1950), Jones (1946), Mowat (1969), Plummer and others (1968), Radford and others (1964), Rehder (1940), St. Pierre and Steeves (1990), Van Dersal (1938).

Figure 1—*Amelachier alnifolia* var. *semiintegrifolia*, Pacific serviceberry (**top**) and *A. laevis*, Allegheny serviceberry (**bottom**): pomes.

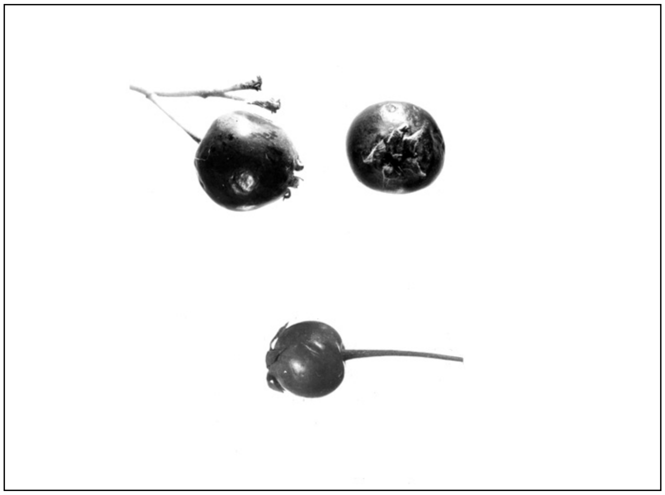


Figure 2—*Amelachier alnifolia,* Saskatoon serviceberry (**left**) and *A. alnifolia* var. *semiintegrifolia,* Pacific serviceberry (**right)**: seeds.

Table 3—*Amelanchier,* serviceberry: height and fruit ripeness criteria

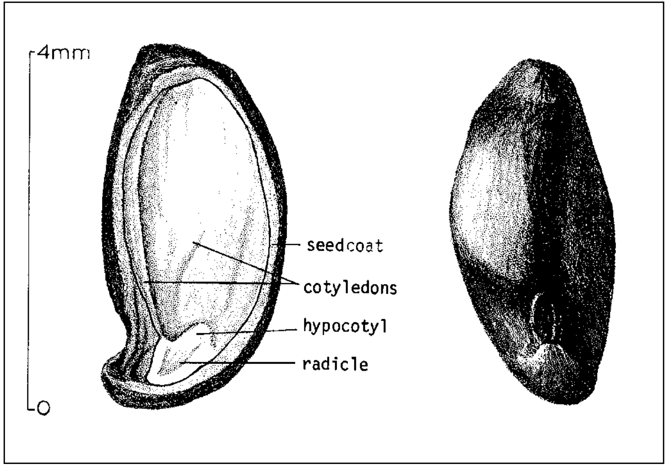
Species	Height at maturity (m)	Year first cultivated	Color of ripe fruit
A. alnifolia	5	1826	Blue purple
var. *semiintegrifolia*	12	1826	Purplish black
A. arborea	18	1623	Reddish purple
A. canadensis	8	1641	Nearly black (sweet)
A. laevis	9	1870	Dark purple
A. sanguinea	3	1824	Dark purple (sweet)

Sources: Fernald (1950), Jones (1946), Petrides (1958), Rehder (1940), Small (1933), Strausbaugh and Core (1953).

eaten by birds or animals as soon as they ripen. Fruit loss of Saskatoon serviceberry can be significant (up to 81% of the potential). These losses occurred because of insects and disease (54%) and frost (27%), with the remaining losses (19%) undetermined (St. Pierre 1989). Fruit loss can exceed 95% in some years and some locations (St. Pierre 1996).

Collection of fruits. To minimize losses to wildlife, fruits must be picked from the shrubs as soon as possible after ripening (table 2). Fruit color is the best way to judge maturity (table 3). Unless the seeds are to be extracted promptly, the fruits should be spread out in thin layers to dry. Loss of viability will result if the fruits are allowed to overheat.

Figure 3—*Amelachier sanguinea*, roundleaf serviceberry: longitudinal section through a seed (**left**) and exterior view (**right**).



Extraction and storage of seeds. Serviceberry seeds are usually extracted by macerating the fruits in water and washing them over screens (Heit 1967; Munson 1986; Peterson 1953), which removes most of the pulp. After this remainder is dried and rubbed through the screens, the seeds and remaining debris are run through a fanning mill to remove small, aborted seeds and bits of fruit (Brinkman 1974). Seed yield and weight data are listed in table 4. Few storage tests have been made of serviceberry seeds, but dry storage in sealed containers at 5 °C is usually recommended (Brinkman 1974; Crocker and Barton 1931). However, excessive drying of seeds may induce a deeper dormancy with consequential decrease in germination rate (St. Pierre 1996).

Pregermination treatments. Embryos of all species show dormancy that can be at least partially overcome by cold stratification (Crocker and Barton 1931), however, control of fungi during this period is critical (McTavish 1986). The seedcoat of some species also may retard germination. Scarification of Allegheny serviceberry in concentrated H_2SO_4 followed by stratification improved germination (Hilton and others 1965). Addition of a mixture of benzyladenine and thiourea enhanced seed germination of Saskatoon serviceberry (Weber and others 1982). The necessary time period of cold stratification varies, but most species require 2 to 6 months (Heit 1968) (table 5). Robinson (1986) reports improved germination from seeds of fruits consumed by cedar waxwings (*Bombycilla cedrorum*).

Germination tests. Germination of Saskatoon serviceberry appears to be genetically controlled and, to a limited extent, can be influenced by environmental fluctua-

Table 4—*Amelanchier*, serviceberry: seed yield data

Species	Place collected	Fruit wt/vol kg/hl	Fruit wt/vol lb/bu	Seed wt/fruit wt kg/45 kg	Seed wt/fruit wt lb/100 lb	Seed wt/fruit vol kg/hl	Seed wt/fruit vol lb/bu	Cleaned seeds (x1,000) /weight Range /kg	Cleaned seeds (x1,000) /weight Range /lb	Cleaned seeds (x1,000) /weight Average /kg	Cleaned seeds (x1,000) /weight Average /lb
A. alnifolia	—	—	—	0.9	2	—	—	80–251	36.3–113.8	181	82
var. *semiintegrifolia*	Oregon	118	42	0.9	2	2.8	1	—	—	119	54
A. arborea	—	—	—	0.5	1	—	—	110–178.6	50–81	176	80
A. sanguinea	Minnesota	—	—	—	—	—	—	—	—	185	84

Sources: Brinkman (1974), McKeever (1938), Mowat (1969).

tions (Acharya and others 1989). Germination of stratified seeds can be tested in sand or a sand–peat mixture. Constant temperatures of 21 °C or alternating day/night temperatures of 30 and 20 °C have been equally successful. Light does not appear to be necessary during tests (table 5). Germination is epigeal (figure 4). Germination of Saskatoon serviceberry seeds often occurs during stratification (St. Pierre 1996). Previously stratified seeds of Saskatoon serviceberry showed 84 to 99% germination at 2 to 5 °C (McKeever 1938; McLean 1967). Under natural conditions, germination could begin in the early spring under snow or shortly after snowmelt.

Nursery practice. Serviceberry seeds may be either sown in the fall or stratified and sown in the spring (Bailey 1935). Many seeds do not germinate until the second spring. It is suggested that the seeds be sown as soon as possible after collection and that the beds be kept mulched until germination begins the following spring (Brinkman 1974). Seeds should be sown in drills at the rate of 80 sound seeds/m (25 seeds/ft) and covered with 6 mm ($^1/_4$ in) of soil. At least for Saskatoon serviceberry, half-shade during the first year apparently is beneficial.

Figure 4—*Amelachier* spp.: seedling development at 3, 5, and 7 days after germination.

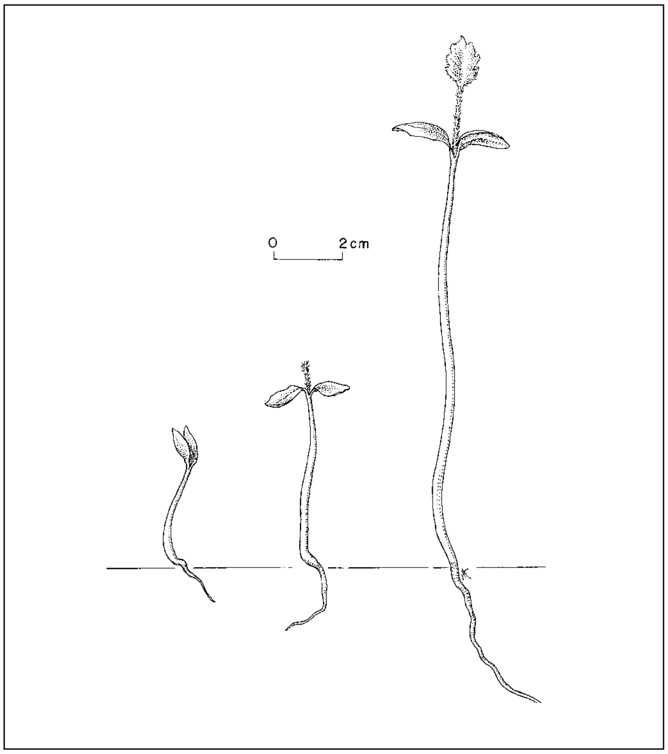


Table 5—*Amelanchier*, serviceberry: cold stratification period, germination test conditions, and results

	Cold stratification*	Germination test conditions					Germination rate		Germination percentage		Purity
Species	(days)	Daily light (hrs)	Medium	Temp (°C) Day	Temp (°C) Night	Days	Amount (%)	Days	Avg (%)	Samples	(%)
A. alnifolia	180+	16	Sand	30	20	30	—	—	—	70	2
	120	0	Sand or blotters	21	21	70	50	8	—	62	10
	98										
A. alnifolia var. *semiintegrifolia*†	30–90	6	Kimpack	30	20	31	—	—	10	2	—
A. arborea	90–120	16	Sand or sand & peat	30	20	—	—	—	54	2	93
A. canadensis	120	—	—	—	—	—	—	—	—	—	—
A. laevis‡	60+	—	Filter paper	20	20	6–7	—	—	61–74	4	—

Sources: Babb (1959), Brinkman (1974), Hilton and others (1965), McKeever (1938), Mclean (1967).

* Stratification was done in a moist medium at temperatures between 1 and 6 °C.

† In an additional test on excised embryos, germination was 82% (Brinkman 1974).

‡ In an additional test on excised embryos, germination was 95% (Hilton and others 1965)

References

Acharya SN, Chu SB, Hermesh R. 1989. Effects of population, environment and their interaction on Saskatoon berry. *Amelanchier alnifolia* Nutt seed germination. Canadian Journal of Plant Science 69: 277–284.

Babb MF. 1959. Propagation of woody plants by seed. Alaska Agricultural Experiment Station Bulletin 26: 1–12.

Bailey LH. 1935. The nursery manual. New York: Macmillan. 456 p.

Brinkman, KA. 1974. *Amelanchier* Med., serviceberry. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 212–215.

Campbell CS, Greene CW, Dickinson TA. 1991. Reproductive biology in subfam. Maloideae (Rosaceae). Systematic Botany 16(2): 333–349.

Crocker W, Barton LV. 1931. After-ripening, germination, and storage of certain rosaceous seeds. Boyce Thompson Institute Contributions 3: 385–404.

Cruise JE. 1964. Studies of natural hybrids in *Amelanchier*. Canadian Journal of Botany 42: 651–633.

Fernald ML. 1950. Gray's manual of botany. New York: American Book Co. 1632 p.

Flessner TR, Darris DC, Lambert SM. 1992. Seed source evaluation of four native riparian shrubs for streambank rehabilitation in the Pacific Northwest. In: Proceedings, Symposium on Ecology and Management of Riparian Shrub Communities: 1991 May 29–31; Sun Valley, ID. Gen. Tech. Rep. INT-289. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 155–162.

Gorchov DL. 1985. Fruit ripening asynchrony is related to variable seed number in *Amelanchier* and *Vaccinium*. American Journal of Botany 72(12): 1939–1943.

Heit CE. 1967. Fall planting of fruit and hardwood seeds. American Nurseryman 126(4): 12–13, 85–90.

Heit CE. 1968. Thirty-five years' testing of tree and shrub seed. Journal of Forestry 66: 632–634.

Hilton RJ, Joswal AS, Teskey BJ, Barabas B. 1965. Rest period studies on seeds of *Amelanchier*, *Prunus*, and *Sorbus.* Canadian Journal of Plant Science 45(1): 79–85.

Jones GN. 1946. American species of *Amelanchier*. Illinois Biological Monographs 20(2): 1–126.

Junttila O, Stushnoff C, Gusta LV. 1983. Dehardening in flower buds of saskatoon-berry, *Amelanchier alnifolia*, in relation to temperature, moisture content, and spring bud development. Canadian Journal of Botany 61(1): 164–170.

Kaurin A, Stushnoff C, Junttila. 1984. Cold acclimation and dormancy of *Amelanchier alnifolia*. Journal of the American Society of Horticultural Science 109(2): 160–163.

Lindstrom OM, Dirr MA. 1989. Acclimation and low-temperature tolerance of eight woody taxa. HortScience 24(5): 818–820.

McKeever DG. 1938. The effect of various methods of treatment on germination of seeds of some plants valuable for game and erosion purposes [MS thesis]. Moscow, ID: University of Idaho School of Forestry. 128 p.

McLean A. 1967. Germination of forest-range species from southern British Columbia. Journal of Range Management 20(5): 321–322.

McTavish B. 1986. Seed propagation of some native plants is surprisingly successful. American Nurseryman 164(4): 55–63.

Meeker JE, Elias JE, Heim JA. 1993. Plants used by the Great Lakes Ojibwa. Odanah, WI: Great Lakes Indian Fish and Wildlife Commission. 440 p.

Moerman DE. 1986. Medicinal plants of Native America, Volume 1. Tech. Rep. 19. Ann Arbor: University of Michigan Museum of Anthropology. 534 p.

Mowat EL. 1969. Phenological observations recorded 1969. Portland, OR: USDA Forest Service, Northwest Forest and Range Experiment Station.

Munson RH. 1986. Extracting seeds from fleshy fruits. Plant Propagator 32(2): 14–15.

Peterson RA. 1953. Comparative effect of seed treatments upon seedling emergence in seven browse species. Ecology 34(4): 778–785.

Petrides GA. 1958. A field guide to trees and shrubs. Boston: Houghton Mifflin. 431 p.

Plummer AP, Christensen DR, Monsen SB. 1968. Restoring big-game range in Utah. Pub. 68-3. Salt Lake City: Utah Department of Natural Resources, Division of Fish and Game. 182 p.

Radford AE, Ahles HE, Bell CR. 1964. Guide to the vascular flora of the Carolinas. Chapel Hill: University of North Carolina Book Exchange. 383 p.

Rehder A. 1940. Manual of cultivated trees and shrubs hardy in North America. New York: Macmillan. 996 p.

Robinson WA. 1986. Effect of fruit ingestion on *Amelanchier* seed germination. Bulletin of the Torrey Botanical Club 113(2): 131–134.

St. Pierre RG. 1996. Personal communication. Saskatoon, SK.

St. Pierre RG. 1989. Magnitude, timing, and causes of immature fruit loss in *Amelanchier alnifolia* (Rosaceae). Canadian Journal of Botany 67: 726–731.

St. Pierre RG, Steeves TA. 1990. Observations of shoot morphology, anthesis, flower number, and seed production in the Saskatoon [serviceberry], *Amelanchier alnifolia* (Rosaceae). Canadian Field-Naturalist 104(3): 379–386.

Scheiner SM, Sharik TL, Roberts MR, Kopple RV. 1988. Tree density and modes of tree recruitment in a Michigan pine–hardwood forest after clear-cutting and burning. Canadian Field-Naturalist 102(4): 634–638.

Small JK. 1933. Manual of the southeastern flora. New York: J.K. Small. 1554 p.

Strausbaugh PD, Core EL. 1953. Flora of West Virginia: Part II. Morgantown: West Virginia University. 1075 p.

Turcek FJ. 1961. Ökologische Beziehungen der Vögel und Gehölze. Bratislava: Verlag Slowakische Akademie der Wissenschaften. 329 p.

Van Dersal WR. 1938. Native woody plants of the United States: their erosion control and wildlife values. Misc. Pub. 303. Washington, DC: USDA. 362 p.

Weber GP, Wiesner LE, Lund RE. 1982. Improving germination of skunkbush sumac and serviceberry seed. Journal of Seed Technology 7(1): 60–71

Fabaceae—Pea family

Amorpha L.

amorpha, indigobush

John C. Zasada and David Martineau

Dr. Zasada retired from the USDA Forest Service's North Central Research Station; Mr. Martineau is the plant division manager at the Prairie Nursery, Westfield, Wisconsin

Growth habit, occurrence, and use. In North America, the amorphas include about 15 species of deciduous shrubs or subshrubs (Wilbur 1975). Wilbur (1975) provides a thorough description of all species with range maps showing distribution. Four of the more common species and their ranges are listed in table 1. Leadplant and indigobush are the 2 most widely distributed and used species in the genus.

Leadplant is common in dry to wet–mesic prairie communities; in Wisconsin, its highest presence values are in the dry to dry–mesic communities (Curtis 1959; Henderson 1995; Johnson and Anderson 1985; Voigt and Mohlenbrock nd). Kotar and others (1988) list leadplant as a diagnostic species for the white oak–pin oak–leadplant habitat type that is transitional between prairie and forest in Wisconsin. Indigobush has a large range and within that range occurs on sites with fairly wet to dry moisture regimes and is relatively more common in riparian areas (Curtis 1959; Glad and Halse 1993). It can be an aggressive invader, as demonstrated by its spread along the Columbia and Snake Rivers in Oregon and Washington (Glad and Hulse 1993). Wilbur (1975) reported that indigobush is highly variable and that it is best described as a complex with variation due to both environmental and genetic factors. In North Dakota, plants from more southern seed sources grow more rapidly and are taller than those from North Dakota sources, but they are also more susceptible to winter damage (Lincoln Oakes Nurseries 1996).

Leadplant and indigobush are reported to hybridize, although hybrids are believed rare (Wilbur 1975). The hybrid has the greatest affinity with leadplant and differs in having a taller growth form as well as in several morphological traits (Wilbur 1975).

The growth form and stature of leadplant results from its tendency to die-back to varying degrees each year. Regrowth from basal stem and root collar buds maintains the above ground stems. Under some conditions, stems will be relatively longer-lived and attain heights of 1.5 to 2 m (table 2). Indigobush is taller than leadplant and its stem longevity is like that of a true shrub.

Leadplant is palatable to domestic livestock and under heavy grazing tends to disappear (Voigt and Mohlenbrock nd); however its palatability for whitetail deer (*Odocoileus virginiana*) was rated as low in a study in the Black Hills (Rosario 1988). A primary use, at present, is for landscaping, where low-maintenance, drought-resistant plants are desirable, and in restoration and reclamation projects (Brown and others 1983; Cox and Klett 1984; Dirr 1990;

Table 1—*Amorpha,* amorpha: nomenclature and occurrence

Scientific name & synonym	Common name(s)	Occurrence
***A. californica* Nutt.**	**mock locust,** false indigo, California amorpha	California Coast Range from Sonoma & Napa Cos. S to Riverside Co.
***A. canescens* Pursh**	**leadplant,** prairie shoestrings	Michigan to Saskatchewan, S to Indiana, W to Arkansas & New Mexico; prairies in region
***A. fruticosa* L.**	**indigobush,** false indigo	S Quebec to N Manitoba, S to Florida & Mexico; S California & Wyoming
***A. nana* Nutt.** *A. microphylla* Pursh	**dwarf indigobush,** fragrant false indigo	Manitoba and Saskatchewan S to Iowa & New Mexico

Sources: Brinkman (1974), Glad and Halsey (1993), Hickman (1993), Niering and Olmstead (1979), Rosario (1988), Voight and Mohlenbrock (nd), Wilbur (1975).

Table 2—*Amorpha,* amorpha: height and year of first cultivation

Species	Height at maturity (m)	Year first cultivated
A. canescens	1–3	1883
A. fruticosa	12–18	1724
A. nana	1–3	1811

Sources: Brinkman (1974), Dirr (1990) Niering and Olmstead (1979), Rehder (1940), Rosario (1988), Smith and Smith (1980), Vines (1960), Wilbur (1975).

Salac and others 1978). Indigobush is used in reclamation of strip-mined areas (Brown and others 1983; Weber and Wiesner 1980). Leadplant is an important prairie plant and is included in restoration projects (Salac and others 1978). All amorpha species are nitrogen-fixers and thus have the potential for improving soil nutrient status. In the traditional medicine of the Great Lakes Ojibwa, a decoction of the root of leadplant was used to treat stomach pain (Meeker and others 1993); leaves were used as a tobacco and for making tea (Niering and Olmstead 1979).

Flowering and fruiting. The irregular, perfect flowers of amorphas are blue to violet purple in color and are borne in the spring or summer (table 3). The inflorescence is a raceme; leadplant can have 200 to 300 flowers/raceme. The fruit is short, indehiscent, somewhat curved and often gland-dotted legume (pod) containing 1 (or sometimes 2) small glossy seed (figures 1 and 2). When ripe in mid to late summer, the legumes are light brown in color. Commercial seed usually consists of the dried legumes.

Good seedcrops of mock locust are borne every 2 years (Brinkman 1974), and similar frequencies probably are typical of the other species. Flowering in leadplant was stimulated by spring burning; periodic burning appears to stimulate both vegetative and reproductive growth (Richards and Landers 1973; Rosario 1988). Periodic, not annual, mowing may also improve seed production (Rosario 1988). Indigobush seed availability may be lowered significantly by seed beetles (Rogers and Garrison 1975). The majority of leadplant seeds are dispersed in September and October, but a few may may remain on the plant during winter.

Figure 1—*Amorpha*, amorpha: legume and seed of *A. fruticosa*, indigobush.

Collection of fruits; extraction and storage of seeds. The ripe legumes can be stripped from the inflorescences and spread out in thin layers for a few days to permit drying.

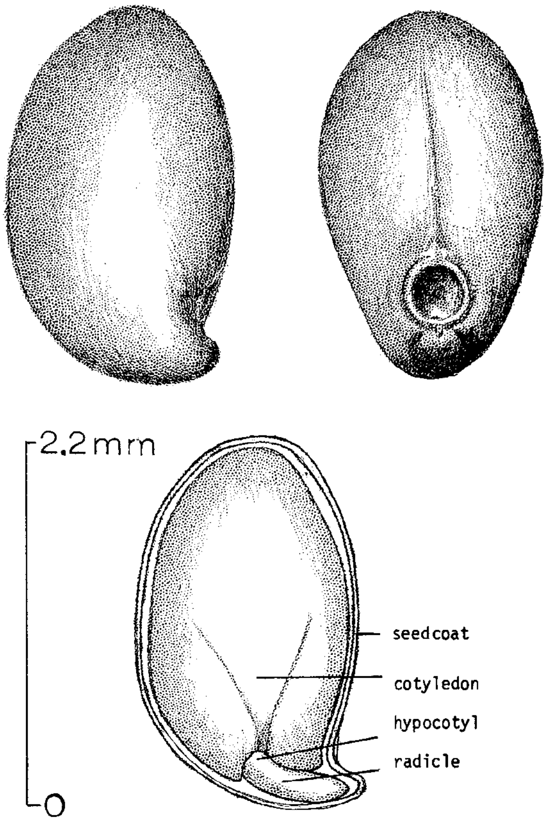
Extraction of seeds is not essential for germination. The legumes are usually 1-seeded, thin walled, and soft enough so that germination does not appear to be reduced significantly if seeds are not removed from the legumes. However, the seeds may be extracted by gently beating or rubbing the legumes. Available data on seed and fruit weights are listed in table 4. Little is known about optimum storage conditions, but all evidence suggests that the seeds are orthodox in storage behavior. Seeds of leadplant stored for 22 months at 41 °C followed by 16 months at room temperature showed little loss in germination; sealed storage at continuous low temperature probably would prolong viability (Brinkman 1974). Seeds of indigobush have retained viabili-

Table 3—*Amorpha,* amorpha: phenology of flowering and fruiting

Species	Flowering	Fruit ripening	Seed dispersal
A. californica	May–July	July–Sept	Aug–Sept
A. canescens	June–late July	Aug–Sept	Sept–Oct
A. fruticosa	May–June	Aug	Sept–Oct
A. nana	May–July	July	July

Sources: Brinkman (1974), Fernald (1950), Lincoln Oakes Nurseries (1996), Mirov and Kraebel (1939), Rehder (1940), Smith and Smith (1980), Van Dersal (1938).

