Fabaceae—Pea family

# *Paraserianthes falcataria* (L.) I. Nielsen

## peacock-plume

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**Synonyms.** *Albizia falcataria* (L.) Fosberg

**Other common names.** Molucca-albizia, *batai, sau,* peacock's plume.

**Growth habit, occurrence, and uses.** Peacock-plume is a large deciduous tree that may reach 30 m in height and 1.2 m in bole diameter. It has a large spreading crown and light gray, smooth bark with small corky warts. This fast-growing native of the Moluccan Islands of Indonesia in the South Pacific has been widely planted throughout many tropical regions of the world and has become naturalized in many of them. The species was introduced into Hawaii in 1917 for ornamental and timber purposes (Rock 1920). The wood is lightweight; moderately weak in bending and compressing strength, and moderately soft and limber (Desch 1941; Gerhards 1966). It has been used for core-stock veneer, pallets, boxes, shelving, and internal furniture parts (Little and Skolmen 1989). In Asia, the wood has been used for fuel, matches, and pulp (Khullar and others 1992). Its lack of resistance to decay and termites, however, limits the value of the wood (Little and Skolmen 1989).

**Flowering and fruiting.** The flower clusters of peacock-plume are large, lateral panicles 8 to 25 cm in length that are borne at the branch tips. The numerous flowers are long (13 mm), stalkless, and greenish yellow to whitish in color. The legumes (pods) are narrow and flat; they measure 10 to 15 cm long and about 2 cm wide (figure 1). Each legume may contain 12 to 20 oblong, flattened, dark brown seeds, about 6 mm in length (Little and Skolmen 1989; Little and Wadsworth 1964; Wick and Walters 1974). In Hawaii, peacock-plume flowers in April and May, with legumes maturing in June to August (Wick and Walters 1974); in India, legumes mature in May and June (Khullar and others 1992).

**Collection, extraction, and storage.** The legumes can be picked from the tree after they turn from green to straw color or from the ground by shaking the branches. After being dried in the sun, the legumes should be run through a

**Figure 1**—*Paraserianthes falcataria,* peacock-plume: legumes (from Little and Skolmen 1989).
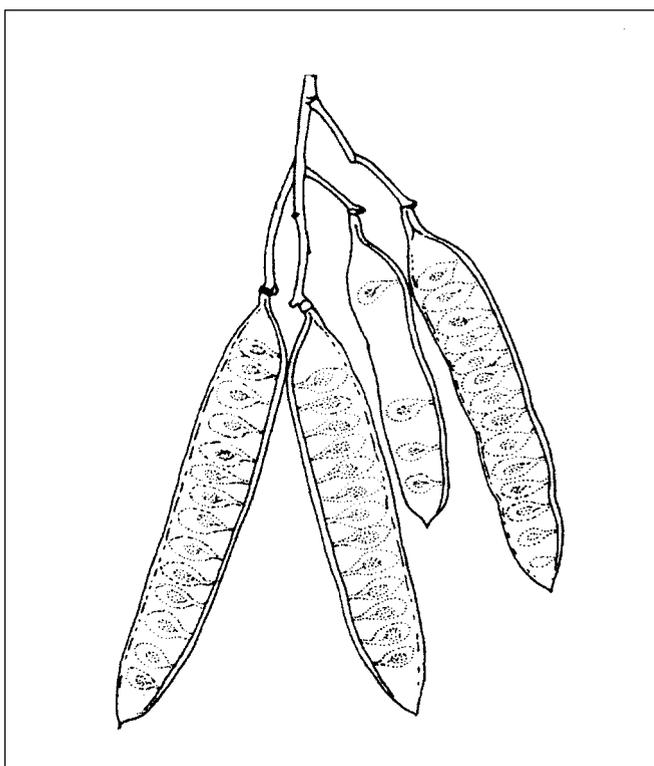


macerator or flailed by hand to extract the seeds. Debris can be removed with aspirators or air-screen cleaners or by simple winnowing. Empty, immature, and damaged seeds can removed by water flotation or by careful blowing in seed aspirators. There are usually 38,000 to 44,000 cleaned seeds/kg (17,000 to 20,000/lb) (Khullar and others 1992; Parrotta 1990; Wick and Walters 1974). Seeds of peacock-plume are orthodox in nature and can be easily stored when dried to about 8 to 10% moisture content. Dried seeds can be stored for at least 2 years in sealed containers at room temperature, but refrigeration at 3 to 5 °C should be used for longer storage (Parrotta 1990). There are no data on the long-term storage potential of these seeds.

**Germination.** Seeds of peacock-plume exhibit seed-coat dormancy that can be overcome with acid scarification, mechanical scarification, or hot-water soaking (Khullar and others 1992; Wick and Walters 1974). The first 2 methods have often produced slightly better results, but hot water soaking is less likely to damage the seeds. Ten to 15 minutes in concentrated sulfuric acid, followed by washing and then 15 minutes of soaking in water has been recommended (Wick and Walters 1974). In hot-water soaking, seeds are immersed in boiling water for 1 to 3 minutes, then soaked in cool water at room temperature for 24 hours immediately before sowing (Parrotta 1990). In a similar method, seeds are immersed in boiling water that is then removed from the heat source and allowed to cool at room temperature; the seeds should remain in the water for 24 hours. Proper treat-ment with any of these methods should produce germination of 70 to 99% within 10 days (Khullar and others 1992; Parrotta 1990; Wick and Walters 1974). Germination is epigeal.

**Nursery practice.** In Hawaii, peacock-plume seeds are sown at densities of 300 to 400 seeds/$m^2$ (28 to 37/$ft^2$) and covered with about 6 to 12 mm ($^1/_4$ to $^1/_2$ in) of soil. Seedlings are usually thinned to the desired seedbed density at maturity of 200 to 250/$m^2$ (20 to 25 seedlings/$ft^2$) and outplanted at 8 to 12 months of age (Wick and Walters 1974). Container seedlings and stumped seedlings can also be used to establish this species (Parrotta 1990).

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## References

Desch HE. 1941. Manual of Malayan timbers, Volume 1. Kuala Lumpur: Malayan Forestry Department. 328 p.

Gerhards CC. 1966. Physical and mechanical properties of *Molucca albizia* grown in Hawaii. Res. Pap. FPL-55. Madison, WI: USDA Forest Service, Forest Products Laboratory. 9 p.

Khullar P, Thapliyal RC, Beniwal BS, Vakshasya RK, Sharma A. 1992. Forest seed. Dehra Dun, India: Indian Council of Forestry Research & Education. 409 p.

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, Wadsworth FH. 1964. Common trees of Puerto Rico and the Virgin Islands. Agric. Handbk. 249. Washington, DC: USDA Forest Service. 548 p.

Parrotta JA. 1990. *Paraserianthes falcataria* (L.) Nielsen: batai, Moluccan sau. Res. Note SO-ITF-SM-31. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 5 p.

Rock JF. 1920. The leguminous plants of Hawaii. Honolulu: Hawaii Sugar Planters' Association. 234 p.

Wick HL, Walters GA. 1974. *Albizia* Durraz., albizia. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: 203–205.

Fabaceae—Pea family

# *Parkinsonia* **L.**

## palo verde

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**Growth habit, occurrence, and uses.** There are 3 noteworthy species of *Parkinsonia* grown in the United States. Two of these—blue palo verde and yellow palo *verde*—were formerly in the genus *Cercidium* but they are now considered to be in *Parkinsonia* (table 1). Palo verde is a thorny, green-barked shrub/small tree that can reach a height of 11 m (Vines 1960). The name is of Spanish-Mexican origin and refers to the very noticeable green (*verde*) color of the smooth trunk of this drought-resistant tree of the hot southern deserts (Jaegar 1940). The open-crowned trees have alternate, bipinnate leaves on slightly zig-zag green twigs (Little and Wadsworth 1964). The species are widely distributed in tropical America and wide-ly planted in the southwestern United States and the Old World tropics (Little 1979; Little and Wadsworth 1964). Palo verde was introduced into Puerto Rico from the south-western United States and is now naturalized (Francis and Liogier 1991). Blue palo verde and yellow palo verde are 2 closely related species, commonly found on the edges of washes, more occasionally in the washes, and scattered in the *bajadas* (Bainbridge and Virginia 1989). Both species drop their leaves when drought-stressed and only the green, thorny branches remain.

The 3 species serve as shelter for animals and rodents (Dean and Milton 1991), and the leaves and legumes (pods) as browse for livestock, rodents, rabbits, other mammals, and many species of birds (Bainbridge and Virginia 1989; Jaeger 1940; Little and Wadsworth 1964; Vines 1960). In the past, the legumes were a fairly important food for Native American inhabitants of the Sonoran Desert (Ebeling 1986; Felger and Moser 1985; Vines 1960). They were picked from July to August and dried; the beans were removed, ground in mortars into flour, and used in mush or cakes (Bean and Saubel 1972). The flowers of palo verde serve as a primary source of forage for megachilid bees in India (Jain and Kapil 1980; Sihag 1982), but the species is considered a weed in Australia (Pearce 1984).

**Flowering and fruiting.** Palo verdes have fragrant 5-petaled, showy, yellow flowers that form in loose racemes 5 to 20 cm long (Little and Wadsworth 1964). Blossoms appear in late March to June and occasionally in August to November after rains. In the past, these trees have been referred to as *fluvia de oro* or "fountain of gold" by Spanish Americans because of their incredible flower show after a generous rainy season. The fruits are 5 to 10 cm long, point-ed legumes that contain 1 to 8 oblong, glossy, yellow-brown

| Table 1—Parkinsonia, palo verde: nomenclature and occurrence | | |
|---|---|---|
| **Scientific name & synonym(s)** | **Common name(s)** | **Occurrence** |
| *P. aculeata* **L.** | **palo verde,** Jerusalem-thorn, horsebean, *retama, palo de ray, palo rayo* | South to trans-Pecos Texas & S Arizona; widely distributed in tropical America; Puerto Rico |
| *P. florida (Benth. ex Gray) S. Wats* <br> *Cercidium floridum* Benth. ex Gray | **blue palo verde** | SW US |
| *P. microphylla* **Torr.** <br> *Cercidium mycrophyllum* (Torr.) Rose & I.M. Johnston | **yellow palo verde** | SW US |
| **Sources:** Bainbridge and Virginia (1989), Little (1979), Little and Wadsworth (1964). | | |

seeds (figures 1 and 2) (Delorit and Gunn 1986; Vines 1960). Both flowers and legumes can occur throughout the year. The fruits are ripe when the legume turns yellow-brown and the seeds rattle (Bainbridge and Virginia 1989). Most legumes of blue palo verde contain only 1 seed (Siemens and Johnson 1995).

**Collection, storage and germination.** Seed collection should be timely because harvesting by animals and birds quickly reduces seed availability. Legumes dehisce upon drying, and small quantities of seeds can be hand-cleaned. A disc mill, meat grinder, or hammermill can be used to clean larger quantities. Reports on seeds per weight for palo verde range from 12,345 to 13,300/kg (5,600 to 6,000/lb) (Francis and Rodríguez 1993; Little and Wadsworth 1964). The seeds are obviously orthodox, since Everitt (1983) found no reduction in seed viability after 2 years storage at room temperature.

Some form of seed scarification is necessary in order to achieve rapid and uniform germination. Francis and Rodríguez (1993) germinated mechanically scarified seeds of palo verde on blotter paper and reported that 59% had germinated after 2 days. Everitt (1983) found that soaking seeds in concentrated sulfuric acid for 45 minutes increased germination from 1% to over 50%. Germination rose to over 87% at continuous temperatures of 15 to 35 °C, or at alternating temperatures of 10/20, 15/25, or 20/30 °C. Although percentage germination and radicle length were little affected by pH, results were enhanced if seeds were buried 1 to 7 cm (0.4 to 2 $^3/_4$ in) rather than left on the surface. Zodape (1991) reported germination of over 80% of seeds soaked in concentrated sulfuric acid. However, Bainbridge and Virginia (1989) found a negative effect of certain abrasion methods—they can create a dust on the seeds that encourages mold growth during germination.

**Figure 1**—*Parkinsonia aculeata*, palo verde:  seed.



Although the seedcoat serves as a barrier to overcome when germinating, it also serves as a protective shield against insect infestation. Janzen (1977) found that the cause of mortality of larvae of the southern cowpea weevil—*Callosobruchus maculatus* F.—in palo verde seeds was not seed toxicity but rather the inability of the larvae to emerge through the seedcoat. Johnson and Siemens (1991) reported a field survival rate of less than 0.1% for *Stator* spp. larvae on palo verde seeds, also attributed to seedcoat density. Bainbridge and Virginia (1989) found that freezing the seeds will kill bruchid beetles, which are a major seed pest.

**Nursery practice and seedling care.** Palo verde seedlings are capable of fast root growth, for example, 35 cm (13.8 in) in 60 days, and may require air- or root-pruning. Young seedlings are susceptible to various damping-off diseases. Washing seeds with dilute hydrogen peroxide or dilute sodium hypochlorite (1:3 laundry bleach with water) before scarification may reduce problems with fungal disease (Bainbridge and Virginia 1989). Seedlings can be grown in a variety of deep, narrow containers. Pots that allow for uninterrupted taproot growth, such as the "tall pot," a 76-cm (30-in) PVC pipe used at the U.S. Department of the Interior National Park Service's Joshua Tree National Park (JTNP) seem to work well for revegetation projects. Soil mix should be sandy and drain well. Mychorrhizal inoculation is not required; however, use of VA-mycorrhizae may be desirable for planting in washes that are usually deficient in soil phosphorous (Virginia 1986).

Palo verde grown in the tall pots have been successfully outplanted without follow-up irrigation at JTNP (Rodgers and Miller 1995). Transplant studies determined that seedlings could be initially established with minimal irrigation. However, seedlings are tempting browse for small mammals, and plants are unlikely to survive without protective screening.

Direct seeding may be successful in the field, provided seeds are pretreated and sown after heavy rains or floods, when moisture and heat stress are low. In 1988, direct seeding trials were undertaken by Bainbridge and Virginia (1989) at the travertine site near the Salton Sea. Seeds were scarified, presoaked, and buried 6 to 12 mm deep in loose soil. Initial treatments of the first trial included control, supplemental water, supplemental water and screening, and supplemental water with screening and shade. After 7 months, only 1 tree was still alive, rated in good condition, in the plot with water and screen. A second trial in the same area in April used presoaked, scarified seeds planted at a density of 100 seeds/m$^2$ (9/ft$^2$). Plots were moistened before and after planting. No germination was observed, probably due

**Figure 2**—*Parkinsonia aculeata*, palo verde:   longitudinal section of a seed.
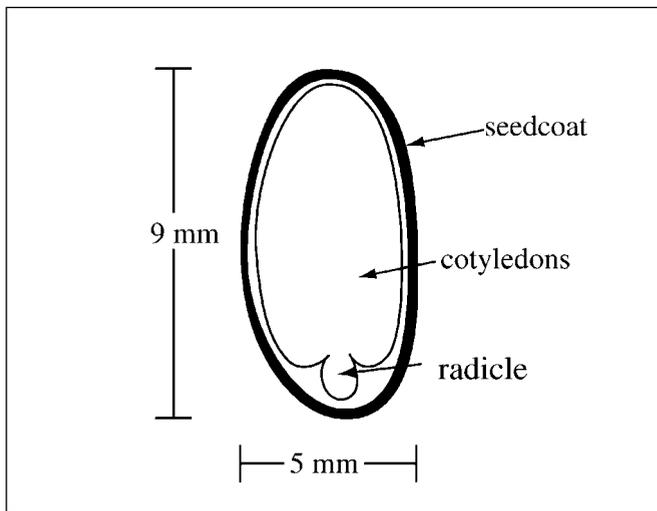


to the late planting date. Results of both trials showed that seedlings in the 2-leaf stage are sensitive to both high winds and freezing; the best time for direct seeding appears to be in late January or early February. Subsequent trials suggest that the use of remote-site irrigation systems—pitchers, porous capsules, and wicks—can improve direct seeding success.

## References

Bainbridge DA, Virginia RA. 1989.   Restoration in the Colorado Desert: Species Notes. Unpublished manuscript prepared for the California Department of Transportation.

Bean LJ, Saubel KS. 1972.   Temalpakh (from the earth): Cahuilla Indian knowledge and usage of plants. Morongo Indian Reservation, CA: Malki Museum Press. 225 p.

Dean WRJ, Milton SJ. 1991.   Patch disturbances in arid grassy dunes: antelope, rodents and annual plants. Journal of Arid Environments 20(2): 231–237 [1992 Herbage Abstracts 62: 2115].

Delorit RJ, Gunn CR. 1986.   Seeds of continental United States legumes (Fabaceae). Park Falls, WI: F.A. Weber & Sons. 134 p.

Ebeling W. 1986.   Handbook of Indian foods and fibers of arid America. Berkeley: University of California Press. 971 p.

Everitt JH. 1983.   Seed germination characteristics of two woody legumes (retama and twisted acacia) from south Texas. Journal of Range Management 36(4): 411–414 [1984 Forestry Abstracts 45: 4409].

Felger RS, Moser MB. 1985.   People of the desert and the sea. Tucson: University of Arizona Press. 435 p.

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.

Jaegar EC. 1940.   Desert wildflowers. Stanford, CA: Stanford University Press. 322 p.

Jain KL, Kapil RP. 1980.   Foraging rhythm of megachilid bees in relation to the flowering of *Medicago sativa* L. and *Parkinsonia aculeata* L. Indian Bee Journal 42(2): 35–38 [Apicultural Abstracts 1973+].

Janzen DH. 1977.   How southern cowpea weevil larvae (Bruchidae: *Callosobruchus maculatus*) die on nonhost seeds. Ecology 58(4): 921–927.

Johnson CD, Siemens DH. 1991.   Expanded oviposition range by a seed beetle (Coleoptera: Bruchidae) in proximity to a normal host. Environmental Entomology 20(6): 1577–1582 [1992 Review of Agricultural Entomology 80: 3799].

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, Wadsworth FH. 1964.   Common trees of Puerto Rico and the Virgin Islands. Agric. Handbk. 249. Washington DC: USDA Forest Service: 180–181.

Pearce GA. 1984.   Research on declared plants and other weeds. Journal of Agriculture of Western Australia 25(1): 34–36 [1985 Weed Abstracts 34: 608].

Rodgers JE, Miller C. 1995.   Unpublished data. Twentynine Palms, CA: USDI National Park Service, Joshua Tree National Park.

Siemens DH, Johnson CD. 1995.   Number of seeds per pod in three species of perennial legumes: a compromise between ecological and physiological constraints? American Midland Naturalist 133: 197–205.

Sihag RC. 1982.   Effect of competition with *Parkinsonia aculeata* L. on pollination and seed production in *Medicago sativa* L. Indian Bee Journal 44(4): 89–90 [1986 Apicultural Abstracts 37: 1044].

Vines RA. 1960.   Trees, shrubs and woody vines of the Southwest. Austin: University of Texas Press. 1104 p.

Virginia RA. 1986.   Soil development under legume tree canopies. Forest Ecology and Management 16: 69–79.

Zodape ST. 1991.   The improvement of germination of some forest species by acid scarification. Indian Forester 117(1): 61–66 [1993 Seed Abstracts 16: 2616].

Vitaceae—Grape family

# *Parthenocissus* Planch.

## creeper

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**Growth habit, occurrence, and use.** About 10 species and many varieties of creepers are native to either eastern Asia or North America. Both of the species discussed here (table 1) are adapted to climbing; Virginia creeper may ascend to about 15 m above ground and Japanese creeper to about 18 m (Robinson 1960). In the 1974 edition of this Manual, thicket creeper—*P. inserta* (Kerner) Fritsch—was treated as a separate species, but it is now considered the same as Virginia creeper. Virginia and Japanese creepers prefer soils that are moist but otherwise grow well in a wide variety of soil types. They are at least moderately tolerant of shading but are most likely to occupy places such as the edges of clearings, fence rows, old walls, and other structures, and stream banks. Chief uses are as ornamentals or for wildlife habitat. The creepers have attractive bluish black fruits and handsome foliage that turns scarlet, crimson, or orange in the fall. They provide food for more than 39 species of wildlife as well as cover for many small birds and mammals (Fisher and others 1935). The creepers are also used for erosion control. Virginia creeper was first cultivated in 1622 and Japanese creeper was first imported about 1862 (Rehder 1949).

**Flowering and fruiting.** The flowers are small and greenish and are borne in rather inconspicuous, long-stemmed clusters. Flowers are usually perfect (bisexual), but some vines have both perfect and unisexual flowers. The periods of flowering and fruiting are listed in table 2. Seed dispersal is largely effected by birds and mammals. Ripe berries (figure 1) of both species are bluish black and usually contain 1 to 4 seeds per fruit (Rehder 1949). Seeds have small embryos (figures 2 and 3). Good seedcrops are borne frequently.

**Collection, extraction, and storage.** After their color has turned to bluish black, fruits can be hand-stripped from the vines. Leaves and other debris mixed with the fruits can be removed by screening or blowing. Seeds can be extracted

| Table 1—*Parthenocissus,* creeper: nomenclature and occurrence | | |
|---|---|---|
| **Scientific name & synonym(s)** | **Common name(s)** | **Occurrence** |
| **P. quinquefolia (L.) Planch.** <br> *P. inserta* (Kerner) Fritsch <br> *Pserda quinquefolia* (L.) Greene | **Virginia creeper,** <br> woodbine | Maine to Manitoba & Florida, to Texas <br> & Rocky Mtns, also California & Mexico |
| **P. tricuspidata (Sieb. & Zucc.) Planch.** <br> *Ampelopsis tricuspidata* Sieb. & Zucc. | **Japanese creeper,** <br> Boston ivy | Japan & Central China; escaped from <br> cultivation in Massachusetts & Ohio |

Sources: Rehder (1949), Robinson (1960), Vines (1960).

| Table 2—*Parthenocissus,* creeper: phenology of flowering and fruiting | | | |
|---|---|---|---|
| **Species** | **Flowering** | **Fruit ripening** | **Fruit drop** |
| *P. quinquefolia* | June–Aug | July–Oct | Aug–Feb |
| *P. tricuspidata* | June–July | Sept–Oct | — |

Sources: Fernald (1950), Gill and Pogge (1974), Rehder (1949), Van Dersal (1938).

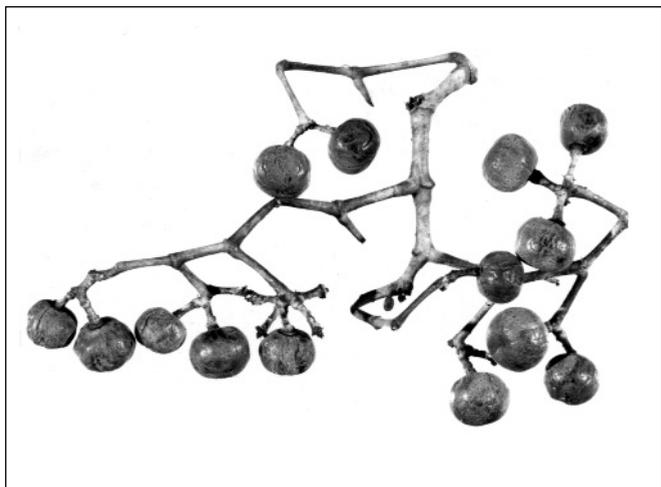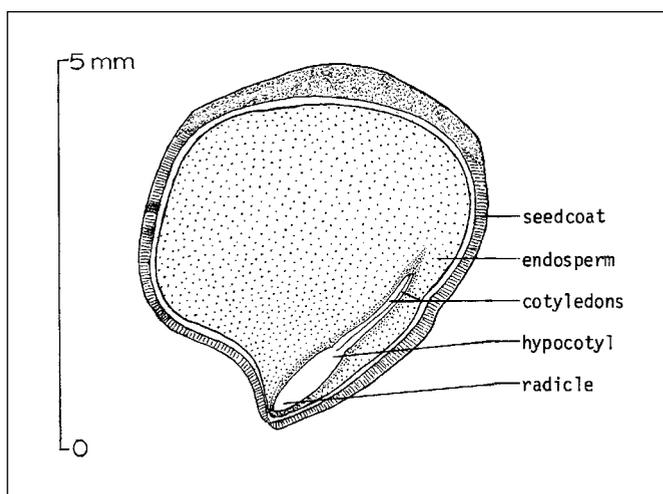**Figure 1**—*Parthenocissus quinquefolia,* Virginia creeper: cluster of berries.



**Figure 2**—*Parthenocissus,* creeper:   seeds of *P. quinquefolia,* Virginia creeper (**left**) and *P. tricuspidata,* Japanese creeper (**right**).