Figure 2—*Amorpha canescens,* leadplant: exterior views of seed and embryo (**top**) and interior of seed (**bottom**).



ty for 3 to 5 years at room temperature (Brinkman 1974); more recent experience indicates that seeds can be stored at 2 °C for at least several years with little loss in viability (Lincoln Oakes Nurseries 1996). The presence of leadplant in prairie soil seed banks also suggests that seeds may have relatively long lives without cold storage (Johnson and Anderson 1985).

Pregermination treatments and germination. The degree and type of dormancy appear to differ among species. As with many woody species, drying of seeds may induce seedcoat dormancy in seeds that would normally germinate without pretreatment (Dirr and Heuser 1987). Both mock locust and leadplant will germinate completely without treatment (Martineau 1996; Mirov and Kraebel 1939). Leadplant seeds obtained from commercial dealers following an unknown period of storage germinated without treatment, but stratification at 3 to 4 °C for 2 and 8 weeks increased the rate of germination; 30 minutes of scarification in sulfuric acid reduced germination by 50% (Cox and Klett 1984). Germination of some seed lots has been improved by soaking the seed in hot water for about 10 minutes. Cold stratification has been used in preparation for spring sowing in a nursery bed (Brinkman 1974). This cold treatment may reduce seedcoat impermeability. Dirr and Heuser (1987) indicate that fresh leadplant seeds germinate without pretreatment but that stored seeds may benefit from acid treatment.

Indigobush and dwarf indigobush appear to have seed coat dormancy. Light scarification of indigobush seeds and soaking seed of both this species and dwarf indigobush in sulfuric acid for 5 to 8 minutes have been used to stimulate germination (Brinkman 1974; Dirr and Heuser 1987). However, fall sowing with no pretreatment results in some, but not complete, germination (Brown and others 1983). Simulated acid rain with pH of less than 5 tended to reduce germination in indigobush, but significant germination occurred at pH 3 and 4 (Lee and Kim 1986). Total seedling dry weight of indigobush increased with decreasing pH of simulated acid rain (Lee and Kim 1986). Germination test conditions and results on pretreated seeds are in table 5. Germination is epigeal (figure 3).

Indigobush is the only species of amorpha that is listed in official seed testing rules. International Seed Testing Association (ISTA 1993) prescriptions call for a 28-day test at alternating temperatures of 20/30 °C on the top of moist

Table 4—*Amorpha,* amorpha or indigobush: fruit and seed data

	Ripe fruit (x1,000)/wt				Cleaned seed (x1,000)/wt			
	Range		Average		Range		Average	
Species	/kg	/lb	/kg	/lb	/kg	/lb	/kg	/lb
A. californica	—	—	—	—	43–146	19–66	84	38
A. canescens	194–233	88–106	211	96	598–651	272–296	624	284
*A. fruticosa**	81–205	37–93	114	52	158–180	72–82	170	77
A. nana	—	—	133	60	—	—	—	—

Sources: Brinkman (1974), Lincoln Oakes Nurseries (1996), Prairie Nursery (1996), Salac and others (1978).
* One hundred pounds of dried fruit will produce about 60 pounds of clean seeds (Swingle 1939).

germination paper. Light is required during the 8 hours at 30 °C, but no pretreatments are called for.

A procedure for tetrazolium testing of depodded seeds of indigobush has been developed (Weber and Wiesner 1980). Seeds are chipped at the distal end to avoid injury to the embryonic axis (the more rounded end in figure 1) and stained for 18 hours. Lactophenol clears the seed coat, making it possible to interpret seed viability without removing the seedcoat. The method distinguishes living from dead seeds (Weber and Wiesner 1980).

Nursery practice. Seedlings can be produced in containers or as bareroot stock. The need for pretreatment of seeds will be determined by species and condition of the seeds, for example, seeds may germinate faster if they are removed from the legume. Timing of sowing in container production is more flexible than in outdoor beds. Seed use may be more efficient in containers than in outdoor beds because temperature and water availability are more easily controlled in the greenhouse environment. Rock (1981) recommends inoculating seeds of leadplant with nitrogen-fixing bacteria before sowing. This recommendation is probably applicable to all amorpha species.

For container production of leadplant in a greenhouse, cleaned seeds (removed from the legumes, inoculated, and unstratified) may be sown at any time during the summer. Initial sowing is in small cells (about 2 to 3 cm^3); germination is completed in about 15 days. When seedlings are at the 3- to 5-leaf stage, they are transplanted to larger containers. Seedlings are kept in the greenhouse until established in the new containers and then moved outside. If seeds are sown in spring, seedlings can be transplanted to ~1 liter containers (~1 qt) in early to midsummer; seedlings will be ready for outplanting by fall (Martineau 1996).

For bareroot production of leadplant, cleaned, inoculated, unstratified seeds are sown in the spring, covered with a few millimeters of soil followed by a layer of sawdust. Seedbeds are lightly compacted and the beds are watered as needed. Germination will occur mostly in the first year with a small amount of carryover to the second growing season. Juvenile leaves (simple, round as in figure 3) are produced part way through the growing season with a transition to the characteristic pinnately compound leaves in mid to late summer. Seedlings will be about 30 to 50 cm (12 to 20 in) tall, with a taproot of equivalent length, after 2 growing seasons. Seedlings are lifted and sold after the second growing season or in the following spring while still dormant. Care should

Figure 3—*Amorpha canescens*, leadplant: seedling development at 1, 2, 8, 20, and 52 days after germination.

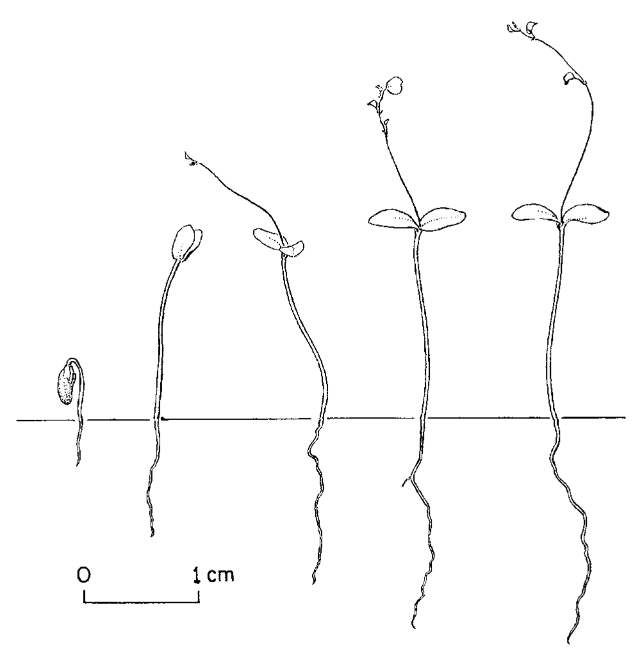


Table 5—*Amorpha.* amorpha: germination test conditions and results

Species	Day/night temp (°C)	Duration (days)	% Germination
A. californica	—	5	42
*A. canescens**	30/20	15–40	28
A. fruticosa	30/20	15–40	63
A. nana	30/20	30–40	70

Sources: Blake (1935), Brinkman (1974), Christiansen (1967), Hutton and Porter (1937), Kraebel (1939), Lincoln Oakes Nurseries (1996), Martineau (1996), Pammel and King (1928), Swingle (1939), Van Dersal (1938).
Note: Temperature is day/night regimen, photoperiod is 8 hours, based on Brinkman (1974).
* Germination of leadplant (*Amorpha canescens*) takes about 2 weeks when sown in nurserybeds in the spring (Lincoln Oakes Nurseries 1996; Martineau 1996).

be taken when lifting, as the roots are split easily (Martineau 1996). Similar procedures are used for leadplant in North Dakota (Lincoln Oakes Nurseries 1996).

The following schedule for growing bareroot indigobush seedlings is reported by the Lincoln Oakes Nurseries (1996):

1. Legumes are hand-stripped from the plants in late September–late October.
2. Stem parts and impurities are removed, but the legumes are not removed.
3. Seeds are cold-stratified for 60 to 90 days in sand before sowing in the spring.
4. Seeds are sown in a single row of 80 to 100 seeds/m (25 to 35 seeds/ft) at a depth of 0.8 cm ($^{1}/_{3}$ in). Seedlings grow to heights of 25 to 35 cm (8 to 14 in) the first year and 0.6 to 1.2 m (2 to 4 ft) the second year.
5. Plants are harvested as 2+0 seedlings.

Seeds can also be sown in the fall to allow natural stratification to occur; this appears to partially eliminate the need for acid treatment in those species where it is recommended (Brown and others 1983; Dirr and Heuser 1987). For leadplant, 0.45 kg (1 lb) of commercial seed has produced about 22,000 usable plants; for indigobush, 1,000 to 5,600 plants (Brinkman 1974).

Amorpha species can be propagated from softwood and semi-hardwood cuttings. Untreated softwood cuttings root readily, but later-season cuttings may require treatment with a rooting compound (Bailey 1939; Dirr 1990; Dirr and Heuser 1987).

References

Bailey LH. 1939. The standard cyclopedia of horticulture. New York: Macmillan. 3639 p.

Blake AK. 1935. Viability and germination of seeds and early life history of prairie plants. Ecology Monograph 5: 405–460.

Brinkman KA. 1974. *Amorpha*, amorpha, false indigo. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk 450. Washington, DC: USDA Forest Service: 216–219.

Brown JE, Maddox JB, Splittstoesser WE. 1983. Performance of trees, shrubs, and forbs seeded directly in the fall on minespoil and silt loam soil. Journal of Environmental Quality 12: 523–525.

Christiansen PA. 1967. Establishment of prairie species in Iowa by seeding and transplanting [PhD thesis]. Ames: Iowa State University. 119 p.

Cox RA, Klett JE. 1984. Seed germination requirements of native Colorado plants for use in the landscape. Plant Propagator 30(2): 6–10.

Curtis JT. 1959. The vegetation of Wisconsin: an ordination of plant communities. Madison: University of Wisconsin. 657 p.

Dirr MA. 1990. Manual of woody landscape plants: their identification, ornamental characteristics, culture, propagation, and uses. Champaign IL: Stipes Publishing. 1007 p.

Dirr MA, Heuser CW Jr. 1987. The reference manual of woody plant propagation: from seed to tissue culture. Athens, GA: Varsity Press. 239 p.

Fernald ML. 1950. Gray's manual of botany. New York: American Book Co. 1632 p.

Glad JB, Halse RR. 1993. Invasion of *Amorpha fruticosa* L. (Leguminosae) along the Columbia and Snake Rivers in Oregon and Washington. Madroño 40(1): 62–63.

Henderson RA. 1995. Plant species composition of Wisconsin prairies. Tech. Bull. 188. Madison: Wisconsin Department of Natural Resources. 58 p.

Hickman JC, ed. 1993. The Jepson manual: higher plants of California. Berkeley: University of California Press. 1400 p.

Hutton ME, Porter RH. 1937. Seed impermeability and viability of native and introduced species of Leguminoseae. Iowa State College Journal of Science 12: 5–24.

ISTA [International Seed Testing Association]. 1993. International rules for seed testing: rules 1993. Seed Science and Technology 21 (Suppl.): 1–59.

Johnson RG, Anderson RC. 1985. The seed bank of a tallgrass prairie in Illinois. American Midland Naturalist 115(1): 123–130.

Lee DK, Kim GT. 1986. Effects of artificial acid rain on seed germination and seedling growth of several woody species. Seoul National University, College of Agricultural Research, Bulletin of Kwanak Arboretum 7: 15–21.

Lincoln Oakes Nurseries. 1996. Personal communication. Bismark, ND.

Martineau D. 1996. Unpublished data. Westfield, WI: Prairie Nursery.

Meeker JE, Elias JE, Heim JA. 1993. Plants used by the Great Lakes Ojibwa. Odanah, WI: Great Lakes Indian Fish and Wildlife Commission. 440 p.

Mirov NT, Kraebel CJ. 1939. Collecting and handling seeds of wild plants. For. Pub. 5. Washington, DC: USDA Forest Service, Civilian Conservation Corps. 42 p.

Niering WA, Olmstead NC. 1979. The Audubon Society field guide to North American wildflowers: eastern region. New York: Knopf. 887 p.

Pammel LH, King CM. 1928. Further studies of the germination and juvenile forms of some trees and woody shrubs, 1927. Proceedings of the Iowa Academy of Science 35: 169–183.

Prairie Nursery. 1996. Wildflowers and native grasses: catalog and growing guide. Westfield, WI: Prairie Nursery. 47 p.

Rehder A. 1940. Manual of cultivated trees and shrubs hardy in North America. New York: Macmillan. 996 p.

Richards MS, Landers RQ. 1973. Responses of species in Kalsow Prairie, Iowa to an April fire. Proceedings of the Iowa Academy of Science 80(4): 159–161.

Rock HW. 1981. Prairie propagation handbook. 6th ed. Hales Corner, WI: Wehr Nature Center. 75 p.

Rogers CE, Garrison JC. 1975. Seed destruction in indigo amorpha by a seed beetle. Journal of Range Management 28(3): 241–242.

Rosario LC. 1988. *Amorpha canescens*. In: Fischer WC, comp. The Fire Effects Information System [database]. Missoula, MT: USDA Forest Service, Intermountain [now Rocky Mountain] Research Station, Intermountain Fire Sciences Laboratory. 12 p.

Salac SS, Jensen PN, Dickerson JA, Gray RW Jr. 1978. Wildflowers for Nebraska landscapes. Misc. Pub. 35. Lincoln: University of Nebraska, Department of Horticulture. 27 p.

Smith JR, Smith BS. 1980. The prairie garden. Madison: University of Wisconsin Press. 52 p.

Swingle CF. 1939. Seed propagation of trees, shrubs, and forbs for conservation planting. SCS-TP-27. Washington, DC: USDA Soil Conservation Service. 198 p.

Van Dersal WR. 1938. Native woody plants of the United States: their erosion control and wildlife values. Misc. Pub. 303. Washington, DC: USDA. 62 p.

Vines RA. 1960. Trees, shrubs, and woody vines of the Southwest. Austin: University of Texas Press. 1104 p.

Voigt JW, Mohlenbrock RH. [nd]. Prairie plants of Illinois. Springfield: Illinois Department of Conservation, Division of Forestry. 272 p.

Weber GP, Wiesner LE. 1980. Tetrazolium testing procedures for native shrubs and forbs. Journal of Seed Technology 5(2): 23–34.

Wilbur RL. 1975. A revision of the North American genus *Amorpha* (Leguminosae-Psoraleae). Rhodora 77 (811): 337–409.

Araliaceae—Ginseng family

Aralia L.

aralia

John C. Zasada and Barton M. Blum

Dr. Zasada retired from the USDA Forest Service's North Central Research Station; Dr. Blum retired from the USDA Forest Service's Northeastern Forest Experiment Station

Growth habit, occurrence, and uses. The genus *Aralia* comprises about 20 species of deciduous trees, shrubs, and herbs found in North America, Asia, Malayasia, and Australia (Blum 1974; Fernald 1950). The main species in North America include 3 subshrubs and a small tree (table 1)—the devil's-walkingstick—that is planted as an ornamental, as is the exotic Japanese angelica-tree—*A. elata* (Miq.) Seem. Animals utilize the vegetative growth and fruits to varying degrees. Two species were used for medicinal purposes by Native Americans. Underground parts are known for their aromatic qualities (Blum 1974; Braun 1961; Dirr 1990; Fernald 1950; Kenfield 1966; Krochmal and others 1969; MacKinnon and others 1992; Meeker and others 1993; Moore 1993; Stupka 1964; Tehon 1951; Voss 1985).

Within their respective ranges, the species occupy different types of sites. Devil's-walkingstick is intolerant of shade, occurring mostly on disturbed sites with no or light forest canopy. It develops best on rich, mesic soils but also occurs on a range of site conditions. Dense stands are formed by shoot production from rhizomes. The stem has prominent spines, hence the species' common name of devil's-walking-stick (Sullivan 1992).

Of the herbaceous perennials, wild sarsaparilla is the most widely distributed. It is a common understory species in a variety of forest types. In Wisconsin, for example, it occurs throughout the state but is most common in northern forests with dry-mesic to wet-mesic moisture regimes (Curtis 1959); it occupies similar sites in Newfoundland, Michigan, and British Columbia (MacKinnon and others 1992; Meades and Moores 1994; Voss 1985). Compound leaves develop annually from a well-developed rhizome system. Clones may be 10 m or more in diameter (Bawa and others 1982; Edwards 1984). The age of the perennial shoot-bearing portion of the rhizome can be determined from leaf scars and frequency of flowering from inflorescence scars (Bawa and others 1982).

Spikenard and bristly aralia are less widespread than wild sarsaparilla. Spikenard occurs on relatively richer sites and is described as one of the largest herbaceous plants in the flora of Michigan (Voss 1985).

Bristly aralia occurs on drier sites. Small clones are formed by development of the rhizome system and consist of vegetative and reproductive ramets (Thomson and Barrett

Table 1—*Aralia,* aralia: nomenclature, occurrence, growth habit, and height

Scientific name	Common name(s)	Occurrence	Year first cultivated	Growth habit	Height at maturity (m)
***A. hispida* Vent.**	**bristly aralia,** wild-alder, bristly sarsaparilla, dwarf-elder	Newfoundland to North Carolina & W to Minnesota & Indiana	1788	Subshrub or perennial herb	0.3–0.9
***A. nudicaulis* L.**	**wild sarsaparilla,** small spikenard	Newfoundland to North Carolina & W to Manitoba & Missouri	1731	Subshrub or perennial herb	0.2–0.4
***A. spinosa* L.**	**devil's-walkingstick,** angelica-tree, Hercules-club, prickly-ash	Pennsylvania to Florida, W to SW Iowa & W Texas; range extended by planting in Massachusetts, Oregon, Washington, & W Europe	1688	Tree	7.7–9.2
***A. racemosa* L.**	**spikenard,** petty morrel, life-of-man	Quebec to Manitoba, Great Lakes region, New England, & SE US	—	Subshrub or perennial herb	0.5–3.0

Source: Blum (1974).

1981). A distinguishing characteristic is the presence of spines on the stem (Curtis 1959; Voss 1985).

Flowering and fruiting. The flowers of *Aralia* are polygamous, white or green, and occur in umbels or panicles (Fernald 1950; Harrar and George 1962). Wild sarsaparilla has 3 to 4 umbels/inflorescence (figure 1) and bristly aralia has approximately 9 umbels/ramet. Flowering occurs from May to September depending on species; fruits mature in late summer or fall (figure 2) (Blum 1974; Fernald 1950). Flowers of wild sarsaparilla develop on a separate stalk that is overtopped by the associated vegetative stalk. In the other species, flowers are terminal and axillary or a combination of the two (Fernald 1950). Fruits are light green when immature, changing to bluish or purplish black when mature (Dirr 1990; Mackinnon and others 1992; Meades and Moores 1994; Soper and Heimberger 1982; Voss 1985). Male flowers retained in bristly aralia umbels with both male and hermaphrodite flowers turn red, making the fruit more conspicuous than if only the fruits were present (Thomson and Barrett 1981).

In bristly aralia, umbels contain male-only and hermaphrodite flowers. During the early stages of flowering, all flowers function as males; the female portion of the hermaphrodite flowers is receptive after the male parts have ceased to function. The number of flowers per umbel ranges from 30 to 40. Twenty-seven to 35% of the flowers are hermaphrodites and more than 90% of these produced fruits (Thomson and Barrett 1981).

Figure 1—*Aralia nudicaulis*, wild sarsaparilla: male inflorescence with 3 umbels, stamens just beginning to appear; the larger vertical stem in the background is the leaf-bearing vegetative shoot.

Figure 2—*Aralia nudicaulis*, wild sarsaparilla: developing fruits with stigmas still attached; additional blurred umbels are part of the same inflorescence.

Wild sarsaparilla is dioecious with complete flowers uncommon (Bawa and others 1982). The sex ratio tends to be male-dominated but varies among sites and with time during the period of flowering, as male and female ramets do not flower synchronously (Barrett and Helenrum 1981). Infloresences on female plants contain on average 55 to 125 flowers. About 68% of the flowers produced fruits. Controlled pollinations produced 90 to 100% fruit set; flowers remain receptive for about 6 days. Some of the main differences between male and female clones are that males have more flowers per inflorescence, greater frequency of flowering, and occur in higher densities and greater numbers of ramets than do females (Barrett and Helenrum 1981; Barrett and Thomson 1982; Bawa and others 1982).

Insects are the major means of pollination in the genus (Bawa and others 1982; Barrett and Helenrum 1981; Thaler and Plowright 1980; Thomson and Barrett 1981; Thomson and others 1982). In areas treated to control spruce budworm, 71% of flowers produced fruits in sprayed and 49% in unsprayed sites, respectively (Thaler and Plowright 1980).

The fruit is a small, berry-like drupe containing 2 to 5 compressed, crustaceous, light reddish brown nutlets that are round, oblong, or egg-shaped. Each nutlet contains 1 compressed, light brown seed with a thin coat that adheres closely to the fleshy endosperm (Sargent 1965; Thomson and Barrett 1981) (figures 2 and 3).

Collection, extraction, and storage. Aralia fruits may be collected when they begin to fall from the plants in autumn (table 2). The seeds are ripe when the endocarps of the nutlets become hard and brittle, and this ripening may occur somewhat later than the ripening of pulp. The fruits should be run through a macerator, with water, immediately after collection. This will prevent fermentation and enable the pulp and empty seeds to float off or be screened out. Small samples can be pulped by rubbing, with water, between 6.35-mm (#16) screens. Purity of seeds cleaned by the macerator technique was 98% (Blum 1974), but soundness in some lots has been only 30 to 60% (Heit 1968). Seed size and weight of cleaned seeds is indicated in figures 3 and 4 and table 3. Refrigerated storage of cleaned seed in sealed containers is recommended (Dirr and Heuser 1987; Heit 1967a), but the duration of viability under these conditions is not known.

Seeds of early successional aralia species from temperate and tropical regions elsewhere in the world have been found in soil seedbanks (Cheke and others 1979; Hirabuki 1988). Seedbanks in beech–birch–maple forests in New England had a minor amount of spikenard, bristly aralia, and wild sarsaparilla (Graber and Thompson 1978). No information was found on buried seeds of devil's-walkingstick, a plant that better fits the ecological characteristics—that is, early successional, intolerant species—of the aralia species found to occupy seedbanks in other parts of the world (Cheke and others 1979; Hirabuki 1988). The longevity of aralia seeds in the forest floor environment is not known.

Germination. Aralia seeds have dormant embryos, and some species, notably bristly aralia, appear to have impermeable endocarps (hardseededness) (Heit 1967b). There may be a combination of both hardseededness and embryo dormancy, requiring either mechanical or chemical scarification of the seedcoat in addition to a prechilling treatment (Heit 1967b). Seed dormancy in devil's-walkingstick can be overcome satisfactorily by 3 months of stratification at low temperatures (Blum 1974; Dirr and Heuser 1987). Hartmann and others (1990) also suggest that 30 minutes of soaking in sulfuric acid in addition to stratification improves germination. Dirr and Heuser (1987) reported 1% germination without stratification and 55% following 3 months of cold treatment. Although pretreatment with sulfuric acid and stratification at low temperatures will partially overcome hardseededness and embryo dormancy, other complications such as immature embryos further hinder germination (Heit 1968). In a study by Nichols (1934), seeds of wild sarsaparilla had 34% germination in 21 to 35 days after pretreating for 71 days at low winter temperatures in a cold frame. However, in this same study, seeds of bristly aralia had only 8% germination after exposure to low temperatures for 83 days. Seeds not exposed to low temperatures, on the other hand, had only 3% germination. Seeds of bristly aralia

Figure 3—*Aralia spinosa*, devil's-walkingstick: nutlets (seeds).

Table 2—*Aralia,* aralia: phenology of flowering and fruiting

Species	Flowering Dates	Fruit Ripening Dates	Seed Dispersal Dates
A. hispida	June–July	A	
A. nudicaulis	May–June	A	
A. spinosa	July–Aug	S	

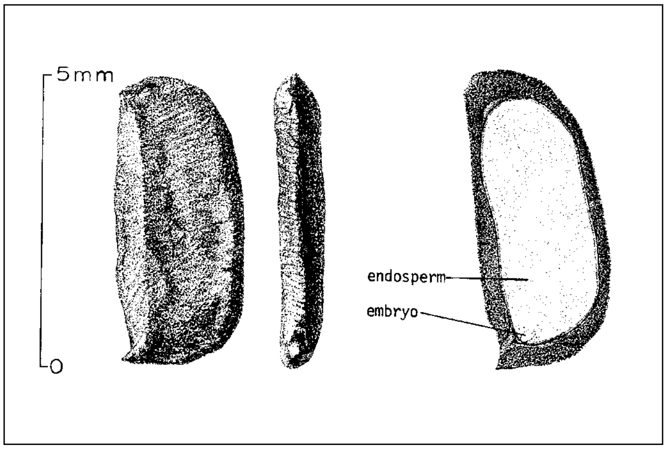
Source: Blum (1974).