**Figure 3**—*Parthenocissus quinquefolia,* Virginia creeper: longitudinal section through a seed.



by running the fruits, with water, through a macerator or a hammermill and then floating off the pulp and empty seeds. Seeds in small lots can be extracted with laboratory blenders run at low speed. Extraction should be done carefully because the seedcoats are often soft and easily injured. An extraction method developed for the soft seeds of wild grapes (*Vitis* spp.) may be satisfactory for creepers also. In this method (Gill and Pogge 1974), the berries are placed in bags made of 14-mesh soil screen and a solid stream of water at a pressure of 2,800 kN (400 lb/in$^2$) is directed onto the berries. Most of the pulp and skins are washed through the screen. The remaining fragments are floated off in a pail of water, and the seeds are recovered from the bottom of the pail. After cleaning, the seeds should be thoroughly dried before storage. Soundness of cleaned seedlots has ranged from 44 to 99% (Swingle 1939). If seed cleaning is not convenient, whole berries can be dried and stored. Cleaned and dried seeds have been stored at room temperatures (Edminster 1947; Fisher and others 1935), but there are no known studies of seed longevity. These seeds are almost certainly to be orthodox in storage behavior, however, so they should keep well for several years at least if stored with low seed moisture (<12%) and at low temperatures (1 to 5 °C). Seeds of another species—*Vitis riparia* (Michx.)—in the same family showed no germination loss after storage for over 2 years in sealed containers at 5 °C (Gill and Pogge 1974).

Cleaned Virginia creeper seeds range from 21,600 to 57,800/kg (9,800 to 26,200/lb) and average 36,500/kg (16,560/lb). No seed yield data on Japanese creeper are available, but they are probably similar to those for Virginia creeper.

**Germination.**    Natural germination takes place during the first or perhaps the second spring following dispersal and is epigeal (Fisher and others 1935) (figure 4). The seeds have an internal dormancy that can be overcome by moist stratification for about 60 days at 5 °C (Gill and Pogge 1974). Outdoor stratification in winter, during which the seeds become frozen, has also increased germination (Adams 1927; Howard 1915). There are no official germination test prescriptions for creepers, but tests can be made in sand flats at alternating temperatures of 20/30 °C. About 30 days is a sufficient test length for stratified seeds, but untreated seeds may require >150 days (Gill and Pogge 1974). Results from a small number of tests suggest that germination of stratified seeds should peak at about 15 days and reach 70 to 80% by 30 days. For untreated seeds, germi-

nation was less than 5% in 4 tests, but 45% in another that ran for 595 days (Adams 1927; Howard 1915; Gill and Pogge 1974). The excised embryo method has also been used to estimate viability (Flemion 1948; Heit 1955).

**Nursery practice.** Untreated seeds may be sown in the fall, but spring sowing of stratified seeds is recommended. Seeds should be sown in drills, and covered with about 1 cm ($^1/_2$ in) of soil or soil and mulch (Edminster 1947). For Virginia creeper, Edminster (1947) recommended sowing seeds at the rate of 750/m$^2$ (70/ft$^2$) with a target bed-density of 108/m$^2$ (10/ft$^2$), but these rates depend on viability, of course. Planting is recommended with either 2+0 or 1+0 stock that has a top height about 15 cm and a stem diameter of about 5 cm, measured 12 mm above the root collar (Edminster 1947).

Creepers can also be propagated vegetatively (Dirr and Heuser 1987). Virginia creeper softwood cuttings taken in June through August should root 100% without hormone treatment, and hardwood cuttings can also be rooted. Japanese creeper softwood cuttings should be treated with 8,000 ppm indolebutyric acid (IBA) in talc. Cuttings should not have tendrils, as buds will not form there.

**Figure 4**—*Parthenocissus quinquefolia,* Virginia creeper: seedling development at 1, 3, and 33 days after germination.
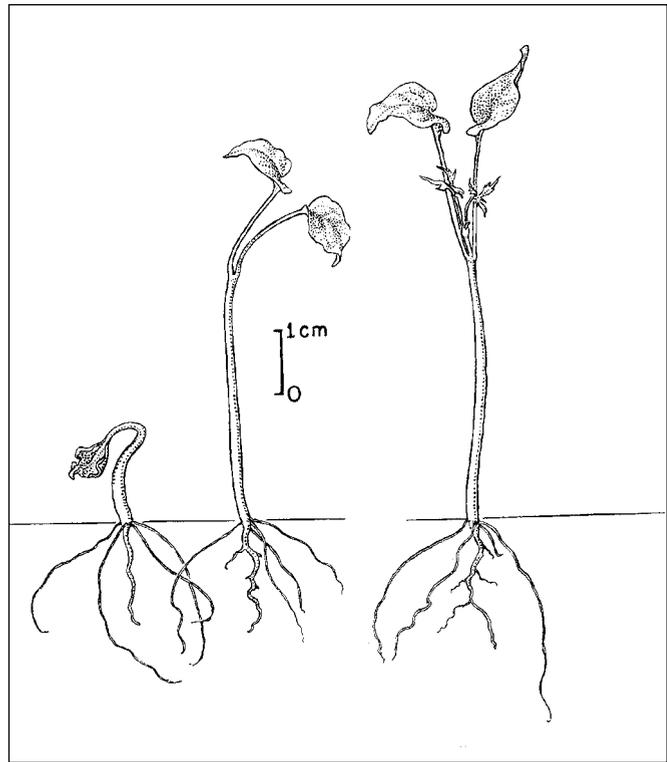
### References

Adams J. 1927. The germination of the seeds of some plants with fleshy fruits. American Journal of Botany 15 (8): 415–428.
Bailey LH. 1914. The standard cyclopedia of horticulture. 6 vol. New York: Macmillan. 3639 p.
Dirr MA, Heuser CW Jr. 1987. The reference manual of woody plant propagation: from seeds to tissue culture. Athens, GA: Varsity Press. 239 p.
Edminster FC. 1947. The ruffed grouse: its life story, ecology and management. New York: Macmillan. 385 p.
Fernald ML. 1950. Gray's manual of botany. 8th ed. New York: American Book Co. 1632 p.
Fisher PL, Briggs AH, Elkins WA, Roe EL. 1935. Propagation of game food and cover plants of the Lake States. St. Paul: USDA Forest Service, Lake States Forest Experiment Station. 81 p.
Flemion F. 1948. Reliability of the excised embryo method as a rapid test for determining the germinative capacity of dormant seeds. Contributions of the Boyce Thompson Institute 15: 229–241.
Gill JD, Pogge FL. 1974. *Parthenocissus* Planch., creeper. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 568–571.

Heit CE. 1955. The excised embryo method for testing germination quality of dormant seed. Proceedings Association of Official Seed Analysts 1955: 108–117.
Howard WL. 1915. An experimental study of the rest period in plants: seeds. Res. Bull. 17. Columbia: Missouri Agricultural Experiment Station. 58 p.
Rehder A. 1949. Manual of cultivated trees and shrubs. Rev. ed. New York: Macmillan. 1116 p.
Robinson FB. 1960. Useful trees and shrubs: reference cards [a card file of data on hardy woody plants in common use as ornamentals]. Champaign, IL: Garrard Press. 427 cards.
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.
Vines RA. 1960. Trees, shrubs, and woody vines of the Southwest. Austin: University of Texas Press. 1104 p.

P

Scrophulariaceae—Figwort family

# *Paulownia tomentosa* (Thunb.) Sieb. & Zucc. ex Steud.

## royal paulownia

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**Other common names.** paulownia, empress tree, princess tree.

**Growth habit, occurrence, and use.** Royal paulownia—*Paulownia tomentosa* (Thunb.) Sieb. & Zucc. ex Steud.—is a common sight along the sides of roads and railroad tracks, as well as near old house sites, in the Northeast and South. A native of eastern Asia, it has been widely planted in North America from Montreal to Florida and west to Missouri and Texas, as well as in some western states (Bonner 1990). It was introduced for its ornamental value in the 19th century and has escaped from cultivation in many localities. This deciduous tree reaches heights of 9 to 21 m at maturity. It has been planted extensively in the South for specialty wood products and for mine spoil reclamation in surface mine areas (Tang and others 1980).

**Flowering and fruiting.** The showy, violet or blue, perfect flowers appear in terminal panicles up to 25 cm long in April to May before the leaves emerge. The fruits are ovoid, pointed, woody capsules about 3 to 4 cm long (figure 1). They turn brown when mature in September and October and persist on the tree through the winter (Vines 1960). The trees start bearing seeds at 8 to 10 years of age and are very prolific (Bonner 1990).

**Collection, extraction, and storage of seed.** The dry fruits can be collected and opened by hand anytime before they disperse their seeds. They can also be collected when still a little green but must be dried completely for seed extraction. One proven extraction method is to place dried capsules in burlap bags and then crush them. Seeds and capsule fragments can then be separated by air (Carpenter and Smith 1979). The tiny, winged, flat seeds are about 1.5 to 3 mm long (figures 2 and 3) and are easily disseminated by wind when the capsules break open on the trees. Fruits collected in southeast Arkansas yielded the following data that appear to be typical for royal paulownia (Bonner and Burton 1974):

| | | |
|---|---|---|
| Fruits per volume | 8,800/hl | 3,100/bu |
| Seeds per fruit | 2,033 | — |
| Seeds per volume of fruit | 2.8 kg/hl | 2.2 lb/bu |
| Seeds per weight | 6,200/g | 175,770/oz |
| Percent moisture content (fresh weight) | 7% | — |

Royal paulownia seeds are orthodox in storage behavior. Carpenter and Smith (1979) reported that samples stored dry at 4 °C germinated 85% or more after 3 years but the rate of germination declined somewhat. Long-term storage performance has not been studied and is therefore unknown.

**Germination.** Royal paulownia seeds exhibit little or no dormancy, but light is necessary for timely germination of fresh seeds (Borthwick and others 1964; Toda and Isikawa 1952). Moist stratification at 3 or 4 °C for up to 8 weeks effectively removes the light requirement (Barnhill and others 1982; Carpenter and Smith 1981). Fresh seedlots from the 1974 Arkansas collection mentioned above had a germinative capacity of 90% in 19 days (4 samples) when tested on moist Kimpak with alternating temperatures of 20 and 30 °C. Eight hours of light were supplied during the

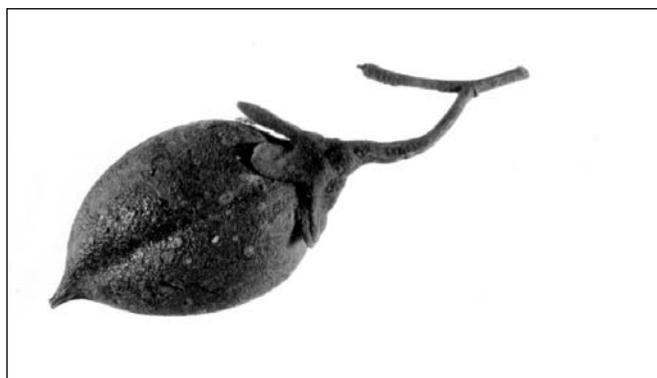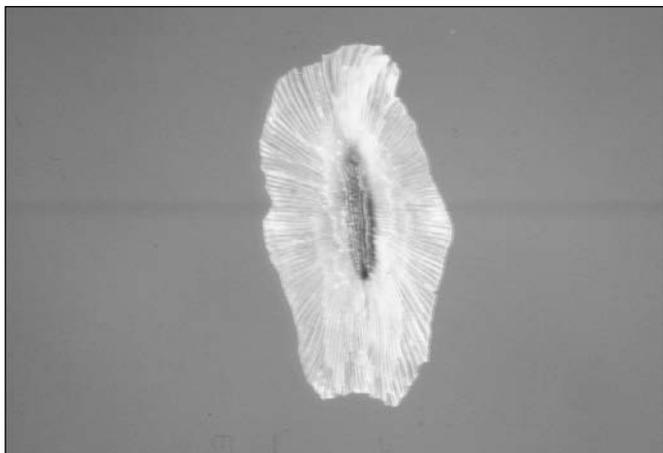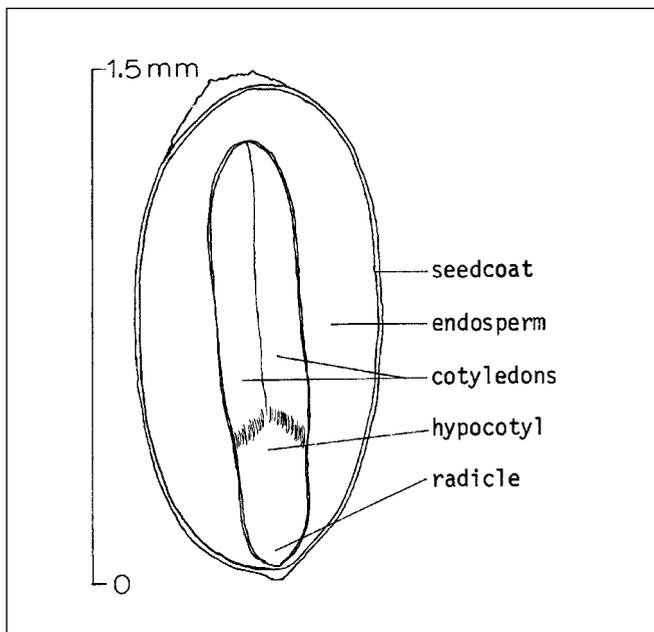**Figure 1**—*Paulownia tomentosa*, royal paulownia: capsule.

**Figure 2**—*Paulownia tomentosa*, royal paulownia: winged seed.



**Figure 3**—*Paulownia tomentosa,* royal paulownia: longitudinal section through a seed.



30 °C cycle. Germination rate was 86% in 9 days (Bonner and Burton 1974). Excellent germination in the laboratory has also been obtained at a constant 20 °C (Carpenter and Smith 1979) and at alternating temperatures of 10/20 °C (Barnhill and others 1982). Stratification is beneficial at these lower temperatures.

**Nursery practice.** Royal paulownia seeds should be broadcast on the surface of nursery beds or planted at a depth of about 3 mm ($^1/_8$ in) with mechanical drills. A desirable bed density is approximately 100 seedlings/m$^2$ (9/ft$^2$). Unstratified seeds sown in the fall should be mulched; seeds sown in the spring should have been stratified (Williams and Hanks 1976). Container production systems have also been developed for this species (Beckjord 1982; Immel and others 1980).

Vegetative propagation is relatively easy with lateral root cuttings, and successful tissue culture techniques are also available (Tang and others 1980; Dirr and Heuser 1987).

## References

Barnhill MA, Cunningham M, Farmer RE. 1982. Germination characteristics of *Paulownia tomentosa*. Seed Science and Technology 10: 217–221.

Beckjord PR. 1982. Containerized and nursery production of *Paulownia tomentosa*. Tree Planters' Notes 33(1): 29–33.

Bonner FT. 1990. *Paulownia tomentosa* (Thunb.) Sieb. & Zucc. ex Steud., royal paulownia. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 2, Hardwoods. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 501–502.

Bonner FT, Burton JD. 1974. *Paulownia tomentosa* (Thunb.) Sieb. & Zucc., royal paulownia. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 572–573.

Borthwick HA, Toole EH, Toole VK. 1964. Phytochrome control of *Paulownia* seed germination. Israel Journal of Botany 13: 122–133.

Carpenter SB, Smith ND. 1979. Germination of paulownia seeds after stratification and dry storage. Tree Planters' Notes 30(4): 4–6.

Carpenter SB, Smith ND. 1981. Germination of paulownia seeds in the presence and absence of light. Tree Planters' Notes 32(4): 27–29.

Dirr MA, Heuser CW Jr. 1987. The reference manual of woody plant propagation: from seed to tissue culture. Athens, GA: Varsity Press. 239 p.

Immel MJ, Tackett EM, Carpenter SB. 1980. Paulownia seedlings respond to increased daylength. Tree Planters' Notes 31(1): 3–5.

Tang RC, Carpenter SB, Wittwer RF, Graves DH. 1980. *Paulownia*: a crop tree for wood products and reclamation of surface-mined land. Southern Journal of Applied Forestry 4: 19–24.

Toda R, Isikawa H. 1952. Effect of diffused light on the germination of *Paulownia* seeds. Journal of the Japanese Forestry Society 34: 250.

Vines RA. 1960. Trees, shrubs, and woody vines of the Southwest. Austin: University of Texas Press. 1104 p.

Williams RD, Hanks SH. 1976. Hardwood nurseryman's guide. Agric. Handbk. 473. Washington, DC: USDA Forest Service. 78 p.

Scrophulariaceae—Figwort family

# *Penstemon* Schmidel

## penstemon, beardtongue

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**Growth habit, occurrence, and use.** The genus *Penstemon* comprises about 230 species of perennial herbs and subshrubs, most of which are found in western North America. Although most of the species are herbaceous, there are many more subshrubby species than are treated here. Several shrubby species from California that were formerly included in the genus *Penstemon* have been transferred to the closely related genus *Keckiella* Straw. In the previous edition of the Seed Manual, Hylton (1974) treated these species under the name *Penstemon*.

Subshrubby penstemon species occur in most vegetation types of the western United States, from warm desert shrublands to alpine fell-fields (table 1). They are most often found on well-drained, rocky or sandy, infertile soils with sunny exposure. Some species, such as Bridges penstemon, are widely distributed and of wide ecological amplitude, whereas others, such as crevice penstemon, are restricted both geographically and ecologically. Many penstemons are pioneer plants that occupy natural disturbances such as rockslides, making them useful for erosion control along roadsides and for mined land reclamation. They are used to some extent as browse by domestic and wild ungulates, and the seeds are used by rodents, birds, and ants. But perhaps the most important use for penstemons is in ornamental horticulture. Many of the penstemons are among our most outstandingly beautiful wildflowers, and the subshrubby species are no exception (Nold 1999). They are easily grown in cultivation, and many species have found their way into garden catalogues specializing in plants for low-maintenance landscapes. One named variety that is commercially available is shrubby penstemon 'Purple Haze'. Some of the warm-desert species are not hardy in cultivation in the North, although some of these, for example, crevice penstemon, can be successfully grown in containers.

**Table 1**—*Penstemon*, penstemon, beardtongue: habitat and geographic distribution

| Scientific name(s) | Common name(s) | Habitat* | Geographic distribution |
|---|---|---|---|
| *P. ambiguus* Torr. | moth penstemon, bush penstemon, gilia beardtongue | Sandy soil; desert shrubland, pinyon–juniper | S Nevada to S Utah, Kansas, & Oklahoma |
| *P. fruticosus* (Pursh) Greene | shrubby penstemon, bush penstemon | Shallow soils; spruce–fir, lodgepole pine | N Rocky Mtns from British Columbia to Idaho |
| *P. leonardii* Rydb. | Leonard penstemon, Leonard's beardtongue | Sagebrush–grassland to aspen–conifer | SE Idaho to S Utah |
| *P. linarioides* Gray | toadflax penstemon | Sagebrush–grassland to ponderosa pine | Utah & Colorado to Arizona & New Mexico |
| *P. petiolatus* Brandeg. | crevice penstemon, petiole beardtongue | Limestone crevices; warm desert shrubland | E Mojave Desert |
| *P. platyphyllus* Rydb. | sidehill penstemon, broadleaf beardtongue | Mountain brush; aspen–conifer | Wasatch Mtns, N Utah |
| *P. rostriflorus* Kellogg P. bridgesii Gray | Bridges penstemon | Warm desert shrubland to alpine | Widespread in W US |
| *P. sepalulus* A. Nels. | littlecup penstemon, littlecup beardtongue | Sagebrush–grasssland to aspen–conifer | Wasatch Mtns, N Utah |

Source: Cronquist and others (1984).
* May include forest type.

**Flowering and fruiting.** Penstemon flowers are borne in elongate racemes that are often held above the leafy stems, though this habit is often less pronounced in the sub-shrubby species. The flowers consist of a 5-toothed cuplike calyx, a tubular or snapdragon-like corolla made of 5 fused petals, 5 stamens mounted on the interior of the corolla tube, and a superior 2-chambered ovary that contains many ovules. One of the 5 stamens is sterile, that is, it has no anther, and is often covered with long hairs and exserted from the corolla, hence the name "beardtongue." The flowers are pollinated by a variety of insects and hummingbirds, and flower form, color, and arrangement in each species reflect specialization to attract particular pollinators. Most penstemons flower in the spring or early summer, though some—for example, Bridges penstemon—are midsummer-flowering. Flowering is indeterminate, with the youngest flowers at the tip of each flowering stalk. After fertilization, the ovaries develop into 2-valved capsules that split open at the tip and sometimes along the sides. The numerous gray to black, angular seeds are dispersed by the shaking action of the wind.

**Seed collection, cleaning, and storage.** Penstemon seeds are usually harvested by hand-stripping or clipping the flowering stalks into containers. Capsules generally begin to split open from 6 to 8 weeks after the plants are in full flower, with those at the base of each stalk ripening first. Stalks can be clipped before the capsules start to open, as long as the seeds can be seen darkening through the ovary wall. If the stalks are clipped after the capsules begin to open, care must be taken to avoid excessive spillage during harvest. For most species, the window of opportunity for harvest is quite wide, as capsules are held upright on the plant and seeds are dispersed only gradually. The harvested material should be dried carefully to avoid molding, espe-

cially if it is collected when somewhat green. The capsules will open after harvest, and for small lots, the seeds can be shaken free and collected by screening. For commercial seedlots, processing with a hammermill or barley de-bearder, followed by a fanning mill, is the usual procedure. Seedlots can readily be cleaned to high purity (>95%).

Penstemon seeds are generally quite small, though size varies considerably among species (table 2). Viability at harvest is usually high (table 2). Damage by seed beetles and other insects during ripening is common, but unfilled and damaged seeds are usually removed in cleaning, so that yield rather than seed quality of the cleaned lot is affected. Penstemon seeds are orthodox in storage behavior, as they keep well in warehouse storage if maintained at moisture contents of 8 to 11%. There is little loss of viability during 5 years, and seeds stored for 15 years may still show viability as high as 50% (Stevens and others 1981, 1996).

**Seed germination and testing.** The germination requirements of penstemon seeds vary widely, both among and within species (Kitchen and Meyer 1991; Meyer and others 1995). Some species have seeds that are germinable without pretreatment and unaffected by chilling, whereas other species have seeds that are nondormant and negatively affected by chilling, and still others have seeds with a positive requirement for chilling (table 3). In general, seeds of species of the desert Southwest and coastal and cis-montane California are the least likely to have a chilling requirement, whereas those from the Great Basin, Rocky Mountains, and Sierras are more likely to require chilling. Within a species (Bridges penstemon, for example), the length of the chilling requirement is positively correlated with the length of time seeds are likely to spend under snow cover in winter (Meyer 1992; Meyer and Kitchen 1994; Meyer and others 1995).

**Table 2**—*Penstemon*, penstemon, beardtongue: seed data

| Species | Seeds/weight | | | | Mean % viability | Samples |
| | Mean | | Range | | | |
| | /g | /oz | /g | /oz | | |
|---|---|---|---|---|---|---|
| *P. ambiguus* | 1,000 | 28,000 | 820–1,270 | 23,000–36,000 | 90 | 6 |
| *P. fruticosus* | 3,500 | 98,000 | 3,230–3,850 | 90,000–108,000 | 68 | 4 |
| *P. leonardii* | 1,250 | 35,000 | 900–2,220 | 25,000–62,000 | 84 | 8 |
| *P. linarioides* | 810 | 23,000 | 720–900 | 20,000–25,000 | 84 | 4 |
| *P. petiolatus* | 2,700 | 77,000 | 2,640–2,800 | 74,000–78,000 | 98 | 2 |
| *P. platyphyllus* | 1,460 | 42,000 | 1,390–1,590 | 39,000–45,000 | 95 | 3 |
| *P. rostriflorus* | 2,260 | 64,000 | 1,560–2,940 | 44,000–82,000 | 87 | 14 |
| *P. sepalulus* | 1,700 | 48,000 | 1,350–2,000, | 38,000–56,000 | 85 | 6 |

**Source:** Meyer (2002).

| Table 3—*Penstemon*, penstemon, beardtongue: germination data after 0 to 24 weeks of chilling* | | | | | | | |
|---|---|---|---|---|---|---|---|
| **Species** | **0 wk** | **4 wk** | **8 wk** | **12 wk** | **16 wk** | **24 wk** | **Samples** |
| *P. ambiguus* | 35 | 21 | 19 | 10 | 16 | 31 | 3 |
| *P. fruticosus* | 6 | 19 | 14 | 19 | 40 | 83 | 4 |
| *P. leonardii* | 0 | 1 | 22 | 82 | 80 | 80 | 2 |
| *P. linarioides* | 0 | 0 | 1 | 6 | 12 | 10 | 2 |
| *P. petiolatus* | 100 | — | — | 100 | 100 | 100 | 1 |
| *P. platyphyllus* | 1 | 55 | 66 | 99 | 97 | 100 | 7 |
| *P. rostriflorus* | 18 | 17 | 54 | 83 | — | 98 | 3 |
| *P. sepalulus* | 3 | 25 | 37 | 83 | 86 | 100 | 2 |

**Sources:** Kitchen and Meyer (1991), Meyer (2002), Meyer and others (1995).
* Germination percentage for seeds subjected to 0 to 24 weeks of chilling at 1 to 2 °C followed by 4 weeks of incubation at 10/20 °C.

The germination requirements of penstemon seeds generally change very little in dry storage; dormancy status is affected only by conditions during time spent in the imbibed state (Meyer and others 1995). For species and populations from middle elevations in the West, there is rarely a natural dormancy-breaking treatment that will remove dormancy in all seeds of a lot. For those that respond positively to chilling, this is manifest as a fraction that will not respond to chilling of any duration. These seeds form a persistent seedbank under natural conditions, and it is not known how they eventually become germinable. Treatment with gibberellic acid can remove seed dormancy or shorten the chilling requirement for many (but not all) species of penstemon (Kitchen and Meyer 1991). This method may or may not be feasible in a production setting, depending on the degree to which gibberellic acid affects seedling quality. Penstemon seeds germinate best at cool temperatures, and germination at temperatures higher than 20 °C may be completely suppressed, a fact to keep in mind when attempting to produce plants from direct sowing in the greenhouse (Allen and Meyer 1990). Light usually has little effect (Meyer and others 1995).

The quality of penstemon seeds may be evaluated using tetrazolium (TZ) staining, a germination test with chilling or gibberellic acid, or a combination of these. A general seed-testing rule for the genus has been adopted by the Association of Official Seed Analysts (Kitchen and others 1999). This test calls for 2 separate procedures. In the first procedure, seeds are placed on blotters saturated with 500 ppm gibberellic acid, chilled at 2 to 5 °C for 60 days, and incubated at 15 or 10/20 °C for 14 days. Post-test viability of ungerminated seeds is then determined with TZ staining. This procedure is used to determine total viability for the seedlot, and TZ staining on non-incubated seeds may be substituted. In the second procedure, seeds are incubated at 15 or 10/20 °C in the light for 28 days. This second procedure is used to determine the size of the nondormant fraction.

Tetrazolium staining is carried out by allowing the seeds to imbibe water for 24 hours, piercing their seedcoats with a needle, immersing them in 1% TZ for 12 hours at room temperature, and then bisecting them longitudinally for evaluation. The embryo is a small, sausage-shaped body embedded in the copious endosperm. Non-viable embryos usually do not stain at all but remain a yellowish color. Even light pink staining indicates a viable embryo, as evidenced by comparisons with maximum germination percentages for numerous seedlots (Kitchen and Meyer 1991). A simple cut test can be used in place of TZ staining for recently harvested seeds, as the presence of a firm, white, viable embryo is quite evident.

**Field planting and nursery practice.** Most penstemon species can be established from direct seeding. Seeds should be broadcast on a firm seedbed and lightly covered, raked, or pressed in. Planting should take place in late fall or early winter for most species, except in the summer rainfall areas of the Southwest, where seeds of nondormant species should be sown just before summer rains. Nondormant species may be spring-seeded in the North but may require supplemental water to establish. Penstemons are susceptible to fusarium wilt diseases in cultivation and should not be fertilized or overwatered. They are more likely to survive in coarse, rapidly draining soils that have not previously been used for agriculture. The young seedlings cannot survive heavy competition from weeds or aggressive perennial grasses.

Penstemons may also be readily produced from seeds in container culture. They grow well in a coarse medium in elongated containers such as those used to produce conifer seedlings. Seeds of nondormant species may be direct-sown, whereas chilled seeds or germlings may be planted for those

species with seeds that require chilling. The seedlings will be ready for hardening-off and outplanting in 3 to 4 months, but they can be held much longer if necessary. Survival of outplanted stock is usually high, as long as plants are watered-in well at the time of transplanting and care is taken to eliminate air pockets around the roots. Plants both from direct seeding and outplanting usually flower the second year, and individuals of the subshrubby species can live for 10 years or more. If seed stalks are not clipped, most plants will readily self-seed.

## References

Allen PS, Meyer SE. 1990. Temperature requirements for seed germination of three *Penstemon* species. HortScience 25: 191–193.

Cronquist, A. Holmgren, AH, Holmgren NH, Reveal JL, Holmgren PK. 1984. Intermountain flora. Volume 4, Subclass Asteridae (except Asteraceae). Bronx, NY: New York Botanical Garden. 573 p.

Hylton LO. 1974. *Penstemon* Mitch., penstemon. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 574–575.

Kitchen SG, Meyer SE. 1991. Seed germination of intermountain penstemons as influenced by stratification and GA$_3$ treatments. Journal of Environmental Horticulture 9: 51–56.

Kitchen SG, Meyer SE, Stevens R, Wilson GR. 1999. Proposed rule: a generalized rule for the genus *Penstemon*, beardtongues. Seed Technologist Newsletter 72(1): 52.

Meyer SE. 2002. Unpublished data. Provo, UT: USDA Forest Service, Rocky Mountain Research Station.

Meyer SE. 1992. Habitat-correlated variation in firecracker penstemon (*Penstemon eatonii*: Scrophulariaceae) seed germination response. Bulletin of the Torrey Botanical Club 119: 268–279.

Meyer SE, Kitchen SG. 1994. Habitat-correlated variation in seed germination response to chilling in *Penstemon* Section Glabri. American Midland Naturalist 132: 349–365.

Meyer SE, Kitchen SG, Carlson SL. 1995. Seed germination timing patterns in intermountain *Penstemon* (Scrophulariaceae). American Journal of Botany 82: 377–389.

Nold R. 1999. Penstemons. Portland, OR: Timber Press. 259 p.

Stevens R, Jorgensen KR, Davis JN. 1981. Viability of thirty-two shrub and forb species through fifteen years of warehouse storage. Great Basin Naturalist 41: 274–277.

Stevens R, Jorgensen KR, Young SA, Monsen SB. 1996. Forb and shrub seed production guide for Utah. Logan: Utah State University Extension Service. 51 p.

Rosaceae—Rose family

# *Peraphyllum ramosissimum* Nutt.

## squaw-apple

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**Growth habit and occurrence.** Squaw-apple—*Peraphyllum ramosissimum* Nutt.— the sole member of its genus, is an intricately and rigidly branched deciduous shrub growing to 2 m tall from numerous, gray-barked basal stems. Leaves are simple, linear-oblanceolate, entire or minutely serrulate, and alternate but fascicled on secondary growth at the ends of short lateral spurs. Squaw-apple occurs mainly in well-drained soils on dry foothill and mountain slopes and is associated with several community types, including oak–sagebrush, mountain brush, pinyon–juniper, and the lower edges of ponderosa pine forests (Hitchcock 1961; Shaw and Monsen 2004; Welsh and others 1987). On a microhabitat scale, squaw-apple often grows in mixed-species clumps. The overall range distribution extends from Grant and Baker Counties in north-central Oregon, south to northeastern California, and east through Nevada, southern Idaho, Utah, western Colorado and northwestern New Mexico (Harrington 1954; Hitchcock and others 1961; Welsh and others 1987). Dayton (1931) reports an altitudinal distribution of 915 m in Oregon to 2,740 m towards the southern range limit.

**Uses.** Wildlife known to eat squaw-apple fruits and seeds or both in Utah include grouse and wild turkeys (family Phasianidae), deer mice (*Peromyscus maniculatus*), chipmunks (*Eutamias* spp.), ground squirrels (*Spermophilus* spp.), and American black bears (*Ursus americanus*) (Auger and others 1995). Deer (*Odocoileus* spp.) browse squaw-apple lightly during the fall and winter (Shaw and others 2004; Smith 1974), and small birds use the intricately branched shrubs as cover even when leaves are not present (Shaw and Monsen 2004). Livestock also browse squaw-apple, and opinions vary widely on its forage value. In central Utah, squaw-apple is said to be almost worthless; in western Colorado, it is considered poor to fair; in eastern Oregon and northeastern California, it is commonly considered fair to moderately good sheep and cattle browse in the spring; and finally, in southwestern Utah, squaw-apple ranks as a valuable browse (Dayton 1931; Plummer and others

1968; Smith 1974). On ranges grazed by cattle during late winter and very early spring, individual plants may be severely hedged (Smith 1974). Even though squaw-apple grows slowly, Monsen and Davies (1985) suggest that it can persist in native plant landscaping for arid environments.

**Flowering and fruiting.** The regular, perfect flowers with their pinkish, spreading, showy petals open in May and June and appear singly or in clusters of 2 to 5. Data from Utah suggest that flowering intensity is greatest for individual plants larger than 1 m in both height and crown (Auger and others 1995). Squaw-apple is pollinated by a variety of insects, and seed production does not appear to be pollen-limited (Auger and others 1995). The fruits, which ripen from late June to early August, are yellowish red, bitter-tasting pomes measuring 8 to 18 mm in diameter, each containing 1 to 8 plump seeds (figure 1). Seeds consist of a brown, leathery testa entirely filled with embryo (figure 2). At 1,070 m in northeastern Oregon, most of the fruits have either dropped or been partially eaten by birds by mid-August (Smith 1974). At 2,500 m in east-central Utah, initiation of fruit removal precedes ripening, and again, most fruits usually have been consumed by mid-August (Auger and others 1995).

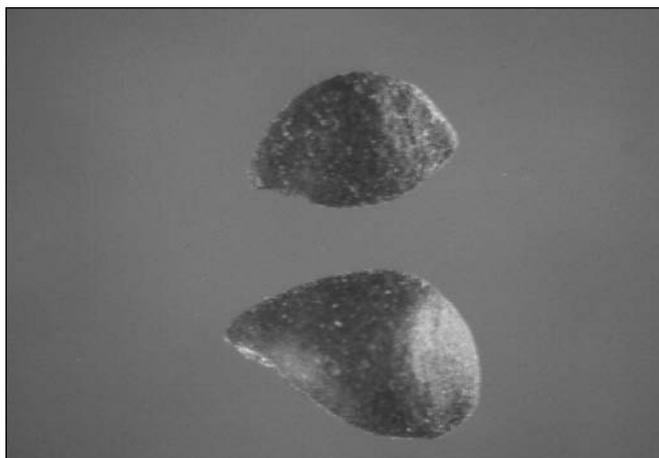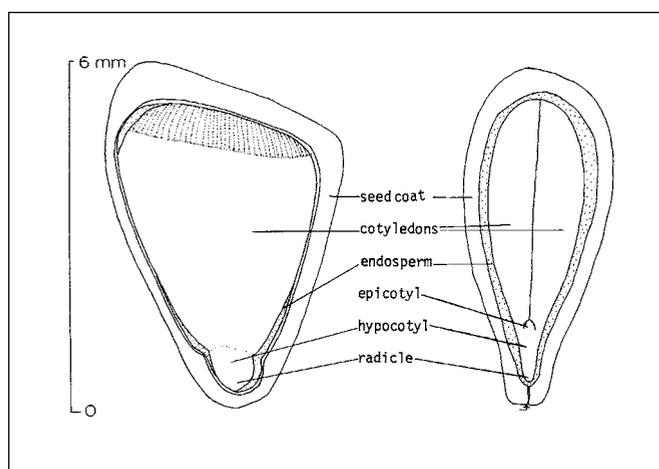**Figure 1**—*Peraphyllum ramosissimum*, squaw-apple: seeds.

**Figure 2**—*Peraphyllum ramosissimum*, squaw-apple: longitudinal sections through a seed.



**Figure 3**—*Peraphyllum ramosissimum*, squaw-apple: germinating seedlings.
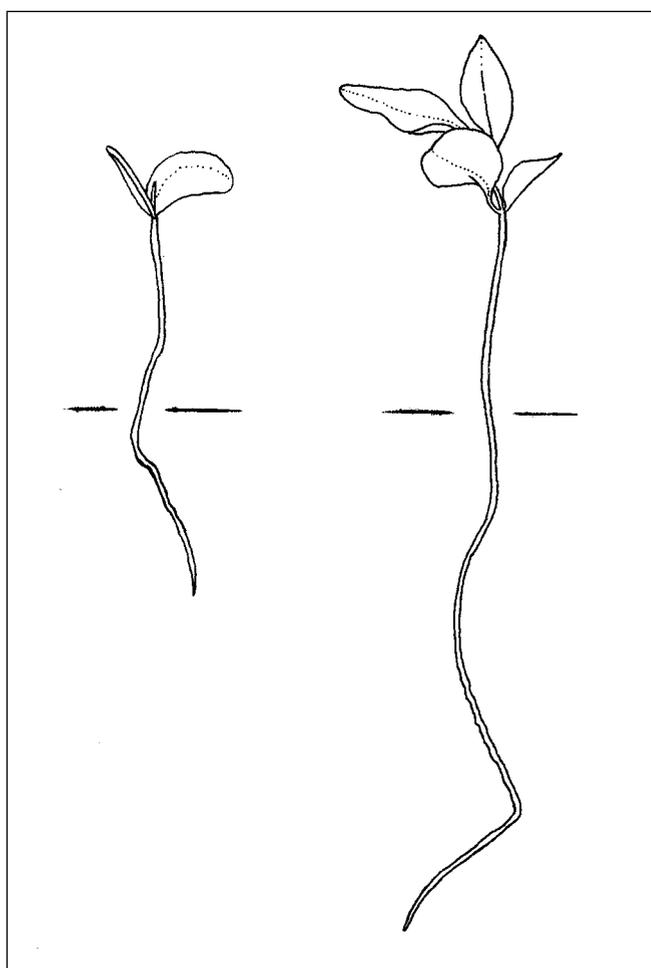


**Collection, extraction, and storage.** Ripe fruits are easily picked from the shrubs. Seeds can be extracted by mashing the fruits in water and floating off the pulp. Any remaining debris may be removed using a fanning mill after the seeds are dry. Seeds stored in a dry, cool, ventilated metal container remained viable up to 5 years (Plummer and others 1968). The yield of pure seeds from 45.5 kg (100 lb) of fresh fruits ranges from 3.0 to 4.7 kg (6.5 to 10.3 lb), and the number of pure seeds per weight ranges from 52,360/kg (23,750/lb) (Plummer and others 1968) to 110,870 (50,290/lb) (Auger and others 1995; Smith 1974). When individual fruits were examined from 2 squaw-apple stands in Utah, filled seeds averaged 71 and 58% of the lot (Auger and others 1995); in another seedlot, fill value was 68% (Smith 1974).

**Germination.** Germination of squaw-apple seeds is epigeal (figure 3) and may occur during cold stratification both in the laboratory and the field. For 1 seedlot, the percentage viability of filled seeds (tetrazolium method) was 79.8% (Auger 1994). Dormancy is embryo-induced. Embryos excised from unstratified seeds and placed on blotters did not germinate when incubated at 10/20 °C (12/12 hours, day/night). Excised embryos required 49 days—the same as intact seeds—before beginning to germinate during cold stratification (Auger 2002). Tests at the USDA Forest Service's Eastern Tree Seed Laboratory (now the National Seed Laboratory) (Smith 1974) indicated that stratification of seeds in a plastic bag for about 45 days at 3 °C maximizes total germination while minimizing germination occurring during stratification.

For a seedlot collected at 2,500 m, viable seeds treated to 70 days of stratification at 1 °C followed by incubation at 10/20 °C (12/12 hours, day/night), showed 79% total germination (Auger 1994). This represented a 71% difference in value for seeds stratified only 35 days. Viable seeds from the same lot kept in low-temperature stratification (1 °C) showed 50% germination by day 82 and about 95% by day 120. Results from seeds collected the next year (1995) were similar. Smith (1974) reported somewhat lower germination percentages at longer chill durations. When seeds were tested at 30/20 °C (8/16 hours, day/night) after 0, 30, 60, and 90 days of cold stratification, germination of squaw-apple averaged 9, 9, 16, and 51% of total seeds.

**Nursery practice.** Squaw-apple is grown in nursery beds only occasionally, usually when requested for transplantation at age 1 to 2 years into native-plant gardens (Prag and Prag 1996). In the greenhouse, squaw-apple seedlings emerge in 6 to 12 days from seeds planted about 5 mm (0.2 in) deep and covered with a thin layer of fine sand (Smith 1974). Overwatering and transplantation during the growing season increase the risk of seedling mortality (Prag and Prag 1996). Establishment is rated fair and persistence is very good (Plummer and others 1968; Shaw and Monsen 2004).

## References

Auger J. 1994. Viability and germination of seeds from seven fleshy-fruited shrubs after passage through the American black bear (*Ursus americanus*) [MS thesis]. Provo, UT: Brigham Young University. 49 p.

Auger J. 2002. Unpublished data. Reno: University of Nevada.

Auger J, Black HL, Meyer SE. 1995. Seed dispersal ecology of squawapple (Rosaceae: *Peraphyllum ramosissimum*). Final report, 29 October 1995 on file. Provo, UT: USDA Forest Service, Intermountain Research Station, Shrub Sciences Laboratory.

Dayton WA. 1931. Important western browse plants. Misc. Pub. 101. Washington, DC: USDA. 214 p.

Harrington HD. 1954. Manual of the plants of Colorado. Denver: Sage Books.

Hitchcock CL, Cronquist A, Ownbey M, Thompson JW. 1961. Vascular plants of the Pacific Northwest. Part 3. Seattle: University of Washington Press. 614 p.

Monsen SB, Davies JN. 1985. Progress in the improvement of selected western North American rosaceous shrubs. In: Carlson JR, McArthur ED, eds. Range Plant Improvement in Western North America; Proceedings, 38th Annual Meeting of the Society for Range Management; 1985 February 11–15; Salt Lake City, UT. Denver, CO: Society for Range Management: 201–220.

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. 183 p.

Prag P, Prag R. 1996. Personal communication. Williams, OR: Forestfarm.

Shaw N, Monsen SB. 2004. The rosaceous shrubs. In: Monsen SB, Stevens R, Shaw NL, eds. Restoring western ranges and wildlands. Gen. Tech. Rep. RMRS–136. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station.

Smith JG. 1974. *Peraphyllum ramosissimum* Nutt., squawapple. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 576–577.

Welsh SL, Atwood ND, Higgins LC, Goodrich S. 1987. A Utah flora. Great Basin Naturalist Memoir 9: 1–894.

Lauraceae—Laurel family

# *Persea borbonia* (L.) Spreng.

## redbay

Franklin T. Bonner

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**Other common names.**    shorebay, swampbay, swamp-bay persea.

**Growth habit, occurrence, and uses.**    There are about 150 species of *Persea*, almost all of which are tropical. The best-known is avocado—*P. americana* P. Mill. Only 1 species, redbay—*P. borbonia* (L.) Spreng.—is native to the continental United States (Little 1979). A variety of redbay, swampbay—*P. borbonia* var. *pubescens* (Pursh) Little—is considered by some to be a separate species (Brown and Kirkman 1990; Little 1979). Redbay is found mainly along streams and swampy sites, and occasionally dry woodlands, in the coastal plain from southern Delaware south to the Florida Keys and west to southern Texas and southwest Arkansas (Little 1979; Sargent 1965). It is a small to medium-sized tree that occasionally reaches heights of 18 to 21 m (Brown and Kirkman 1990). The wood is used locally for cabinets and boatbuilding. The fruits are eaten by birds, and the leaves are widely used to flavor soups and meat dishes (Brendemuehl 1990; Brown and Kirkman 1990). The tree is also planted as an ornamental because of its fruit and evergreen foliage.

**Flowering and fruiting.**    Redbay's small (6 mm long), yellow, perfect flowers are borne in axillary panicles that appear from May to June. The fruits are oblong, dark blue, single-seeded drupes that are covered with a thin, fleshy tissue; the endocarp is firm, but pliant (figure 1). Average fruit size is 7 to 10 mm in diameter and 10 mm in length. Seed size is 0.5 to 1 mm less than fruits (figures 2 and 3). The fruits, which are borne on yellow-orange peduncles 12 to 25 mm long, mature in September to October (Brown and Kirkman 1990; Radford and others 1968; Vines 1960).

**Collection, extraction, and storage.**    Redbay fruits can be easily collected by hand from the branches when the exteriors of the fruits turn dark blue or purple. Even though the fruits persist for a short while on the trees, early collection may be necessary to prevent predation by birds. Removal of the fleshy exocarp should not be necessary if

**Figure 1**—*Persea borbonia*, redbay:    fruits.



**Figure 2**—*Persea borbonia*, redbay:    cleaned seed.
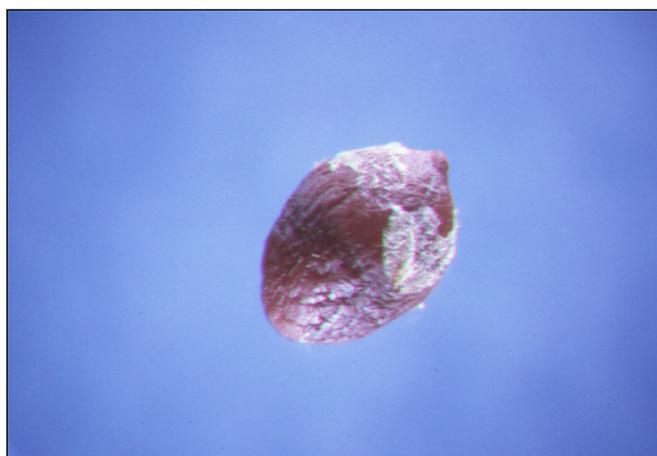


seeds are to be planted immediately. If they are to be stored temporarily, removal of this tissue may help avoid damage from pathogens. There are about 3,680 seeds/kg (1,670/lb) (the sample came from Mississippi). Storage data are not available for redbay, so viability retention under typical storage conditions is unknown. Avocado, however, is considered to be recalcitrant in nature and difficult to store (King and

**Figure 3**—*Persea borbonia*, redbay:   longitudinal section through a seed.

**References**

Brendemuehl RH. 1990.   *Persea borbonia* (L.) Spreng., redbay. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 2, Hardwoods. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 503–506.
Brown CL, Kirkman LK. 1990.   Trees of Georgia and adjacent states. Portland, OR: Timber Press. 292 p.
King MW, Roberts EH. 1980.   Maintenance of recalcitrant seeds in storage. In: Chin HF, Roberts EH, eds. Recalcitrant crop seeds. Kuala Lumpur: Tropical Press: 53–89.
Little EL Jr. 1979.   Checklist of United States trees (native and naturalized). Agric. Handbk. 541. Washington, DC: USDA Forest Service. 375 p.
Radford AE, Ahles HE, Bell CR. 1968.   Manual of the vascular flora of the Carolinas. Chapel Hill: University of North Carolina Press. 1183 p.
Sargent CS. 1965.   Manual of the trees of North America (exclusive of Mexico). 2nd. Ed., corrected and reprinted. New York: Dover. 934 p.
Vines RA. 1960.   Trees, shrubs, and woody vines of the Southwest. Austin: University of Texas Press. 1104 p.

Roberts 1980), and redbay may be the same. Some research is clearly needed on this subject.

**Germination tests and nursery practice.**   Redbay apparently has some type of seedcoat dormancy. Tests with 1 sample from Mississippi yielded 44% germination after 56 days for seeds that had part of their seedcoats removed with a longitudinal cut. Untreated seeds and seeds stratified for 28 days at 3 °C had zero germination in the same test. All seeds were germinated on moist blotter paper at alternating temperatures of 20 °C at night for 16 hours and 30 °C for 16 hours in the light. There are no recommended test procedures from official seed testing organizations for redbay. Germination is hypogeal (Brendemuehl 1990).

There are no specific directions for nursery production of redbay. Avocado is commonly propagated from seeds or cuttings (Vines 1960), and redbay may respond to similar practices.

Rutaceae—Rue family

# *Phellodendron amurense* Rupr.

## Amur corktree

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**Growth habit, occurrence, and use.** Amur corktree—*Phellodendron amurense* Rupr.—is native to northern China, Manchuria, Korea, and Japan. This small to medium deciduous tree—25 to 50 feet tall—has been cultivated in the Far East and eastern Europe. It was introduced into the United States around 1865, and its thick, corky bark and massive, irregular branches have made it of special interest for landscape and environmental plantings in the northern and western United States (Blackburn 1952; Everett 1964; Hoag 1965; Lewis 1957). In tests in Kansas, however, the tree did not perform well and was not recommended for general use (Hensley and others 1991). It is a potential source of industrial cork (Izmodenov 1972; Ota and others 1965), important as a nectar-bearing species in bee-keeping areas of the Russian Far East (Necaev and Pelemenev 1965), and of possible importance for the insecticidal properties of its fruit oils (Schechter 1943). In Byelorussia it is considered a "soil builder" when mixed with Scots pine—*Pinus sylvestris* L. (Letkovskij 1960). It tolerates a wide range of soil conditions, pH, drought, and pollution; it is easily transplanted and generally free of pests.

**Flowering and fruiting.** The species is dioecious, and female plants develop tend to have a bushier form than males (Hensley and others 1991). Small, yellowish green flowers, in large clusters of terminal panicles, appear in May and June (Krecetova 1960; Rehder 1940; Schechter 1943). Climate affects the time of day when flowers open, pollination, and the longevity of flowers (Starshova 1972).