Table 3—*Aralia,* aralia: seed data

	Cleaned seeds/weight				
	Range		Average		
Species	/kg	/lb	/kg	/lb	Samples
A. hispida	207,740–218,790	94,000–99,000	203,320	92,000	2
A. nudicaulis	185,640–245,310	84,000–111,000	218,300	99,000	3
*A. spinosa**	232,050–346,970	105,000–157,000	288,850	131,000	2

Source: Blum (1974).
* 100 pounds of fruit have yielded 11 pounds of seed.

Figure 4—*Aralia nudicaulis*, wild sarsaparilla: exterior views of nutlets in 2 planes and longitudinal section.



were shown to benefit from after-ripening at temperatures ranging between 1 to 10 °C; optimum 5 °C for 90 to 120 days before planting in a greenhouse (Crocker 1948).

Japanese angelica-tree may benefit from 3 months of warm followed by 3 months of cold treatment; however, 70% germination has been reported following cold treatment only (Dirr and Heuser 1987).

Warm plus cold stratification of wild sarsaparilla brought about germination of 24% (with a potential germination of 66 to 92%). The seeds were stratified for 60 days at 20 °C (night) to 30 °C (day), plus 60 days at 5 °C, plus 60 more days at 20 to 30 °C, plus 60 more days at 5 °C. Similar treatment brought about only 0.5% germination of bristly aralia (Blum 1974). Obviously, this species still needs further study before fully satisfactory seed treatments can be developed (Heit 1967a).

Nursery practice. Heit (1968) recommends treating small lots of aralia seeds with sulfuric acid for 30 to 40 minutes and broadcast sowing in September. The aralias also may be propagated vegetatively. Root and rhizome cuttings offer the best method of vegetative propagation (Dirr and Heuser 1987).

References

Barrett SCH, Helenrum K. 1981. Floral sex ratios and life history in *Aralia nudicaulis* (Araliaceae). Evolution 35: 752–762.

Barrett SCH, Thomson JD. 1982. Spatial pattern, floral sex ratios, and fecundity in dioecious *Aralia nudicaulis* (Araliaceae). Canadian Journal of Botany 60: 1662–1670.

Bawa KS, Keegan CR, Voss RH. 1982. Sexual dimorphism in *Aralia nudicaulis* L. (*Araliaceae*). Evolution 36(2): 371–378.

Blum BM. 1974. *Aralia* L., aralia. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 220–222.

Braun LE. 1961. The woody plants of Ohio. Columbus: Ohio State University Press. 362 p.

Cheke AS, Nanakorn W, Yankoses C. 1979. Dormancy and dispersal of seeds of secondary forest species under the canopy of a primary tropical rain forest in northern Thailand. Biotropica 11(2): 88–95.

Crocker W. 1948. Growth of plants. New York: Reinhold Publishing. 90 p.

Curtis JT. 1959. The vegetation of Wisconsin. Madison: University of Wisconsin Press. 657 p.

Dirr MA. 1990. Manual of woody landscape plants: their identification, ornamental characteristics, culture, propagation and uses. Champaign, IL: Stipes Publishing. 1007 p.

Dirr MA, Heuser CW Jr. 1987. The reference manual of woody plant propagation: from seed to tissue culture. Athens, GA: Varsity Press. 239 p.

Edwards J. 1984. Spatial pattern and clone structure of the perennial herb *Aralia nudicaulis*. Bulletin of the Torrey Botanical Club 111: 28–33.

Graber RE, Thompson DF. 1978. Seeds in the organic layers and soil of four beech–birch–maple stands. Res. Pap. NE-401. Upper Darby, PA: USDA Forest Service, Northeastern Forest Experiment Station. 8 p.

Fernald, ML. 1950. Gray's manual of botany. New York: American Book Co. 1632 p.

Harrar ES, George J. 1962. Guide to southern trees. New York: Dover Publications. 709 p.

Hartmann HT, Davies DE, Davies FT Jr. 1990. Plant propagation: principles and practice. 5th ed. Englewood Cliffs, NJ: Prentice Hall. 647 p.

Heit CE. 1967a. Propagation from seed: 11. Storage of deciduous tree and shrub seeds. American Nurseryman 126(10): 12–13, 86–94.

Heit CE. 1967b. Propagation from seed: 6. Hardseededness—a critical factor. American Nurseryman 125(10): 10–12, 88–96.

Heit CE. 1968. Propagation from seed: 15. Fall planting of shrub seeds for successful seedling production. American Nurseryman 128(4): 8–10, 70–80.

Hirabuki Y. 1988. Significance of viable seeds of several woody pioneers stored in the soil of a temperate mixed forest. Ecological Review 21(3): 163–168.

Kenfield WG. 1966. The wild gardener in the wild landscape. New York: Hofner Publishing. 232 p.

Krochmal A, Walters RS, Doughty RM. 1969. A guide to medicinal plants of Appalachia. Res. Pap. NE-138. Upper Darby, PA: USDA Forest Service, Northeastern Forest Experiment Station. 291 p.

MacKinnon A, Pojar J, Coupe R. 1992. Plants of northern British Columbia. Edmonton, AB: Lone Pine Publishing. 345 p.

Meades WJ, Moores L. 1994. Forest site classification manual: a field guide to the Damman forest types of Newfoundland. FRDA Rep. 003. Cornerbrook, NF: Natural Resources Canada, Canadian Forest Service.

Meeker JE, Elias JE, Heim JA. 1993. Plants used by the Great Lakes Ojibway. Odanah WI: Great Lakes Indian Fish and Wildlife Commission. 440 p.

Moore M. 1993. Medicinal plants of the Pacific West. [Santa Fe, NM]: Red Crane Books. 359 p.

Nichols GE. 1934. The influence of exposure to winter temperatures upon seed-germination in various native American plants. Ecology 15(4): 364, 373.

Sargent CS. 1965. Manual of trees of North America. New York: Dover Publishing. 934 p.

Soper JH, Heimburger ML. 1982. Shrubs of Ontario. Toronto: Royal Ontario Museum.

Stupka A. 1964. Trees, shrubs, and woody vines of Great Smoky Mountains National Park. Knoxville: University of Tennessee Press. p. 96.

Sullivan J. 1992. *Aralia spinosa*. In: Fischer WC, comp. Fire Effects Information System [database]. Missoula, MT: USDA Forest Service, Intermountain [now Rocky Mountain] Research Station, Fire Sciences Laboratory.

Tehon LR. 1951. The drug plants of Illinois. Circ. 44. Urbana: Illinois Natural Historical Survey. 23 p.

Thaler GR, Plowright RC. 1980. The effect of aerial insecticide spraying for spruce budworm control on the fecundity of entomophilous plants in New Brunswick. Canadian Journal of Botany 58: 2022–2027.

Thomson JD, Barrett SCH. 1981. Temporal variation in gender in *Aralia nudicaulis* Vent. (Araliaceae). Evolution 35: 1094–1107.

Thomson JD, Maddison WP, Plowright RC. 1982. Behavior of bumble bee pollinators of *Aralia hispia* Vent. (Araliaceae). Oecologia 54: 326–336

Voss EG. 1985. Michigan flora: 2. Dicots (Saururaceae–Cornaceae). Cranbrook Institute of Science Bulletin 59: 1–724.

Araucariaceae—Araucaria family

Araucaria Juss.

araucaria

Gerald A. Walters and John K. Francis

Dr. Walters retired from the USDA Forest Service's Pacific Southwest Forest and Range Experiment Station;
Dr. Francis retired from the USDA Forest Service's International Institute of Tropical Forestry

Growth habit, occurrence, and use. The araucarias are 15 species of evergreen coniferous trees that are generally confined to the Southern Hemisphere. They are found in South America, Australia, New Guinea, New Caledonia, the New Hebrides Islands, and Norfolk Island under tropical, subtropical, and temperate climates (Dallimore and Jackson 1954; Howcroft 1978a&b; Ntima 1968; Record and Hess 1943; Veblen and Delmastro 1976; Webb and others 1984). They are noted for their long, straight, clear boles and symmetrical crowns; many are useful for timber and some are cultivated as ornamental trees and houseplants (Streets 1962).

Several species have been introduced to California, Oregon, Washington, Florida, Hawaii, Puerto Rico, the U.S. Virgin Islands, Guam, American Samoa, and other U.S. territories in the South Pacific region (table 1) (Francis 1988; Walters 1974). Araucaria species are generally found on sites at elevations from sea level to 2,100 m, with 1,200 to 2,400 mm of rainfall and well-drained soils. Cook-pine and Norfolk-Island-pine have been widely planted in Hawaii (Menninger 1964; Walters 1974). The botanical identities of these 2 species are often confused, and no one (not even visiting foresters from Australia) is absolutely sure which species is which! Recipients of araucaria seeds shipped out of Hawaii should be made aware of this confusion. All data on phenology and methods reported here are based on information obtained from the areas of natural occurrence. Norfolk-Island-pine is also a very common ornamental tree in Florida, California, Puerto Rico, and the U.S. Virgin Islands.

Flowering and fruiting. Araucarias generally begin to flower and set seeds between the age of 15 to 20 years. Most hoop-pine trees begin producing female flowers and fruits when they are between 10 and 12 years old and 6 to 10 m tall. Flowering and fruiting is very intermittent from year to year, and pollen production begins when trees are 22

Table 1—*Araucaria,* araucaria: nomenclature, occurrence, and heights attained

Scientific name & synonym(s)	Common name(s)	Occurrence		Maximum height (m)
		Native	US	
A. angustifolia **(Bertol.) Kuntz**	**parana-pine,** candelabra tree, Brazilian-pine	Brazil, Argentina, & Paraguay	Hawaii & Puerto Rico	36
A. araucana **(Molina.) K. Koch.** *A. imbracata* Par.	**monkey-puzzle tree,** monkey-puzzle, Arauco-pine, Chilean-pine	Chile & Argentina	California, Oregon, & Washington	50
A. bidwillii **Hook.**	**bunya-pine,** bunya-bunya	Australia	California, Florida, Hawaii, & Puerto Rico	43
A. columnaris **(Forster) Hook.** *A. excelsea* (Lamb.) R. Br.	**Cook-pine,** columnar araucaria	New Caledonia	Hawaii, Florida, & Puerto Rico	60
A. cunninghamii **Aiton ex D. Don)**	**hoop-pine,** Moreton-Bay-pine	New Guinea & Australia	California, Hawaii, & Puerto Rico	60
A. heterophylla (Salisb.) Franko	**Norfolk-Island-pine,** Australian-pine	Norfolk Island	California, Florida, Hawaii, & Puerto Rico	60
A. hunsteinii K. Schum. & Hollrung *A. schummaniana* Warb. *A. klinkii* Laut.	**klinki-pine**	New Guinea	Hawaii & Puerto Rico	80

Sources: Dallimore and Jackson (1954), LHBH (1976), Walters (1974).

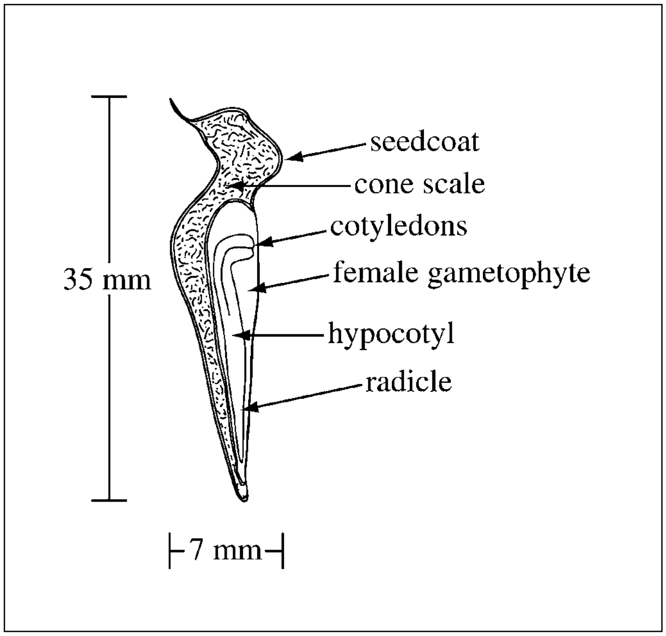
to 27 years old and are about 20 m tall (Haines and Nikles 1987). Male and female flowers are generally found on different parts of the same tree. Male flowers usually appear at the base of the crown in young trees and the female flowers at the top. As the tree grows older, the male and female flowers come closer to each other. Bisexual flowers are also found. After pollination, the female flowers develop slowly, with the cones maturing in about 2 years (Ntima 1968). The mature cones are ovoid or almost spherical, ranging in size from 10 by 5 cm for hoop-pine to 30 by 20 cm for bunya-pine (Ntima 1968). In natural stands, seedlots collected from hoop-pines are rarely more than 65% viable (Haines and Nikles 1987).

Upon maturing, cones turn from green to brown (Ntima 1968; Walters 1974). Cones disintegrate on the tree or fall to the ground and disintegrate. The brown seeds are kite-shaped and have papery wings on either side (figures 1 and 2) or are thick and heavy with much endosperm. Araucaria seeds may be carried a short distance from the mother tree by wind, but generally the seeds fall within the periphery of the crown (Ntima 1968). Animals and birds that prey on the seeds are the most effective natural dispersers of the heavy seeds. The time of flowering, seed development, and seed dispersal, as well as seedcrop intervals are listed for 5 species in table 2.

Collection, cleaning, and storage. Most of the seeds of hoop-pine collected for planting are grown in seed orchards (Haines and Nikles 1987). Collection of cones should begin when the first trace of brownness is observed on the cone. In natural stands, the second-year cones are generally picked by climbing or felling trees (Howcroft 1978; Ntima 1968; Walters 1974). Cone collection must be timed correctly to get the highest proportion of mature and fertile seeds. A method for timing cone matureness is to pick a cone and measure the time it takes to disintegrate; ripe cones spontaneously disintegrate within 7 days. Collected cones should be spread on shelves in single layers for drying and turned daily. The cones normally will begin to disintegrate within a few days. Cones that fail to disintegrate within 10 days should be discarded, as they are considered too immature (Ntima 1968; Walters 1974). The average number of seeds per weight ranges from 77/kg (35/lb) for bunya-pine to 4,400/kg (1,995/lb) for hoop-pine (table 3) (Howcroft 1986; Walters 1974).

Figure 1—*Araucaria,* araucaria: seeds of *A. columnaris*, Cook-pine **(left)** and *A. heterophylla,* Norfolk-Island-pine (**right**).

Figure 2—*Araucaria heterophylla*, Norfolk-Island-pine: longitudinal section through a seed.



Most araucaria are recalcitrant (that is, intolerant of dessication). Their seeds have short viability under atmospheric conditions and normally should be sown within a month of collection (Ntima 1968). If the seeds cannot be sown immediately, they should be stored under cold, moist, and airtight conditions at a temperature of 3 °C (Ntima 1968; Walters 1974). Klinki-pine seeds can be stored for at least 6 months with 32% moisture at a temperature of 3.5 °C (Willan 1991). Damp storage at 4 to 7 °C was best for monkey-puzzle-tree seeds. After 3 months of storage, these seeds began to germinate after 21 days at 25 to 30 °C and reached 70 to 90% germination after 7 days (Swindells 1980). Hoop-pine seeds appear to be orthodox (that is, tolerant of dessication); air-dried seeds stored at temperatures ranging from 1.7 to –15 °C showed little reduction in germination percentage for 17 months of storage (46 to 50% germination), but

Table 2—*Araucaria,* araucaria: phenology of flowering, seed development and dispersal, and seedcrop intervals

Species	Flowering	Seed ripening	Seed dispersal	Crop intervals (yrs)
A. angustifolia	—	Apr–May	May–Aug	1
A. bidwillii	Sept–Oct	Jan–Feb	Jan–Feb	1–2
A. columnaris	Dec–Jan	Dec–Feb	Dec–Feb	3–4
A. cunninghamii				
Early-flowering races	Dec–Jan	Dec	Dec	4–5
Late-flowering races	Apr–May	—	—	—
A. heterophylla	Sept	Apr	Apr–May	3–4

Source: Walters (1974).
Note: Information for all species is based on their natural ranges.

Table 3—*Araucaria,* araucaria: seed data

	Cleaned seeds/weight			
	Range		Average	
Species	/kg	/lb	/kg	/lb
A. angustifolia	—	—	108	50
A. bidwillii	66–88	30–40	77	35
A. columnaris	1,980–2,640	900–1,200	2,200	1,000
A. cunninghamii	3,300–6,600	1,500–3,000	4,400	2,000
A. heterophylla	550–620	250–280	573	260
A. hunsteinii	2,000–2,500	900–1,100	—	—

Sources: Howcroft (1986b), Walters (1974).

decreased significantly between 17 and 100 months of storage. However, after 100 months of storage, germination still ranged from 25 to 44% (Shea and Armstrong 1978). Tompsett (1984) found that seeds of monkey-puzzle-tree, parana-pine, klinki-pine, and bunya-pine could not be safely dried below 25 to 40% moisture content; seeds of cook-pine and 2 other araucarias (*A. nemorosa* de Laubenfels and *A. scopulorum* de Laubenfels) cannot be dried below 12%; and seeds of hoop-pine could be dried to 2% without damage. Seeds in the second 2 groups dried to moisture contents just above the critical levels can be stored at –18 °C and thus appear to be orthodox. Parana-pine, monkey-puzzle-tree, and bunya-pine seeds are classified as recalcitrant (Farrant and others 1989; Ramos and others 1988). Plastic bags are good containers (Ntima 1968). Seeds of hoop-pine can be stored up to 8 years (Shea and Armstrong 1978).

Germination. No pregermination treatments are needed for araucaria seed (Ntima 1968; Walters 1974). Under suitable moisture and temperature (21 to 30 °C) conditions, germination (which is cryptogeal in this genus) may begin about 10 days after sowing. Germination is delayed by cooler temperatures, sometimes taking 50 days or more (Ntima 1968). Seed quality varies from year to year; if sufficient pollen is available to the parent trees, seed quality is generally good (Walters 1974).

Twenty-nine and 45% of a large number of hoop-pine and klinki-pine seeds germinated within 9 weeks in a germination test (Thong 1974). Klinki-pine seeds are pregerminated (incubated until the radicle begins to show) before sowing into containers. In a test with 3 replications of 1,200 seeds each, germination averaged 85% in 22 days. Of those seeds not germinating, 54% were dead, 30% were rotten, and 16% had not germinated yet. Survival of seedlings in containers to outplanting size was 88%. Broadcasting seeds on the surface of wet sawdust with a second shadecloth a few centimeters above the bed gave better germination than covering seeds with sawdust or germinating them without the second shadecloth covering (Howcroft 1974). Tompsett (1984) obtained 80 to 100% germination of 6 species tested when seed moisture contents were optimal.

Nursery practice. Araucarias can be grown under high shade or low shade. For both types of shade, seeds are sown during spring. Norfolk-Island-pine seeds are placed on a bed of sand–soil–peat mix to germinate with the pointed end of the seed slightly embedded. About 70% of fresh seedlots germinate in 4 to 12 days (Logsdon 1973). Seeds should be treated with a fungicide to prevent damping-off. Fungi pathogenic to seedlings can be isolated from seed collected from the ground and even from seeds extracted from cones collected from trees (El-Lakany and others 1981). *Rhizoctonia solani* Kühn—the fungal species causing most of the cases of pre- and post-emergence damping-off—was one of the most commonly isolated fungi from *Araucaria* seeds (Kamara and others 1981). Control of seedborne and soilborne fungi should be undertaken before planting. With high shade, the seeds of all species except bunya-pine are sown in flat-bottomed drills about 1.25 cm ($^{1}/_{2}$ in) deep and then covered with the same amount of softwood sawdust (fungicide-treated hardwood sawdust may also be suitable).

Bunya-pine seeds are sown in drills 7 to 10 cm (3 to 4 in) deep or on shaded, moist media. A few months after sowing, fusiform radicles, called "tubers," are formed. The seedbeds are re-dug, and these tubers are collected and then either planted directly into containers or stored at room temperature until required for planting. Exposure of the tubers to sunlight before re-planting breaks their dormancy, and the plants begin to grow. Almost every seed produces a tuber and all of these develop into plants (Walters 1974).

With low shade, the seeds are broadcast on well-prepared nursery beds and covered with about 2 cm ($^{3}/_{4}$ in) of sawdust. The aim in both types of sowing is to have a stocking of 130 to 180 plants/m^2 (12 to 17/ft^2) (Ntima 1968; Walters 1974).

Newly sown beds should be given full overhead shade within several days of sowing. Best shoot development occurs when the seedbeds are given 75% shade for the first few months and 5% shade for the next 3 months (except for hoop-pine). Shading should be removed in 2 steps after this shading treatment to give full exposure 2 weeks before transplanting to containers. Full light is not admitted until nearly 1 year after sowing hoop-pine. When 75% of the seedlings are 15 to 22 cm (6 to 9 in) tall, the seedlings should be transplanted. Lifting and planting need to be done carefully to minimize damage to the roots. Transplanting should be done about 5 months before field planting. The seedlings should be spaced 5 by 20 cm (2 to 8 in) apart (stem to stem) and given full shade. The shade should be gradually removed to give full sunlight to the seedlings for at least a month before transferring them to the planting site (Ntima 1968). About 50 to 60% of the seeds will develop into plantable seedlings. Seedlings are generally outplanted when 2 years old (Ntima 1968). Norfolk-Island-pine seedlings grown in nursery beds or containers will be 15 to 20 cm (6 to 8 in) tall in 1 year and 60 to 76 cm (24 to 30 in) tall in 2 years (Logsdon 1973).

References

Dallimore W, Jackson AB. 1954. A handbook of Coniferae and Ginkgoaceae. London: Edward Arnold, Publisher. 686 p.

El-Lakany MH, Kamara AM, Badran OA, Attia YG. 1981. Seed pathology of *Araucaria* spp.: 2. Fungal species associated with *Araucaria heterophylla* seed. Australian Forestry Research 11(3/4): 275–281.

Farrant PM, Pammenter NW, Berjak P. 1989. Germination-associated events and the desiccation sensitivity of recalcitrant seeds: a study on three unrelated species. Planta 178(2): 189–198.

Francis JK. 1988. Araucariaceae in Puerto Rico. Turrialba 38(3): 202–207.

Haines RJ, Nikles DG. 1987. The *Araucaria araucana* gene resource in Chile. For. Occ. Pap. 1976/1. Rome: FAO: 2–6.

Howcroft NHS. 1974. Pregermination techniques for *Araucaria hunsteinii*. Trop. For. Res. Note SR.27. Boroko, Papua New Guinea: Department of Forests. 10 p.

Howcroft NHS. 1978a. Exploration and provenance seed collection in Papua New Guinea 1976/1977. For. Occ. Pap. 1978/2. Rome: FAO: 5–11.

Howcroft NHS. 1978b. Data sheet on *Araucaria hunsteinii* K. Schumann. For. Occ. Pap. 1978/2. Rome: FAO: 31–37.

Kamara AM, El-Lakany MH, Badran OA, Attia YG. 1981. Seed pathology of *Araucaria* spp.: 1. A survey of seed-borne fungi associated with four *Araucaria* spp. Australian Forest Research 11(3/4): 269–274.

LHBH [Liberty Hyde Bailey Hortorium]. 1976. Hortus third: a concise dictionary of plants cultivated in the United States and Canada. New York: Macmillan: 98.

Logsdon BB. 1973. Growing the Norfolk Island pine. Tree Planters' Notes 24(1): 33–36.

Menninger EA. 1964. Seaside plants of the world. New York: Hearthside Press. 303 p.

Ntima OO. 1968. Fast growing timber trees of the lowland tropics: the araucarias. Oxford: Commonwealth Forestry Institute. p. 139.

Ramos A, Carneiro JG de A, Souza GB de, Banchelli A. 1988. Biochemical and physiological alterations of *Araucaria angustifolia* (Bert.) O. Ktze. seeds immediately after oven drying. In: Carneiro JG de A and others, eds. Proceedings, Bilateral Symposium (Brazil–Finland) on Forestry Activities; 16–22 October 1988; Cuitiba, Parana, Brazil. Cuitiba, Parana, Brazil: Instituto Agronomico do Parana: 108–117.

Record SJ, Hess RW. 1943. Timbers of the new world. New Haven, CT: Yale University Press. 640 p.

Shea GM, Armstrong PA. 1978. The effect of postharvest environmental factors on the longevity of hoop pine seed. Res. Note 24. Brisbane, Australia: Queensland Department of Forestry. 2 p.

Streets RJ. 1962. Exotic forest trees in the British Commonwealth. Oxford, UK: Clarendon Press. 765 p.