Fruits are subglobose drupes about 1 cm in diameter (figure 1), green to yellowish green, turning black when ripe in September and October (Read 1974). They remain on the terminal panicles long after the leaves have dropped. Fruits are borne singly on short stalks (figure 1) and are very oily and aromatic. Each fruit usually contains 2 or 3 full-sized seeds and 3 or 4 aborted seeds (Read 1974). Seeds are brown to black, 5 mm long, 2 mm wide, and about 1 mm thick (figures 2 and 3); they have a moderately hard, stony coat (Gorokhova 1981; Read 1974).

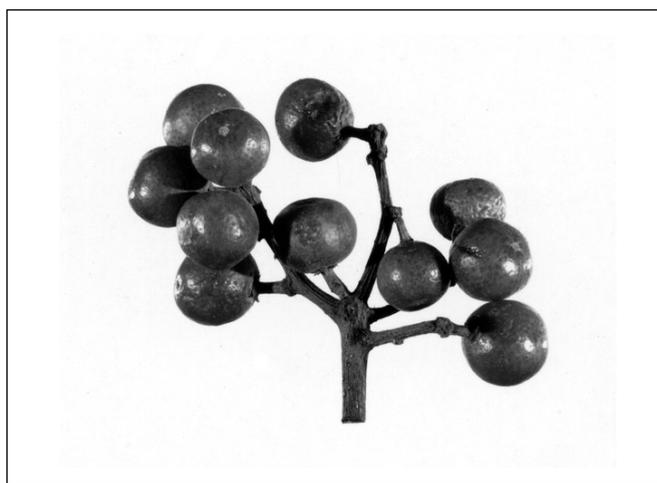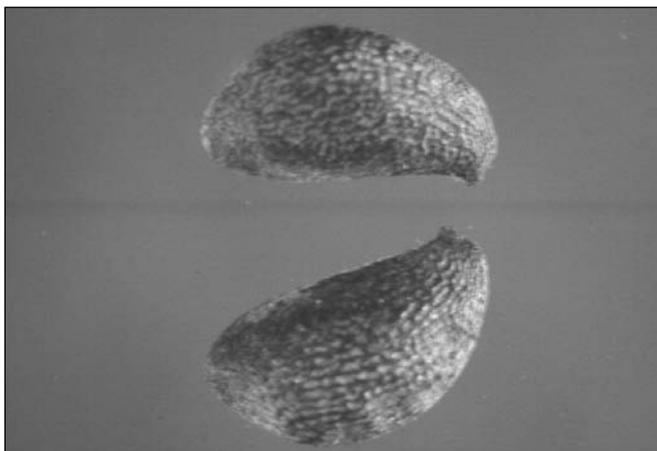**Figure 1**—*Phellodendron amurense*, Amur corktree: fruit cluster.



**Figure 2**—*Phellodendron amurense*, Amur corktree:



Minimum seed-bearing age is 7 to 13 years, both within the natural range and where the species has been introduced (Atkimockin 1960; Gorokhova 1981; Maljcev 1950; Read 1974; Starshova 1972). No data are available on the frequency of seedcrops. Severe drought had no marked effect on the

**P**

**Figure 3**—*Phellodendron amurense,* Amur corktree: longitudinal section through 2 planes of a seed.
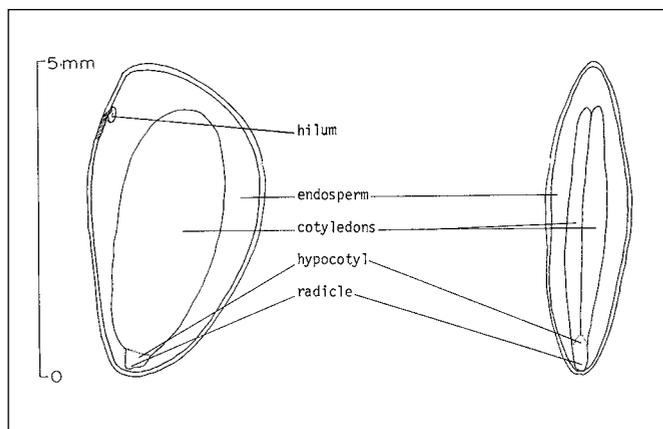


morphology of fruits and seeds, but appeared to reduce seed quality (Gorokhova 1986).

**Collection, extraction, and storage.**   The terminal panicles of fruit may be harvested with pruning shears in late September through October after leaf fall. After that, although many fruits remain tightly on the tree, some will have fallen. Fruits should be spread out in shallow layers to prevent heating and mildew during air-drying. Fruits may be soaked in water and seeds squeezed from the fleshy matter by hand; large lots can be run through a macerator and separated from the pulp by flotation. Fresh fruits weigh about 57 kg/hl (44 lb/bu) and yield about 0.9 kg (2 lb) of cleaned seeds (Read 1974). Based on seeds from 2 different lots, 1 kg contained 58,960 to 80,000 (26,800 to 36,363/lb) and 96,800 to 105,600 (44,000 to 48,000/lb) cleaned seeds (Read 1974; Swingle 1939). Seeds collected from plants growing in the natural range had similar seed weights (Gorokhova 1981).

**Germination.**   Fresh seeds germinate well without pretreatment (Dirr 1990; Read 1974). However, there are a number of reports of greatly improved germination following stratification. Stratification is recommended for seeds stored any length of time (Dirr and Heuser 1987).

Germination for a seedlot (for which the handling and storage history was not described) was best following cold moist, underground stratification for 166 days (Timm 1989). In another study, seeds stratified for 8 weeks had a higher germination rate and the same germination percentage as seeds stratified 4 weeks; germination of unstratified seeds was less than half that of stratified seeds (Mukai and Yokoyama 1985). Based on the information available, it is recommended that seeds be stratified if the history of collection, handling, and storage is not documented. Seeds of other *Phellodendron* spp. vary in their requirements for stratification (Dirr and Heuser 1987; Lin and others 1994).

Seeds germinate best at alternating temperatures. Both Lin and others (1979) and Mukai and Yokoyama (1985) reported germination of 3% or less at constant temperatures and 75 to 90% at alternating temperatures. The best temperature regimes were 35/5 °C and 35/15 °C (day length and high temperature for 8 hours).

**Nursery practice and natural regeneration.**   In its natural range, natural regeneration sometimes occurs in dense groups. Although the corktree has been reported to sucker from its roots (Dirr and Heuser 1987), this dense regeneration is believed to be from seeds present in the forest floor (Soludukin 1977). Light fire or disturbances that result in drying and warming of the forest floor are believed to promote this development. There was no indication regarding the longevity of the seeds in the forest floor environment, however the endocarp is moderately hard and might facilitate longevity under these conditions (Soludukin 1977).

In the nursery, untreated seeds may be sown in the fall (Read 1974) or stratified through winter for spring-seeding (Yerkes 1945). It is suggested that the best time for spring sowing is when the mean daily soil temperature has reached 8 to 10 °C (Antonyuk 1987). Trees may also be propagated vegetatively by root cuttings or shoot cuttings (Bailey 1947; Dirr and Heuser 1987).

**References**

Antonyuk ED. 1987.   Growth of seedlings in a polythene greenhouse in relation to sowing times. Lesnoe Khozyaistvo 4: 36–37.
Atkimockin NG. 1960.   [in Russian: Trials with *Phellodendron* spp. at the Forest-Steppe Experiment Station [abstract]. Byulleten Glavnogo Botanicheskogo Sada [Moskva] 37: 30–33.
Bailey LH. 1947.   Standard cyclopedia of horticulture. 2nd ed. New York: Macmillan. 1388 p.
Blackburn BC. 1952.   Trees and shrubs of eastern North America. New York: Oxford University Press. 358 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 cultivation: from seed to tissue culture. Athens, GA: Varsity Press. 239 p.
Everett TH. 1964.   New illustrated encyclopedia of gardening. Volume 8. New York: Greystone Press: 1455–1456.
Gorokhova GI. 1981.   Fruiting of far-eastern species of plants under conditions of the forest steppe zone of western Siberia. Soviet Journal of Ecology 12 (4): 219–222 [translated and published 1982].
Gorokhova GI. 1986.   Effect of drought on the seed quality of exotic plants from the Soviet East [abstract]. Byulleten Glavnogo Botanicheskogo Sada [Moskva] 139: 85–89.
Hensley DL, Wiest SC, Long CE, Pair JC, Gibbons FD III. 1991.   Evaluation of 10 landscape trees for the Midwest. Journal of Environmental Horticulture 9(3): 149–155.

Hoag DG. 1965. Trees and shrubs of the northern plains. Minneapolis: Lund Press. 376 p.

Izmodenov AG. 1972. Multiple use of *Pinus koraiensis* forests [English abstract]. Moscow: Lenaya Promyshlenoost. 122 p.

Krecetova NV. 1960. [in Russian: The biology of flowering and fertilization in *P. amurense*. abstract]. Botanicheskii Zhurnal 45(9): 1336–1340.

Letkovskij AI. 1960. [in Russian: Planting *Phellodendron amurense* to increase the productivity of Scots pine forest (in Belorussia.)] Lesnaya Hortus 12(1): 36–37 [Forestry Abstracts 23: 548, 1962].

Lewis CE. 1957. American elm substitutes. American Nurseryman 106(10): 10–11, 50–51.

Lin TP, TW Hu, Leu JJ. 1979. The effect of alternating temperatures on the germination of the seed of *Phellodendron* spp. [abstract]. Bulletin of the Taiwan Forest Research Institute 322: 1–10.

Lin TP, Chen MH, Lin CH. 1994. Dormancy in seeds of *Phellodendron wilsonii* is mediated in part by abscisic acid. Plant Cell Physiology 35(1): 115–119.

Mukai Y, Yokoyama T. 1985. Effect of stratification on seed germination of *Phellodendron amurense* [abstract]. Journal of the Japanese Forestry Society 67(3): 103–104.

Necaev AD, Pelmenev VK. 1965. [in Russian: The importance of *Phellodendron amurense* as a nectar-bearing species.] Rastitel'nye Resursy [Moskva] 1(3): 419–423 [Forestry Abstracts 28: 621; 1967].

Ota M and others. 1965. [in Japanese: A study of the manufacturing conditions and properties of SIS hardboard from the inner bark of Kihada (*Phellodendron amurense* Rupr.).] Wood Industries Tokyo 20(6): 13–16 [Forestry Abstracts 27: 1475; 1966].

Read RA. 1974. *Phellodendron amurense* Rupr., Amur corktree. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 578–579.

Rehder A. 1940. Manual of cultivated trees and shrubs. 2nd ed. New York: Macmillan. 996 p.

Schechter MS. 1943. The insecticidal principle in the fruit of Amur corktree (*Phellodendron amurense*). Journal of Organic Chemistry 8: 194–197.

Soludukhin ED. 1977. Features of the regeneration of *Phellodendron amurense* [abstract]. Lesnoe Khozyaistvo 4: 32–33.

Starshova NP. 1972. The 'anthecology' of *Phellodendron amurense* in the middle Volga region: 1. Ecology of flowering. Botanicheskii Zhurnal 57(11): 1402–1412.

Swingle CF, comp. 1939. Seed propagation of trees, shrubs, and forbs for conservation planting. SCS-TP-27, Washington, DC: USDA Soil Conservation Service. 198 p.

Timm GT. 1989. Effect of stratification on the field germination rate of some tree seed. Journal of the Korean Forestry Society 78(1): 26–29.

Yerkes GE. 1945. Propagation of trees and shrubs. Farm. Bull. 1567 (rev.) Washington, DC: USDA. 54 p.

Hydrangeaceae—Hydrangea family

# *Philadelphus* L.

## mock orange

Nancy L. Shaw, Emerenciana G. Hurd, and Peter F. Stickney

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**Growth habit, occurrence, and use.** The mock oranges—*Philadelphus* spp.—have been placed in several families: Saxifragaceae (Harrington 1954), Hydrangeaceae (Hitchcock and others 1961), and more recently, the Philadelphaceae (Hickman 1993). Hydrangeaceae, however, is the most widely accepted placement (Cronquist and others 1997; USDA NRCS 2001). There are about 50 to 65 species of mock orange, occurring primarily in temperate and subtropical areas of the Northern Hemisphere. Four or five species are native to the United States. Two of these—Lewis mock orange (*Philadelphus lewisii* Pursh) and littleleaf mock orange (*P. microphyllus* Gray)—occur in the western United States and are used in wildland as well as in ornamental plantings (table 1). Both western species are erect to rounded, multi-stemmed, deciduous shrubs with opposite, entire or nearly entire leaves and fragrant white flowers (Hickman 1993; Munz amd Keck 1973; Welsh and others 1987).

Lewis mock orange, the state flower of Idaho, was named for Captain Meriwether Lewis, who collected the plant in 1806. It is an extremely variable plant, growing from 1.5 to 3 m tall and producing leaf blades that are 25 to 75 mm long. The species is distributed from British Columbia to California and eastward into Montana (table 1).

It exhibits wide ecological amplitude, growing in riparian areas and on cliffs, talus slopes, and rocky hillsides from the big sagebrush (*Artemisia tridentata* Nutt.) zone to ponderosa pine (*Pinus ponderosa* Dougl.) and lodgepole pine (*Pinus contorta* Dougl.) forests at elevations from sea level to 2,440 m (Hitchcock and others 1961; Hopkins and Kovalchik 1983).

Littleleaf mock orange is a smaller plant, ranging from 0.9 to 2 m in height and producing leaf blades 8 to 25 mm long. It is distributed from Utah to central Mexico (table 1) and grows in pinyon–juniper, mountain brush, aspen (*Populus tremuloides* Michx.), lodgepole pine, Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and white fir (*Abies concolor* Lindl.) communities (Hitchcock 1943; Welsh and others 1987).

Both species furnish excellent cover and habitat for wildlife. Lewis mock orange provides good browse for deer (*Odocoileus* spp.) and elk (*Cervus elaphus*), especially on some winter ranges (Kufeld 1973; Leege 1968; Marchant and Sherlock 1984; USDA Forest Service 1937). It is usually not grazed heavily by livestock, but in some areas it does receive fair amounts of use (Leege 1968; USDA Forest Service 1937). Plants resprout and are often more palatable following fire (Leege and Hickey 1971; USDA Forest

| Table 1—*Philadelphus,* mockorange: nomenclature and occurrence | | |
|---|---|---|
| **Scientific name & synonym(s)** | **Common name(s)** | **Occurrence** |
| ***P. lewisii* Pursh**<br>*P. californicus* Benth.<br>*P. gordonianus* Lindl.<br>*P. columbianus* Koehne<br>*P. gordonianus* var. *columbianus* Rehd. | **Lewis mock orange,**<br>Indian arrowwood,<br>syringa*, wild mock orange | British Columbia, SW Alberta, Washington,<br>Oregon, Idaho N of the Snake River,<br>Montana E of the Continental Divide, & N California |
| ***P. microphyllus* Gray**<br>*P. nitidus* A. Nels.<br>*P. stramineus* Rydb. | **littleleaf mock orange,**<br>little-leaf mock orange,<br>desert mockorange | Idaho, Nevada, Utah, SE Wyoming, W Colorado,<br>SE California, Arizona, New Mexico,<br>W Texas, N Mexico |

Sources: Conquist and others (1997), Davis (1952), Hickman (1974), USDA ARS (2002), Welsh and others (1987).
* This common name, although widely used, creates some confusion, as it also the generic name of the lilacs, to which the mock orange bears some resemblance.

Service 1937). Quail (*Callipepla* spp.) and squirrels consume Lewis mock orange seeds (Van Dersal 1938). Mule deer (*O. hemionus*) browse littleleaf mock orange (Patton and Ertl 1982).

Mock oranges are valuable plants for revegetating disturbances on steep, rocky, unstable slopes within their native ranges (Stevens and others 2004). Seedlings or larger stock are recommended for planting such sites. Mock oranges are also useful for planting in drier areas of degraded riparian zones.

Mock orange species and their cultivars are used as ornamentals. Lewis mock orange was first cultivated in 1823 or 1884, and littleleaf mock orange in 1883 (Rehder 1940). Both are used as borders, screens, and hedges or as isolated specimens in sunny areas. They can also be used for low-maintenance landscaping and in recreational area plantings (Kruckeberg 1982, Sutton and Johnson 1974, Wright 1980). They do well on a wide variety of soils and require little maintenance. Plants grow vigorously, flower reliably, and are generally free of insect and disease problems.

Native Americans used stems of Lewis mock orange for making arrows (USDA FS 1937). Flowers are used in preparing perfumes and teas (Taylor 1972).

**Genetic variation and hybridization.** Natural variability in mock orange floral and vegetative characteristics is extensive and has contributed to development of the complex synonymy for each species (Cronquist and others 1997; Hickman 1993; Hitchcock and others 1961; Holmgren and Reveal 1966; Hu 1955; Rydberg 1905). This variability has been exploited to develop numerous hybrids (Rehder 1940; Rydberg 1905) and several ornamental cultivars (Wright 1980). 'Waterton' Lewis mock orange, selected from the Waterton Lakes area of Alberta, is a hardy, bushy shrub with flowers scattered over the crown of the plant (Taylor 1972). The *P. lemoinei* (*P. coronarius* × *P. microphyllus*) group of hybrids exhibit the pineapple scent and beauty of their littleleaf mock orange parent (Sutton and Johnson 1974; Wright 1980).

**Flowering and fruiting.** Mock orange flowers are white, fragrant, and showy, with 4 (5) petals and numerous stamens. They are produced in few-flowered cymes at the ends of shoots formed the previous year. Western species flower from May to July (Hitchcock and others 1961; Munz and Keck 1973; Orme and Leege 1980). Fruits are woody, turbinate, loculicidal capsules that mature in late summer (figure 1); those of Lewis mock orange dehisce in September or October (Marchant and Sherlock 1984; Orme and Leege 1980). The seeds are dispersed by wind and gravity.

Seeds of both species are slender, 3 mm long, pale brown, and caruncular with a thick, brown seedcoat (Hurd 1995; Taylor 1972) (figures 1 and 2). The embryo is cylindrical and well developed (figure 2). A thin layer of endosperm adheres to the seedcoat. Lewis mock orange plants grown from seed may begin flowering in the second or third year (Everett 1957).

**Figure 1**—*Philadelphus lewisii,* Lewis mock orange: capsules and cleaned seed.



**Figure 2**—*Philadelphus lewisii,* Lewis mock orange: longitudinal sections of a seed.
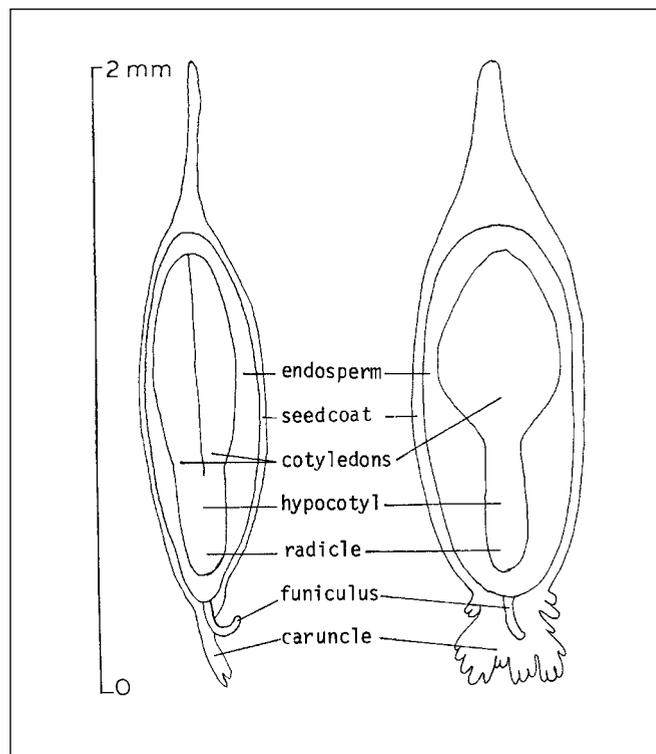
**Collection, cleaning, and storage of seeds.** Mock orange seeds are collected in late summer by hand-stripping the capsules after they have turned dark brown and the valves have just begun to open (Stevens and others 2004). After drying, seeds are extracted by crushing the capsules with a barley de-bearder, or if most capsules have opened, seeds are separated from coarse debris using an aspirator or air-screen machine (Glazebrook 1941). Shaking or crushing the dried capsules and screen to remove debris cleans small lots. The number of cleaned seeds of Lewis mock orange was estimated at 11,600,000/kg (5,300,000/lb), with a range of 7,700,000 to 18,000,000 (3.5 to 8 million/lb) (Glazebrook 1941; Hurd 1995; Mirov and Kraebel 1939; Swingle 1939). Fill of cleaned seedlots varies with rigor of cleaning. Acceptable purity for commercial seed purchases is 95% and acceptable germination is 65% (Jorgensen 2004).

Seeds of Lewis mock orange can be sown as soon as they are ripe or placed in storage for later planting. Reports of longevity vary, but the seeds appear to be orthodox in storage behavior. Refrigerated storage has been recommended (Marchant and Sherlock 1984). Taylor (1972) reported that dry seeds could be stored in airtight containers in a cool place for 1 year.

**Germination.** Seeds of Lewis mock orange reportedly require light for germination (Dirr and Heuser 1987), but exposure to continuous light or darkness may be inhibitory (Glazebrook 1941). Germination is enhanced by 20 to 75 days of wet prechilling at 0 to 5 °C (Dirr and Heuser 1987; Marchant and Sherlock 1984; Stickney 1974). Germination seeds from 2 sources that were chilled for 8 weeks at 5 °C and incubated at 22 to 26 °C was 64% (Glazebrook 1941) and 52% (Mirov and Kraebel 1939). Without prechilling, germination of seeds from 4 Idaho and Oregon collections incubated at 15 or 20/10 °C (8/16 hours) for 28 days was 12% or less (Shaw 1995) (table 2). A 28-day prechill at 3 to 5 °C improved germination with the increase greater when seeds were incubated at 15 °C compared to 20/10 °C (table 2).

Littleleaf mock orange is readily propagated from seeds (Sutton and Johnson 1974; Swingle 1939). Germination of untreated seeds collected in New Mexico was 12 times greater when they were incubated at 15 compared to 20/10 °C (8/16 hours) for 28 days (Shaw 1995) (table 2). Prechilling for 28 days at 3 to 5 °C improved germination if seeds were subsequently incubated at 20/10 °C, but decreased germination if they were incubated at 15 °C (table 2). Germination of both species is epigeal.

**Nursery practice.** Bareroot stock of Lewis mock orange may be produced by fall-seeding untreated seeds or by spring-seeding prechilled seeds (Stevens and others 2004). Uniformity of seed spacing may be improved by diluting the small seeds with rice hulls. Seeds should be covered very lightly. Seedlings develop rapidly and can be transplanted as 1-year-old stock.

Container stock may be grown from seeds (Atthowe 1993). Seedlings should be provided with shade for the first month and not watered excessively, as they are fragile and susceptible to damping-off (Taylor 1972). The 3-leaf stage should be attained before seedlings are transferred to larger containers.

**Table 2**—*Philadelphus,* mock orange: germination test conditions and results

| Species, seed source, & elevation | Seed fill (%) | Viability (%) | Wet prechill (days) | Percentage germination 15 °C | Percentage germination 20/10 °C |
|---|---|---|---|---|---|
| *P. lewisii* | | | | | |
| Banks, ID (830 m) | 98 | 96 | 0 | 1 | 1 |
| | 98 | 96 | 28 | 57 | 16 |
| Craters of the Moon National | 100 | 92 | 0 | 12 | 6 |
| Monument, ID (1,680 m) | 100 | 92 | 28 | 41 | 23 |
| Grant Co., OR (1,020 m) | 100 | 90 | 0 | 8 | 5 |
| | 100 | 90 | 28 | 47 | 33 |
| Idaho City, ID (1,650 m) | 99 | 96 | 0 | 2 | 2 |
| | 99 | 96 | 28 | 34 | 33 |
| *P. microphyllus* | | | | | |
| Sandoval Co., NM (2,380 m) | 98 | 63 | 60 | 5 | |
| | 98 | 63 | 28 | 44 | 20 |

**Sources:** Shaw (1995).
**Note:** Seeds were prechilled at 3 to 5 °C and then incubated at 15 or 20/10 °C (8/16 hours) for 0 or 28 days. The percentage germination was then determined. For 28 days of incubation, seeds were exposed to 8 hours of light (PAR=350 $\mu$Mol/m$^2$/sec) each day. Exposure corresponded to the high temperature period of the alternating temperature regime. Viability is based on the percentage of viable seeds to germinate normally.

Mock orange is easily propagated from softwood or hardwood cuttings, rooted suckers, divisions, or layers (Hartmann and others 1990; Macdonald 1986; Sutton and Johnson 1974). Softwood cuttings harvested in midsummer root readily under a mist system. Root production is enhanced by treatment with 1,000 ppm indole butyric acid (IBA) (Dirr and Heuser 1987; Marchant and Sherlock 1984). Hardwood cuttings may be harvested and planted in fall or early spring (Hartmann and others 1990; Macdonald 1986). These should be treated with 2,500 to 8,000 ppm IBA. Both types of cuttings can also be rooted in a cold frame (Macdonald 1986; Marchant and Sherlock 1984).

**Field practice.** Mock orange seeds may be broadcast seeded on a rough seedbed and covered lightly or spot-seeded on prepared seedbeds (Stevens and others 2004). Seeds may also be surface-planted using a seeder that presses the seeds into the soil surface. Best results are obtained if seeds are planted in well-drained sites free of herbaceous competition. Seeds may be mixed with other shrub seeds that require surface or shallow planting.

Mock orange seedlings quickly develop a fibrous root system and transplant easily as bareroot or container stock (Everett 1957; Sutton and Johnson 1974). Youtie (1991, 1992) obtained good survival of Lewis mock orange planting stock grown from cuttings and planted on a disturbed site in the Columbia River Gorge. Plant growth is reportedly slow for Lewis mock orange (Taylor 1972) and moderate to rapid for littleleaf mock orange (Sutton and Johnson 1974).

### References

Atthowe H. 1993. Propagation of riparian and wetland plants. In: Landis TD, tech. coord. Proceedings, Western Forest Nursery Association; 1992 September 14–18; Fallen Leaf Lake, CA. Gen. Tech. Rep. RM-221. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: 78–81.

Cronquist A, Holmgren NH, Holmgren PK. 1997. Intermountain flora, vascular plants of the Intermountain West, U.S.A. Volume 3, Part A subclass Rosidae (except Fabales). Bronx., NY: New York Botanical Garden. 446 p.

Dirr MA, Heuser CW. 1987. The reference manual of woody plant propagation. Athens, GA: Varsity Press. 239 p.

Everett PC. 1957. A summary of the culture of California plants at the Rancho Santa Ana Botanic Garden. Claremont, CA: Rancho Santa Ana Botanic Garden. 223 p.

Glazebrook TB. 1941. Overcoming delayed germination in the seed of plants valuable for erosion control and wildlife utilization [thesis]. Moscow, ID: University of Idaho. 97 p.

Harrington HD. 1954. Manual of the plants of Colorado. Denver: Sage Books. 665 p.

Hartmann HT, Kester DE, Davies FT Jr. 1990. Plant propagation principles and practices. 5th ed. Englewood Cliffs, NJ: Prentice-Hall. 657 p.

Hickman JC. 1993. The Jepson manual: higher plants of California. Berkeley: University of California Press. 1400 p.

Hitchcock CL. 1943. The xerophyllous species of *Philadelphus* in southwestern North America. Madroño 17: 35–56.

Hitchcock CL, Cronquist A, Ownbey M, Thompson JW. 1961. Vascular plants of the Pacific Northwest: 3. Saxifragaceae to Ericaceae. Seattle: University of Washington Press. 614 p.

Holmgren AH, Reveal JL. 1996. Checklist of the vascular plants of the Intermountain Region. Res. Pap. INT-32. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station.

Hopkins WE, Kovalchik BL. 1983. Plant associations of the Crooked River National Grassland. R6 Ecol. 133-1983. Portland, OR: USDA Forest Service, Pacific Northwest Region. 98 p.

Hu SY. 1955. A monograph of the genus *Philadelphus*. Journal of the Arnold Arboretum 36: 52–109.

Hurd EG. 1995. Unpublished data. Boise, ID: USDA Forest Service, Intermountain Research Station.

Jorgensen K. 2004. Appendix II. In: Monsen SB, Stevens R, Shaw NL, comps. Restoring western ranges and wildlands Gen. Tech. Rep. RMRS-136. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station.

Kruckeberg AR. 1982. Gardening with native plants of the Pacific Northwest. Seattle: University of Washington Press. 252 p.

Kufeld RC. 1973. Foods eaten by the Rocky Mountain elk. Journal of Range Management 26: 106–113.

Leege TA. 1968. Prescribed burning for elk in northern Idaho. Proceedings of the Annual Tall Timbers Fire Ecology Conference 8: 235–253.

Leege TA, Hickey WO. 1971. Sprouting of northern Idaho shrubs after prescribed burning. Journal of Wildlife Management. 35(3): 508–515.

Macdonald B. 1986. Practical woody plant propagation for nursery growers. Vol. I. Portland, OR: Timber Press. 669 p.

Marchant C, Sherlock J. 1984. A guide to selection and propagation of some native woody species for land rehabilitation in British Columbia. For. Res. Rep. RR-84007-HQ. Victoria, BC: Ministry of Forests. 117 p.

Mirov NT, Kraebel CJ. 1939. Collecting and handling seeds of wild plants. For. Pub. 5. Washington, DC: USDA Civilian Conservation Corps. 42 p.

Munz PA, Keck DD. 1973. A California flora and supplement. Berkeley: University of California Press. 1681 p.

Orme ML, Leege TA. 1980. Phenology of shrubs on a north Idaho elk range. Northwest Science 54: 187–198.

Patton DR, Ertl MG. 1982. Run wild: wildlife/habitat relationships. Wildlife Unit Tech. Ser. Washington, DC: USDA Forest Service. 49 p.

Rehder A. 1940. Manual of cultivated trees and shrubs. 2d ed. New York: Macmillan. 996 p.

Rydberg PA. 1905. North American Flora 22: 162–175.

Shaw NL. 1995. Unpublished data. Boise, ID: USDA Forest Service, Intermountain Research Station.

Stevens R, Monsen SB, Shaw NL. 2004. Shrubs of other families. In: Monsen SB, Stevens R, comps. Restoring western ranges and wildlands Gen. Tech. Rep. RMRS-136. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station.

Stickney PF. 1974. *Philadelphus lewisii* Pursh, Lewis mockorange. In: Shopmeyer CS, tech. coord. Seeds of woody plants in the United States. USDA Agric. Handbk. 450. Washington, DC: USDA Forest Service: 580–581.

Sutton R, Johnson CW. 1974. Landscape plants from Utah's mountains. EC-368. Logan: Utah State University. 137 p.

Swingle CF, comp. 1939. Seed propagation of trees, shrubs, and forbs for conservation planting. SCS-TP-27. Washington, DC: USDA Soil Conservation Service. 198 p.

Taylor S. 1972. *Philadelphus lewisii* Pursh 'mock orange' or 'syringa'. Davidsonia 3: 4–7.

USDA ARS [USDA Agricultural Research Service]. 2001. Germplasm Information Network (GRIN)[online datbase]. Beltsville, MD: National Genetic Resources Program.

USDA Forest Service. 1937. Range plant handbook. Washington, DC. 512 p.

USDA NRCS [USDA National Resources Conservation Service]. 2001. The PLANTS Database, version 3.1[http://plants.usda.gov]. Baton Rouge, LA: USDA NRCS National Plant Data Center.

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.

Welsh SL, Atwood ND, Higgins LC, Goodrich S. 1987. A Utah flora. Great Basin Naturalist 9: 1–894.

Wright D. 1980. *Philadelphus*. Plantsman 2: 104–116.

Youtie BA. 1991. Native plants delight visitors at Columbia Gorge plot. Park Science 11: 4–5.

Youtie BA. 1992. Biscuit scabland restoration includes propagation studies (Oregon). Restoration & Management Notes 10: 79–80

Rosaceae—Rose family

# *Heteromeles arbutifolia* (Lindl.) M. Roemer
## Christmasberry

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**Growth habit, occurrence, and uses.** The genus *Heteromeles* has only a single species—*H. arbutifolia* (Lindl.) M. Roemer, also known as *H. salicifolia* (K. Presl.) Abrams (Phipps 1992). It is closely related to the large tropical genus *Photinia* Lindl., to which it has sometimes been referred. Christmasberry, also known as toyon, California-holly, and hollywood, is a long-lived shrub or small tree, 2 to 10 m in height, that sprouts freely after fire from a subterranean burl. It has shiny, leathery, evergreen leaves that are sharply toothed along the margins. A common constituent of chaparral vegetation throughout California and Baja California, it is usually found on less harsh, more mesic microsites. Christmasberry is useful for erosion control, is a source of honey, and has leaves and fruits that provide food for wildlife. It has also been widely planted in California as an ornamental for park, freeway, and home landscape use (Magill 1974). The attractive foliage and fruits are cut and used for their decorative value.

**Flowering and fruiting.** Unlike many chaparral shrubs, Christmasberry is summer-flowering (Magill 1974). The numerous, small flowers are borne in flat-topped or convex terminal inflorescences. The flowers are perigynous and have 5 separate petals, 10 stamens, and a 2- to 3-carpellate ovary. The fruits are bright red to orange, 2- or 3-seeded juicy pomes that are 6 to 10 mm in diameter. They ripen from October through January and are dispersed by birds. Good crops are reported to occur yearly (Keeley 1992).

**Seed collection, cleaning, and storage.** Christmasberry fruits may be clipped or stripped from the branches once they have attained a bright red or orange color (Magill 1974). They should be soaked in water and allowed to ferment slightly. (However, too-long a soaking period can damage the seeds, which have soft, pliable seedcoats.) The seeds (figure 1 and 2) may then be separated from the pulp by passage through a macerator, followed by flotation to remove the pulp. Small lots can be hand-rubbed through a large-holed screen. The seeds may then be allowed to dry. Once dry, any flat, unfilled seeds can be removed by screening.

**Figure 1**—*Heteromeles arbutifolia,* Christmasberry: seeds.



Christmasberry seed weight is apparently highly variable. Magill (1974) reported a mean seed weight of 19 mg and count of 52,630 seeds/kg (23,900/lb), whereas Keeley (1991) reported a seed weight of 5.5 mg and count of 181,820/kg (82,500/lb). Martineja and Bullock (1997) examined Christmasberry seed weight as a function of habitat variables. They found no correlation with latitude or annual precipitation but did find a significant increase in seed weight with increasing elevation. Overall mean seed weight for their 12 Christmasberry populations was 36 mg and seed count was 27,800 seeds/kg (12,600/lb), with weight ranges of 28 to 49 mg and counts of 20,400 to 35,700 seeds/kg (9,200 to 16,200/lb).

Christmasberry seeds have limited longevity at room temperature, but they are probably orthodox in storage behavior. Keeley (1991) reported a shelf life of less than 1 year in laboratory storage. The seeds were also damaged or killed by high temperature treatments. One hour at 70 °C reduced viability from 99 to 33%, and 5 minutes at 120 °C resulted in essentially complete mortality (Keeley 1987). Magill (1974) recommended sealed storage at low tempera-

**Figure 2**—*Heteromeles arbutifolia*, Christmasberry: longitudinal section through a seed.



**Figure 3**—*Heteromeles arbutifolia*, Christmasberry: young seedling (**left**) and older seedling (**right**).
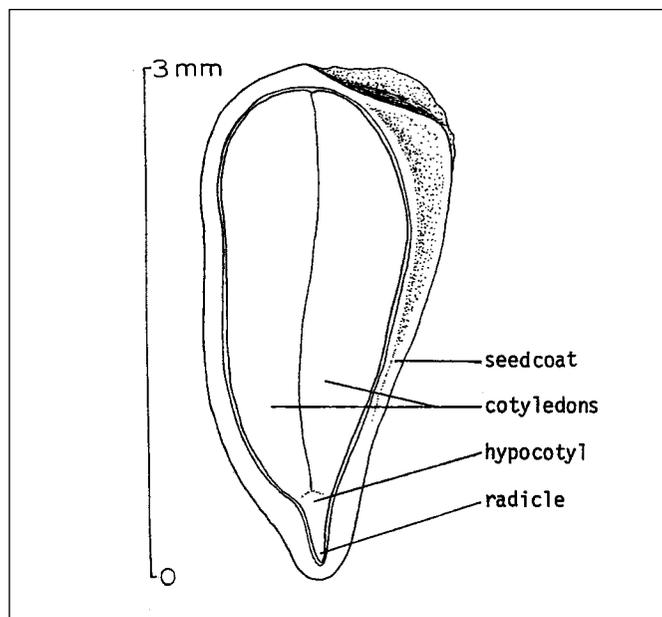


ture but did not give any data on viability retention under these conditions.

**Germination and seed testing.** Christmasberry seeds are reported to be nondormant at dispersal (Emery 1988; Keeley 1987; Magill 1974), whereas seeds that have been stored are rendered secondarily dormant and require 3 months of chilling at 3 to 5 °C in order to germinate. Under field conditions, Christmasberry seeds germinate within a few months of dispersal and do not form a persistent seedbank (Parker and Kelly 1989). Germination is epigeal (figure 3). Recruitment of new individuals is rarely observed. Although winter seedling emergence is a common occurrence, the seedlings almost invariably die, either from herbivory or summer drought (Parker and Kelly 1989). Because of the transient seed bank, there can be no recruitment after fire, and new recruitment is in fact restricted to chaparral stands that have been free of fire for at 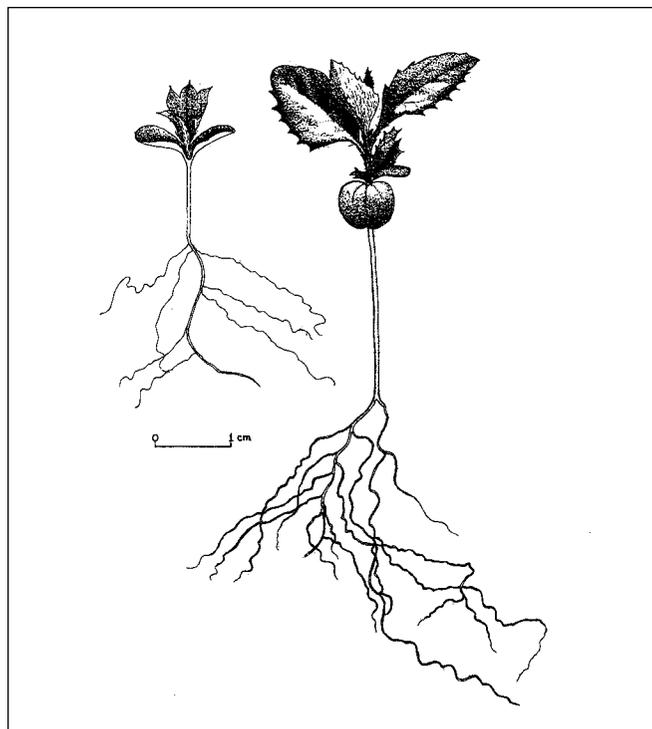least 50 years (Keeley 1992). The seedlings are not very drought-tolerant and seem to need the shade and the deep litter that develops under adult shrub canopies in old stands in order to survive.

Recently harvested lots of Christmasberry seeds that are well-cleaned to remove unfilled seeds generally have high fill and high viability. Keeley (1987) reported germination of 99% at 23 °C. Such lots should be relatively easy to evaluate, either with a germination test or with tetrazolium staining. A 3-month chill at 5 °C followed by a germination test of 28 days at 20 or 25 °C should give maximum germination. Christmasberry seeds have no endosperm, and the embryo completely fills the seed cavity (figure 2). A procedure similar to that used for apple (*Malus* spp.) or bitter-

brush (*Purshia* spp.) can be used for tetrazolium evaluation. The seeds should be soaked in water overnight, then clipped at the cotyledon end. The embryos can then be gently squeezed out, immersed in 1% tetrazolium chloride for 6 hours at room temperature, and examined for staining patterns. Older seedlots that have begun to lose viability and germinate sporadically will probably also have ambiguous tetrazolium staining patterns.

**Field seeding and nursery practice.** Christmasberry would probably be difficult to direct-seed in a wildland setting because of its establishment requirements (Keeley 1992). The seedlings require shady, moist conditions and deep litter, so they would have difficulty getting established on the open disturbances that characterize most wildland seeding projects. Christmasberry is easily propagated from seeds in a nursery setting, however. The seeds maybe planted in flats in sand or soil. If freshly harvested seeds are used, no pretreatment is necessary, and seedlings emerge over a period of 10 to 40 days (Magill 1974). Emergence of 73% has been reported in one case. The seeds may also be planted outdoors in nursery beds. Chilling before spring-planting is recommended (Magill 1974). Greever (1979) reported 100% emergence from March sowing in sand and that there was little difference in seedling size between December and March sowings by May. Propagation by grafting or cuttings is also practiced (Greever 1979; Magill 1974).

## References

Emery DE. 1988. Seed propagation of native California plants. Santa Barbara, CA: Santa Barbara Botanic Garden. 107 p.

Greever PT. 1979. Propagation of *Heteromeles* (*Photinia*) *arbutifolia* by softwood cuttings or by seed. Plant Propagator 25 (2): 10–11.

Keeley JE. 1987. Role of fire in seed germination of woody taxa in California chaparral. Ecology 68: 434–443.

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.

Magill AW. 1974. *Photinia arbutifolia* Lindl., Christmasberry. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 582–583.

Martineja NE, Bullock SH. 1997. Geographic variation in seed mass in the chaparral shrub *Heteromeles arbutifolia* (Rosaceae). Southwestern Naturalist 42: 119–121.

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: 231–255.

Phipps JB. 1992. *Heteromeles* and *Photinia* (Rosaceae, subfam. Maloideae) of Mexico and Central America. Canadian Journal of Botany 70: 2138–2182.

Rosaceae—Rose family

# *Physocarpus* (Camb.) Raf.

## ninebark

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**Growth habit, occurrence, and use.** The genus *Physocarpus* includes about 6 species of deciduous, spiraea-like shrubs with exfoliating bark, alternate and lobed leaves resembling *Ribes*, and small white to pinkish flowers in corymbs. The common name, ninebark, probably refers to the use of the plant in a number of medicinal cures (Stokes 1981) or the numerous layers of bark that peel off (Strausbaugh and Core 1978). Five species are native to North America, and one is introduced from Asia (table 1). Three subspecies of dwarf ninebark—*P. alternans* ssp. *alternans, P. a*. ssp. *annulatus* J.T. Howell, and *P. a*. ssp. *panamintensis* J.T. Howell—are recognized (USDA NRCS 2001). Although the genus is not wide-spread, certain species may be locally abundant because of root sprouting. Atlantic ninebark and common ninebark, 2 varieties of *opulifolius* — the specific epithet refers to *Viburnum opulus,* an introduced species from Europe (Stokes 1981)—are the most common species in the eastern United States and are found along streams, riverbanks, and moist hillsides. Atlantic ninebark grows to 1.5 m, whereas common ninebark may be twice that height. A dense, compact cultivar of Atlantic ninebark named 'Nugget' produces golden yellow foliage in the spring that matures to orange-bronze (Higginbotham 1990). Of the western species, dwarf ninebark is found mostly in rocky canyons and low-elevation forests of California and grows to 1 m in height; mountain ninebark is found from foothill forests to mountain tops of the central and southern Rocky Mountains and grows to 1 m in height; mallow ninebark is found in rocky canyons and low-elevation open forests throughout the Rocky Mountains and grows to 2 m; and Pacific ninebark is found in moist to wet lowlands or foothills mostly west of the Cascade Range and grows to 3 m. A prostrate and rhizomatous cultivar of Pacific ninebark named 'Tilden Park' grows to a height of 1.5 m (Straley 1989).

Ninebark species and cultivars generally are hardy, do best in full sunlight or thin shade, and tolerate a wide variety of soil types (Krüssmann 1985). They are used primarily as ornamentals in landscaping or for watershed protection. Most of the species have been cultivated in the United States for nearly 100 years (table 1). In the wild, mallow ninebark sprouts prolifically from the root crown after spring and fall fires (Lea and Morgan 1993). Although the genus is reported to be remarkably free from insects and diseases (Everett 1981; Gill and Pogge 1974), at least 17 flower-eating, 63 leaf-and-stem-eating, and 4 seed-eating insects have been identified on common ninebark, including the flower-specialist mirids *Plagiognathus punctatipes* Knight and *Psallus physocarpi* Henry and seed-specialist torymids *Megastigmus gahani* Milliron and *M. physocarpi* Crosby (Wheller and Hoebeke 1985).

**Flowering and fruiting.** Flowers are complete, regular, and clustered together in terminal corymbs consisting of a few in mountain and mallow ninebarks, 3 to 6 in dwarf ninebark, and many in Pacific and common ninebarks. Flowers are from 0.5 to 1 cm in diameter, the corolla mostly white, sometimes pinkish to light pink in Pacific and mountain ninebarks. The 5 sepals are densely stellate pubescent to tomentose, except in Pacific ninebark, where they are sometimes glabrous (Krüssmann 1985). Flowers of Pacific ninebark appear in April through June, those of mountain ninebark appear in May through June, and those of mallow and common ninebarks in June.

The fruits are small, firm-walled, inflated follicles (figure 1); the generic name *Physocarpus* is derived from the Greek *physa* ("bladder" or "bellows") and *karpos* ("fruit"), referring to the bladder-shaped follicles (Stokes 1981). Follicles range in size from 5 mm in dwarf ninebark to 11 mm in Pacific ninebark. They are solitary in dwarf ninebark and sometimes mountain ninebark; paired in mallow ninebark and sometimes mountain ninebark; and

**Table 1**—*Physocarpus,* ninebark:   nomenclature, occurrence, and first cultivation

| Scientific name & synonyms | Common name | Occurrence | First cultivated |
|---|---|---|---|
| **P. alternans (M.E. Jones) J.T. Howell**<br>*Neillia monogyna* var. *alternans* Jones<br>*Opulaster alternans* Heller | **dwarf ninebark** | California to Nevada | — |
| **P. amurensis (Maxim.) Maxim.**<br>*Spiraea amurensis* Maxim. | **Amur ninebark** | Manchuria & Korea | 1856 |
| **P. capitatus (Pursh) Kuntze**<br>*Spiraea capitatus* Pursh | **Pacific ninebark** | Alaska, British Columbia,<br>Montana, south to California | 1827 |
| **P. malvaceus (Greene) Kuntze**<br>*Neillia malvacea* Greene<br>*Opulaster malvaceus* (Greene) Kuntze ex Rydb.<br>*Opulaster pauciflorus* (Torr. & A. Gray) Heller<br>*Opulaster pubescens* Rydb.<br>*P. pubescens* (Torr. & A. Gray) Piper<br>*P. pubescens* (Rydb.) A. Nels.<br>*P. pauciflorus* Piper ;   *Spiraea opulifolia* L. | **mallow ninebark** | British Columbia to Montana,<br>south to Oregon, Utah, &<br>Wyoming | 1897 |
| **P. monogynus (Torr.) Coult.**<br>*Opulaster hapmanii* Rydb.<br>*Opulaster monogynus* Kuntze<br>*P. torreyi* (S. Wats.) Maxim. | **mountain ninebark** | South Dakota to Texas,<br>Arizona, Nevada | 1889 |
| **P. opulifolius (L.) Maxim.**<br>*Opulaster alabamensis* Rydb.    *O. australis* Rydb.<br>*O. opulifolius* (L.) Kuntze;    *O. stellatus* Rydb.<br>*Spiraea opulifolia* L. | **common ninebark** | Maine to Minnesota, S<br>to Tennessee & Florida | 1687 |
| **P. opulifolius (L.) Maxim. var.<br>  intermedius (Rydb.) Robins.**<br>*Opulaster intermedius* Rydb.<br>*P. intermedius* (Rydb.) Schneid.<br>*P. missouriensis* Daniels;    *P. ramaleyi* A. Nels. | **Atlantic ninebark**<br><br>Missouri | Quebec to North Dakota,<br>S to Colorado, Arkansas, & | 1908 |

number 3 to 5 in Amur, Pacific, common, and Atlantic ninebarks. When mature, the follicles tend to be brown, reddish, or coppery in color, glabrous in common ninebark and sometimes Pacific ninebark, otherwise stellate-pubescent. Follicles burst open at both sutures when mature. They seldom fall of their own weight but are easily dislodged by wind or snow. Some fruits may persist until the end of winter (Gill and Pogge 1974). Each follicle may contain several seeds, which are shiny and pyriform (figures 1 and 2). Seed ripening is indeterminate and does not always result in good fill (Link 1993).

**Collection, extraction, and storage.**    Ripe fruits can be picked from the shrubs or shaken onto dropcloths, dried either naturally or with artificial heat, and then threshed with a hammermill, and cleaned. Seeds of common and Atlantic ninebark are extracted by dry maceration followed by hand-screening to remove debris and follicle fragments (Yoder 1995). Yields are about 1,650 clean seeds/g (46,800/oz) for mallow ninebark (Link 1993), 1,550 clean seeds/g (43,750/oz) for Pacific ninebark (USDA NRCS 2001), and

**Figure 1**—*Physocarpus opulifolius*, common ninebark: follicles (**above**) and seeds (**below**).
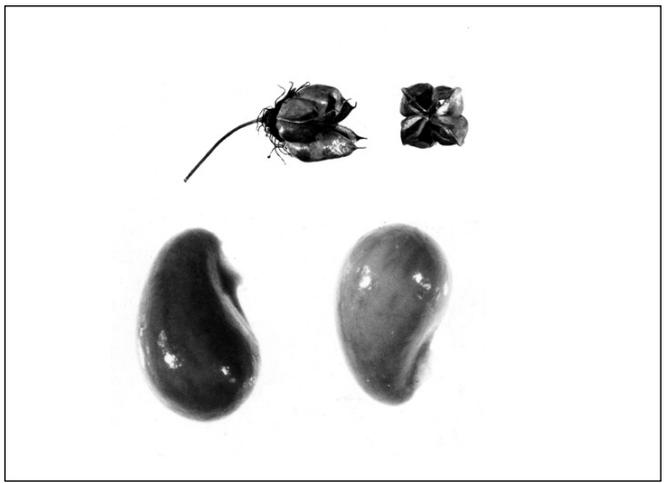


1,000 to 3,650 clean seeds/g (28,350 to 103,500/oz) for common ninebark (Gill and Pogge 1974). Viability is usually less than 50%. The seeds are orthodox and may be stored for at least 5 years when cool and dry (Link 1993).