Swindells P. 1980. Monkey puzzle. Garden Chronicle and Horticultural Trade Journal 187(11): 17–19.

Thong HL. 1974. Germination and seedling survival of *araucaria* with Demosan (chloroneb, 1,4- dichloro-2,5-dimethoxybenzene) treatment. Malaysian Forester 37(1): 54–61.

Tompsett PB. 1984. Desiccation studies in relation to the storage of *Araucaria* seed. Annals of Applied Biology 105: 581–586.

Veblen TT, Delmastro R. 1976. The *Araucaria araucana* gene resource in Chile. For. Occ. Pap. 1976/1. Rome: FAO: 2–6.

Walters GA. 1974. *Araucaria*, araucaria. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 223–235.

Webb DB, Wood PJ, Smith JP, Henman GS. 1984. A guide to species selection for tropical and sub-tropical plantations. Oxford, UK: Commonwealth Forestry Institute. 256 p.

Willan RL. 1991. A guide to forest seed handling. For. Pap. 20/2. Rome: FAO. 379 p.

Ericaceae—Heath family

Arbutus menziesii Pursh

Pacific madrone

Philip M. McDonald

Dr. McDonald is a research silviculturist at the USDA Forest Service's
Pacific Southwest Research Station, Redding, California

Other common names. madrone, arbutus, madroño.

Occurrence and growth habit. Pacific madrone—*Arbutus menziesii* Pursh—is 1 of 3 species of *Arbutus* native to the western United States (Little 1979). It is an evergreen tree that occurs in coastal mountains from southwestern British Columbia to southern California, and also in the Sierra Nevada of north central California. It often is found as a single tree or in groves, only rarely occupying extensive areas (McDonald and Tappeiner 1990; McDonald and others 1983). Seldom does Pacific madrone form pure stands; usually it is found in mixture with several conifer and hardwood species. It also competes successfully in both overstory and understory canopies (Sawyer and others 1977). Although some trees originate from seed, most begin life as root crown sprouts. Tree height and form vary widely: height from 8 to 38 m, and form from straight to crooked (Sudworth 1908). Stand density is a prime determinant of form and also affects tree height. In general, the more dense the stand, the better the form and the greater the height. On good sites with well-stocked stands, plentiful moisture, and some shade, the tree grows straight and tall with a narrow crown. On poorer sites with lower stocking and inadequate soil moisture, the tree becomes short and crooked, with a relatively wide crown. Clumps of trees are prevalent and increase as stands become more open. The species seems to be phototropic and trees are often observed leaning into gaps in the canopy. Asymmetric bole development is common. Over the entire range, the majority of Pacific madrone trees have some lean and some crook. Forking also is common.

Use. The strong, smooth, fine-grained wood has been utilized for many purposes, ranging from lumber, veneer, and fuelwood to furniture, flooring, interior trim, and paneling (EDA 1968; Overholser 1968). In the past, the wood of Pacific madrone was prized for making charcoal for gunpowder (Koch 1973) and was found to be without peer when made into bobbins and spools. This species was first cultivated in 1827 and has been planted occasionally as an ornamental tree in Europe and the United States (McMinn and Maino 1959).

Flowering and fruiting. Flowers, which bloom from March to June, are formed on a panicle 12 to 15 cm long. The 8-mm flowers consist of 5 sepals fused at the base with 5 fused urn-shaped petals and 10 stamens. The anthers split open when ripe, the awns are elongate, and the superior ovary is rough and bumpy with 5 chambers (Hickman 1993). The fruit is a berry, also rough and bumpy, less than 12 mm in diameter (figure 1). The generic name derives from *arboise*, a Celtic word for "rough fruit" (Roy 1974). The thin-skinned berry has rather dry, mealy flesh and generally is 5-celled (figures 1 and 2). McDonald (1978) found that, in northern California, the number of seeds per berry ranged from 2 to 37, with an average of 20. The berries ripen in September through November but often remain on the trees through December. Fully ripe berries are bright red

Figure 1—*Arbutus menziesii*, Pacific madrone: exterior view of the fruit (**left**) and transverse section of fruit showing its 5 carpels (**right**).

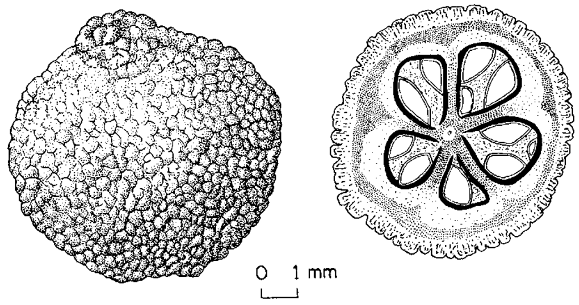
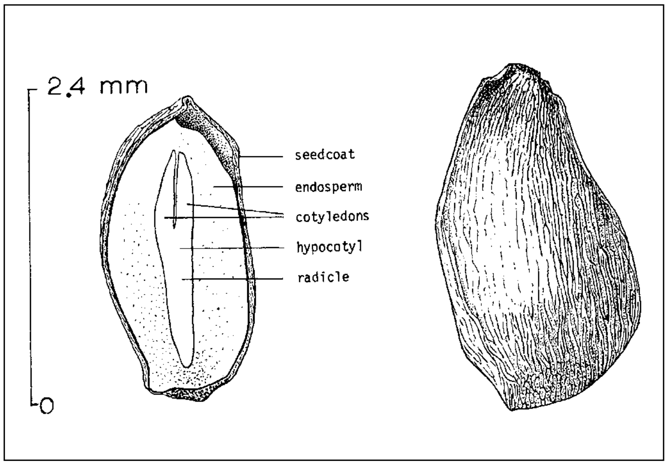


Figure 2—*Arbutus menziesii*, Pacific madrone: longitudinal section through a seed (**left**) and exterior view of a seed (**right**).



or bright reddish orange (Peattie 1953). However, the smaller numbers of yellowish orange or yellowish green berries that are usually present at the same time also furnish viable seeds (McDonald 1978).

The minimum seed-bearing age (from root crown sprouts) is 4 years but more commonly at least 8 years. Older trees have tremendous capability to produce seeds. On a good site in northern California, the number of berries produced during a light seed year for 3 representative trees that were 23, 36, and 41 cm in dbh ranged from 13,320 to more than 107,000/tree and related best to amount of living crown (McDonald 1978). On this same site, annual records showed that during a 24-year period (1958–1981), Pacific madrone produced 2 medium to heavy and 10 very light to light seedcrops (McDonald 1992). In years when the overall seedcrop is poor or nonexistent, madrone trees may be stimulated to produce heavy crops by logging and thinning. Apparently, the reduced stand density provides additional water and nutrients that become manifest in reproductive material.

A recent phenomenon that has greatly reduced seed production (Thornburgh 1994) is dieback and death of Pacific madrone trees infected by the madrone canker—*Botryosphaeria dothidea Moug.:F*r.) Ces. & De Not.—which is virulent in northern California (McDonald and Tappeiner 1990).

Collection, extraction, and storage. Berries of Pacific madrone can be collected during the ripening period, dried thoroughly, and stored at room temperature for 1 or 2 years (Mirov and Kraebel 1939). Separating the seeds from the pulp after soaking and maceration of the berries probably is best (McDonald 1978). Only dry seeds should be stored, probably in sealed containers at temperatures just above freezing (Roy 1974). Fresh berries picked in the northern Sierra Nevada numbered 1,390 to 2,490/kg (630 to 1,130/lb), and the yield of cleaned seeds was 1.6 to 2.0 kg/45 kg (3.6 to 4.4 lb/100 lb) of fruit. The number of seeds ranged from 434,310 to 705,470/kg or 197,000 to 320,000/lb (McDonald 1978). Dried berries from an unknown source numbered 900/kg (2,000/lb) (Mirov and Kraebel 1939).

Pregermination treatments. Because the seeds exhibit strong embryo dormancy, stratification is critical. McDonald (1978) found that only 1 of 400 sound seeds germinated without stratification. For stratification, much evidence shows that storage in a plastic bag containing a small amount of moist paper or peat moss at temperatures just above freezing for 35 to 45 days is all that is needed to break dormancy (McDonald 1978; Roy 1974). With this treatment, 78 to 90% of a seedlot will have germinated in 10 days.

Germination tests. Only sound seeds should be used in germination trials. For red berries, darker color and slight rounding at the pointed end proved diagnostic for separating sound from unsound seeds; for yellowish berries, only seed size was a worthwhile indicator—larger seeds were more likely to be sound than small ones (McDonald 1978). Extensive trials in laboratory and field have shown the perils of germinating seeds in berries. If berries were present, so were virulent fungi and consumers. Indeed, in a field trial, snaptraps baited with a single red madrone berry caught more white-footed deer mice (*Peromyscus maniculatus*) than those baited with peanut butter and wheatflakes.

Nursery practice. Pacific madrone can be propagated by germinating seeds in flats and transplanting the seedlings to individual containers. Losses from damping-off fungi, however, can be huge. Hundreds of seedlings die overnight and the number available for planting often is small. Van Dersal (1938) noted that a yield of about 450 usable plants/kg of seeds (1,000/lb) was the best that could be expected. Although this species has been propagated vegetatively by grafting, layering, and rooting of cuttings (Roy 1974), no operational application of these techniques is known.

Seedling care. The problem of fungi does not end after the germinants become seedlings. Even after transfer to peat pots or other containers, the seedlings need to be protected from fungi. And even after great care, survival and growth in a conventional (sunlit) plantation is poor. In a trial on a high site in the northern Sierra Nevada, survival of seedlings in large containers (plugs) on competition-free ground was 33% after 6 years (McDonald 1978). All seedlings died back at least once, developed multiple stems of poor form, and grew poorly. Natural seedlings developing in the wild also have a dismal establishment record, with first-year survival rates of 0 to 6%. Damping-off fungi, drought, predation by invertebrates, and litterfall, often interacting together, seriously limit the reproductive efforts of Pacific madrone (McDonald 1978; Pelton 1962; Tappeiner and others 1986). Based on this evidence, the best environment for establishment of both natural and planted seedlings is bare mineral soil and moderate shade (McDonald and Tappeiner 1990). However, the rate of seedling growth and its consistency in this environment is unknown.

References

EDA [Economic Development Administration]. 1968. The Hoopa Valley Reservation hardwood study report. Washington, DC: USDC. 154 p.
Hickman JC, ed. 1993. The Jepson manual of higher plants of California. Berkeley: University of California Press. 1400 p.
Koch M. 1973. Santa Cruz County: parade of the past. Fresno, CA: Valley Publishers: 33–43.
Little EL Jr. 1979. Checklist of United States trees (native and naturalized). Agric. Handbk. 541. Washington, DC: USDA Forest Service. 375 p.
McDonald PM. 1978. Silviculture-ecology of three native California hardwoods on high sites in north-central California [PhD dissertation]. Corvallis: Oregon State University, Department of Forest Science. 309 p.
McDonald PM. 1992. Estimating seed crops of conifer and hardwood species. Canadian Journal of Forest Research 22: 832–838.
McDonald PM, Tappeiner JC II. 1990. *Arbutus menziesii* Pursh, Pacific madrone. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Vol. 2, Hardwoods. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 124–132.
McDonald PM, Minore D, Atzet T 1983. Southwestern Oregon–Northern California hardwoods. In: Burns RM, tech. comp. Silvicultural systems for the major forest types of the United States. Agric. Handbk. 445. Washington, DC: USDA Forest Service: 29–32.
McMinn HE, Maino E. 1959. An illustrated manual of Pacific Coast trees. Berkeley: University of California Press. 490 p.
Mirov NT, Kraebel CJ. 1939. Collecting and handling seeds of wild plants. For. Pub. 5. Washington, DC: USDA Forest Service, Civilian Conservation Corps. 5 p.
Overholser JL. 1968. Oregon hardwood sawtimber. Rep. G-9. Corvallis: Oregon State University, Forest Products Laboratory. 52 p.
Peattie DC. 1953. A natural history of western trees. Boston: Houghton-Mifflin. 751 p.
Pelton J. 1962. Factors influencing survival and growth fo a seedling population of *Arbutus menziessii* in California. Madrono 16: 237–276.
Roy DF. 1974. *Arbutus menziesii* Pursh, Pacific madrone. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 226–227.
Sawyer JO, Thornburgh DA, Griffin JR. 1977. Mixed evergreen forest. In: Barbour MG, Major J, eds. Terrestrial vegetation of California. New York: John Wiley and Sons: 359–381.
Sudworth GB. 1908. Forest trees of the Pacific slope. Washington, DC: USDA Forest Service. 441 p.
Tappeiner JC II, McDonald PM, Hughes TF. 1986. Survival of tanoak (*Lithocarpus densiflorus*) and Pacific madrone (*Arbutus menziesii*) seedlings in forests of southwestern Oregon. New Forests 1: 43–55.
Thornburgh DA. 1994. Personal communication. Arcata, CA: Humboldt State University, Department of Forestry.
Van Dersal WR. 1938. Native woody plants of the United states: their erosion-control and wildlife values. Misc. Pub. 303. Washington, DC: USDA. 362 p.

Ericaceae—Heath family

Arctostaphylos Adans.

manzanita

Susan E. Meyer

Dr. Meyer is a research ecologist at the USDA Forest Service's Rocky Mountain Station,
Shrub Sciences Laboratory, Provo, Utah

Growth habit, occurrence, and uses. The shrub genus *Arctostaphylos,* or manzanita, comprises about 50 species, 90% of which are endemic to California and adjacent areas (Munz and Keck 1959). Three species—greenleaf manzanita, Mexican manzanita, and rosybract manzanita—are widely distributed in the southwestern United States and Mexico. One species—bearberry or kinnickinnick—is circumboreal in distribution (table 1). The manzanita habit varies from mat-forming (bearberry) to nearly arborescent (bigberry manzanita). About a quarter of the species have subterranean burls that generate new sprouts both after fire and throughout the long life of the plant (Keeley 1992; Wells 1969). The leaves of manzanitas are leathery, entire, and evergreen. They are major components of chaparral and are also common understory species in montane coniferous forest types, especially ponderosa (*Pinus ponderosa* Dougl. ex Laws.) and Jeffrey (*P. jeffreyi* Grev. & Balf.) pines. They are most abundant in the fire-prone vegetation of regions with dry summers.

The manzanitas are moderately important as winter browse plants for wild ungulates but are less important for domestic livestock (Berg 1974). They are used principally after fire, when new shoots or seedlings are produced in abundance. The fruits are eaten by bears (*Ursus* spp.), grouse (*Dendragapus* spp.), and coyotes (*Canis latrans*) (Belcher 1985; Kauffmann and Martin 1991) and the seeds by various rodents (Keeley and Hays 1976). The sprouting species are particularly important for watershed protection after fire, and many species could be used in revegetation for erosion control. Manzanitas also have great potential for use as ornamentals. Their smooth red bark; interesting, twisted growth forms; and bright evergreen leaves make them attractive year-round. Bearberry has found wide

Table 1—*Arctostaphylos,* manzanita: habitat requirements and geographic distribution

Scientific name	Common name(s)	Habit	Habitat	Distribution
A. canescens **Eastw.**	**hoary manzanita**	Shrubby, without burl	Ponderosa pine forest, chaparral	N California to Oregon
A. glandulosa **Eastw.**	**Eastwood manzanita**	Shrubby, with burl	Ponderosa pine forest, chaparral	California to Oregon
A. glauca **Lindl.**	**bigberry manzanita**	Shrubby or treelike, without burl	Chaparral, joshua tree woodland	S California to Baja California
A. patula **Greene**	**greenleaf manzanita**	Shrubby, with burl	Ponderosa pine forest	California to Oregon, Arizona, & Colorado
A. pungens **Kunth**	**Mexican manzanita,** pointleaf manzanita	Shrubby, without burl	Ponderosa pine forest, chaparral, pinyon-juniper woodland	S California, E to Utah & Texas & S into Mexico
A. pringlei **Parry**	**rosybract manzanita,** Pringle manzanita	Shrubby, without burl	Ponderosa pine forest, chaparral, mixed warm desert shrubland	S California, S to Baja California & E to Arizona & SW Utah
A. uva-ursi **(L.) Spreng.**	**bearberry,** kinnickinnick	Mat forming, without burl	Coniferous forest mostly at high elevation	Circumboreal, S to California, New Mexico, Illinois, & Georgia

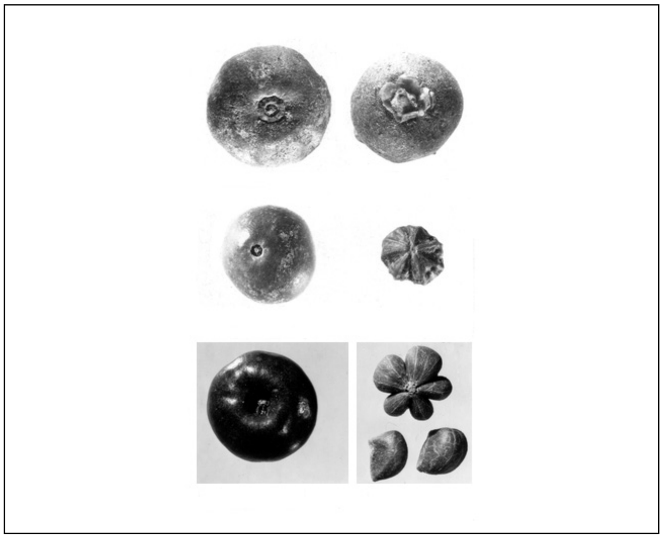
Source: Munz and Keck (1959).

acceptance as a versatile groundcover (Dirr 1983) and has also been used medicinally (Belcher 1985).

Flowering and fruiting. Small urn-shaped white to pink perfect flowers appear on the plants from early winter through spring. The bud primordia are formed the previous year, and flowering and fruiting intensity is positively correlated with the previous year's precipitation (Keeley 1977). The flowers are pollinated by insects, principally bees and flies (Fulton and Carpenter 1979). Obligately seeding species (that is, those unable to sprout after fire) may have a higher investment in pollinator attraction than sprouting species, as evidenced as higher flower density and nectar production (Fulton and Carpenter 1979). They may also be more likely to be self-fertile and to have higher seed-set overall as measured by the incidence of inviable or unfilled seeds (Keeley and Zedler 1978). Many of the sprouting species are tetraploids, and Kelly and Parker (1991) report that lower seed set may be associated with polyploidy rather than the sprouting habit per se.

Fruits ripen about 2 months after full-flowering, generally from June to September, depending on elevation. The fruits are drupe-like, with a hard, bony endocarp enclosing multiple seeds, a mealy mesocarp, and a thin exocarp (figure 1). Each seed is borne in a nutlet-like section. Ripe fruits may persist on the plant for several months but eventually fall. They may be dispersed by birds or mammals, especially coyotes (*Canis latrans)* (Kauffman and Martin 1991). The nutlets themselves may be dispersed by scatter-hoarding rodents, but rodents most often consume the seeds *in situ* and thus act solely as seed predators (Keeley 1977).

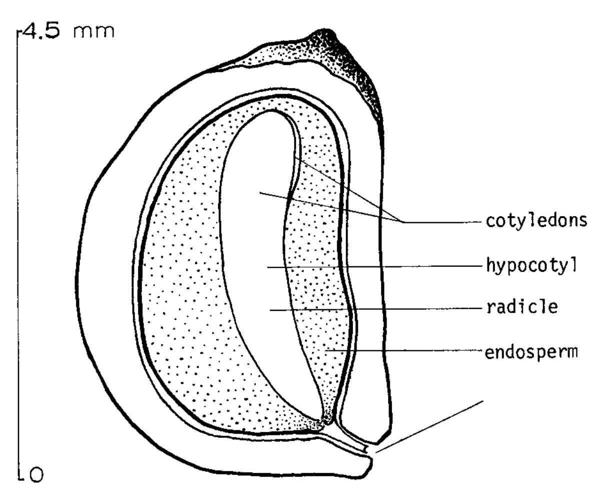
Figure 1—*Arctostaphylos*, manzanita: *A. glauca*, bigberry manzanita bottom (**left**) and top (**right**) views of a drupe; *A. glandulosa*, Eastwood manzanita: drupe (**left**) and coalesced nutlets (**right**); *A. patula*, greenleaf manzanita, drupe (**left**) and partially coalesced nutlets plus 2 separated nutlets (**right**).



The nutlets may break apart at maturity or remain variously fused. In some species (for example, bigberry manzanita) the nutlets are completely coalesced, whereas in most species, including Eastwood and greenleaf manzanitas, the stone breaks irregularly into 1- to several-seeded-segments. The endocarp wall surrounding each seed is usually thick, hard, resinous, and impervious (figure 2). The wall has a channel (periole) at the basal or micropylar end. This channel is plugged with tissue that is not as hard as the endocarp itself. When the seed germinates, the radicle and hypocotyl are forced out through this periole (Berg 1974). The endocarp wall is thought to have a protective function, especially with regard to heat damage during fire. Seeds surrounded by very thick endocarps or contained within fused nutlets are apparently more likely to survive fire than those borne singly or with thinner endocarps (Keeley 1977). The testa itself is thin and membranous, and the well-developed straight or curved embryo is embedded in abundant endosperm (Berg 1974).

Seed collection, cleaning and storage. Good seed crops are produced on average every 2 to 3 years, usually the year following a year of high precipitation (Keeley 1977). The fruits range from pink or red to black when ripe, depending on species. They may be hand-stripped or picked up off the ground. Seed fill is often low, and considerable insect damage may be evident (Keeley and Hays 1976). Fill

Figure 2—*Arctostaphylos uva-ursi*, bearberry: longitudinal section through a nutlet.



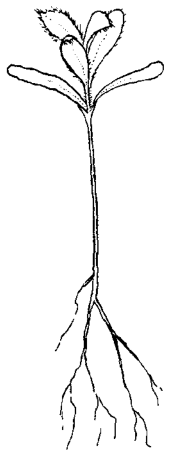
may be checked in the field by cutting the fruits transversely, preferably before the endocarp hardens (Berg 1974). Kelly and Parker (1991) reported a mean set (percentage of ovules forming seeds) of 62% for 14 California species, with a range from 50 to 80%.

To clean manzanita seeds, the fruits should be soaked in water, then macerated by hand or in a macerator to separate the pulp from the stones. The pulp may be removed by flotation, or the material may be dried, after which nutlets may be separated from the dried pulp using screens or a fanning mill (Berg 1974). Seedlots may be cleaned to high purity (Belcher 1985). Representative seed unit weights are given in table 2. Seed unit weights are highly variable even within a seedlot because a seed unit may be single or multiple-seeded, depending on the degree of coalescence of the nutlets.

Manzanita seeds form persistent seed banks and are apparently long-lived under field conditions (Kelly and Parker 1990). There is little information on longevity in warehouse storage, but it is probable that seedlots would maintain viability over periods of 10 years or more.

Germination and seed testing. In natural stands, new seedlings (figure 3) of most species of manzanita grow only after fire, and the seeds of these species are considered to be refractory, that is, germinating only in response to fire-related environmental cues (Keeley 1991, 1995). But unlike the refractory seeds of most chaparral shrubs, manzanita seeds apparently do not become germinable through heat shock (Kauffman and Martin 1991; Keeley 1987a). There is evidence that charate leached from incompletely burned wood can trigger germination in manzanita seeds, but the maximum percentages attained using recently collected seeds were not high (13% for Eastwood manzanita and 19% for greenleaf manzanita (Keeley 1987a, 1991). It is probable that, under field conditions, the seeds change in some way following dispersal (perhaps through dry after-ripening at the embryo level) that renders them more responsive to the charate stimulus. Parker and Kelly (1989) report that hoary manzanita seeds retrieved from the soil seedbank germinated readily in response to charate, whereas hand-harvested seeds less than 1 year old did not. In spite of the massive endocarp, manzanita nutlets are permeable to water, and the enclosed seeds are capable of imbibition without any pretreatment, at least in greenleaf manzanita (Meyer 1997). This explains how charate rather than heat shock could trigger germination. Presumably the charate stimulus enters the seed through the periole.

Figure 3—*Arctostaphylos patula,* greenleaf manzanita: seedling at 1 month.



Even though manzanitas form persistent seedbanks, there is evidence that these seedbanks turn over fairly quickly, as there was no net gain in size of the seedbank in the absence of fire over 10 years for 2 chaparral species (bigberry and Eastwood manzanitas), even in the face of massive inputs (Keeley 1987b). Most of the seed loss appears to be due to rodent predation rather than germination or loss of

Table 2—*Arctostaphylos,* manzanita: seed weights and filled seed percentages

Species	Seed unit	Seeds/weight /kg	Seeds/weight /lb	Filled seeds (%)	Sample
A. glandulosa	1–2 seeded	66,150–97,020	30,000–44,000	—	2
A. glandulosa	1–3 seeded	55,125	25,000	58	2
A. glauca	Entire stone	990–1,760	450–800	83	5
A. patula	Variable	36,690–55,125	18,000–25,000	—	1+
A. patula	1-seeded	44,100	20,000	85	1
A. uva-ursi	1-seeded	59,535–90,405	27,000–41,000	—	3+

Sources: Belcher (1985), Berg (1974), Keeley (1977, 1991), Keeley and Hayes (1976), Meyer (1997).

viability (Keeley and Hays 1976). This suggests that the seeds available for seedling recruitment after fire probably belong mostly to recently produced cohorts.

Even though manzanita nutlets are water-permeable, most reports on germination describe the seeds as hard-seeded, and the traditional pretreatment is sulfuric acid scarification for 3 to 15 hours (Belcher 1985; Berg 1974; Carlson and Sharp 1975; Emery 1988). Because the periole is much weaker than the endocarp wall, acid can enter there and damage the embryo long before the endocarp wall is stripped away, so care must be taken to remove the seeds before this damage occurs (Belcher 1985; Berg 1974). Coalesced nutlets generally require more time in acid than solitary nutlets, perhaps because the perioles, which are on the inner face of each nutlet, are better-protected when the nutlets are coalesced. Chaparral species such as bigberry and Eastwood manzanitas may be rendered immediately germinable by acid scarification, although reported percentages are low—3 to 8% (Berg 1974). Populations of greenleaf manzanita required both acid scarification (2 to 4 hours) and subsequent chilling for 60 days (Berg 1974) and 90 days (Carlson and Sharp 1975). Final germination percentages were 20 to 50%. Bearberry has been reported to respond to warm plus cold stratification following a 3- to 6-hour acid treatment—60 to 120 days at 25 °C, followed by 60 to 90 days at 5 °C (Berg 1974). Final germination percentages ranged from 30 to 60%. Belcher (1985) reported that warm plus cold stratification of bearberry resulted in 40 to 60% germination without acid scarification, but that acid scarification for 3 hours could be substituted for warm stratification. In bearberry, even excised embryos were dormant prior to chilling (Giersbach 1937).

Emery (1988) reported that a fire treatment (burning 3 to 4 inches of pine straw or excelsior over the planted seeds) in fall resulted in some emergence the following spring for many species of manzanitas, but the mechanism of dormancy loss under these conditions was not further explored. Charate could have been the stimulus responsible for this effect. It would be worth experimenting with charate as a germination stimulant in a nursery propagation setting.

Formal seed quality evaluation in manzanita is rendered difficult by the lack of reliable germination tests and by the thick endocarp. Tetrazolium staining requires excision of the seed from the endocarp by twisting it open along the suture or by cutting the nutlet off-center longitudinally, procedures difficult to carry out without damage (Belcher 1985). A seed unit may contain multiple seeds, only 1 of which has to be viable for the seed unit to be considered viable. For seedlots that have not been incorrectly handled (for example, stored at high moisture content) or stored for long periods, a cut test to determine fill is probably the best way to get a quick idea of total viability.

Field seeding and nursery practice. It will probably continue to be very difficult to obtain manzanita from direct seeding until there is a much better understanding of factors controlling release from dormancy. The absence of manzanita seedlings in unburned chaparral (Keeley 1992) coupled with the regular appearance of thousands of manzanita seedlings per hectare following fire, as reported by Keeley (1977), strongly suggests that a successful seeding prescription would include a seed pretreatment simulating fire-related germination cues. The sulfuric acid–stratification treatments described above and the fire treatment of Emery (1988) are currently the only published procedures for nursery seed propagation. The mazanitas are much more easily propagated from cuttings than from seeds, and in practice most nursery propagation is probably accomplished in this way (Berg 1974; Emery 1988).

References

Belcher E. 1985. Handbook on seeds of browse-shrubs and forbs. Tech. Pub. R8-8. Atlanta: USDA Forest Service, Southern Region. 246 p.

Berg AR. 1974. *Arctostaphylos* Adans., manzanita. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 228–231.

Carlson JR, Sharp WC. 1975. Germination of high elevation manzanitas. Tree Planters' Notes 26(3): 10–11, 25.

Dirr MA. 1983. Manual of woody landscape plants: their identification, ornamental characteristics, culture, propagation, and uses. Champaign, IL: Stipes Publishing. 826 p.

Emery DE. 1988. Seed propagation of native California plants. Santa Barbara, CA: Santa Barbara Botanic Garden. 107 p.

Fulton RE, Carpenter FL. 1979. Pollination, reproduction, and fire in California *Arctostaphylos*. Oecologia 38: 147–157.

Giersbach J. 1937. Germination and seedling production of *Arctostaphylos uva-ursi.* Contributions to the Boyce Thompson Institute 9: 71–78.

Kauffman JB, Martin RE. 1991. Factors influencing scarification and germination of three montane Sierra Nevada shrubs. Northwest Science 65: 180–187.

Keeley JE. 1977. Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and nonsprouting chaparral shrubs. Ecology 58: 820–829.

Keeley JE. 1987a. Role of fire in seed germination of woody taxa in California chaparral. Ecology 68: 434–443.

Keeley JE. 1987b. Ten years of change in seed banks of the chaparral shrubs *Arctostaphylos glauca* and *A. glandulosa*. American Midland Naturalist 117: 446–448.

Keeley JE. 1991. Seed germination and life history syndromes in the California chaparral. Botanical Review 57: 81–116.

Keeley J. 1992. Recruitment of seedlings and vegetative sprouts in unburned chaparral. Ecology 73: 1194–1208.

Keeley JE. 1995. Seed germination patterns in fire-prone Mediterranean climate regions. In: Arroyo MTK, Zedler PH, Fox MD, eds. Ecology and biogeography of Mediterranean ecosystems in Chile, California, and Australia. New York: Springer-Verlag: 239–273.

Keeley JE, Hays RL. 1976. Differential seed predation on two species of *Arctostaphylos* (Ericaceae). Oecologia 24: 71–81.

Keeley JE, Zedler PH. 1978. Reproduction of chaparral shrubs after fire: a comparison of sprouting and seeding strategies. American Midland Naturalist 99: 142–161.

Kelly VR, Parker VT. 1990. Seed bank survival and dynamics in sprouting and nonsprouting *Arctostaphylos* species. American Midland Naturalist 124: 114–123.

Kelly VR, Parker VT. 1991. Percentage seed set, sprouting habit, and ploidy level in *Arctostaphylos* (Ericaceae). Madroño 38 (4): 227–232.

Meyer SE. 1997. Personal observation. Provo, UT: USDA Forest Service, Rocky Mountain Research Station.

Munz PA, Keck DD. 1959. A California flora. Berkeley: University of California Press. 1681 p.

Parker VT, Kelly VR. 1989. Seed banks in California chaparral and other Mediterranean climate shrublands. In: Leck MA, Parker VT, Simpson RL, eds. Ecology of soil seed banks. San Diego: Academic Press: 231–253.

Wells PV. 1969. The relation between mode of reproduction and extent of speciation in woody genera of the California chaparral. Evolution 23: 264–267.

Rosaceae—Rose family

Aronia Medik

chokeberry

John D. Gill, Franz L. Pogge, and Franklin T. Bonner

Dr. Gill and Mr. Pogge retired from the USDA Forest Service's Northeastern Forest Experiment Station;
Dr. Bonner is a scientist emeritus at the USDA Forest Service's Southern Research Station,
Mississippi State, Mississippi

Growth habit, occurrence, and uses. The chokeberries—genus *Aronia*—discussed here are 2 closely related species (red and black chokeberries) and 1 hybrid deciduous shrub (purple chokeberry) (table 1). Black chokeberry is small, only 0.5 to 1 m tall. Red chokeberry and purple chokeberry are medium sized, 3 to 4 m tall. Red and black chokeberries hybridize readily and may be difficult to distinguish. Red and purple chokeberries are practically identical ecologically (Van Dersal 1938), and the only satisfactory way to distinguish between them is by the color of their ripe fruit. Both have pubescence on younger branches, leaf stems, and lower leaf surfaces. In contrast, black chokeberry is smooth or has only a few scattered hairs on these parts (Gleason 1963). The combined ranges of these 3 include most of the eastern United States and southern parts of adjacent Canadian provinces (table 1). All are moderately tolerant of shading and prefer moist soils, which usually are acidic. The most likely habitats are bogs and swamps, low woods, clearings, and damp pine barrens. However, each species will tolerate drier conditions, and black chokeberry is better adapted than the others to growth in drier thickets or clearings on bluffs or cliffs (Fernald 1950; Gleason 1963). All are valuable as food sources for wildlife in fall and winter (Hosely 1938). Their handsome foliage, flowers, and fruits also make them attractive as ornamentals, but none has been cultivated extensively. Red and black chokeberries were first cultivated about 270 years ago (Rehder 1940).

Flowering and fruiting. The white, bisexual flowers bloom for 2 to 3 months during March to July, the local flowering period depending on latitude and elevation. Fruit ripening dates are similarly dependent and range from August to November (table 2). Fruits drop from the plants shortly after ripening and may continue through the winter and spring. The fruits are rather dry, berrylike pomes (figure 1) containing 1 to 5 seeds (figure 2), some of which may be empty (aborted). Natural seed dispersal is chiefly by animals. Black chokeberry fruits shrivel soon after ripening,

Table 1—*Aronia,* chokeberry: nomenclature, occurrence, and height at maturity

Scientific name & synonym(s)	Common name	Occurrence	Height (m)
***A. arbutifolia* (L.) Pers.** *A. arbutifolia* var. *glabra* Ell. *Pyrus arbutifolia* (L.) L. f. *Sorbus arbutifolia* (L.) Heynh.	**red chokeberry**	Nova Scotia to S Ontario & S to Florida & E Texas	1–4
***A. melanocarpa* (Michx.) Ell.** *A. nigra* (Willd.) Koehne *Pyrus melanocarpa* (Michx.) Willd. *Pyrus melanocarpa* (Michx.) Heynh. *Sorbus melanocarpa* (Michx.) Heynh.	**black chokeberry,** *gueles noires*	Newfoundland to Minnesota & S to Tennessee & South Carolina	0.5–1
***A. x prunifolia* (Marsh.) Rehd. (pro sp.)** *A. arbutifolia* var. *atropurpurea* (Britt.) Seymour *A. atropurpurea* Britt.; *A. floribunda* (Lindl.) Spach *Pyrus arbutifolia* var. *atropurpurea* (Britt.) B.L. Robins. *Pyrus floribunda* Lindl. *Sorbus arbutifolia* var. *atropurpurea* (Britt.) Schneid.	**purple chokeberry,** hybrid chokeberry	Newfoundland to Ontario & S to Indiana & Virginia	1–4

Source: Gill and Pogge (1974).

Table 2—*Aronia,* chokeberry: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening
A. arbutifolia	Texas	Mar–Apr	Oct–Nov
	West Virginia	Mar–May	Sept–Oct
	North	Apr–July	Sept–Nov
A. melanocarpa	South	Mar–June	Aug
	North	Apr–July	Aug–Oct
	West Virginia	June	Sept–Oct
A. x *prunifolia*	—	Apr–July	Aug–Oct

Sources: Ammons (1975), Fernald (1950), McDonald (1960), Mahlstede and Maber (1957), Van Dersal (1938).

Figure 1—*Aronia arbutifolia*, red chokeberry: leaf and cluster of fruits (pomes).

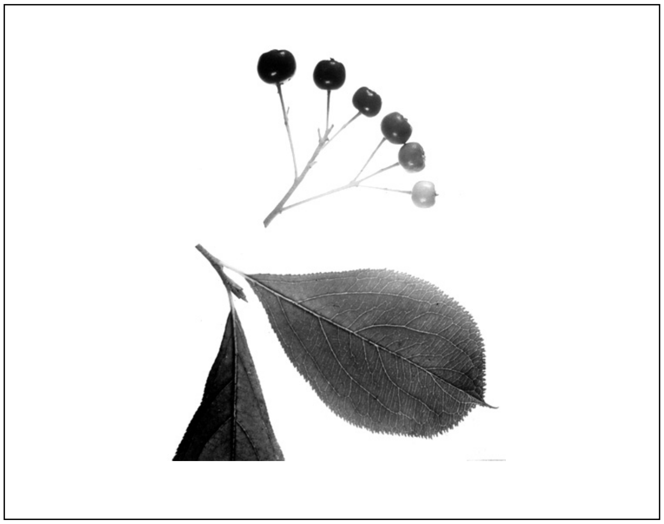
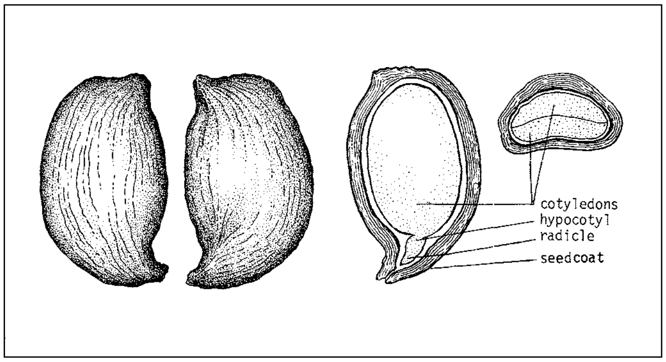


Figure 2—*Aronia melanocarpa*, black chokeberry: exterior views of seed, as well as longitudinal and transverse



and most of them drop. Purple chokeberry fruits shrivel at the beginning of winter, whereas fruits of red chokeberry remain plump and bright into the winter. Red chokeberry may yield fruit first at 2 years of age (Spinner and Ostrum 1945) and produces good seedcrops almost every year. Black chokeberry yields a good crop about every second year (Gill and Pogge 1974).

Collection of fruits; extraction and storage of seeds. If loss to birds is a hazard, fruits should be handpicked as soon as they ripen. Otherwise, they should be picked within a month or so. The delay should be least with black chokeberries and can be longest with red chokeberry. Fruits of the latter species collected in January and cleaned and sown right away will germinate in 2 weeks (Dirr and Heuser 1987). Commercial seeds usually consist of the dried pomes or "dried berries" as usually listed in seed catalogs. There are about 16,220 dried pomes/kg (7,355/lb) of red choke berry (Swingle 1939). Although seed extraction and cleaning may be impractical on a large scale, small lots of seeds can be extracted by rubbing fresh fruits over screens and floating off the debris. If the fruits have dried, they can be soaked in water until the pulp is soft enough to come off (Mahlstede and Maber 1957). A kitchen blender can be useful for extracting seeds from small lots of several kinds of small berries and other soft fruits, including chokeberries (Morrow and others 1954; Munson 1986). Cleaned seeds per weight average about 564,480/kg (256,000/lb) for red chokeberry and 608,580/kg (276,000/lb) for black chokeberry (Gill and Pogge 1974; Swingle 1939). No data were found on longevity of seeds, but drying before storage is recommended (Chadwick 1935), so they are undoubtedly orthodox in storage behavior.

Pregermination treatments and germination tests. Chokeberry seeds have an internal dormancy that can be overcome by stratification in a moist medium at temperatures of 1 to 5 °C. A higher stratification temperature 10 °C also was effective on seeds of purple chokeberry (Crocker and Barton 1931). Optimum duration of stratification may be 60 to 120 days and varies with the species (table 3).

Table 3—*Aronia,* chokeberry: cold stratification periods, germination test conditions and results

Species	Cold stratification period (days)	Germination test conditions: Temp (°C) Day	Night	Days	Germinative capacity: Amount (%)	Samples
A. arbutifolia	90	20	20	30	94	4
A. melanocarpa	90–120	30	20	30	22	4
A. x *prunifolia*	60	20	20	30	96	2

Sources: Crocker and Barton (1931), Gill and Pogge (1974).

There are no official test prescriptions for chokeberries, but tests of stratified seeds can be done on paper or in soil, sand, or peat for 28 days, at diurnally alternating temperatures of 30 (day) and 20 °C (night) or at a constant 20 °C. Gemination starts after about 8 days and may be virtually complete in 20 to 30 days (Crocker and Barton 1931). Germination of seeds stratified as recommended here was mostly in the 90 to 100% range (table 3). Germination of unstratified seed was quite low, 0 to 15%, in tests that extended into a second year (Adams 1927). Germination is epigeal.

Nursery practice. In some nurseries, the dried fruits are soaked in water for a few days and mashed and then the whole mass is stratified until spring. Limiting the stratification period to 60 days for purple, 90 days for red, and 120 days for black chokeberry may increase germination in the nursery. Fall planting is done by some growers (Dirr and Heuser 1987). The recommended sowing depth is about 10 mm ($^1/_3$ in) (Sheat 1948). Germination mostly takes place within a few days after sowing. As a rule of thumb, 0.45 kg (1 lb) of cleaned seed may yield about 10,000 usable plants (Van Dersal 1938). Outplanting may be done with 2-year-old seedlings (Sheat 1948).

Vegetative propagation is possible with red chokeberry (and perhaps the others). Softwood cuttings taken in July and treated with 4,000 ppm of indole-butyric acid solution root very well. Cuttings taken in December or January will root also (Dirr and Heuser 1987). Irrigation of the mother plant a few days before the cuttings are taken will help rooting (Dehgan and others 1989).

References

Adams J. 1927. The germination of the seeds of some plants with fleshy fruits. American Botanist 15(8): 415–428.

Ammons N. 1975. Shrubs of West Virginia. Grantsville, WV: Seneca Books. 127 p.

Chadwick LC. 1935. Practices in propagation by seeds: stratification treatment for many species of woody plants described in fourth article of series. American Nurseryman 62(12): 3–9.

Crocker W, Barton LV. 1931. After-ripening and storage of certain roseaceous seeds. Contributions of the Boyce Thompson Institute 3: 385–404.

Dehgan B, Gooch M, Almira F, Kane M. 1989. Vegetative propagation of Florida native plants: 3. Shrubs. Proceedings of the Florida State Horticultural Society 102: 254–266 [Seed Abstracts 1991; 14(4): 1155].

Dirr MA, Heuser CW Jr. 1987. The reference manual of woody plant propagation: from seeds to tissue culture. Athens, GA: Varsity Press. 239 p.

Fernald ML. 1950. Gray's manual of botany. 8th ed. New York: American Book Co. 1632 p.

Gill JD, Pogge FL. 1974. *Aronia* Medik, chokeberry. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 232–234.

Gleason HA. 1963. The new Britton and Brown illustrated flora of the Northeastern United States and adjacent Canada. 3 vol. New York: Hafner Publishing.

Hosely NW. 1938. Woody plants used by wildlife in the northeastern United States [PhD thesis]. Ann Arbor: University of Michigan. 409 p.

McDonald EE. 1960. Fruiting trees. Texas Game and Fish 18 (5): 9.

Mahlstede JP, Maber ES. 1957. Plant propagation. New York: John Wiley and Sons. 413 p.

Morrow EB, Darrow GM, Scott DH. 1954. A quick method of cleaning berry seed for breeders. American Society of Horticultural Science Proceeddings 63: 265.

Munson RH. 1986. Extracting seeds from fleshy fruits. Plant Propagator 32(2): 14–15.

Rehder A. 1940. Manual of cultivated trees and shrubs. 2nd ed. New York: Macmillan. 996 p.

Sheat WG. 1948. Propagation of trees, shrubs and conifers. London: MacMillan. 479 p.

Spinner GP, Ostrum GF. 1945. First fruiting of woody food plants in Connecticut. Journal of Wildlife Management 9(1): 79.

Swingle CF, comp. 1939. Seed propagation of trees, shrubs and forbs for conservation planting. SCS-TP-27. Washington, DC: USDA Soil Conservation. Service. 187 p.

Van Dersal WR. 1938. Native woody plants of the United States: their erosion-control and wildlife values. Misc. Pub. 303. Washington, DC: USDA. 362 p.

Asteraceae—Aster family

Artemisia L.

sagebrush

Susan E. Meyer

Dr. Meyer is a research ecologist at the USDA Forest Service's Rocky Mountain Research Station, Shrub Sciences Laboratory, Provo, Utah

Growth habit, occurrence, and use. Sagebrush—*Artemisia* L.—species are probably the most common shrubs in western North America. Big sagebrush alone occupies an estimated 60 million ha as a landscape dominant or codominant in the semiarid interior, and related species of the subgenus Tridentatae are estimated to occupy an additional 50 million ha (Beetle 1960; McArthur and Stevens in press). Sagebrush-dominated vegetation occurs mostly under semiarid climatic regimes characterized by cold winters and predominantly winter precipitation. The genus is circumboreal in distribution and consists of about 400 species of mostly evergreen shrubs, subshrubs, and herbaceous perennials.

The 20 or so shrubby sagebrush species in the United States differ widely in their growth form, ecology, distribution, and abundance (table 1). Big, black, silver, and low sagebrushes are widely distributed, polymorphic species of relatively broad ecological amplitude, whereas most of the remaining species are either more geographically restricted or more specialized in their habitat requirements. The subshrub fringed sagebrush, common and widespread in both the Old and New Worlds, may be the most widely distributed sagebrush taxon. Sand sagebrush is an important species on sandy soils on the Great Plains and in the Southwest, whereas the summer-deciduous subshrub budsage is the principal sagebrush species of salt desert shrub vegetation in the Great Basin.

Because of their status as regional dominants, sagebrush species—especially those of the subgenus *Tridentatae*—have been the object of a great deal of study (McArthur and Welch 1986). Many have long been regarded as undesirable plants by the ranching industry because of their perceived low palatability to livestock and propensity for increase under conditions of abusive grazing. However, they provide a principal source of browse on winter ranges for both wild and domestic ungulates, and undoubtedly are central to the habitat requirements of many other wildlife species.

Most sagebrush species rely on seeds for regeneration and have neither the ability to resprout following burning—with notable exceptions (McArthur and others 2004)—nor a long-lived soil seedbank (Young and Evans 1975, 1989; Meyer 1990). Invasion by exotic annual grasses and the associated increase in fire frequency has resulted in loss of big sagebrush over vast acreages of its former area of dominance (Billings 1990; D'Antonio and Vitousek 1992). This loss has led to a realization of the importance of the shrub overstory for maintaining the integrity of the ecosystem and also to a renewed interest in seed propagation of sagebrush species (Meyer 1994). Sagebrush has been seeded as part of big-game winter-range rehabilitation and mined-land reclamation efforts for over 30 years, so there is a considerable fount of knowledge to draw upon (Plummer and others 1968).

Subspecies and ecotypes. The more complex sagebrush species are made up of series of subspecies that are morphologically and ecologically distinct. In addition, many sagebrush taxa have been shown through common garden studies to be made up of numerous ecotypes that result from adaptation to local conditions through the process of natural selection (McArthur and others 1979). Such site-specific adaptation may be reflected in traits such as frost or drought hardiness, growth rate, competitive ability, flowering time, and seed germination regulation (McArthur and Welch 1982; Meyer and Monsen 1990). This means that the use of seed from locally adapted or at least habitat-matched populations is important to successful long-term restoration of these species.

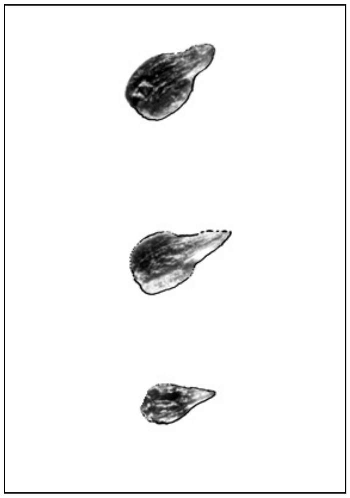
An alternative to using adaptedness as the principal criterion for ecotype selection has been to identify native germplasms with desirable traits such as high winter-forage-quality for wild ungulates (for example, Welch and others 1986). Their use is recommended in artificial seedings with specific management objectives on sites that fall within their range of adaptation.