**Figure 2**—*Physocarpus malvaceus*, mallow ninebark: long-itudinal sections through a seed.
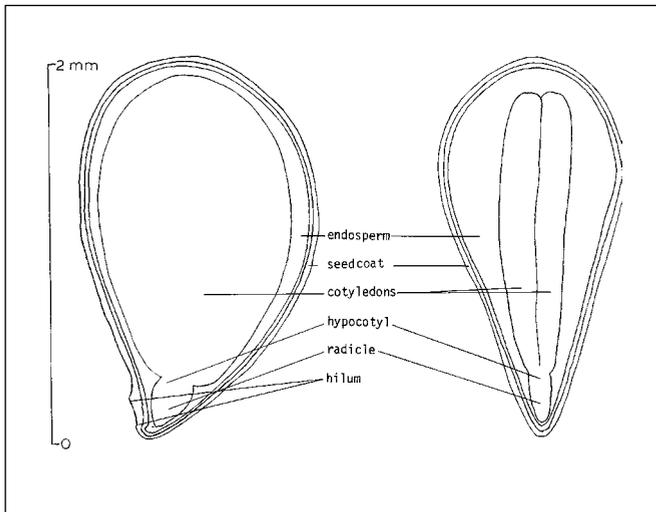


**Nursery practices.** Mallow ninebark seeds may be planted in the fall or planted in the spring after 30 days of prechilling (Link 1993). Seeds of common ninebark and Atlantic ninebarks are sown in raised beds either in the fall or in the spring after 60 days of prechilling (Yoder 1995). Seeds are mixed one part seeds to three parts (by volume) dry, sifted sawdust to provide bulk and facilitate even distribution; sown at a depth of about 3 mm ($^1/_8$ in); and mulched with a layer of sawdust about 6 mm ($^1/_4$ in) thick (Yoder 1995). The ninebarks are easily propagated by softwood cuttings planted under mist, or hardwood cuttings planted in the field (Everett 1981; Dirr and Heuser 1987).

## References

Dirr MA, Heuser CW Jr. 1987. The reference manual of woody plant propagation: from seed to tissue culture. Athens, GA: Varsity Press. 239 p.

Everett TH. 1981. The New York Botanical Garden illustrated encyclopedia of horticulture. New York: Garland Publishing. 3601 p.

Gill JD, Pogge FL. 1974. *Physocarpus,* ninebark. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 584–586.

Higginbotham JS. 1990. New plants for 1990. American Nurseryman 171(4): 26–40.

Lea SM, Morgan P. 1993. Resprouting response of ninebark (*Physocarpus malvaceus*) shrubs to burning and clipping. Forest Ecology and Management 56: 199–210.

Link E, ed. 1993. Native plant propagation techniques for National Parks, interim guide. East Lansing, MI: USDA Soil Conservation Service, Rose Lake Plant Materials Center. 240 p.

Krüssmann G. 1985. Manual of cultivated broad-leaved trees and shrubs. Vol. II. Portland, OR: Timber Press.

Strausbaugh PD, Core EL. 1978. Flora of West Virginia, 2nd ed. Grantsville, WV: Seneca Books. 1079 p.

Stokes DW. 1981. The natural history of wild shrubs and vines. New York: Harper & Row. 246 p.

Straley GB. 1989. A new cultivar of *Physocarpus capitatus* (Rosaceae). Baileya 23(1): 51–53.

USDA NRCS USDA Natural Resources Conservation Service]. 2001. PLANTS, Version 3.1 [database available at http://plants.usda.gov]. Baton Rouge, LA: National Plant Data Center.

Wheller AG, II, Hoebeke ER. 1985. The insect fauna of ninebark, *Physocarpus opulifolius* (Rosaceae). Proceedings of the Entomological Society of Washington 87(2): 356–370.

Yoder WG. 1995. Personal communication. Licking, MO: George O. White State Forest Nursery.

Pinaceae—Pine family

# *Picea* A. Dietr.

## spruce

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**Growth habit, occurrence, and use.** The spruce genus—*Picea*—includes 40 to 50 species of evergreen conifers native to the temperate and boreal regions of the Northern Hemisphere, occurring in Europe, Asia Minor, the Caucasus, Siberia, China, Japan, the Himalayas, and North America (table 1). The genus evolved from primordial ancestors in the northeastern mainland of Asia, with present-day Korean spruce likely the most primitive species. Most North American species probably arose through eastward migrated and mutation of Ezo spruce (Wright 1955). More recent work suggests a strong relation between the Old World Serbian spruce and the New World black spruce (Fowler 1980). At least 12 species occur in China (Li and others 1990). Seven species are native in North America, excluding the rare and localized occurrence of Chihuahua spruce—*P. chihuahuana* Martinez—in northwest Mexico (Rushforth 1986; Patterson 1988). The genus name is derived from the Latin *pix* or *picis,* "pitch", referring to the resinous qualities of the trees (Everett 1981) or of a pitch pine, probably Scots pine (*Pinus sylvestris* L.) (Little 1979).

The genus includes medium to tall conifers that range in height at maturity from 9 to over 70 m. Crowns of most species appear conical in outline. The generally small branches occur in whorls with common internodal branches. The needle-like leaves are borne on peg-like projections (pulvini) on the twigs, have angled or flattened cross section, and persist for several years. Needles fall readily from twigs on drying. The slender boles gradually taper along their entire length, sometimes from a buttressed base. The thin and scaly bark sometimes has furrows at the base of old trees. The generally shallow root systems have many long, stringy, and tough rootlets. Open-grown trees retain live branches to the ground, and in black spruce and sometimes Norway, Ezo, and white spruces, layering occurs when branch tips come in contact with moist soil, take root, and develop into full-size trees (Nienstaedt and Zasada 1990; Nikolov and Helmisaari 1992; Stone and McKittrick 1976; Viereck and Johnston 1990).

Members of the spruce genus grow on various soils and at all elevations up to treeline in the more northern latitudes. In more southern latitudes, spruce species usually inhabit cold, wet, or shallow soils of bogs or higher elevations on mountain slopes. Shade-tolerant spruce species often replace stands of birch (*Betula*), quaking aspen (*Populus tremuloides* Michx.), or other pioneer species on disturbed areas (Dallimore and Jackson 1967). Nursery and greenhouse cultivation currently provide seedlings and transplants of 7 North American and 8 introduced species for forestry or horticultural purposes in the United States (table 1).

The strong, light-weight, light-colored, fine-grained, even-textured, long-fibered wood of Engelmann, white, black, red, and Sitka spruces result in high-value timber. However, the restricted range, occurrence in inaccessible locations, and propensity for developing knots limits the commercial timber value of Brewer spruce (Thornburgh 1990). Specialty products have included violin faces and piano soundboards from Engelmann, white, red, and Sitka spruces; aircraft parts from Engelmann and Sitka spruces; and house logs from Engelmann and white spruces. The occurrence of most species at high elevations and on steep slopes or wet soils makes them important watershed protectors. The genus also provides important winter shelter for wildlife in the higher latitudes. Although some animals such as snowshoe hare (*Lepus americanus*), porcupine (*Erethizon dorsatum*), and black bear (*Ursus americanus*) may sometimes browse on spruce foliage or inner bark, neither wild or domestic animals prefer spruce as a food source (Alexander and Shepperd 1990; Blum 1990; Dallimore and Jackson 1967; Harris 1990; Nienstaedt and Zasada 1990; Viereck and Johnston 1990).

Tolerance of extreme exposure to wind and cold temperatures makes spruce especially well-suited to some shelterbelt planting. White, Norway, blue, and Sitka spruces have been widely used for this purpose. The relatively shallow root systems of Engelmann, white, blue, red, and Sitka spruces make these species susceptible to windthrow, how-

| Table I—*Picea*, spruce: nomenclature and occurrence of native and cultivated species in North America | | |
|---|---|---|
| **Scientific name & synonym(s)** | **Common name(s)** | **Occurrence** |
| **P. abies (L.) Karst.**<br>*P. excelsa* Link | **Norway spruce** | Native of Fennoscandia, W Europe<br>to Ural Mtns of central Russia;<br>widely planted in NE & central US |
| **P. asperata Mast.**<br>*P. crassifolia* Kamarov | **dragon spruce,**<br>Chinese spruce | Native of NW China; occasionally<br>cultivated in US |
| **P. breweriana S. Wats.** | **Brewer spruce,** weeping spruce | NW California & SW Oregon |
| **P. engelmannii Parry ex Engelm.**<br>*P. columbiana* Lemmon<br>*P. glauca* ssp. *engelmann* (Parry<br>  ex Engelmann) T.M.C. Taylor<br>*P. engelmanii* var. *glabrata* Goodman | **Engelmann spruce,**<br>mountain spruce | Rocky Mtns from British Columbia S<br>to Arizona & New Mexico; Cascade Range<br>in Washington & Oregon |
| **P. glauca (Moench) Voss**<br>*P. alba* (Aiton) Link<br>*P. alba* var. *albertiana* (S. Brown) Beiss.<br>*P. albertiana* S. Brown;    *P. canadensis* B.S.P.<br>*P. canadensis* var. *albertiana* (S. Brown) Rehder<br>*P. glauca* var. *albertiana* (S. Brown) Sarg.<br>*P. glauca* var. *posildii* Raup<br>*P. nigra* var. *glauca* Carr. | **white spruce,** Canadian<br>spruce, skunk spruce,<br>cat spruce, Black Hills spruce,<br>western & white spruce,<br>Alberta spruce, Porsild spruce | Norton Sound to Gulf of Alaska, E across<br>Canada from British Columbia SW Alberta<br>to Labrador, Newfoundland; also<br>in Black Hills of South Dakota |
| **P. glehnii (Fr. Schmidt) Mast.** | **Sakhalin spruce** | Native to Sakhalin & Hokkaido; planted in NE<br>US to Newfoundland |
| **P. jezoensis (Siebold & Zucc.) Carr.**<br>*P. ajanensis* (Lindley & Gordon)<br>  Fischer ex Carr.<br>*P. kamchatkensis* LaCassagne<br>*P. komarovic* Vasiljev<br>*P. microsperma* (Lindley) Carr. | **Ezo spruce,** yeddo spruce,<br>yezo spruce | Native of SE Russia, Shantar Islands,<br>Kamchatka Peninsula, Sakhalin Island,<br>S to NE China, N Korea, & N Japan |
| **P. koraiensis Nakai** | **Korea spruce,** Koyama spruce | N Korea, NE China, & Sikhote-Alin<br>Mtns of SE Russia |
| **P. mariana (Mill.) B.S.P .** | **black spruce,** bog spruce,<br>swamp spruce, eastern spruce | Alaska to Labrador, Newfoundland;<br>NE & N central US |
| **P. obovata Ledeb.**<br>*P. abies* var. *obovata* Lindquist | **Siberian spruce** | From White Sea & Kola Peninsula E<br>across Russia to Sea of Okhotsk |
| **P. omorika (Pancic) Purk.** | **Serbian spruce** | SE Europe |
| **P. pungens Engelm.**<br>*P. commutata* Horton *P. parryana* Sarg. | **blue spruce,** Colorado spruce,<br>Colorado blue spruce | Rocky Mtns in Wyoming, Utah, &<br>Colorado, scattered in Arizona & New Mexico |
| **P. rubens Sarg.**<br>*P. australis* Small<br>*P. nigra* (Ait.) Link var. *rubra* (Du Roi) Engelm.<br>*P. rubra* (DuRoi) Link (not A. Dietrich) | **red spruce,** West Virginia<br>spruce, eastern spruce,<br>yellow spruce, he-balsam | Nova Scotia, S Quebec, New York,<br>& S in Appalachian Mtns to North Carolina |
| **P. sitchensis (Bong.) Carr.**<br>*P. sitchensis* Bong.<br>*P. falcata* (Rafin.) Suringar<br>*P. menziesii* (D. Don) Carr.<br>*Abies falcata* Rafin.<br>*A. menziesii* (D. Don) Lindley<br>*Pinus menziesii* Douglas | **Sitka spruce,,** coast spruce,<br>tideland spruce, yellow spruce,<br>Alaska spruce | Gulf of Alaska & Kodiak Island to<br>N California |
| **P. smithiana (Wall.) Boss.**<br>*P. morinda* Link<br>*P. ramaleyi* A. Nels. | **Himalayan spruce,**<br>west Himalayan spruce | N India & Pakistan |

**Sources:** USDA ARS (2005), NRCS (2001).

ever, especially when growing on sites with moist soils or high water tables. The conical form and dense, persistent branches of spruce species make them highly desirable for environmental plantings. All 7 North American species and the introduced Norway, Ezo, dragon, and Serbian spruces are planted as ornamentals. Many cultivars featuring variations or extremes in crown height, shape and symmetry, or thickness; rate of height growth; branch angle and degree of twig droop; and needle color exist (Everett 1981, Huxley 1992). In general, spruce species do not tolerate droughty

sites but do thrive on slightly acidic and moist but well-drained soils. Of all the species, Serbian spruce may best tolerate industrial air pollution (Dallimore and Jackson 1967).

**Geographic races and superior strains.** The wide ranges and diverse environments to which the spruce species have adapted provide an array of individual, ecological, and geographic variations. Natural hybridization and introgression commonly occur where ranges of compatible species overlap. Hybridization between white spruce and Sitka spruce (first reported by Little 1953 as *P. × lutzii)*, occurs in British Columbia and throughout the Kenai Peninsula in Alaska (Copes and Beckwith 1977). This hybrid has demonstrated a genetically based resistance to attack by the Sitka spruce weevil—*Pissodes strobi* Peck—which causes severe height growth and stem form reduction in Sitka spruce (Mitchell and others 1990). Hybridization between white spruce and Engelmann spruce occurs in northern Montana and British Columbia (Daubenmire 1974). Artificial crosses of Engelmann spruce with Sitka spruce and with blue spruce suggest the close relatedness of these North American species (Fowler and Roche 1977). Electrophoresis has yet to clearly identify hybrids of Engelmann spruce and blue spruce along a 1,200-m elevational transect in the front range of the Colorado Rocky Mountains, where the species grow together. Morphological similarity between the 2 species, such as number of bud scales, number of stomatal rows, and location of resin sacs, however, suggests either convergent evolution or the influence of environmental variation on the morphological characters (Mitton and Andalora 1981). Natural introgression between the maritime Sitka spruce and the more interior complex of white and Engelmann spruces occurs in a portion of British Columbia, and the hybrid fraction was estimated by restriction fragment length polymorphisms of the nuclear ribosomal RNA genes (Sutton and others 1994). Differences in monoterpene composition from black spruce oleoresin (including

α–pinene, 3-carene, and terpinolene) vary among geographic origins in an east–west pattern, except for seeds from sources in New England that have close affinity in monoterpene composition to red spruce (Chang and Hanover 1991). Natural introgression of black spruce into red spruce may result in greater height and diameter growth in New Brunswick, yet the hybrid performed unpredictably in managed stands (Fowler and others 1988).

Early crosses within the genus have provided a thorough background in potential crossability of the genus, including specimens from artificial crosses between nonsympatric species (Wright 1955). Analysis of morphological characteristics and monoterpene composition from artificial crosses

between white, red, and blue spruces later verified the hybridity of the seedlings, evaluated the utility of spruce hybrids, and clarified the evolutionary relation among members of the genus (Bongarten and Hanover 1982). Height growth of Engelmann spruce × Sitka spruce hybrids proved unsuitable for reforestation purposes in the north central interior of British Columbia (Kiss 1989). Hybrids of black spruce and Serbian spruce out-performed the black spruce parents in height and diameter growth and can be produced sexually en masse in seed orchards (Fowler 1980).

Seed source identification and provenance testing of native as well as exotic spruce species are important in selecting suitable races for various purposes. Seeds intended for use in artificial reforestation usually are collected from "superior" trees growing in the same area that is to be replanted. Measurements of phenology and growth—both adaptive characters closely related to survival and optimal utilization of the growing season—indicated a clinal variation pattern with photoperiod and temperature as primary factors in 100 seed sources of black spruce from natural stands in Alaska to Newfoundland. A 1° shift in latitude changed the seedlings' total height 2 to 11% (Morgenstern 1978). On a smaller scale, clinal variation in black spruce in the maritime provinces resulted in 3 overlapping breeding zones (Park and Fowler 1988). Within the range of black spruce, extensive gene flow between stands discourages formation of distinctive provenances. Phenotypic characteristics of cones, needles, twigs, percentage survival, and growth generally differ more within-populations than between-populations (Fowler and Mullin 1977; Parker and others 1983; Thomson and others 1990). In Alberta, black spruce populations growing on strongly contrasting environments, such as uplands adjacent to peatlands, exhibited similarity in isozyme variability (Wang and MacDonald 1992). In contrast, populations near the margins of the range, such as coastal regions in Newfoundland, better reflected provenance effects (Khalil 1984; Yeh and others 1986).

Genetic variation of Engelmann spruce may correlate with latitude and elevation; the species grows at 762 to 1,067 m in British Columbia and as high as 3,658 m in the southern Rocky Mountains (Alexander 1987). After 10 years, seedlings from more northern and lower elevation sources grew better than those from other sources within this wide geographical and elevational distribution when planted together at 2,930 m in central Colorado (Shepperd and others 1981). Lack of genetic variation of red spruce at the provenance level suggests a single broad seed and breeding zone for the maritime provinces (Fowler and others 1988). Genetic variation in natural populations of blue spruce has received considerable attention and seems to conform to a discontinuous (rather than clinal) pattern with extensive stand-to-stand and individual-tree variation

(Diebel and Fechner 1988; Fechner 1985; Hanover 1975). Provenance research in genetic variation of white spruce indicates that distinct populations have evolved within broad ecological regions, thereby resulting in differences in rate of juvenile growth, response to calcium nutrition, wood density, late-season initiation of needle primordia, nuclear volume, DNA content, branch to bud morphology, optimal temperature for seed germination, terpene biochemistry, and isoenzymes (Alden 1985). A range-wide provenance study planted in Minnesota showed large differences for tree height at ages 9 and 19 among populations with relatively poor performance by northern and western populations. Yet, no apparent geographic pattern existed in allozyme variation due to high outcrossing rates and strong inbreeding depression (Furnier and others 1991).

Norway spruce, perhaps the most intensively studied non-native species, shows strong latitudinal and elevational gradients. Seeds from northern latitudes and higher elevations weigh less than seeds from southern latitudes and lower elevations (Heit 1968; Tyszkiewics 1968). Seed source

also influences mineral nutrient content of seeds (Youngberg 1951) and early growth of seedlings in nursery beds (Heit 1968). Seed source of Serbian spruce can affect the crown shape and susceptibility to frost (Dirr and Heuser 1987).

**Flowering and fruiting.** The reproductive cycle in spruce takes 2 years; timing of various processes has been studied in detail for Engelmann spruce (Harrison and Owens 1983), white spruce (Owens and Molder 1977; 1984) (figure 1), and Sitka spruce (Owens and Molder 1976). Production of cones and filled seed varies with (1) the number of central or fertile ovuliferous scales formed in the cone-primordium; (2) the success of pollination and fertilization; (3) the degree of self-pollination; and (4) the loss to seed-eating animals and disease organisms (Caron and Powell 1989). Male and female strobili arise in spring in axils of elongating shoots, usually on different branches of the same tree. Bisexual cones occasionally occur; in interior Alaska, white spruce bisexual cones with the female portion at the apex are more common than those with the male portion at the apex (Zasada and others 1978). The pendant, yellow,

**Figure 1**—*Picea glauca*, white spruce: reproductive cycle (from Owens and Molder 1984, used with permission of the author and publisher).
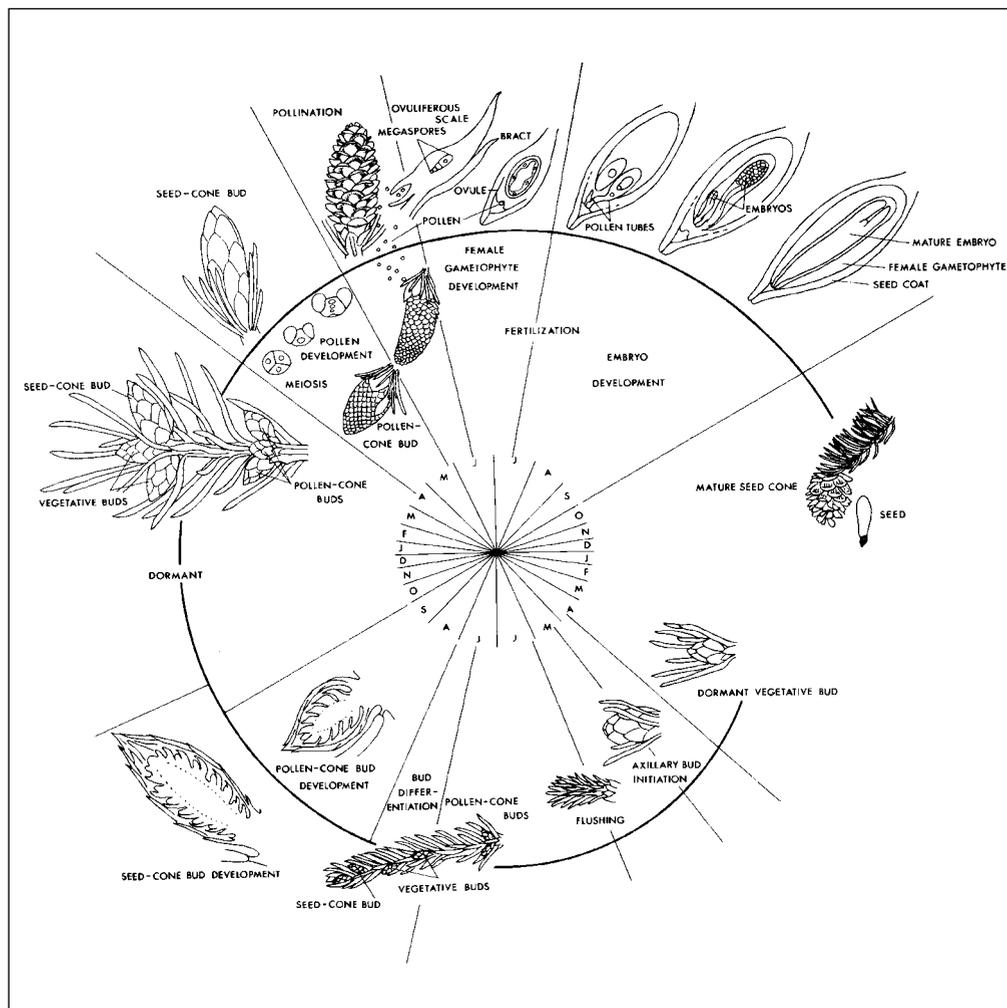
bright purple, or crimson male strobili have ovoid to cylindrical shape and uniform distribution over the crown. Each scale (microsporophyll) bears 2 pollen sacs (microsporangia) and are spirally arranged on a central axis. Male strobili dry out and fall off soon after pollen-shedding.

The timing of female strobili differentiation is similar for most species of spruce that have been studied; female strobili become anatomically determined at the end of the period of bud-scale initiation and the end of lateral shoot elongation (Owens 1986). Female strobili arise near the apex of shoots on upper branches in crowns of Engelmann, Sitka, and white spruces; the seed-cone zone in black spruce occurs on the most vigorous 1-, 2-, and 3-year-old branches at the top of the tree (Caron and Powell 1992). Initially the female strobili are erect, yellowish green, crimson, or purple; cylindrical; and 5 to 20 mm in diameter. The ovuliferous scales are spirally arranged on a central axis and each bears 2 ovules (megasporangia) at the base. Each species has a characteristic number of spirals per cone, and the number of seeds per cone depends in part on the pitch and diameter of the spirals as well as the length of the cones (Fogal and Alemdag 1989). The size of the preceding cone crop and climatic conditions at the time of cone bud differentiation influence the number of reproductive buds formed in white spruce (Zasada and others 1978). Checking female strobili in the fall preceding the seed year provides an early means of predicting potential size of the cone crop (Eis 1973).

Female strobili receive pollen when fully open, a period that lasts only a few days. Fechner (1974) determined that female strobili of blue spruce become receptive 1 to 5 days after the first pollen release, depending on elevation, and that cones tip over and become pendent within 3 to 4 weeks of initial receptivity. Fertilization may follow pollination within a few days or may be delayed until after cones become pendent (Fechner 1974); cones mature in late summer or autumn, depending on summer growing conditions (table 2). Embryo development (figure 2) of white spruce seeds in Alaska generally proceeds rapidly during July after completion of shoot, stem, and cone growth, although on any specific date, embryo length, percentage of embryo length, cotyledon length, and relative cotyledon length will differ among trees within a stand (Zasada 1988). Embryos of white spruce–Engelmann spruce hybrids in British Columbia typically fill the embryo cavity well before the seeds mature (Eremko and others 1989). Cotyledon number between species differs from 4 to 15 (Dallimore and Jackson 1967) and may be under strong maternal control (Diebel and Fechner 1988).

The size of a cone crop for individual trees and stands tends to follow the phenomenon of alternate bearing, with heavy crops followed by light or no crops, because cones develop in terminal positions on the shoots, leaving fewer available locations for flower production the year after a

**Table 2**—*Picea*, spruce: height, seed-bearing age, and phenology of flowering and fruiting

| Species | Mature height (m) | Minimal seed-bearing age (yr) | Flowering | Cone ripening | Cone size (cm) | Dispersal | Years between large seedcrops | Preripe cone color | Ripe cone color |
|---|---|---|---|---|---|---|---|---|---|
| *P. abies* | 30–60 | 40–60 | Apr–June | Sept–Nov | 10–18 | Sept–Apr | 4–13 | — | Brown |
| *P. asperata* | 45 | — | — | — | 8–13 | — | — | — | — |
| *P. breweriana* | 25–30 | 20–30 | — | Sept–Oct | — | Sept–Oct | 2 | Green | Dark brown, black |
| *P. engelmannii* | 25–30 | 15–40 | May–June | Aug–Sept | 3–6 | Sept–Oct | 2–6 | Green | Brown |
| *P. glauca* | 15–30 | 30 | May | Aug | 3–5 | Aug–May | 2–13 | Green | Pale brown |
| *P. glehnii* | 30 | — | — | — | 6 | — | — | — | Shiny brown |
| *P. jezoensis* | 30–45 | 20–25 | — | — | 5–8 | — | 2–4 | Crimson | Brown |
| *P. koraiensis* | 18 | — | — | — | — | — | — | Green | Brown |
| *P. mariana* | 9–27 | 10 | May–June | Sept | 2–4 | Oct* | 4 | Green | Purple–brown |
| *P. obovata* | — | — | — | Sept | — | — | 12–13 | Green | — |
| *P. omorika* | 30 | — | May | — | 5 | — | — | Bluish black | Cinnamon brown |
| *P. pungens* | 21–50 | 20 | Apr–June | — | 7–10 | — | 1–3 | Green | Pale brown |
| *P. rubens* | 21–30 | 30–50 | Apr–May | Sept–Oct | — | Oct–Mar | 3–8 | Green | Brown |
| *P. sitchensis* | 18–73 | 20 | May | Aug–Sept | — | Aug–Sept | 3–4 | Yellow–green | Brown |
| *P. smithiana* | 61 | 20 | Apr–May | Oct–Nov | 10–18 | Oct–Nov | — | Bright green | Brown |

**Sources:** Alden (1955), Alexander (1987), Alexander and Shepperd (1984), Edwards (1980), Fechner (1974), Fechner (1985), Nikolov and Helmisaari (1992), Safford (1974), Zasada and Viereck (1970).
* Cones of *P. mariana* are semi-serotinous and release seeds throughout the year for several years.

**Figure 2**—*Picea glauca,* white spruce: diagrammatic longitudinal section of a mature seed at dispersal, showing seedcoat, gametophyte, and fully developed embryo (from Alden 1985, used with permission of the author and publisher).
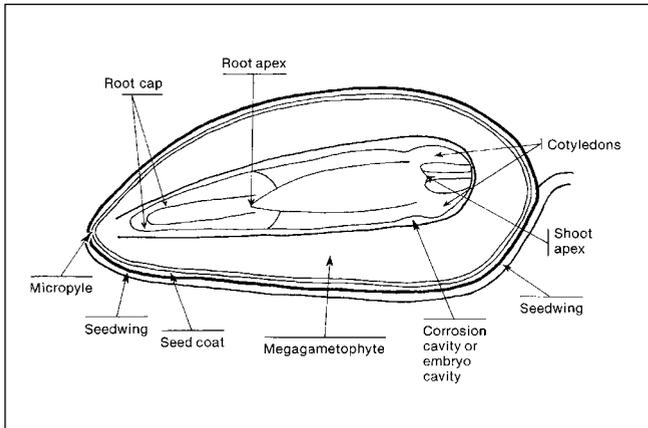


good crop (Edwards 1986; Fechner 1985). Annual production of cones and seeds differs considerably, however, with the intervals between good cone crops ranging from 2 years in Brewer spruce to as long as 13 years in white and Norway spruces (table 2). Between 1969 and 1994, Engelmann spruce in central Colorado produced good cone crops in 8 of the 26 years (Shepperd 1995). Between 1957 and 1978, irregular production of white spruce cones and seeds in interior Alaska varied with environmental factors such as temperature during cone initiation; nutrient deficiencies; and losses to insects, diseases, and squirrels (Zasada 1980; Zasada and Viereck 1970).

At maturity, the pendent cones open to shed seeds during autumn and winter (table 2). Persistent cone scales on mature cones may have rounded, pointed, irregular, notched, or reflexed ends. Most species shed cones at the end of the season, but some cones may remain on the tree throughout the next growing season. Cones should be harvested before inclement weather reduces workers' productivity or losses to squirrels increase (Curran and others 1987). Cones may be collected before they are fully ripe and, if artificially ripened, release seeds with maximal germination capacity (Edwards 1980). Cones may be collected from standing trees, slash, or animal caches, although cones that have been in contact with the forest floor may acquire seed-killing fungi. Seeds generally reach maturity before cones show their characteristic ripe color (table 2). Time of ripening varies among cones on an individual tree and among trees in a single stand (Fechner 1974; Jensen and others 1967; Zasada 1988). Various measures of estimating seed maturity have emphasized (1) physical attributes such as color and firmness of cones; (2) moisture content and specific gravity of cones; (3) color of testa and brittleness of seeds (Crossley 1953; Edwards 1980); (4) a cone moisture content of 30% or less for Norway spruce; (5) specific gravity between 0.78

and 0.95 (Winston and Haddon 1981; Zasada 1973) and a soft "spongy feel" of cones when squeezed in the fingers for white spruce; or (6) dark brown or black testa and seeds that "snap" when cut with a sharp instrument. All of these indicate that cones are sufficiently ripe for harvest.

Morphological characteristics of seed maturity for white spruce embryos show 75 to 95% complete embryo development by the end of the growing season, depending on site characteristics of the stand. Continued embryo development in seeds of cones collected in high latitude forests at this stage of seed maturity requires careful handling of the cones (Zasada 1988). Changes in sugar content provide a biochemical measure of maturity in ripening seeds of Norway and Sitka spruces (Jensen and others 1967). Computation of average daily temperature and growing degree-day summations also indicates seed maturity. Zasada (1973) recommends 625 growing degree-days (above a threshold of 5 °C and summed from pollination date) as a minimal time for white spruce embryos in interior Alaska to fully develop; this heat sum is reached in early August. Other optimal growing degree-day sums include 912 for white spruce in Ontario (Winston and Haddon 1981) and 955 for white spruce and 1,050 for black spruce in Newfoundland (Curran and others 1987). Maximal cone maturity in blue spruce, measured as seed germinability, occurs 6 weeks before natural seed release for low-elevation trees and 4 weeks before natural seed release for high-elevation trees (Fechner 1974).

Recent work has expanded the understanding of seed production in relation to crown structure and cone size. Cones of black spruce on trees of intermediate crown class initially produce almost twice as many seeds as those of either the dominant or the co-dominant trees, but disperse their seeds at a much faster rate during the first 5 to 6 seed-bearing years (Payandeh and Haavisto 1982). The number of black spruce seeds per cone and number of filled seeds per cone relate to cone size: cones in New Brunswick averaged from 26 to 30 mm long with 10 to 37 filled seeds per cone (Caron and Powell 1989) and the most common size of black spruce cones in Ontario averaged 20 to 28 mm long with potential yields of 74 to 94 seeds per cone and 38 to 44 filled seeds per cone (Haavisto and others 1988). Cones of white spruce from Ontario averaged 39 to 47 mm in length and contained an average of 46 to 62 filled seeds per cone; regression models developed from these results estimate the number of sound seeds per cone as a function of seeds per cone section, cone length, and cone diameter (Fogal and Alemdag 1989).

Attempts to enhance seed yields in seed orchard programs have been hampered by the relatively long period of tree growth before flowering begins. Documented minimal seed-bearing age (table 2) for most species ranges from 10 to 60 years, although crops of sufficient quantity to warrant collection may not occur until much later. Efforts to stimulate flowering in younger trees have involved girdling of the

bole, nitrogen fertilization, and root pruning. Top-pruning of grafted white spruce in seed orchards, done to maintain the cone-bearing branches at a height within reach of a short ladder, may also increase cone production and decrease the cost of cone collection (Nienstaedt 1981).

Several lines of research have attempted to define the physiological processes and procedures for large-scale stimulation of flowering to either shorten the length of breeding programs or to increase production of cones and seeds. Application of gibberellins $A_4$, $A_7$, and $A_9$ stimulated female cone production in grafted Norway spruce clones, although the response differed by year and clone (Dunberg 1980). Gibberellin $A_{4/7}$ applied in the top 2 branch whorls of mature Sitka spruce grafts increased female flowering and seed production (Tompsett and others 1980); girdling in combination with stem injections of gibberellin $A_{4/7}$ in grafted clones of Sitka spruce may stimulate pollen-cone production (Philipson 1985a); and top-pruning and stem injection of gibberellin $A_{4/7}$ may increase cone production in the lower crown and increase the ease of cone collection (Philipson 1985b). Heat and drought also promote flowering, although by a different induction mechanism. Potted grafts of Engelmann spruce produced high numbers of both male and female cone buds after exposure to high temperature within heated polyethylene-covered houses when the exposure occurred during the late stage of slow shoot elongation, whereas drought during the period of rapid shoot elongation after vegetative bud burst enhanced female cone production (Ross 1985). Optimal daytime temperature is 22 to 25 °C (Ross 1988a). In contrast, polyhouse temperatures that frequently exceed 30 °C during the pollination sequence of Engelmann spruce resulted in accelerated pollen shed, increased underdevelopment of pollen cones, and reduced yields of seed (Ross 1988b). These results suggest a need for a year's rest between treatments to allow time for cone maturation and vegetative replenishment of shoots. Repeated injection of gibberellin $A_{4/7}$ into container-grown grafts of Sitka spruce in a polyhouse during May and June effectively stimulated flowering (Philipson 1992). Application of gibberellin $A_{4/7}$ also stimulated flowering of white spruce (Ho 1988b; Marquard and Hanover 1984), even though white spruce has been classed as recalcitrant because of its sporadic flowering and usually nominal response to gibberellin $A_{4/7}$ alone (Pharis and others 1986). Stem injection of gibberellin $A_{4/7}$ in combination with nondestructive girdling greatly increases flowering in mature white spruce trees (Pharis and others 1986) and grafted clones (Ross 1992). Whole-tree spraying of branches at relatively high concentrations (800 mg/liter gibberellin $_{4/7}$) during May through July promoted cone production the next year (Ho 1988b). In the Great Lakes region, elongating shoots sprayed in May produced more male and female strobili than shoots sprayed in June (Cecich 1985). Flowering of white spruce responded to heat similar to that of Engelmann spruce by enhanced

pollen-cone production after subjecting potted grafts to 30 °C for 10 hours, whereas seed-cone production was enhanced after 5 hours at 20 °C (Ross 1991). Seed-cone production of black spruce also has been stimulated by application of gibberellin; the greatest increase occurred with 200 mg/liter of gibberellin $A_{4/7}$ sprayed repeatedly on young grafts during the period of rapid shoot elongation (Ho 1991). Seed-cone production also may be enhanced in field-grown seed orchards by applying a foliar spray of 400 mg/liter gibberellin $A_{4/7}$ during the period before lateral shoot elongation and bud-type differentiation (Ho 1988a), and in seed orchards of seedling origin by applying a foliar spray of 200 to 800 mg/liter gibberellin $A_{4/7}$ (Hall 1988). Attempts with several species to promote male flowering preferentially by the synthetic auxin naphthalene acetic acid (NAA) have been inconclusive (Hall 1988; Ross 1992).

Spruce seeds are small (2.5 to 5.0 mm long), oblong to acute at the base, with a single well-developed wing that is 2 to 4 times the length of the seed (figure 3). Wind is the primary agent for dispersal (Dobbs 1976; McCaughey and Schmidt 1987; Youngblood and Max 1992; Zasada and Lovig 1983). Dispersal of white spruce seeds begins in late August and extends throughout winter; however, seeds released before mid-October have higher viability because they tend to come from well-developed central cone scales, whereas seeds released either earlier or later tend to come from less-developed basal and apical scales (Dobbs 1976; Youngblood and Max 1992; Zasada and others 1978). Cones of red spruce release seeds in a similar manner. The semi-serotinous cones of black spruce remain partially closed, and disperse seeds for several years as the cone scales flex with repeated wetting and drying (Haavisto and others 1988; Viereck and Johnston 1990). Seed viability decreases only slightly during the first 3 years, then decreases rapidly to about 5% in cones up to 12 years old, and may remain almost constant for older cones (Payandeh and Haavisto 1982). Nonlinear equations have been developed to model dispersal of filled seeds into openings for Engelmann spruce (Alexander 1986; McCaughey and Schmidt 1987), white spruce (Dobbs 1976; Youngblood and Max 1992) and black spruce (Payandeh and Haavisto 1982). Once dispersed, spruce seeds remain viable for only a short period; Fraser

**Figure 3**—*Picea,* spruce:  seeds with wings of *P. breweriana,* Brewer spruce; *P. engelmannii,* Engelmann spruce; *P. glauca,* white spruce; *P. mariana,* black spruce; *P. rubens,* red spruce; and *P. sitchensis,* Sitka spruce (**left to right**).
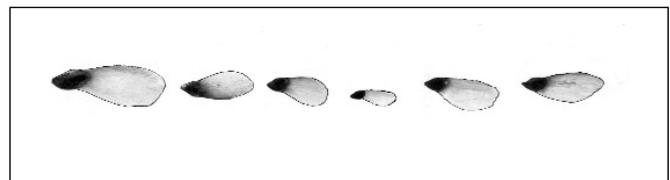
| Table 3—*Picea*, spruce: common cone- and seed-damaging insects | | | |
|---|---|---|---|
| **Insect species** | **Common name** | **Damage** | **Affected species\*** |
| *Choristoneura occidentalis* Freeman | western spruce budworm | Larvae feed externally on cones | ***P. engelmannii*** |
| *Dasineura canadensis* Felt | spruce cone gall midge | Larvae form gall on cone scale | ***P. glauca*** |
| *Dasineura rachiphaga* Tripp | spruce cone axis midge | Larvae mine through scales into axis | ***P. engelmannii, P. glauca,*** *P. sitchensis,P. mariana* |
| *Dioryctria abietivorella* Grote | fir cone moth | Larvae mine & riddle cone | ***P. mariana, P. glauca,*** *P. engelmannii, P. pungens,* |
| *Henricus fuscodorsanus* Kearfott | cone cochylid | Larvae feed on scales & seeds | ***P. sitchensis, P. glauca*** |
| *Hylemya anthracina* Czerny | spruce cone seed maggot | Larvae tunnel around cone axis | ***P. mariana, P. glauca, P. engelmannii, P. sitchensis*** |
| *Laspeyresia youngana* Kerfott | spruce seed moth | Larvae feed on seeds | ***P. engelmannii, P. glauca,*** *P. mariana, P. pungens, P. rubens, P. sitchensis* |
| *Mayetiola carpophaga* Tripp | spruce seed midge | Larvae feed on seeds | ***P. glauca*** |
| *Megastigmus atedius* Walker | spruce seed chalcid | Larvae feed on seeds | All native *Picea* |
| *Strobilomyia neanthracina* Michelson | spruce cone maggot | — | ***P. mariana*** |

**Sources:** Cameron and Jenkins (1988), Schmid and others (1981).
\* Major hosts in **boldface type.**

(1976) reported that on a natural forest floor seedbed, black spruce seeds may lose viability completely after 16 months.

**Cone and seed losses.** Various agents destroy cones and seeds, including killing frosts, insects, diseases, birds, and mammals. Late frost during the spring may damage cones of white spruce; affected conelets become flaccid, die and turn black and do not produce seeds (Zasada 1971). Frost also commonly damages cones of Engelmann spruce (Cameron and Jenkins 1988).

Many insects feed on seeds and cone parts (table 3). Just 2 species—spruce cone seed maggot (*Hylemya anthracina* Czerny) and spruce seed moth (*Laspeyresia* × = *Cydia*) *youngana* Kearfott)—cause the most widespread damage (Cameron and Jenkins 1988; Hedlin 1973; Hedlin and others 1980; Schmid and others 1981). Insect populations fluctuate with cone crop abundance and differ among spruce communities having dissimilar stand structure (Fogal and Larocque 1992). Greater seed and cone losses usually occur in years of below-average cone production (Schmid and others 1981; Werner 1964). Above-average summer temperatures may ameliorate seed losses in Ontario from *Laspeyresia* by contributing to greater insect mortality and preventing prolonged insect diapause (Fogal 1990). Damage to cones and seeds by insects has been reduced by soil application of carbofuran (Cerezke and Holmes 1986) or stem implants of acephate (West and Sundaram 1992).

Basidiospore production of the inland spruce cone rust—*Chrysomyxa pirolata* Winter—coincides with the period when most spruce cones are receptive to pollen. This fungus sometimes causes severe damage to the cones of white, blue, Engelmann, and black spruces. Diseased cones contain fewer seeds, with reduced viability, and germinants may be abnormal (Summers and others 1986, Sutherland 1990). Coastal spruce cone rust—*Chrysomyxa monesis* Ziller—causes similar damage in Sitka spruce (Bega and Scharpf 1993). Pre-emergence seed losses caused by a soil-borne fungus—*Geniculodendron pyriforme* G.A. Salt—in Sitka spruce nurseries occur after cones come in contact with the ground during collection and cleaning of seeds (Sutherland and Woods 1978). Similarly, another fungus—*Caloscypha fulgens* (Pers.) Boudier—infects cones lying on the forest floor or in squirrel caches; spreads during stratification and presowing storage; and kills seeds of white, black, and Sitka spruces (Sutherland 1990). The seed-borne blight caused by *Sirococcus strobilinus* Preuss may damage seedlings of Engelmann, Sitka, and white spruces, and their hybrids (Sutherland and others 1981).

Many species of birds consume spruce seeds. Several finches (families Fringillidae and Estrildidae) feed almost exclusively on conifer seeds, including the common (red) crossbill (*Loxia curvirostra*), the two-barred (white-winged) crossbill (*L. leucoptera)*, and the pine siskin (*Carduelis pinus*). Spruce seeds often provide an important winter food source for the American goldfinch—*C. tristis*. In addition,

the pine siskin and the pine grosbeak—*Pinicola enucleator*—may feed on reproductive buds (Benkman 1987; Clement and others 1993).

Pine squirrels (*Tamiasciurus hudsonicus fremonti*) harvest and cache Engelmann spruce cones (Alexander 1987). Red squirrels (*T. hudsonicus*) and northern red-backed voles (*Clethrionomys rutilus*) consume great quantities of seeds of white spruce during winter (Brink and Dean 1966; West and deGroot 1990; West and others 1980). Red squirrels also consume seeds of black spruce and clip twigs and terminals and eat reproductive and vegetative buds of red spruce (West 1989). In Newfoundland, the proportion of black spruce cones per tree harvested by red squirrels in years with small cone crops ranged from 64 to 96%, whereas in a year with a good cone crop, less than 1% of cones were taken (West 1989).

**Extraction and storage of seeds.** Spruce seeds require careful extraction and storage because cones often are collected before fully mature and seeds may continue to ripen within the cones (Caron and others 1990; Edwards 1980, 1986; Zasada 1973). Post-harvest ripening of prematurely collected cones, however, allows flexibility in collecting operations and extends the collection period by allowing the use of immature cones (Edwards 1986). Cones of white spruce may air-dry in half-filled burlap sacks or on open screens for a few weeks at 5 to 15 °C and 60 to 75% relative humidity (Alden 1985), or for up to 3 months at 5 °C and 75 to 90% relative humidity (Winston and Haddon 1981). Cones also may dry under field conditions of outside storage if ventilation is good (Caron and others 1990; Zasada 1973). Cones of Engelmann Sitka, and white spruces have been safely stored for up to 5 months without loss of seed quality (Edwards 1986).

Improper extraction, even from mature cones, will reduce viability of spruce seeds. Mature cones usually require additional drying with heat to fully flex the cone scales and ensure maximal seed recovery. Cones of Engelmann, Sitka, and white spruces require exposure to an air flow of gradually decreasing moisture content and increasing temperature in a convection kiln for 6 to 24 hours at 38 to 49 °C (Edwards 1986). Other workers suggest slightly lower maximal temperatures for white spruce (Alden 1985; Curran and others 1987). Kiln-drying requires careful monitoring of temperature because high temperature can cause physiological injury (Carmichael 1958). After drying, tumbling or shaking loosens seeds from opened cones. If cones fail to open fully, complete extraction of seeds may require remoistening and redrying followed by additional tumbling or crushing (Alden 1985; Edwards 1986).

Black spruce cones present a greater challenge for seed extraction because of the tightly bonded scales. The following special extraction procedure has been developed for these semi-serotinous cones (Haavisto and others 1988):

1. Cones are soaked in lukewarm water for 2 hours.
2. Cones are oven-dried at 40 °C for 20 to 22 hours.
3. Cones are tumbled in a revolving screened drum for 30 minutes.
4. Steps 1 to 3 can be repeated for up to 16 times for complete extraction of seeds.

The weakly bonded seedwings separate readily from the seeds with little abrasive action (Edwards 1986). For small seedlots, the seeds can be gently rubbed by hand inside a moistened cotton bag (Alden 1985; Caron and others 1990). For larger lots, wings and chaff are separated from seeds using any commercial seed-processing device: an oscillating screen scalper, a fanning mill, an air-screen cleaner, or a small rotating cement mixer, for example (Alden 1985; Edwards 1986; Stiell 1976). In some cases, seeds may need remoistening with a fine mist to aid in cleaning, after which they can be dried again. Air and gravity separators not only remove empty seeds, wings, and debris, but also sort seeds into different density fractions. Cleaned seeds are prepared for storage by conditioning with low heat to achieve 4 to 8% moisture content. The number of cleaned seeds per weight ranges from about 50,000 to almost 900,000/kg (110,200 to 1,984,200/lb) for the various species (table 4).

Because cone- and seed-crops differ between years, seeds collected during good to excellent years are stored for use during poor crop years. Seeds from most species of spruce seem fairly similar in longevity characteristics and storage requirements; seeds have been safely stored for 10 to 20 years at moisture content of 4 to 8% and temperatures between –10 and +3 °C (Wang 1974). Seeds of Norway spruce, stored at 0 to 2 °C and 6 to 8% moisture content in glass carboys sealed with cork and wax, retained high percentage germination for 17 years (Hill 1976). Seeds of white spruce stored at –18 to +3 °C and 7% moisture content for 7 years retained their initial percentage germination (Stiell 1976). To assure maximal seed longevity, the specified moisture content must be maintained during the entire storage period. Polyethylene bags (4- to 10-mil) make satisfactory storage containers. Seeds treated with rodent repellent have longevity characteristics similar to untreated seeds (Radvanyi 1980). For longer storage, metabolic processes are halted; Ahuja (1986) found that Norway spruce seeds stored in liquid nitrogen (–196 °C) retained full germinability, suggesting this as a long-term storage method.