Table 1—*Artemisia,* sagebrush: distribution and ecology of principal shrubby species in the United States

Scentific name	Common names(s)	Distribution	Habitat
SUBGENUS *TRIDENTATAE*			
***A. arbuscula* Nutt.**	**low sagebrush**	Widely distributed, mostly intermountain	Shallow, rocky soils in mtns
***A. bigelovii* Gray**	**Bigelow sagebrush,** rimrock sagebrush	SW deserts	Shallow rocky soils at middle to low elevations bottoms or
***A. cana* Pursh**	**silver sagebrush**	NW Great Plains, N intermountain region & N Sierras	Deep sandy soils in valley snow catchment basins in mtns
***A. nova* A. Nels.**	**black sagebrush**	Widely distributed, mostly intermountain	Shallow soils over bedrock at middle to low elevations region
***A. pygmaea* Gray**	**pygmy sagebrush**	Utah & adjacent parts of Nevada & Colorado	Fine-textured calcareous soils at low elevations
***A. rigida* (Nutt.) Gray**	**stiff sagebrush,** scabland sagebrush	Columbia Plateau, E Washington & Oregon	Shallow rocky soils over basalt at low elevations
***A. tridentata* Nutt.**	**big sagebrush**	Widely distributed, W North America	Wide ecological amplitude
***A.t.* ssp. *tridentata* Nutt.**	**basin big sagebrush**	See species	Mostly on deep well-drained soils of valley bottoms
***A.t.* ssp. *vaseyana* (Rydb.) Beetle**	**mountain big sagebrush,** Vasey sagebrush	See species	Mostly on coarse soils at middle to high elevations benchlands
***A.t.* ssp. *wyomingensis* Beetle & Young**	**Wyoming big sagebrush**	See species	On coarse to fine soils of at middle to low elevation
***A. tripartita* Rydb.**	**threetip sagebrush**	Columbia Plateau E into Wyoming	Deep to shallow mostly volcanic soils at low elevations
OTHER SUBGENERA			
***A. filifolia* Torr.**	**sand sagebrush,** old man sagebrush	W Great Plains & SW deserts	Sandy soils at low to middle elevations
***A. frigida* Willd.**	**fringed sagebrush**	W North America to central Asia	Very wide ecological amplitude
***A. spinescens* D.C. Eat.** *Picrothamnus desertorum* Nutt.	**budsage**	Widely distributed, mostly N intermountain region	Semiarid bottoms, benches, & foothills, salt desert shrublands

Flowering and fruiting. Most North American sagebrush species flower in late summer or autumn and ripen fruit from September through December. Seeds of high-elevation populations generally ripen earlier than those of low-elevation populations. Budsage, which flowers in March or April and sets seed in May or June before entering summer dormancy, is a major exception. The tiny yellowish or brownish flowers are wind-pollinated and are borne in groups of about 2 to 70 (depending on species) in small heads enclosed in overlapping bracts with thin, dry margins. The numerous heads are arranged in spikelike or open panicles that occur terminally on the branches of current-season growth. Each fertile floret within a head may develop into a small, 1-seeded fruit (achene) that lacks any special appendages for dispersal (figure 1). The pericarp of the achene is papery and membranous, whereas the seedcoat of the enclosed seed is firmer and somewhat shiny. The endosperm is reduced to a membrane fused to the inner wall of the seedcoat, whereas the embryo is well-developed and fills the interior of the seed. Mucilaginous nerves on

Figure 1—*Artemisia*, sagebrush: achenes (cleaned seeds) of *A. arbuscula*, low sagebrush (**top**); *A. nova*, black sagebrush (**middle**); and *A. tridentata*, big sagebrush (**bottom**).



the exterior of the pericarp may aid in adhesion to the soil surface during radicle penetration (Walton and others 1986). The hypocotyl hairs that develop as a first manifestation of germination have been shown to have a similar function (Young and Martens 1991).

The fruits fall or are shaken from the plant by wind within a few weeks of maturation. The potential yearly seed production of a single plant of big sagebrush is prodigious, on the order of hundreds of thousands of seeds (Welch and others 1990). However, many factors operate to restrict seed production in wildland stands, including excessive browsing (Fairchild 1991; Wagstaff and Welch 1991), intraspecific competition (Fairchild 1991; Young and others 1989), insect and disease attack (Welch and Nelson 1995), and cycles of dry years (Young and others 1989). Sagebrush in field cultivation for seed production yields harvestable crops within 2 years of establishment and generally produces high yields yearly (Welch and others 1990). Wildland stands vary in the consistency and quality of their seedcrops, depending on the factors listed above and also on the taxon under consideration and on site quality factors. An alternative to field cultivation for needed ecotypes that produce minimal numbers of seeds in the wild is management of wildland stands through thinning or protection from browsing to maximize seed production.

Seed collection, cleaning, and storage. Sagebrush seeds (actually, the 1-seeded achenes) are collected by beating or stripping them into shoulder hoppers, baskets, or bags. They are much more easily harvested by beating when dry than wet. Usually there is considerable among-bush variation in ripening date within a population. Harvesting too late may result in a high proportion of half-filled and aborted fruits.

Purity on a dry-weight basis before cleaning is often 10% or less. Passage through a barley de-bearder serves to break up the inflorescences to release the seeds; hammermilling is less desirable, as it tends to make the material ball-up and may damage the seeds (McArthur and others 2004). Screening and fanning can then be used to remove sticks and other debris, resulting in lot purities of 50% or more. This cleaning procedure may strip many of the seeds of their membranous pericarps, but this has no effect on viability or storage life, although it may reduce seed dormancy or light requirement somewhat (Meyer and others 1990; Welch 1995). Sagebrush seeds are not easily damaged in cleaning equipment because of their small size (Welch 1995). Advantages to cleaning to relatively high purities include improved accuracy in quality evaluation; reduced shipping, handling, and storage costs; better regulation of moisture content during storage; and better metered flow through seeding devices (Welch 1995). On the other hand, sagebrush seeds are so small that lots at high purity must be diluted with a carrier in order to achieve realistic seeding rates. Seed size varies substantially among species and also among populations within species (table 2). Seeding rates should take seed size and therefore seed number per unit weight into account.

Sagebrush seeds are not long-lived in warehouse storage. Seedlots commonly hold full viability for 2 or 3 years (Stevens and others 1981). Seedlots of initial low quality lose viability more quickly than high-quality lots. Careful attention to moisture content (6 to 8% is optimal) and storage at relatively low temperatures (<10 °C) can extend storage life to 5 years and possibly longer. Because of late ripening dates, almost all sagebrush seed is held at least 1 year (until the following autumn) before planting.

Germination. We have good information on seed germination patterns for only a few species of sagebrush, but evidence indicates that this information may be broadly applicable to other species (Meyer and Monsen 1991, 1992; Meyer and others 1990). Variation in germination response is generally related to climatic variation at collection sitse rather than to specific or subspecific identity. Timing mechanisms are keyed to a pattern of winter or early spring germination and early spring emergence for all species examined so far. Sagebrush seeds are characterized by relatively low levels of dormancy at dispersal but may be more or less strongly light-requiring or slow to germinate. Both dormancy and light requirement are removed through moist chilling (stratification), so that most seeds become germinable during winter. After-ripening in storage also tends to reduce dormancy or light requirement. In the studies of big sagebrush germination ecophysiology cited above, patterns of variation in dormancy, light requirement, and germination rate were shown to be linked to collection site habitat. Seeds of populations from montane habitats with long, snowy winters tend to be dormant, light-requiring, or slow to germinate at autumn temperatures. These traits protect them from autumn germination, a risk for seeds dispersed in early autumn into relatively mesic environments. Seeds of populations from habitats with short, mild winters and hot, dry springs are dispersed later. They tend to be nondormant, not light-requiring, and quick to germinate, which facilitates germination during winter, when conditions are most favorable on warm desert fringe sites.

Germination under winter snowcover conditions is also keyed to habitat. Seeds of montane populations may take 20 weeks or more to germinate under conditions simulating snowcover in the field, whereas those of warm desert fringe populations may do so in as little as 1 week. Seeds of montane populations can also sense and respond with increased germination rates to the shift from dark to light in the cold that results from thinning snow cover in the early spring. These habitat-correlated patterns apparently hold for black, silver, and low sagebrushes as well as for big sagebrush, based on preliminary data (table 3). Germination under snowcover seems to be a common pattern for sagebrush, ensuring emergence in very early spring just as the snow is melting (Meyer 1990; Meyer and Monsen 1990; Monsen and Meyer 1990).

Most big sagebrush seeds germinate during the winter and spring following the autumn of their production. They have no apparent mechanisms for seed bank carryover from year to year, and studies on *in situ* seed banks have failed to detect any substantial carryover (Young and Evans 1975, 1989). The tiny fraction of seeds that sometimes carries over (Hassan and West 1986) is probably made up of buried seeds whose light requirement has not yet been overcome because of inadequate chilling (Meyer and others 1990).

The observation that sagebrush seeds germinate over a broad range of temperatures (see for example, Bai and Romo 1994; McDonough and Harniss 1974; Weldon and

Table 2— *Artemisia,* sagebrush: seed data (pure live seeds)

	Cleaned seeds (million)/weight			
	Mean		Range	
Species	**/kg**	**/lb**	**/kg**	**/lb**
A. arbuscula	1.81	0.82	1.13–2.15	0.15–0.98
A. bigelovii	5.54	2.52	—	—
A. cana	2.87	1.30	1.81–4.90	0.82–2.23
A. nova	2.03	0.92	2.00–2.12	0.91–0.96
A. pygmaea	1.04	0.47	—	—
A. rigida	1.10	0.50	—	—
A. tridentata				
spp. *tridentata*	5.26*	2.38*	4.25–5.67*	1.93–2.58*
spp. *vaseyana*	4.30	1.95	4.23–4.36	1.92–1.98
spp. *wyomingensis*	4.72	2.14	4.00–5.42	1.82–2.46
A. tripartita	4.87	2.21	—	—
A. filifolia	3.20	1.45	—	—
A. frigida	10.0	4.55	—	—
A. spinescens	3.06	1.39	2.25–3.70	1.02–1.68

Sources: Belcher (1985), Deitschman (1974), McArthur and others 2004, Meyer (1990).

* Subspecies not distinguished.

Table 3—*Artemisia,* sagebrush: germination data

	Germination percentage* on day 14 at 15 °C				Days to 50% germination at 1 °C (light)		
	Mean		Range				
Species	**Light**	**Dark**	**Light**	**Dark**	**Mean**	**Range**	**Lots #**
A. arbuscula	100	—	—	—	38.2	38	1
A. bigelovii	100	—	—	—	—	—	1
A. cana,	100	81.5	100	75–88	56.0	54–58	2
A. nova	92.3	21.2	75–100	3–57	47.6	17–80	5
A. tridentata							
ssp. *tridentata*	94.6	18.6	84–100	0–46	54.0	27–95	5
ssp. *vaseyatia*	85	12.2	64–94	0–24	49.2	16–98	5
ssp. *wyomingensis*	98.4	13.4	94–100	2–46	55.2	18–98	5
A. filifolia	100	—	—	—	—	—	1
A. spinescens	92.7	72.6	87–98	52–93	45.5	38–53	2

Sources: All data from Meyer (1990) except for *A. tridentata* lots stored 4 months (Meyer and others 1990).

* Expressed as percentage of viable seeds.

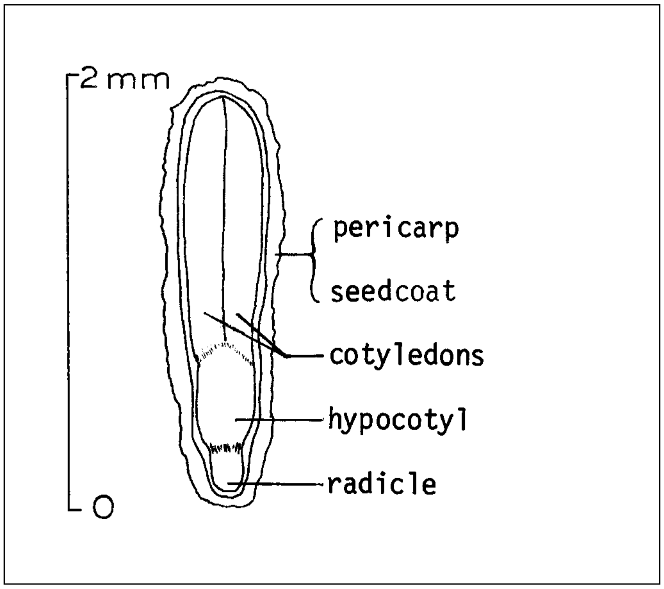
others 1959; Wilson 1982) probably stems from the fact that sagebrush seeds have no need for protection from germination at summer temperature, as they almost never encounter summer regimes. Budsage, a species with seeds that ripen in early summer but do not germinate until the following early spring, shows strong germination suppression at summer temperatures (Meyer and Kitchen 1997).

Germination testing for sagebrush species is a relatively straightforward process. We recommend a 21-day test at 15 or 20 °C with light as the standard for big sagebrush and black sagebrush, with a 2-week chill (stratification) for more dormant lots (AOSA 1993; Meyer and others 1988a, 1988b). Because many dormant sagebrush seeds will not germinate in response to a short chilling, the viability of ungerminated seeds should be evaluated with tetrazolium.

Tetrazolium staining also represents an alternative to the germination test for evaluating the viability of sagebrush seeds. The fruits are pierced with a needle through the center of the cotyledon region of the embryo (figure 2) and immersed in buffered 1% tetrazolium chloride solution for 6 hours at 25 °C. The pericarp and seedcoat are then slit with a needle at the cotyledon end, and the embryos are squeezed out. Embryos stained a uniform bright red may be classed as viable.

The principal source of inconsistent results in sagebrush seed testing comes from decisions made during the purity evaluation. The inclusion of non-viable half-filled and aborted fruits in the pure seed fraction has little effect on the value for percentage purity but can affect the viability percentage considerably. In research, we routinely exclude such fruits and only occasionally encounter recently collected or properly stored lots whose viability is less than 90%. The seed analyst has a more difficult problem and we hope that the advent of better cleaning procedures for sagebrush seeds will help to make these difficulties unnecessary.

Figure 2—*Artemisia nova*, black sagebrush: longitudinal section through an achene.



Nursery and field practice. Many species of sagebrush have been successfully grown both as container and as bareroot stock (Long 1986; McArthur and others 2004; Welch and others 1986). In addition, the practice of transplanting wildlings has been particularly successful with sagebrush (McArthur and others 2004). Planting is best carried out in early spring, when moisture conditions are favorable. Container stock requires careful hardening (Long 1986).

Sagebrush species are among the few native shrubs that can be reliably established by direct seeding. Seedling recruitment is regularly observed on small-scale disturbances in wildland stands where competition from adult plants and from weedy understory species is not too severe. Artificial seeding should mimic natural processes of dispersal. Seeding in late fall or onto snow in winter is most successful; spring-seeding is not recommended. Seeding rates that result in an average of 50 to 100 seeds/m^2 (5 to 9/ft^2) usually result in adequate stands. This corresponds to a rate of 0.1 to 0.2 kg/ha (1.5 to 3 oz/ac) on a pure live seed (PLS) basis for a lot that averages 4 million seeds/kg (113,400/oz). The seeds should be planted at or near the surface of a firm but not compacted seedbed. Because of their small size, drilling or broadcasting seeds into a loose, sloughing seedbed may bury them too deeply for successful emergence (Jacobsen and Welch 1987; Monsen and Meyer 1990).

Sagebrush plants are generally quite long-lived, and successful recruitment from seeds every year is not necessary for perpetuation of the stand. On drier sites, winter snowfall may be inadequate for successful emergence and establishment in a typical year, especially on the bare, windswept surfaces of artificial seedings. Small-scale use of snow-fencing has been shown to enhance sagebrush stand establishment under such marginal conditions (Monsen and others 1992). Once nuclear stands are established, the shrubs themselves may act as both seed sources and living snow entrapment structures. It is common to see newly establishing seedlings spread out on the leeward side of an adult plant, where drifting snow accumulates.

Sagebrush species have been successfully seeded onto drastic disturbance sites such as mine- waste rock dumps, but adding topsoil (even minimally) often greatly enhances success, perhaps through re-inoculation with essential symbionts such as mycorrhizae (Monsen and Richardson 1984). Fertilization per se usually favors herbaceous competitors over the shrub seedlings and is not generally recommended.

Reports on seedling competitiveness in sagebrush are somewhat contradictory. In the era of sagebrush control on rangelands, managers often remarked on the ability of sagebrush to reestablish in perennial forage grass plantings (Pechanec and others 1944). Follow-up moisture in the summer appears to facilitate shrub seedling survival in competition with perennial grasses. Success in mixed seedings may be enhanced by separating the seeds spatially, for example, in separate drop boxes on the seeding implement, or by interseeding into scalps (McArthur and others 2004).

Sagebrush seedings in the presence of strong exotic annual grass competition have almost universally been failures (Monsen 1995). It may be that, in order to restore big sagebrush–bunchgrass communities on many sites now dominated by exotic annuals like cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* (L.) Nevski), seeding and establishment of the native perennial understory is a necessary prerequisite to successful establishment of sagebrush. More-expensive weed-control measures are often not an option on the large acreages involved.

References

AOSA [Association of Official Seed Analysts]. 1993. Rules for testing seeds. Journal of Seed Technology 16(3): 1–113.

Bai Y, Romo JT. 1994. Germination of previously-buried seeds of fringed sage (*Artemisia frigida*). Weed Science 42: 390–397.

Beetle AA. 1960. A study of sagebrush: the section Tridentatae of *Artemisia*. Wyoming Agriculture State Bulletin 368: 1–83.

Belcher E. 1985. Handbook on seeds of browse-shrubs and forbs. Tech. Pub. R8-8. Atlanta: USDA Forest Service, Southern Region. 246 p.

Billings WD. 1990. *Bromus tectorum*, a biotic cause of ecosystem impoverishment in the Great Basin. In: Woodell GM, ed. The Earth in transition: patterns and processes of biological impoverishment. Cambridge, UK: Cambridge University Press: 301–322.

D'Antonio CM, Vitousek PM. 1992. Biological invasions by exotic grasses, grass-fire cycle, and global change. Annual Review of Ecology and Systematics 23: 63–88.

Deitschman GH. 1974. *Artemisia*, sagebrush. In: Schopmeyer CS, tech coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 235–237.

Fairchild JA. 1991. Plant community and shrub vigor responses to one-way and two-way chaining of decadent big sagebrush on a critical mule deer winter range in east central Utah [PhD dissertation]. Provo, UT: Brigham Young University.

Hassan MA, West NE. 1986. Dynamics of soil seed pools in burned and unburned sagebrush semi-deserts. Ecology 67: 269–272.

Jacobsen TLC, Welch BL. 1987. Planting depth of 'Hobble Creek' mountain big sagebrush. Great Basin Naturalist 47: 497–499.

Long LE. 1986. Container nursery production of *Artemisia* and *Chrysothamnus* species. In: McArthur ED, Welch BL, comps. Proceedings, Symposium on the Biology of *Artemisia* and *Chrysothamnus*. 1984 July 9–13; Provo, UT. Gen. Tech. Rep. INT-200. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 395–396.

McArthur ED, Welch BL, eds. 1986. Proceedings, Symposium on the Biology of *Artemisia* and *Chrysothamnus*. 1984 July 9–13; Provo, UT. Gen. Tech. Rep. INT-200. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 398 p.

McArthur ED, Blauer AC, Plummer AP, Stevens R. 1979. Characteristics and hybridization of important Intermountain shrubs: 3. Sunflower family. Res. Pap. INT-220. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 82 p.

McArthur ED, Stevens R, Shaw NL. 2004. Composite shrubs. In: Monsen SB, Stevens R, eds. Restoring western ranges and wildlands. Ogden, UT: USDA Forest Service Rocky Mountain Research Station.

McDonough WT, Harniss RO. 1974. Effects of temperature on germination in three subspecies of big sagebrush. Journal of Range Management 27: 204–205.

Meyer SE. 1990. Unpublished data. Provo, UT: USDA Forest Service, Rocky Mountain Research Station.

Meyer SE. 1990. Seed source differences in germination under snowpack in northern Utah. In: Munkshower F, ed. Fifth Billings Symposium on Disturbed Land Reclamation. Volume 1. 1990 March 25–30; Billings, MT. Pub. 9003. Bozeman: Montana State University Reclamation Research Unit: 184–191.

Meyer SE. 1994. Germination and establishment ecology of big sagebrush: implications for community restoration. In: Monsen SB, Kitchen SG, eds. Proceedings, Ecology and Management of Annual Rangelands. 1992 May 18–22; Boise, ID. Gen. Tech. Rep. INT-313. USDA Forest Service, Intermountain Research Station: 244–251.

Meyer SE, Kitchen SG. 1997. Unpublished data. Provo, UT: USDA Forest Service, Rocky Mountain Research Station.

Meyer SE, Monsen SB. 1990. Seed-source differences in initial establishment for big sagebrush and rubber rabbitbrush. In: McArthur ED, Romney EM, Smith SD, Tueller PT, eds. Symposium, Cheatgrass Invasion, Shrub Die-off and Other Aspects of Shrub Biology and Management. 1989 April 5–7; Las Vegas. Gen. Tech. Rep. INT-276. Ogden, UT: USDA Forest Service, Intermountain Research Station: 200–208.

Meyer SE, Monsen SB. 1991. Habitat-correlated variation in mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*: Asteraceae) seed germination patterns. Ecology 72: 739–742.

Meyer SE, Monsen SB. 1992. Big sagebrush germination patterns: subspecies and population differences. Journal of Range Management 45: 87–93.

Meyer SE, Kitchen SG, Wilson GR, Stevens R. 1988a. Proposed rule for *Artemisia nova*. Association of Official Seed Analysts Newsletter 62(1): 16–17.

Meyer SE, Kitchen SG, Wilson GR, Stevens R. 1988b. Proposed rule for *Artemisia tridentata*. Association of Official Seed Analysts Newsletter 62(1): 17–18.

Meyer SE, Monsen SB, McArthur ED. 1990. Germination response of *Artemisia tridentata* to light and chill: patterns of between-population variation. Botanical Gazette 152: 176–183.

Monsen SB. 1995. Personal communication. Provo, Utah: USDA Forest Service Rocky Mountain Research Station.

Monsen SB, Meyer SE. 1990. Seeding equipment effects on establishment of big sagebrush on mine disturbances. In: Munkshower F, ed. Fifth Billings Symposium on Disturbed Land Rehabilitation. Volume 1, Hardrock waste, analytical, and revegetation. 1990 March 25–30; Billings, MT. Pub. 9003. Bozeman: Montana State University, Reclamation Research Unit: 192–199.

Monsen SB, Richardson BL. 1984. Seeding shrubs and herbs on a semiarid minesite with and without topsoil. In: Tiedemann AR, McArthur ED, Stutz HC, Stevens R, Johnson KL, eds. Proceedings, Symposium on the Biology of *Atriplex* and Related Chenopods. 1983 May 2–6; Provo, UT. Gen. Tech. Rep. INT-172. Ogden, UT: USDA Forest Service, Intermountain Research Station: 298–305.

Monsen SB, Meyer SE, Carlson SL. 1992. Sagebrush establishment enhanced by snowfencing. In: Rangeland Technology and Equipment Council, USDA Forest Service Technology and Development Program 2200-Range: 1992 Annual Report: 6-8.

Pechanec JF, Plummer AP, Robertson JH, Hull AC. 1944. Eradication of big sagebrush (*Artemisia tridentata*). Res. Pap. 10. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 23 p.

Plummer AP, Christensen DR, Monsen SB. 1968. Restoring big game range in Utah. Pub. 68-3. Salt Lake City: Utah Division of Fish and Game 183 p.

Stevens R, Jorgensen KR, Davis JN. 1981. Viability of seed from thirty-two shrub and forb species through fifteen years of warehouse storage. Great Basin Naturalist 41: 274–277.

Wagstaff FJ, Welch BL. 1991. Seedstalk production of mountain big sagebrush enhanced through short-term protection from heavy browsing. Journal of Range Management 44: 72–74.

Walton TP, White RS, Wambolt CL. 1986. Artemisia reproductive strategies: a review with emphasis on plains silver sagebrush. In: McArthur ED, Welch BL, eds. Symposium on the Biology of *Artemisia* and *Chrysothamnus*. 1984 July 9–13; Provo, UT. Gen. Tech. Rep. INT-200. Odgen, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 67–74.

Welch BL. 1995. Beyond twelve percent purity. In: Roundy BA, McArthur ED, Haley JS, Mann DK, comps. Proceedings, Symposium on Arid Lands Ecology and Restoration. 1993 October 19–21; Las Vegas. Gen. Tech. Rep. INT-315. Ogden, UT: USDA Forest Service, Intermountain Research Station: 126–129.

Welch BL, Nelson DL. 1995. Black stem rust reduces big sagebrush seed production. Journal of Range Management 48: 398–401.

Welch BL, McArthur ED, Nelson DL, Pederson JC, Davis JN. 1986. 'Hobble Creek'—a superior selection of low-elevation mountain big sagebrush. Res. Pap. INT-370. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 10 p.

Welch BL, Wagstaff FJ, Jorgensen GL. 1990. 'Hobble Creek' mountain big sagebrush seed production. In: McArthur ED, Romney EM, Smith S, Tueller PT, eds. Symposium on Cheatgrass Invasion, Shrub Die-off, and Other Aspects of Shrub Biology and Management. 1989 April 5–7; Las Vegas. Gen. Tech. Rep. INT-276. Ogden, UT: USDA Forest Service, Intermountain Research Station: 166–170.

Weldon LW, Bohmont DW, Alley HP. 1959. The interrelation of three environmental factors affecting germination of sagebrush seed. Journal of Range Management 12: 236–238.

Wilson RG. 1982. Germination and seedling development of fringed sagewort (*Artemisia frigida*). Weed Science 30: 102–105.

Young JA, Evans RA. 1975. Germinability of seed reserves in a big sagebrush (*Artemesia tridentata*) community. Weed Science 23: 358–364.

Young JA, Evans RA. 1989. Dispersal and germination of big sagebrush (*Artemisia tridentata*) seeds. Weed Science 37: 201-–06.

Young JA, Martens E. 1991. Importance of hypocotyl hairs in germination of *Artemisia* seeds. Journal of Range Management 43: 358–366.

Young JA, Evans RA, Palmquist DE. 1989. Big sagebrush (*Artemisia tridentata*) seed production. Weed Science 37: 47–53.

Annonaceae—Custard-apple family

Asimina Adans.

pawpaw

Franklin T. Bonner

Dr. Bonner is a scientist emeritus at the USDA Forest Service's Southern Research Station, Mississippi State, Mississippi

Growth habit and use. Of the 9 species of the genus *Asimina*, seed data are available only for small-flower pawpaw and pawpaw (table 1). Both form shrubs or small deciduous trees (Vines 1960). Their fruits provide food for wildlife and are also eaten by humans. There is some interest in commercial fruit production of pawpaw, and cultivar selections have been made since the early part of the century (Peterson 1990).

Flowering and fruiting. Flowers of the pawpaw genus are solitary, perfect, and greenish purple. They appear in the spring during March to May, about the same time as the leaves. In natural stands of pawpaw, pollination and seed set are very poor (Norman and others 1992; Willson and Schemske 1980), conditions that discourage commercial productions. In central Illinois, pawpaw averaged 3.5 to 10.5 seeds/fruit (Willson and Schemeske 1980). Pawpaw fruits are 5 to 17 cm long, whereas those of small-flower pawpaw are 5 to 12 cm long (Halls 1973). Pawpaw fruits are greenish yellow before maturity and turn brown to black as they ripen in July to August and fall to the ground in August and September. Seeds of small-flower pawpaw mature while the fruit coat is still green (Norman and others 1992). The fruits are fleshy berries that contain several dark brown, shiny seeds (figure 1). The fleshy part of the fruit is considered edible, but there appear to be 2 different fruit types. Those with white flesh are barely edible, whereas others are larger and have a yellowish or orange flesh with a much better taste (Bonner and Halls 1974). The seeds themselves are oblong, rounded, flat, and bony (figures 1 and 2).

Figure 1— *Asimina*, pawpaw: fruits and seeds of *A. parviflora*, small-flower pawpaw (**top**) and *A. triloba*, pawpaw (**bottom**).

Collection and extraction. Pawpaw fruits should be picked or shaken from the trees as soon as the flesh is soft. The seeds may be extracted by macerating the fruits in water and floating off the pulp, but the entire fruit may be sown (Bonner and Halls 1974). Seed yield, purity, and

Table 1— *Asmina,* pawpaw: nomenclature, occurrence, and size

Scientific name	Common name(s)	Occurrence	Height at maturity (m)
***A. parviflora* (Michx.) Dunal**	**small-flower pawpaw,** small-fruited pawpaw, small custard-apple, dwarf pawpaw	Texas E to Florida; N to Virginia	3.5
***A. triloba* (L.) Dunal**	**pawpaw,** custard-apple common pawpaw	Texas & Arkansas E to Florida; N to New York, Michigan, & Nebraska	12

Source: Vines (1960).

soundness are as follows (Bonner and Halls 1974; Vines 1960):

	small-flower pawpaw	pawpaw
Cleaned seeds/wt	2,860/kg (1,300/lb)	1,540/kg per (700/lb)
Purity (%)	98	100
Sound seeds (%)	94	96

There is no storage information available on these species.

Germination. Germination is usually very slow because seeds have dormant embryos, and seedcoats are slowly permeable. Moist stratification for 60 days at 5 °C resulted in germination of 50, 62, and 82% for 3 samples of pawpaw seeds (Bonner and Halls 1974). Stratification for 100 days has been recommended, but germination still may be slow and irregular. Fall-sowing of untreated seeds does not improve results (Bonner and Halls 1974). No specific test conditions have been reported, but alternating temperatures of 20 °C during the day and 30 °C at night on a moist medium have been satisfactory for most species of the northern temperate zone.

Nursery practice. Pawpaw seeds may be sown in the fall without pretreatment, or stratified and sown in the spring. Seeds should be covered about 20 mm ($^3/_4$ in) deep. Some shade is helpful to germinating seedlings (figure 3). Another method is to plant fresh seeds, before they dry, in pots of sand and then to keep them in a cool cellar or similar place. As the seeds sprout, they can be picked out and transplanted into nursery beds. Pawpaws can also be propagated by layering and root cuttings (Bonner and Halls 1974) but apparently not by stem cuttings (Dirr and Heuser 1987).

References

Bonner FT, Halls LK. 1974. *Asimina*, pawpaw. In: Schopmeyer CS, tech. coord. Seeds of woody plants of the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 238–239.

Dirr MA, Heuser CW. 1987. The reference manual of woody plant propagation. Athens, GA: Varsity Press. 239 p.

Halls LK. 1973. Flowering and fruiting of southern browse species. Res. Pap. SO-90. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 10 p.

Norman EM, Rice K, Cochran S. 1992. Reproductive biology of *Asimina parviflora* (Annonaceae). Bulletin of the Torrey Botanical Club 119: 1–5.

Peterson RN. 1990. Pawpaw (*Asimina*). In: Moore JN, Ballington JR, eds. Genetic resources of temperate fruit and nut crops. Acta Horticulturae 290: 567–600.

Vines RA. 1960. Trees, shrubs, and woody vines of the Southwest. Austin: University of Texas Press. 1104 p.

Willson MF, Schemske DW. 1980. Pollinator limitation, fruit production, and floral display in pawpaw (*Asimina triloba*). Bulletin of the Torrey Botanical Club 107: 401–408.

Figure 2—*Asimina parviflora*, small-flower pawpaw: longitudinal section through a seed.

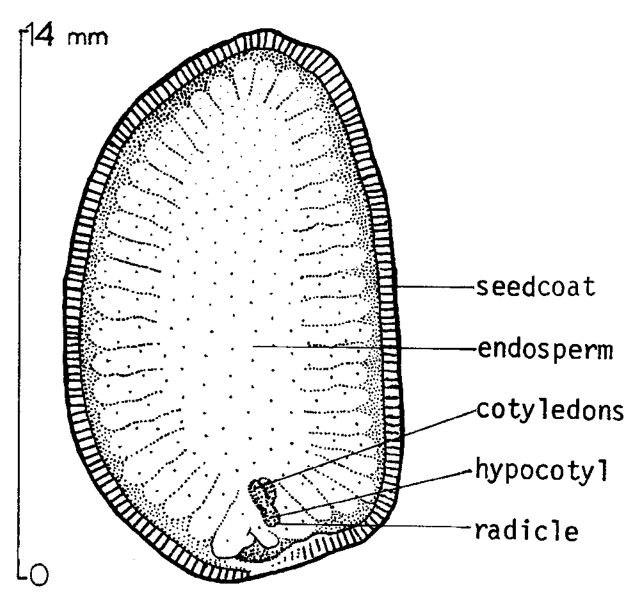
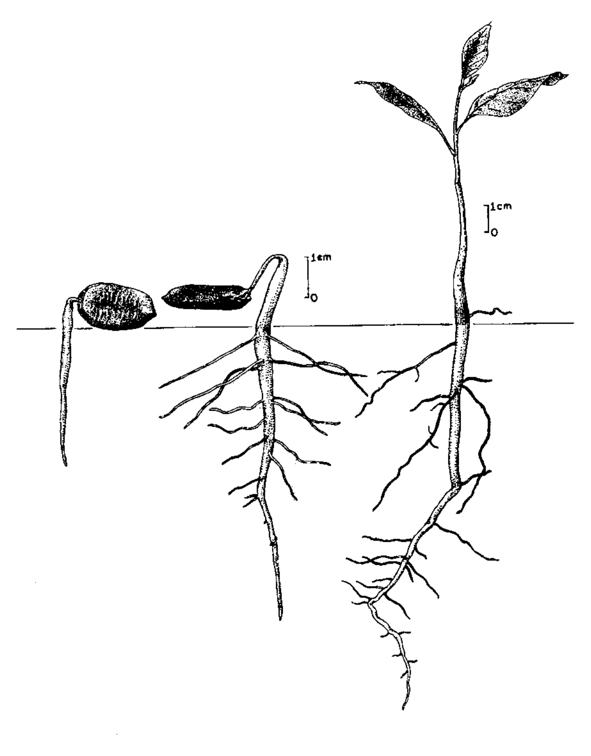


Figure 3—*Asimina triloba*, pawpaw: seedling development at 2, 9, and 20 days after germination.



Chenopodiaceae—Goosefoot family

Atriplex L.

saltbush

Susan E. Meyer

Dr. Meyer is a research plant ecologist at the USDA Forest Service's Rocky Mountain Research Station, Shrub Sciences Laboratory, Provo, Utah

Growth habit, occurrence, and use. The genus *Atriplex* L.—saltbush—is cosmopolitan in distribution and comprises about 250 species of annual and perennial herbs, subshrubs, and shrubs (McArthur and Sanderson 1984). Most species are halophytic (at least to some degree) and occupy salt desert, coastal strand, or saltmarsh habitats. Shrubby species are important in arid and semiarid regions throughout the world, with centers of diversity in south central Asia, Australia, temperate South America, and western North America. Western North America is an area of particularly high genetic diversity, with more than 20 principal species of shrubs and subshrubs as well as countless hybrids and variants; 12 of these species are described here (table 1). The genus is in a state of active evolution in the Intermountain region (Stutz 1978, 1984). The drying up of Pleistocene lakes 10,000 or so years ago opened up vast areas of unexploited salt-desert habitat. Shrubby saltbush species migrated in rapidly from several directions and hybridized freely, giving rise to the rich complex of forms in the region today.

In terms of areal extent, the most important species are probably shadscale and Gardner saltbushes (Blauer and others 1976). These species are regional dominants over millions of hectares in the Intermountain and northwestern Great Plains regions, respectively. Shadscale saltbush mostly occurs with winterfat (*Krascheninnikovia lanata* (Pursh) Guldenstaedt.); budsage (*Artemesia spinescens* D.C. Eaton); and other salt-desert shrubs, whereas Gardner saltbush is able to maintain codominance with perennial grasses (Stutz 1978). In the Mojave Desert, desert-holly is an upland landscape dominant, particularly in the Death Valley region, whereas allscale saltbush is a dominant species on playa fringes. Fourwing saltbush is the most widely distributed shrubby saltbush in North America and is often an important component of grassland communities, especially in the Chihuahuan Desert and western Great Plains. Sickle and basin saltbushes are inconspicuous but common components of northern Intermountain salt-desert vegetation.

Shrubby saltbush species are extremely important as forage plants for livestock and wildlife in arid and semiarid regions worldwide (Goodall 1982). They provide palatable and nutritious feed on a year-round basis and are especially important on winter ranges. As a consequence, they have been studied and used in range rehabilitation far more extensively than most other shrubs (Jones 1970; McArthur and Monsen in press; Osmond and others 1980; Tiedemann and others 1984). There is also considerable interest in utilizing saltbush species as irrigated forage crops on marginal, salinized agricultural land (Glenn and others 1992; Watson and O'Leary 1993). Some shrubby saltbush species are also used extensively for the stabilization of drastically disturbed land because of their ability to establish and grow on harsh sites.

Geographic races and hybrids. An important feature of infraspecific variation in many saltbush species is the presence of series of races at different ploidy levels (Sanderson and others 1990; Stutz 1978; Stutz and Sanderson 1979). Polyploid races often show dwarfing and adaptation to extremely harsh environments. The tendency to evolve polyploid races has also been important in facilitating the formation and stabilization of interspecific hybrids. Saltbush species possess a wealth of genetic variability, both within and among ploidy levels for numerous traits that may be important for survival both of local populations in nature and of the products of artificial seedings. Hybrid forms, even those that have not yet formed stabilized populations in nature, may possess attributes that make them useful in specific disturbed land rehabilitation applications (Stutz 1995).

Common garden studies with fourwing saltbush have demonstrated ecotypic variation in growth form, growth rate, winter-greenness, drought and cold hardiness, palatability, nutrient status, seed size, and seed germination and establishment traits (McArthur and others 1983; Springfield 1970; Van Epps 1975; Welch and Monsen 1981, 1984). It is

Table 1—*Atriplex,* saltbush: ecology and distribution

Scientific name	Common name(s)	Geographic distribution	Ecology
A. canescens **(Pursh) Nutt.**	**fourwing saltbush,** chamisa	Widely distributed in W North America	Wide ecological amplitude; mostly in sandy uplands & gravelly washes
A. confertifolia **(Torr. & Frem.) S. Wats.**	**shadscale saltbush,** spiny saltbush, sheepfat	Widely distributed in W North America	Wide ecological amplitude; mostly on silt or clay soils of low to moderate salinity
A. corrugata **S. Wats.**	**mat saltbush**	Colorado Plateau N to Red Desert of Wyoming	Restricted to heavy saline clays on shale outcrops
A. cuneata **A. Nels.**	**Castle Valley saltbush**	Colorado Plateau	Restricted to heavy saline clays on shale outcrops
A. falcata **(M.E. Jones) Standl.**	**sickle saltbush,** falcate saltbush, Nuttall saltbush	N Great Basin	Subsaline soils of benches & alluvial fans
A. gardneri **(Moq.) D. Dietr.**	**Gardner saltbush**	NW Great Plains, Wyoming, & Montana	Mostly on saline or subsaline clay soils
A. hymenelytra **(Torr.) S. Wats.**	**desert-holly**	Mojave Desert	Clay flats & gravelly fans under extreme aridity
A. lentiformis **(Torr.) S. Wats.**	**big saltbush,** quailbush, lensscale	Mojave Desert; cismontane & coastal California	Mostly around saline springs & seeps
A. obovata **Moq.**	**mound saltbush,** broadscale saltbush	Chihuahuan Desert	Saline flats
A. polycarpa **(Torr.) S. Wats.**	**allscale saltbush,** cattle saltbush, desert saltbush	Mojave Desert; Central Valley of California	Saline & subsaline slopes & flats
A. semibaccata **R. Br.**	**Australian saltbush,** trailing saltbush	Introduced from Australia	Along roadsides & in saline disturbances
A. tridentata **Kuntze**	**basin saltbush,** trident saltbush	NE Great Basin, & Uinta Basin of Utah	Saline flats

Sources: Ansley and Abernathy (1985), Meyer (1996), Mikhail and others (1992), Young and others (1980).

likely that other widely distributed saltbush species possess similar ecotypic differentiation. Many researchers who have studied saltbush establishment from artificial seedings emphasize the importance of using not just adapted species, but locally adapted ecotypes of these species (Bleak and others 1965; McArthur and others 2004; Nord and others 1971; Plummer and others 1968; Springfield 1970).

Cultivar development for saltbush has also emphasized ecotypic adaptation. The 3 released cultivars of fourwing saltbush were developed for warm winter ('Marana'), intermountain cold desert ('Rincon'), and northwestern Great Plains ('Wytana') planting applications (Carlson 1984). 'Wytana' was developed from a fourwing saltbush × Gardner saltbush hybrid entity known as *Atriplex aptera* A. Nels.

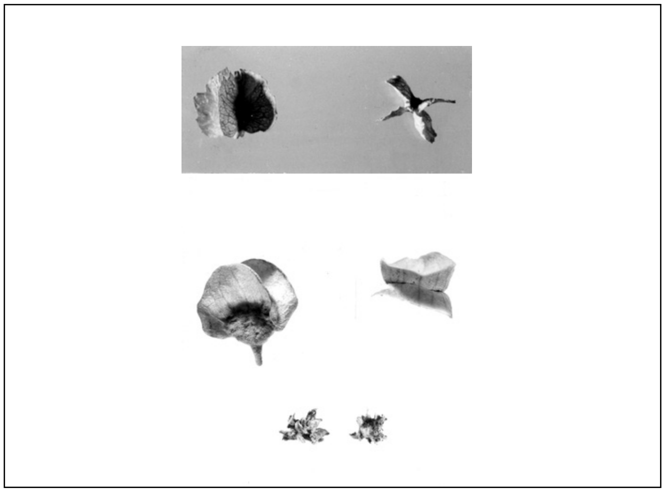
Flowering and fruiting. The flowers of saltbush are yellowish or brownish, inconspicuous, and unisexual, and are borne in the axils of the upper leaves or in terminal spikes. The male flowers consist of groups of stamens within a shallow 5-toothed calyx; petals are absent. Both petals and calyx are absent in the female flowers. The naked 1-seeded ovary is borne instead between 2 leaflike bracteoles.

Most native shrubby saltbush species are dioecious, that is, the sexes are borne on separate plants. Fourwing saltbush possesses a unique gender system known as trioecy, with genetically male plants, genetically female plants, and a third category that can switch sexes depending on environmental conditions (McArthur and others 1992). Australian saltbush is monoecious, that is, the flowers are unisexual and both sexes are present on the same plant.

Saltbush species flower in early to late summer, and fruits ripen from early fall to winter. The flowers are wind-pollinated. The leaflike bracteoles stay green and photosynthetically active until quite late in the ripening process and probably provide resources directly to the ripening ovule within. The fruits often persist on the bushes at least until spring, and it is not uncommon to find 2 generations of fruits on a plant simultaneously. Harvestable seedcrops of fourwing saltbush are produced on average 3 of every 5 years, whereas some of the more xerophytic species, such as mat saltbush, produce good seedcrops only occasionally.

The terminology describing the fruits of saltbush has been a source of confusion. The family Chenopodiaceae as a whole is characterized by a fruit type known as a utricle, which is defined as a small, bladdery 1-seeded fruit with a thin, membranous pericarp (Munz 1974). The utricle in saltbush is contained within the bracteoles, which enlarge in size and become more or less sealed, forming a false-fruit, which will hereafter be referred to simply as "the fruit" (figure 1). The bracteoles are not fused to the utricle, but in native species they usually enclose it so completely that threshing is not possible. In Australian saltbush, the bracteoles are not fused across the top and the utricles may be threshed free (figure 2) (Foiles 1974).

Figure 1—*Atriplex*, saltbush: bract-enclosed utricles ("fruits") of; *A. canescens*, fourwing saltbush (**top**), *A. confertifolia*, shadscale saltbush (**middle**); and *A. falcata*, sickle saltbush (**bottom**).



The saltbush seed itself is contained within the utricle and is generally not separable from it (figure 3). The disk-shaped seed has a curved embryo on its outer perimeter and a scanty provision of storage tissue (in this case perisperm) in the center. In most native species, the ovule (and thus the seed) is inverted within the fruit, meaning that the radicle end points upward. This facilitates radicle emergence from between the bracteoles, which often have their only opening or weakest point at the tip. The degree of woody thickening of the bracteole walls varies among and within species and may be linked to the persistent seed dormancy often encountered.

Seed collection, cleaning and storage. Saltbush seeds are harvested by stripping or beating the ripe fruits into shoulder hoppers, boxes, or bags, or onto tarps spread under the bushes. Vacuum or reel-type harvesters may also be used (McArthur and others 2004). In field cultivation, 'Wytana' fourwing and Gardner saltbushes have been cut and windrowed with a hay-swather and then combine-harvested. Seeds shattered during combining were salvaged using a vacuum harvester (Carlson and others 1984).

Seed collections of fourwing and shadscale saltbushes are commonly hammermilled to remove the bracteole wings (McArthur and others 2004). This reduces bulk by half and facilitates cleaning, handling, and seeding through conventional drills. Hammermilling has little effect on dormancy of

Figure 2—*Atriplex semibaccata,* Australian saltbush: bract-enclosed utricle

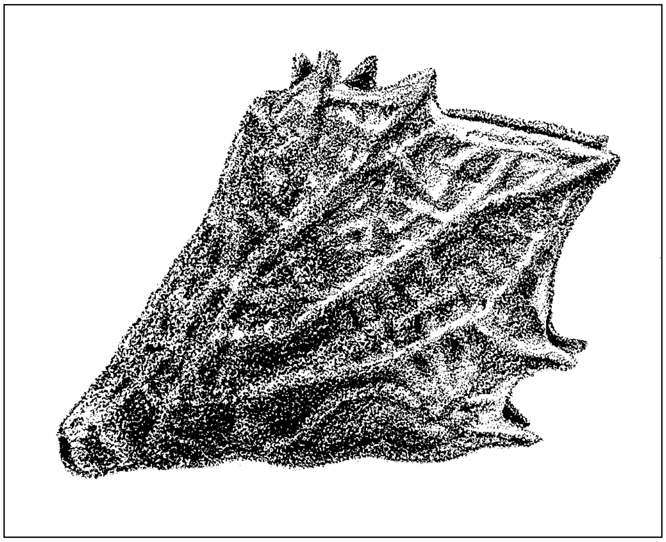
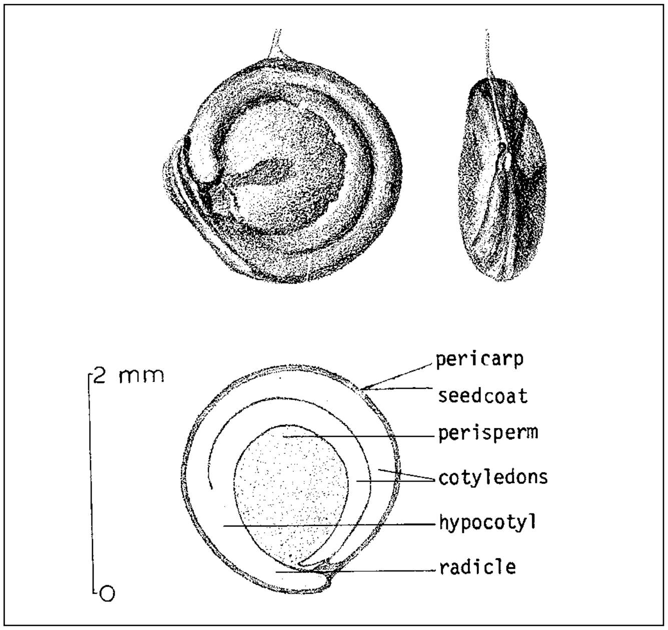


Figure 3—*Atriplex semibaccata,* Australian saltbush: exterior views in 2 planes of utricles removed from their bracts and a longitudinal section through a utricle.



fourwing saltbush but may speed the germination of nondormant seeds somewhat (Gerard 1978; Springfield 1970). Collections of wingless small-fruited species such as Gardner, sickle, and mat saltbushes do not require hammermilling. Seed collections of all species may be cleaned by screening and blowing in a fanning mill (McArthur and others 2004).

Even relatively high-quality seedlots of saltbush may average only 50% fill. A cut test to determine fill is often carried out before harvest. Fills of 40% or less are usually considered substandard. Such a seedlot would not normally be worth the expense of harvesting, cleaning, and transporting. Field-grown saltbush seedlots often have higher fill than wild-collected lots (Briggs 1984; Carlson and others 1984; McArthur and others 1978; Stroh and Thornberg 1969). Most of the weight of a saltbush fruit is in the bracteole walls, even after de-winging. Filled and unfilled fruits thus have similar density, making it impossible to remove unfilled fruits by fanning. Also, the variation in fruit size within a lot is not highly correlated with fill, so that screening to improve fill is not feasible.

Fruit size varies considerably among and within lots, especially for fourwing and shadscale saltbushes (table 2). Polyploid races often have smaller fruits. This variation in fruit size makes it essential to explicitly consider number of fruits per unit weight as well as fill percentage when planning seeding rates.

Seeds of most saltbush species are long-lived in dry storage and can be stored in an open warehouse for at least 5 to 10 years with little or no loss of viability (Springfield 1970; Stevens and others 1981). Controlled storage presents little advantage over open warehouse storage for these species. Attack by seed-destroying insects such as dermestid beetles (*Dermestes* spp.) during storage has been reported (Haws and others 1984)

Germination. Seeds of saltbush species as a group are characterized by high levels of dormancy and complex multiple dormancy mechanisms. The most universal characteristic seems to be the tendency to lose dormancy, or after-ripen, under dry conditions. For less-dormant species and lots this is manifested as an increase through time in the fraction of seeds germinable without pretreatment, or in the fraction of seeds able to germinate under non-optimum conditions, for example, osmotic stress. For more dormant species, after-ripening is manifested as an increase through time in storage in the response to dormancy-breaking treatments such as chilling (table 3).

In general, species and populations from warm desert and California cis-montane habitats produce seeds that are relatively nondormant, after-ripen quickly, and do not require chilling (Cornelius and Hylton 1969; Edgar and Springfield 1977; Kay and others 1977a&b; Mikhiel and others 1992; Springfield 1970; Warren and Kay 1984; Young and others 1980) (tables 1 and 3). Seeds of species and populations from cold desert, foothill, and northern plains habitats often require chilling for germination even after an after-ripening period (Ansley and Abernethy 1985; Meyer and others 1998) (tables 1 and 3). Shadscale saltbush seeds

Table 2—*Atriplex,* saltbush: fruit yield data

	Fruit (x1,000) /weight			
	Range		Average	
Species	/kg	/lb	/kg	/lb
A. canescens				
intact	17–120	8–55	68	31
de-winged	29–326	13–148	118	54
A. confertifolia	65–277	30–126	142	65
A. corrugata	—	—	174	79
A. cuneata	—	—	180	82
A. falcata	—	—	434	197
A. gardneri	210–262	95–119	233	106
A. hymenelytra	—	—	477	217
A. lentiformis	900–2,000	409–909	1,957	890
A. obovata	—	—	457	208
A. polycarpa	785–1,370	357–623	1,078	490
A. semibaccata	165–317	75–144	—	—
A. tridentata	120–370	55–168	280	128

Sources: Belcher (1985), Foiles (1974), McArthur and others 2004).

Table 3—*Atriplex,* saltbush: germination data

Species	Storage (months)	Incubation treatment	Germination (%)		Samples
			Mean	Range	
A. canescens	3	15 °C	32	4–96	23
	24	15 °C	54	10–100	23
	3	4 wk @ 1–15 °C	41	4–93	23
	24	4 wk @ 1–15 °C	69	21–100	23
A. confertifolia	3	5/15 °C	0	0–1	15
	36	5/15 °C	2	0–6	15
	3	16 wk @ 1–5/15 °C	16	0–47	15
	36	16 wk @ 1–5/15 °C	46	4–83	15
A. gardneri	3	Mean multiple treatments	26	—	1
	15	Mean multiple treatments	48	—	1
A. hymenelytra	8	5/15 °C	33	—	1
A. lentiformis	8	10/20 °C	56	29–71	3
	24	Mean multiple treatments	39	39–40	2
	24	Best treatment 10/25 %C	68	—	1
A. obovata	8	10/20 °C & 0.05 M NaCl	42	—	1
A. polycarpa	8	10/20 °C	53	11–94	2
	8	20/30 °C	50	21–79	2
A. semibaccata	24	Mean multiple treatments	41	37–46	3
	24	Best treatment 10/25 °C	69	—	1

Sources: Ansley and Abernathy (1985), Meyer (unpublished data), Mikhail and others (1992), Young and others (1980).
Note: Germination period is 28 days and germination is expressed as percentage of filled fruits, except for *A. gardneri* data, where germination is 14 days, and for *A. lentiformis* and *A. semibaccata* data, where germination is expressed as percentage of total fruits.

rarely become germinable without chilling, regardless of their habitat of origin (Mikhiel and others 1992) (table 3).

Other treatments that have sometimes been found to remove dormancy include scarification and leaching (Ansley and Abernethy 1985; Graves and others 1975; Nord and Whitacre 1957; Sabo and others 1979; Twitchell 1955; Young and others 1980). Scarification apparently acts by weakening the bracteole walls. Actual rupture of the membranous utricle wall is usually damaging to the seed (Sabo and others 1979). After-ripening may also act on the bracteole walls, as evidenced by work with a seedlot of the South American species *A. repanda* Phil., for which optimum time for sulfuric acid scarification decreased from 7 to 2 hours during 5 years in dry storage (Fernandez 1978). The bracteole walls may also be weakened by the action of saprophytic fungi under field conditions (Vest 1952). Hand-removal of the bracteoles promotes increased germination in many species but does not necessarily remove dormancy completely, suggesting that either the utricle wall or the testa interacts with the embryo to impose dormancy even in excised fruits. The failure of excised fruits to germinate suggests a chilling requirement. Sanderson and others (1990) found that excised fruits of warm-winter populations of shadscale saltbush were more likely to germinate without chilling than those of cold winter populations.

Leaching probably promotes germination by removing some inhibitor from the fruit, either inorganic salts such as sodium chloride (Beadle 1952) or an organic inhibitor such as saponin (Nord and Van Atta 1960). It is important to remove excess water after soaking, as germination can be inhibited by inadequate aeration (Beadle 1952; Young and others 1980). Rates of leaching under field conditions are probably controlled by the osmotic potential of the seedbed. In the highly saline litter underneath bushes of many species, the salts in the bracteole walls would make only a minor contribution.

The complex dormancy mechanisms shown by many saltbush species function both to time germination appropriately within a given year and to ensure carryover of a persistent seedbank between years (Garvin and others 1996). Seed pretreatments to circumvent these mechanisms have limited application in field plantings but may be useful in seed quality evaluation and in nursery propagation.

Seed quality evaluation in saltbush is complicated by dormancy problems. Seedlots are usually cleaned to high purity, making the purity analysis quite simple. For fourwing saltbush, we proposed a 21-day germination test at 15 °C, a recommendation that was subsequently accepted as the official testing procedure (Meyer and others 1986). The most important determinant of viability is the fill percentage, that is, the proportion of fruits that contain an undamaged seed with a well-developed embryo. Post-test viability determination is essential in fourwing saltbush. Germination percentage may vary as a function of after-ripening status, or the test temperature may not be optimum for a particular lot. Post-test evaluation is even more essential for species of saltbush with less-known germination requirements.

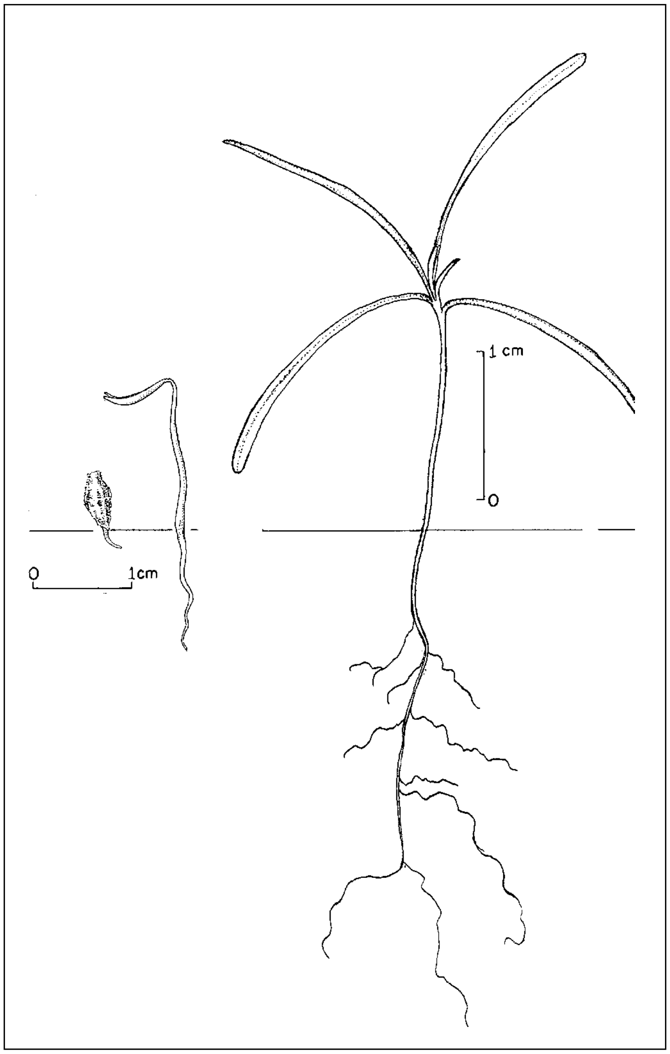
In practice, few seedlots of saltbush are evaluated using a germination test. Because of dormancy problems, the tetrazolium test has become the standard method. The general method is to soak the intact (bracteoled) fruit for several hours or overnight and extract the utricle by either prying open the bracts, clipping at the stem end, or off-center longitudinal bisection (Belcher 1985). The utricles are then pierced in the center and placed in 1% tetrazolium solution for several hours, and the staining patterns on the linear embryos are evaluated. Saltbush seed quality is somewhat difficult to evaluate using tetrazolium. Staining is often weak and incomplete for embryos that are germinable, resulting in viability estimates that tend to be low (Ansley and Abernethy 1984; Springfield 1970).

Nursery and field practice. Saltbush species have been successfully propagated in the nursery, both as container stock (Ferguson 1980) and as bareroot stock (Shaw and Monsen 1984). Most of the information available is for fourwing saltbush, but it is probably broadly applicable to other species. Propagation may be from seeds or from stem cuttings (McArthur and others 1984; Richardson and others 1979). The latter are advantageous for obtaining clonal material of known sex for the establishment of seed orchards with optimal sex ratios (McArthur and others 1978). When high-quality seedlings of an adapted ecotype are outplanted during periods of optimal moisture, survival can be high (Foiles 1974; McArthur and others 2004). Wildlings of fourwing saltbush have also been used as transplant stock.

Saltbush species may also be direct-seeded successfully, although results have been inconsistent (McArthur and others 2004). Pitfalls include poor choice of species or ecotypes; using poor-quality seeds (low fill); planting too deep; planting at the wrong season; excessive competition from weeds or seeded grasses; interactions with pathogenic fungi such as damping-off diseases; and seedling predation by grasshoppers, rabbits, or other animals. Fourwing saltbush fruits are apparently not particularly attractive to granivorous rodents (Everett and others 1978), possibly because of the saponin content of the bracts (Sanderson and others 1986), so pre-emergence seeds predation is rarely a problem. Seeding rates of 4 to 8 kg/ha (3.5 to 7 lb/ac) have been recommended for de-winged lots of fourwing saltbush. This corresponds to about 200 to 530 live seeds/m^2 (25 to 50/ft^2) for a seedlot of average fruit size (122,000/kg) and fill (50%). In regions of low and unpredictable precipitation, saltbush seedlings may fail to emerge or survive in dry years even when all planting guidelines are followed. As annual recruitment is not necessary for the perpetuation of natural stands, this poses a problem only in artificial revegetation. Once seedlings establish, however, young plants grow rapidly (figure 4) and may become reproductively mature in their second growing season.

The large fruits may create the impression that saltbush should be drill-seeded at considerable depth, but seed reserves are small, as bracteole tissue is not nutritive. Most

Figure 4—*Atriplex canescens*, fourwing saltbush: seedling development at 1 and 2 days after germination, and at a later time.



authors recommend drilling at depths of 0.5 to 1 cm. Broadcast seeding followed by chaining has produced good stands of fourwing saltbush (Plummer and others 1966). Most species probably need shallow coverage. Young and others (1980) reported that surface seeding prevented emergence of quailbush and reduced that of Australian saltbush by half, even under conditions of unlimited moisture.

Optimal season for planting varies according to precipitation patterns. In winter precipitation zones such as the Intermountain area and the Mojave Desert, fall or early winter planting has been most successful (Kay and others 1977a&b; McArthur and others 2004; Plummer and others 1968). In summer precipitation zones such as the southern Great Plains and Chihuahuan Desert, spring and midsummer plantings are more likely to succeed (Springfield 1970). Northern Great Plains species with a chill requirement, such as Gardner saltbush, are probably best fall-seeded, whereas fourwing saltbush could be fall- or spring-seeded in the northern Great Plains area.

The expectation that highly dormant seedlots will emerge during the first year after planting is possibly the major source of disappointment in saltbush seedings. Knowledge of after-ripening patterns in the genus suggests that the best way to circumvent this problem is to use seedlots that have been given ample opportunity to after-ripen in dry storage prior to planting.

References

Ansley RJ, Abernethy RH. 1984. Seed pretreatments and their effects on field establishment of spring-seeded gardner saltbush. Journal of Range Management 37: 509–513.

Ansley RJ, Abernethy RH. 1985. Environmental factors influencing Gardner saltbush seed dormancy alleviation. Journal of Range Management 38: 331–335.

Beadle NCW. 1952. Studies in halophytes: 1. The germination of the seed and establishment of the seedling of five species of *Atriplex* in Australia. Ecology 33: 49–62.

Belcher E. 1985. Handbook on seeds of browse-shrubs and forbs. Tech. Pub. R8-TP8. Atlanta: USDA Forest Service Southern Region. 246 p.

Blauer AC, Plummer AP, McArthur ED, Stevens R, Giunta BC. 1976. Characteristics and hybridization of important Intermountain shrubs: 2. Chenopod family. Res. Pap. INT-177. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 42 p.

Bleak AT, Frischknecht NC, Plummer AP, Eckert RE. 1965. Problems in artifical and natural revegetation in the arid shadscale vegetation zone of Utah and Nevada. Journal of Range Management 18: 59–63.

Briggs JA. 1984. Seed production of *Atriplex canescens* in southern Arizona. In: Tiedemann AR, McArthur ED, Stutz HC, Stevens R ,Johnson KL, compilers. Proceedings, Symposium on the Biology of *Atriplex* and Related Chenopods; 1983 May 4–6; Provo, UT. Gen. Tech. Rep. INT-172. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 187–190.

Carlson JR. 1984. *Atriplex* cultivar development. In: Tiedemann AR, McArthur ED, Stutz HC, Stevens R, Johnson KL, comps. Proceedings, Symposium on the Biology of *Atriplex* and Related Chenopods; 1983 May 4–6; Provo, UT. Gen. Tech. Rep. INT-172. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 176–182.

Carlson JR, Scheetz JG, Oaks WR. 1984. Seed production techniques of two chenopods: Gardner saltbush and winterfat. In: Tiedemann AR, McArthur ED, Stutz HC, Stevens R, Johnson KL, comps. Proceedings, Symposium on the Biology of *Atriplex* and Related Chenopods; 1983 May 4–6; Provo, UT. Gen. Tech. Rep. INT-172. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 191–195.

Cornelius DR, Hylton LO. 1969. Influence of temperature and leachate on germination of *Atriplex polycarpa*. Agronomy Journal 61: 209–211.

Edgar RL, Springfield HW. 1977. Germination characteristics of broadscale: a possible saline-alkaline site stabilizer. Journal of Range Management 30: 296–298.

Everett RL, Meewig RO, Stevens R. 1978. Deer mouse preference for seed of commonly planted species, indigenous weed seed, and sacrifice foods. Journal of Range Management 31: 70–73.

Ferguson RB. 1980. Potting media for *Atriplex* production under greenhouse conditions. Res. Note INT-301. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 4 p.

Fernandez HG. 1978. Aumento de la germinacion en *Atriplex repanda*: 2. Efecto de diferentes tratamientos quimicos al pericarpio. Phyton 36: 123–127.

Foiles MW. 1974. *Atriplex*, saltbush. In: Schopmeyer CS, ed. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 240–243.

Garvin SC, Meyer SE, Carlson SL. 1996. Seed germination studies in *Atriplex confertifilia* (Torr. and Frem.) Wats. In: Barrow JR, McArthur ED, Sosebee RE, Tausch RJ, comps. Proceedings, Shrubland Ecosystem Dynamics in a Changing Environment; 1995 May 23–25; Las Cruces, NM. Gen. Tech. Rep. INT-338. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: 165–169.

Gerard JB. 1978. Factors affecting fruit fill and seed germination of fourwing saltbush (*Atriplex canescens* (Pursh) Nutt.). In: Hyder DN, ed. Proceedings, 1st International Rangeland Congress. Denver: Society for Range Management.

Glenn EP, Watson MC, O'Leary JW, Axelson RD. 1992. Comparison of salt tolerance and osmotic adjustment of low-sodium and high-sodium subspecies of the C4 halophyte, *Atriplex canescens*. Plant, Cell and Environment 15: 711–718.

Goodall DW. 1982. Chenopod shrubland communities: a global perspective. International Journal of Ecology and Environmental Science 9: 85–99.

Graves WL, Kay BL, Williams WA. 1975. Seed treatment of Mojave Desert shrubs. Agronomy Journal 67: 773–777.

Haws BA, Bohart GE, Meadows RW, Coombs EM, Roe AR. 1984. Status of information concerning insects associated with selected species of *Atriplex*. In: Tiedemann AR, McArthur ED, Stutz HC, Stevens R, Johnson KL, comps. Proceedings, Symposium on the Biology of *Atriplex* and Related Chenopods; 1983 May 4–6; Provo, UT. Gen. Tech. Rep. INT-172. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 226–236.

Jones R. 1970. The biology of *Atriplex*. Canberra, Australia: CSIRO. 128 p.

Kay BL, Brown CR, Graves WL. 1977a. Desert saltbush. Mojave Reveg. Notes 18. Davis: University of California, Department of Agronomy and Range Science. 7 p.

Kay BL, Brown CR, Graves WL. 1977b. Fourwing saltbush. Mojave Reveg. Notes 17. Davis: University of California, Department of Agronomy and Range Science. 12 p.

McArthur ED, Sanderson SC. 1984. Distribution, systematics, and evolution of Chenopodiaceae: an overview: In: Tiedemann AR, McArthur ED, Stutz HC, Stevens R, Johnson KL, comps. Proceedings, Symposium on the Biology of *Atriplex* and Related Chenopods; 1983 May 4–6; Provo, UT. Gen. Tech. Rep. INT-172. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 14–23.

McArthur ED, Blauer AC, Noller GL. 1984. Propagation of fourwing saltbush by stem cuttings. In: Tiedemann AR, McArthur ED, Stutz HC, Stevens R, Johnson KL, comps. Proceedings, Symposium on the Biology of *Atriplex* and Related Chenopods; 1983 May 4–6; Provo, UT. Gen. Tech. Rep. INT-172. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 261–264.

McArthur ED, Freeman CD, Luckinbill LS, Sanderson SC, Noller GL. 1992. Are trioecy and sexual lability in *Atriplex canescens* genetically based? Evidence from clonal studies. Evolution 46: 1708–1721.

McArthur ED, Monsen SB, Shaw NL. 2004. Chenopod shrubs. In: Monsen SB Stevens R. Shaw NL, eds. Restoring western ranges and wildlands. USDA Forest Service, Intermountain Research Station.

McArthur ED, Plummer AP, Van Epps GA, Freeman DC, Jorgensen KR. 1978. Producing fourwing saltbush seed in seed orchards. In: Heyder DC, ed. Proceedings, 1st International Rangeland Congress. Denver: Society for Range Management: 406–410.

McArthur ED, Stevens R, Blauer AC. 1983. Growth performance comparisons among 18 accessions of fourwing saltbush (*Atriplex canescens*) at two sites in central Utah. Journal of Range Management 36: 78–81.

Meyer SE, Allen PS, Wilson GR, Davis TD, Davis JN, Stevens R, Jorgensen K. 1986. Proposed rule for *Atriplex canescens*. Association of Official Seed Analysts Newsletter 60(1): 14–15.

Meyer SE, Carlson SL, Garvin SC. 1998. Seed germination regulation and field seed bank carryover in shadscale (*Atriplex confertifolia*: Chenopodiaceae). Journal of Arid Environments 38: 255–267.

Mikhiel G, Meyer SE, Pendleton RL. 1992. Variation in germination response to temperature and salinity in shrubby *Atriplex* species. Journal of Arid Environments 22: 39–49.

Munz PA. 1974. A flora of southern California. Berkeley: University of California Press. 1086 p.

Nord EC, Whitacre JE. 1957. Germination of fourwing saltbush seed improved by scarification and grading. Forest Research Notes 125: 1–5.

Nord EC, Hartless PF, Nettleton WD. 1971. Effects of several factors on saltbush establishment in California. Journal of Range Management 24: 216–223.

Nord EC, Van Atta GR. 1960. Saponin: a seed germination inhibitor. Forest Science 6: 350–353.

Osmond CB, Bjorkman O, Anderson DJ. 1980. Physiological processes in plant ecology: toward a synthesis with *Atriplex*. Berlin: Springer-Verlag.

Plummer AP, Monsen SB, Christensen DR. 1966. Fourwing saltbush, a shrub for future game ranges. Pub. 66-4. Salt Lake City: Utah State Department of Fish and Game: 1–12.

Plummer AP, Christensen DR, Monsen SB. 1968. Restoring big game range in Utah. Pub. 68-3. Salt Lake City: Utah Division of Fish and Game. 183 p.

Richardson SG, Barker JR, Van Epps GA. 1979. Factors affecting rooting stem cuttings of salt desert shrubs. Journal of Range Management 32: 280–283.

Sabo DG, Johnson DV, Martin WC, Aldon EF. 1979. Germination requirements of 19 species of arid land plants. Res. Pap. RM-210. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: 1–26.

Sanderson SP, Pendleton RL, McArthur ED, Harper KT. 1986. Saponin effect on small mammal forage preference in a planting of *Atriplex canescens*. In: Provenza FJ, Flinders JT, McArthur ED, comps. Proceedings, Wildland Shrub Symposium on Plant–Herbivore Interactions. Gen. Tech. Rep. INT-222. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 74–77.

Sanderson SC, Stutz HC, McArthur ED. 1990. Geographic differentiation in *Atriplex confertifolia*. American Journal of Botany 77: 490–498.

Shaw N, Monsen SB. 1984. Nursery propagation and outplanting of bareroot chenopod seedlings. In: Tiedemann AR, McArthur ED, Stutz HC, Stevens R, Johnson KL, comps. Proceedings, Symposium on the Biology of *Atriplex* and Related Chenopods; 1983 May 4–6; Provo, UT. Gen. Tech. Rep. INT-172. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 251–260.

Springfield HW. 1970. Germination and establishment of fourwing saltbush in the southwest. Res. Pap. RM-55. Fort Collins, CO: USDA Forest Service, Rocky Mounntain Forest and Range Experiment Station: 1–48.

Stevens R, Jorgensen KR, Davis JN. 1981. Viability of seed from thirty-two shrub and forb species through fifteen years of warehouse storage. Great Basin Naturalist 41: 274–277.

Stroh JR, Thornberg AA. 1969. Culture and mechanical harvest of fourwing saltbush grown under irrigation. Journal of Range Management 22: 60–62.

Stutz HC. 1978. Explosive evolution of perennial *Atriplex* in western North America. Great Basin Naturalist Memoirs 2: 161–168.

Stutz HC. 1984. *Atriplex* hybridization in western North America. In: Tiedemann AR, McArthur ED, Stutz HC, Stevens R, Johnson KL, comps. Proceedings, Symposium on the Biology of *Atriplex* and Related Chenopods. 1983 May 4–6; Provo, UT. Gen. Tech. Rep. INT-172. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 25–27.

Stutz HC. 1995. Personal communication. Provo, UT: Brigham Young University.

Stutz HC, Sanderson SC. 1979. The role of polyploidy in the evolution of *Atriplex canescens*. In: Goodin JR, Northington DK, eds. Arid land plant resources. Lubbock: Texas Tech University, International Center for Arid and Semi-arid Land Studies: 615–621.

Tiedemann AR, McArthur ED, Stutz HC, Stevens R, Johnson KL, comps. 1984. Proceedings, Symposium on the Biology of *Atriplex* and Related Chenopods; 1983 May 4–6; Provo, UT. Gen. Tech. Rep. INT-172. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 308 p.

Twitchell LT. 1955. Germination of fourwing saltbush as affected by soaking and chloride removal. Journal of Range Management 8: 218–220.

Van Epps GA. 1975. Winter injury to fourwing saltbush. Journal of Range Management 28: 157–159.

Vest ED. 1952. A preliminary study of some of the germination characteristics of *Atriplex confertifolia* [MS thesis]. Salt Lake City: University of Utah. 46 p.

Warren DC, Kay BL. 1984. Pericarp inhibition of germination in *Atriplex confertifolia*. In: Tiedemann AR, McArthur ED, Stutz HC, Stevens R, Johnson KL, comps. Proceedings, Symposium on the Biology of *Atriplex* and Related chenopods; 1983 May 4–6; Provo, UT. Gen. Tech. Rep. INT-172. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 158–174.

Watson MC, O'Leary JW. 1993. Performance of *Atriplex* species in the San Joaquin Valley, California, under irrigation and with mechanical harvests. Agriculture, Ecosystems and Environment 43: 255-266.

Welch BL, Monsen SB. 1981. Winter crude protein differences among accessions of fourwing saltbush grown in a common garden. Great Basin Naturalist 41: 343–346.

Welch BL, Monsen SB. 1984. Winter nutritive value of accessions of fourwing saltbush grown in a common garden. In: Tiedemann AR, McArthur ED, Stutz HC, Stevens R, Johnson KL, comps. Proceedings, Symposium on the Biology of *Atriplex* and Related Chenopods. 1983 May 4–6; Provo, UT. Gen. Tech. Rep. INT-172. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 138–144.

Young JA, Kay BL, George H, Evans RA. 1980. Germination of three species of *Atriplex*. Agronomy Journal 72: 705–709..