**Pregermination treatments.** Seeds of most species of spruce germinate promptly without pretreatment, but seeds of black, blue, Brewer, Engelmann, Ezo, Norway, Sakhalin, Sitka, and white spruces may germinate more rapidly after a stratification treatment. Seeds of Norway spruce may be stratified by conditioning for 3 weeks at cold temperature and may be soaked in water for 24 hours ("priming") before planting (Dirr and Heuser 1987). Seeds of red and white spruces stratified in newspaper and moist sand at 0 to 3 °C

**Table 4—*Picea*, spruce: weight of cleaned seeds, methods of testing for laboratory germination, and additional directions**

| Species | Seeds/weight | | Substrate | Test (days) | Additional directions |
|---|---|---|---|---|---|
| | /kg | /lb | | | |
| P. abies | 105,600–462,300 | 47,000–209,700 | TB | 16 | — |
| P. asperata | 154,300–165,400 | 70,000–75,000 | — | — | — |
| P. breweriana | 112,500–163,200 | 51,000–74,000 | — | — | Prechill |
| P. engelmannii | 152,200–710,000 | 69,000–322,000 | TB,P | 16 | Prechill; light; sensitive to excess moisture; if dormant, use $KNO_3$ |
| P. glauca | 298,000–884,200 | 135,000–401,000 | TB | 21 | Prechill 14–21 days at 3–5 °C; light |
| P. glehnii | — | — | TB,P | 14 | Prechill 21 days at 3–5 °C |
| P. jezoensis | 395,100–508,500 | 179,200–230,600 | TB,P | 14 | Prechill 21 days at 3–5 °C |
| P. koraiensis | 209,500–242,500 | 95,000–110,000 | TB | 21 | Light |
| P. mariana | 739,000–1,464,100 | 335,000–664,000 | TB | — | Prechill or soak; light |
| P. omorika | 277,000–377,500 | 125,600–171,200 | TB | 16 | Light; sensitive to excess moisture |
| P. pungens | 176,400–359,000 | 80,000–163,000 | TB,P | 16 | Prechill |
| P. rubens | 220,500–637,000 | 100,000–289,000 | TB | 28 | Light |
| P. sitchensis | 342,000–882,000 | 155,000–400,000 | TB,P | 21 | Soak; prechill; light; sensitive to excess moisture; if dormant, use $KNO_3$ |
| P. smithiana | 53,000–88,200 | 24,000–40,000 | — | — | — |

**Sources:** Dirr and Heuser (1987), Jeglum and Kennington (1993), Nikolov and Helmisaari (1992), Safford (1974), Stein and others (1986), Willan (1985).

**Note:** TB = top of blotters; P = petri dishes covered with blotters, filter paper, or sand.

for 14 months showed only a slight loss of percentage germination; under these conditions black spruce lost about one-third of its percentage germination and germination of all 3 species declined to about 10% of the original capacity after 27 months (MacGillivary 1955). Prechilling, or cold stratification, may widen the range of temperatures over which seeds can subsequently germinate, increase the maximal percentage germination at some temperatures, and increase the rate of germination at almost any temperature (Gosling and Rigg 1990). Prechilling of white spruce seeds at 2 to 4 °C for 6 weeks results in high percentage germination (Caron and others 1990). Other researchers have prechilled white spruce seeds by soaking them in cold running water for 24 hours, blotting them dry, and then refrigerating them at 4 °C for 3 weeks (Chanway and others 1991). Storage of cones at 5 °C for 4 weeks, however, may eliminate any subsequent need for stratification of white spruce seeds (Winston and Haddon 1981). White spruce seeds from high-latitude sites in Alaska (> 55° latitude) do not undergo dormancy, and stratification is detrimental for mature seeds (Alden 1995). Before nursery sowing, Engelmann spruce seeds need to be primed for 24 hours, then prechilled for 6 to 8 weeks at 2 °C in loosely closed polyethylene bags (Tanaka and others 1986). Unstratified seeds of black spruce incubated for 24 days at 3 or 20 °C germinated completely within 18 days with 14:10 (light:dark) hours of fluorescent light, whereas moist seeds prechilled for 24 hours at 3 °C in a polyethylene bag in the dark reached 95% germination within 12 days when incubated at 5 to 30 °C, regardless of lighting regime (Farmer and others 1984). Priming black spruce seeds for 5 to 6 days in water (until the radicles nearly emerge) and surface-drying before sowing accelerated germination by about 1 week (Malek 1992). Seeds of black spruce from high latitudes in Alaska, collected and immediately extracted in the spring, will germinate in 2 to 6 days after becoming fully imbibed with water; no dormancy exists and stratification is not required (Alden 1995). Dormancy of Sitka spruce seeds is broken and 95% germination is possible after priming for 72 hours (until seeds reach 30% moisture content), then chilling for 6 weeks in loosely closed polyethylene bags at 4 °C (Gosling and Rigg 1990).

Treating seedlots with various fumigants, insecticides, fungicides, and rodent repellents in storage or before sowing may reduce germination of seeds. Germination of white spruce seeds treated with a finely ground rodent repellent mixed with graphite declined slightly from that of untreated seeds after more than 5 years of storage (Radvanyi 1980). Aluminum powder, which is used as a lubricant on Sitka and white spruce seeds in bareroot nurseries in Canada, may decrease the percentage germination of treated seeds and reduce first-year survival of seedlings (Sutherland and others 1978). Embedding black spruce seeds in pellets may discourage their consumption by small mammals, depending

on the material surrounding the seeds (Martell 1981). As always, pesticide users should closely follow the manufacturer's recommended dosages.

Seedlots of all spruce species should meet the quality standards of 95% purity and 80% viability recommended by the International Seed Testing Association and the Association of Official Seed Analysts for most species. Many spruce seedlots contain a fairly high percentage of empty seeds when extracted from the cones. Failure to remove these empty seeds during the cleaning process can seriously affect germination test results. Methods of germination testing are summarized in table 4 (Safford 1974; Stein and others 1986). In all species, germination tests call for alternating temperatures of 20 °C for 16 hours and 30 °C for 8 hours (Stein and others 1986).

**Germination and nursery practices.** Germination of spruce seeds is epigeal (figure 4). Growers raise seedlings of spruce species in North America either as bareroot stock (2+0 or 3+0) in nursery beds or as container seedlings (1+0 or 2+0) in greenhouses. Nursery-grown transplants (2+2) of slow-growing species such as black spruce may have greater survivability (Mullin 1980). Seeds of blue, Engelmann, and Korean spruces may germinate at low temperatures in the fall and die over winter, making fall-sowing of these species in nursery beds highly risky (Heit 1968).

Under natural conditions, most species of spruce germinate on various media, including rotten wood, shallow duff, and mixtures of mineral and organic soil. Mineral soil makes an ideal seedbed because of greater water availability. Commercial growers raise white spruce seedlings with high stem caliper and stem height and heavy stem and root weights as container seedlings in either (1) a commercially prepared mixture composed of equal parts of sphagnum peat moss and vermiculite or (2) a mixture of equal parts of sphagnum peat moss, peat moss, and vermiculite (Lackey and Alm 1982). Germination of some seedlots of Sitka spruce has been improved by moistening the substrate with a 0.2% solution of potassium nitrate (Safford 1974).

Seeds of most species germinate promptly and completely under a wide range of temperatures either with or without light. Once germinated, seedlings in greenhouses require extended daylength to accelerate growth and prevent dormancy. Continuous fluorescent lighting providing about 150 $\mu$mol/m$^2$/sec photosynthetically active radiation at 25 °C allows continuous vigorous growth of blue spruce seedlings (Young and Hanover 1978). White spruce seedlings respond favorably to photoperiodic lighting intensities of about 414 to 4,150 $\mu$mol/m$^2$/sec, although Engelmann spruce has a much narrower response range of about 210 to 520 $\mu$mol/m$^2$/sec (Arnott and Macey 1985). Seedlings of white spruce also have been grown with photosynthetically active radiation at the seedling canopy level of about 300 $\mu$mol/m$^2$/sec in a 16-hour photoperiod at 23 °C and a night temperature of 17 °C (Chanway and others

1991). Failure of the lighting system for only a few days reduced the effectiveness of extended or intermittent photoperiod, leading to increased root rather than shoot growth in white spruce seedlings (Arnott and Simmons 1985). Under laboratory or greenhouse conditions, newly germinated seedlings of red spruce require a light period of at least 16 hours to prevent the onset of dormancy (Safford 1974).

In greenhouse management, imposing a reduced photoperiod will induce bud scale formation leading to dormancy and hardening-off in spruce seedlings. Without this stimulus, first- or second-year seedlings may not enter dormancy, regardless of temperature. Imposing nitrogen stress and moisture stress will also induce dormancy (Young and Hanover 1978). Once dormant, seedlings of most species require 4 to 6 weeks of cold treatment at 0 °C or lower to initiate new growth (Safford 1974).

Macro- and micro-nutrients introduced in the irrigation system commonly support spruce seedlings in accelerated growth conditions within a greenhouse (Landis and others 1989). In addition to fertilizer, addition of growth-promoting rhizobacteria such as *Bacillus* strains may stimulate the

**Figure 4**—*Picea pungens*, blue spruce: seedling development at 2, 5, and 7 days after germination.
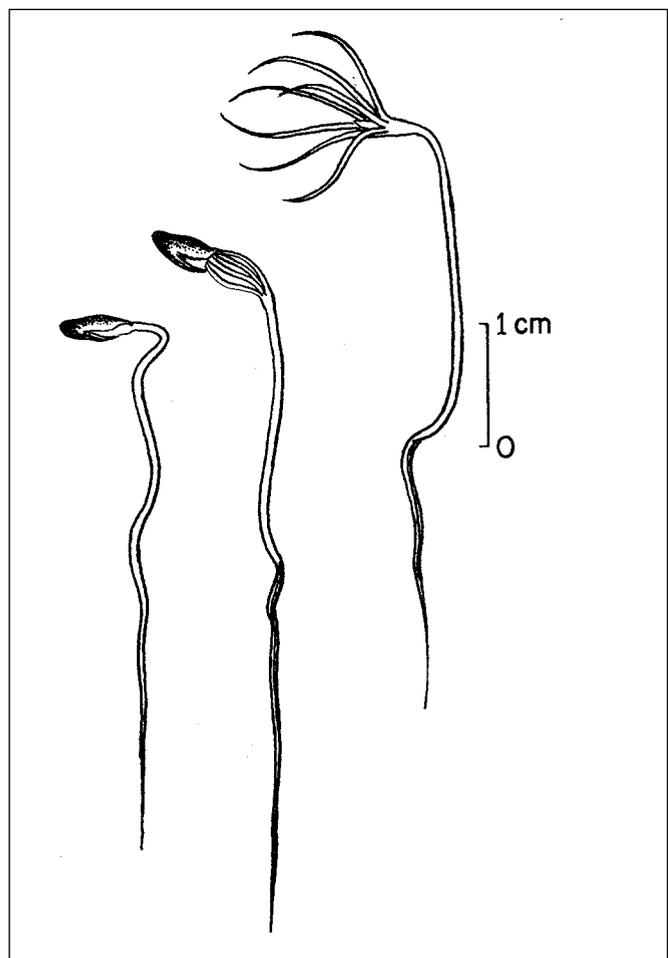
emergence rate of white spruce seedlings, possibly through induction of root elongation and the formation of lateral and adventitious roots (Chanway and others 1991). In nurseries in the Great Lakes region, stunting of first-year white spruce seedlings—described as early cessation of growth, purple discoloration of foliage, and low foliage phosphorus concentration without a soil phosphorus deficiency—may result from poor mycorrhizal development after soil fumigation (Croghan and others 1987).

Ectomycorrhizae may play an important role in seedling establishment, and a growing number of researchers are investigating the formation of mycorrhizae on seedlings. Black spruce seedlings inoculated soon after emergence with fungal plugs of the ectomycorrhizae-forming *Laccaria bicolor* (Maire) Orton or *L. laccata* (Fries) Berkely & Broome showed more second-order lateral roots and greater seedling dry weight and height (Thomson and others 1990).

## References

Ahuja MR. 1986. Storage of forest tree germplasm in liquid nitrogen (−196 °C). Silvae Genetica 35: 5–6.

Alden J. 1985. Biology and management of white spruce seed crops for reforestation in subarctic taiga forests. Bull. 69. Fairbanks: University of Alaska , School of Agriculture and Land Resources Management, Agricultural and Forestry Experiment Station. 51 p.

Alden J. 1995. Personal communication. Fairbanks: University of Alaska.

Alexander RR. 1986. Engelmann spruce seed production and dispersal, and seedling establishment in the central Rocky Mountains. Gen. Tech. Rep. RM-134. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 9 p.

Alexander RR. 1987. Ecology, silviculture, and management of the Engelmann spruce–subalpine fir type in the central and southern Rocky Mountains. Agric. Handbk. 659. Washington, DC: USDA Forest Service. 144 p.

Alexander RR, Shepperd WD. 1990. *Picea engelmannii*. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 187–203.

Arnott JT, Macey DE. 1985. Effect of supplemental light intensity on white spruce, Engelmann spruce, and mountain hemlock seedlings grown under an extended photoperiod. Canadian Journal of Forest Research 15: 295–300.

Arnott JT, Simmons CS. 1985. The effect of failure in extended and intermittent photoperiodic lighting on the growth of white spruce container seedlings. Canadian Journal of Forest Research 15: 734–737.

Bega RV, Scharpf RF. 1993. Rusts. In: Scharpf RF, tech. coord. Diseases of Pacific Coast conifers. Agric. Handbk. 521. Washington, DC: USDA Forest Service: 83–111.

Benkman CW. 1987. Food profitability and the foraging ecology of crossbills. Ecological Monographs 57: 251–267.

Blum BM. 1990. *Picea rubens*. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 250–259.

Bongarten BC, Hanover JW. 1982. Hybridization among white, red, blue, and white × blue spruces. Forest Science 28: 129–134.

Brink CH, Dean FC. 1966. Spruce seed as a food of red squirrels and flying squirrels in interior Alaska. Journal of Wildlife Management 30: 503–512.

Cameron DE, Jenkins MJ. 1988. Engelmann spruce cone losses caused by insects in northern Utah in a year of low cone production. Great Basin Naturalist 48: 508–511.

Carmichael AJ. 1958. Determination of the maximum air temperature tolerated by red pine, jack pine, white spruce and black spruce seeds at low relative humidities. Forestry Chronicle 34: 387–392.

Caron GE, Powell GR. 1989. Cone size and seed yield in young *Picea mariana* trees. Canadian Journal of Forest Research 19: 351–358.

Caron GE, Powell GR. 1992. Patterns of cone distribution in crowns of young *Picea mariana*: 1. Effect of tree age on seed cones. Canadian Journal of Forest Research 22: 46–55.

Caron GE, Wang BSP, Schooley HO. 1990. Effect of tree spacing, cone storage, and prechilling on germination of *Picea glauca* seed. Forestry Chronicle 66: 388–392.

Cecich RA. 1985. White spruce (*Picea glauca*) flowering in response to spray application of gibberellin A$_{4/7}$. Canadian Journal of Forest Science 15: 170–174.

Cerezke HF, Holmes RE. 1986. Control studies with carbofuran on seed and cone insects of white spruce. Info. Rep. NOR-X-280. Edmonton, AB: Canadian Forest Service, Northern Forest Centre. 10 p.

Chang J, Hanover JW. 1991. Geographic variation in the monoterpene composition of black spruce. Canadian Journal of Forest Research 21: 1796–1800.

Chanway CP, Radley RA, Holl FB. 1991. Inoculation of conifer seed with plant growth promoting *Bacillus* strains causes increased seedling emergence and biomass. Soil Biology and Biochemistry 23: 575–580.

Clement P, Harris A, Davis J. 1993. Finches and sparrows: an identification guide. Princeton, NJ: Princeton University Press. 500 p.

Copes DL, Beckwith RC. 1977. Isoenzyme identification of *Picea glauca, P. sitchensis*, and *P. lutzii* populations. Botanical Gazette 138: 512–521.

Croghan CF, Palmer MA, Wolosiewicz M. 1987. Stunting of white spruce (*Picea glauca* (Moench) Voss) associated with ectomycorrhizal deficiency. Tree Planters' Notes 38: 22–23.

Crossley DI. 1953. Seed maturity in white spruce (*Picea glauca*). Silviculture Research Notes [Canadian Forest Service, Research Division] 104: 1–16.

Curran WJ, Tricco P, Hall JP. 1987. Optimal dates for collection of conifer seed in central Newfoundland. Info. Rep. N-X-248. St. John's, NF: Canadian Forestry Service, Newfoundland Forestry Centre. 15 p.

Dallimore W, Jackson AB. 1967. A handbook of Coniferae and Ginkgoaceae. 4th ed. Harrison SG, rev. New York: St. Martin's Press. 729 p.

Daubenmire R. 1974. Taxonomic and ecologic relationships between *Picea glauca* and *Picea engelmannii*. Canadian Journal of Botany 52: 1545–1550.

Diebel KE, Fechner GH. 1988. Natural variation among seedlings from Colorado sources of blue spruce. Western Journal of Applied Forestry 3: 106–109.

Dirr MA, Heuser CW Jr. 1987. The reference manual of woody plant propagation: from seed to tissue culture. Athens, GA: Varsity Press. 239 p.

Dobbs RC. 1976. White spruce seed dispersal in central British Columbia. Forestry Chronicle 52: 225–228.

Dunberg A. 1980. Stimulation of flowering in *Picea abies* by gibberellins. Silvae Genetica 29: 51–53.

Edwards DGW. 1980. Maturity and quality of tree seeds: a state of the art review. Seed Science and Technology 8: 625–657.

Edwards DGW. 1986. Cone prediction, collection, and processing. In: Shearer RC, comp. Proceedings, Conifer Tree Seed in the Inland Mountain West Symposium; 1985 August 5–6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 78–102.

Eis S. 1973. Predicting white spruce cone crops. Tech. Note BC-P-7. Victoria, BC: Environment Canada, Pacific Forest Research Centre. 4 p.

Eremko RD, Edwards DGW, Wellinger D. 1989. Guide to collecting cones of British Columbia conifers. Forest Resource Development Agreement Rep. 055. Victoria, BC: Forestry Canada, British Columbia Ministry of Forestry. 114 p.

Everett TH. 1981. The New York Botanical Garden illustrated encyclopedia of horticulture. New York: Garland Publishing. 3601 p.

Farmer RE, Charrette P, Searle IE, Tarjan DP. 1984. Interaction of light, temperature, and chilling in the germination of black spruce. Canadian Journal of Forest Research 14: 131–133.

Fechner GH. 1974. Maturation of blue spruce cones. Forest Science 20: 47–50.

Fechner GH. 1985. Silvical characteristics of blue spruce. Gen. Tech. Rep. RM-117. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 19 p.

Fogal WH. 1990. White spruce cone crops in relation to seed yields, cone insect damage, and seed moth populations. In: West RJ, ed. Proceedings, Cone and Seed Pest Workshop; 1990 October 4; St. John's, NF. Info. Rep. N-X-274. St. John's, NF: Forestry Canada, Newfoundland and Labrador Region: 76–88.

Fogal WH, Alemdag IS. 1989. Estimating sound seeds per cone in white spruce. Forestry Chronicle 65: 266–270.

Fogal WH, Larocque G. 1992. Development of flowers, cones, and seeds in relation to insect damage in two white spruce communities. Forest Ecology and Management 47: 335–348.

Fowler DP. 1980. Hybridization of black spruce and Serbian spruce. Info. Rep. M-X-112. Fredericton, NB: Canadian Forestry Service, Maritimes Forest Research Centre. 30 p.

Fowler DP, Mullin RE. 1977. Upland–lowland ecotypes not well developed in black spruce in northern Ontario. Canadian Journal of Forest Research 7: 35–40.

Fowler DP, Roche L. 1977. Genetics of Engelmann spruce. Res. Pap. WO-30. Washington, DC: USDA Forest Service. 13 p.

Fowler DP, Park YS, Gordon AG. 1988. Genetic variation of red spruce in the Maritimes. Canadian Journal of Forest Research 18: 703–709.

Fraser JW. 1976. Viability of black spruce seed in or on a boreal forest seedbed. Forestry Chronicle 52: 229–231.

Furnier GR, Stine M, Mohn CA, Clyde MA. 1991. Geographic patterns of variation in allozymes and height growth in white spruce. Canadian Journal of Forest Research 21: 707–712.

Gosling PG, Rigg P. 1990. The effect of moisture content and prechill duration on the efficiency of dormancy breakage in Sitka spruce (*Picea sitchensis*). Seed Science and Technology 18: 337–343.

Haavisto VF, Fleming RL, Skeates DA. 1988. Potential and actual yields of seed from black spruce cones. Forestry Chronicle 64: 32–34.

Hall JP. 1988. Promotion of flowering in black spruce using gibberellins. Silvae Genetica 37: 135–138.

Hanover JW. 1975. Genetics of blue spruce. Res. Pap. WO-28. Washington, DC: USDA Forest Service. 12 p.

Harris AS. 1990. *Picea sitchensis*. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 260–267.

Harrison DLS, Owens JN. 1983. Bud development in *Picea engelmannii*: 1. Vegetative bud development, differentiation, and early development of reproductive buds. Canadian Journal of Botany 61: 2291–2301.

Hedlin AF. 1973. Spruce cone insects in British Columbia and their control. Canadian Entomologist 105: 113–122.

Hedlin AF, Yates HO, Tovar DC, Ebel BH, Koerber TW, Merkel EP. 1980. Cone and seed insects of North American conifers. Victoria, BC: Environment Canada, Canadian Forestry Service [with USDA Forest Service and Secretaria de Agricultura y Recuros Hidraulicos, Mexico]. 122 p.

Heit CE. 1968. Propagation from seed: 13. Some western and exotic spruce species. American Nurseryman 127: 12–13, 51–63.

Hill JA. 1976. Viability of several species of conifer seeds after long term storage. Tree Planters' Notes 27: 2–3.

Ho RH. 1988a. Gibberellin $A_{4/7}$ enhances seed-cone production in field-grown black spruce. Canadian Journal of Forest Research 18: 139–142.

Ho RH. 1988b. Promotion of cone production on white spruce grafts by gibberellin $A_{4/7}$ application. Forest Ecology and Management 23: 39–46.

Ho RH. 1991. Promotion of cone production in potted black-spruce grafts, using gibberellins, heat-treatment and root-pruning. Forest Ecology and Management 40: 261–269.

Huxley A. ed. 1992. The new Royal Horticultural Society dictionary of gardening. New York: Stockton Press. 3353 p.

Jeglum JK, Kennington DJ. 1993. Strip clearcutting in black spruce: a guide for the practicing forester. Sault Ste. Marie, ON: Forestry Canada, Ontario Region, Great Lakes Forestry Centre. 102 p.

Jensen A, Stephansen K, Løken A. 1967. Seed ripening of Norwegian coniferous trees: 2. Variation in the chemical content and germination of seeds of *Picea abies* (L.) Karst. and *Picea sitchensis* (Bong.) Carr. Forest Research Institute West Norway Report 44: 191–222.

Khalil MAK. 1984. All-range black spruce provenance study in Newfoundland: performance and genotypic stability of provenances. Silvae Genetica 33: 63–71.

Kiss GK. 1989. Engelmann × Sitka spruce hybrids in central British Columbia. Canadian Journal of Forest Research 19: 1190–1193.

Lackey M, Alm A. 1982. Evaluation of growing media for culturing containerized red pine and white spruce. Tree Planters' Notes 33: 3–7.

Landis TD, Tinus RW, McDonald SE, Barrett JP. 1989. The container tree nursery manual. Volume 4, Seedling nutrition and irrigation. Agric. Handbk. 674. Washington DC: USDA Forest Service. 112 p.

Li J, Than H, Ge J. 1990. Spruce forests in northeast China. In: Titus BD, Lavigne MB, Newton PF, Meades WJ, eds. The silvics and ecology of boreal spruces: Proceedings of the IUFRO Working Party S1.05-12 Symposium; 1989 August 12–17; St. John's, NF. Info. Rep. N-X-271. St. John's, NF: Forestry Canada: 91–95

Little EL Jr. 1953. A natural hybrid spruce in Alaska. Journal of Forestry 51: 745–747.

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

MacGillivary JH. 1955. Germination of spruce and fir seeds following different stratification periods. Forestry Chronicle 31: 365.

Malek L. 1992. Priming black spruce seeds accelerates container stocking in techniculture single-seed sowing system. Tree Planters' Notes 43: 11–13.

Marquard RD, Hanover JW. 1984. Sexual zonation in the crown of *Picea glauca* and the flowering response to exogenous $GA_{4/7}$. Canadian Journal of Forest Research 14: 27–30.

Martell AM. 1981. Effects of pelleting and repellent coating of conifer seeds on feeding by deer mice. Info. Rep. O-X-330. Sault Ste. Marie, ON: Canadian Forestry Service, Great Lakes Forest Research Centre. 9 p.

McCaughey WW, Schmidt WC. 1987. Seed dispersal of Engelmann spruce in the Intermountain West. Northwest Science 61: 1–6.

Mitchell RG, Wright KH, Johnson NE. 1990. Damage by the Sitka spruce weevil (*Pissodes strobi*) and growth patterns for 10 spruce species and hybrids over 26 years in the Pacific Northwest. Res. Pap. PNW-434. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 12 p.

Mitton JB, Andalora R. 1981. Genetic and morphological relationships between blue spruce, *Picea pungens*, and Engelmann spruce, *Picea engelmannii*, in the Colorado Front Range. Canadian Journal of Botany 59: 2088–2094.

Morgenstern EK. 1978. Range-wide genetic variation of black spruce. Canadian Journal of Forest Research 8: 463–473.

Mullin RE. 1980. Comparison of seedling and transplant performance following 15 years of growth. Forestry Chronicle 56: 231–232.

Nienstaedt H. 1981. Top pruning white spruce seed orchard grafts. Tree Planters' Notes 32(2): 9–13.

Nienstaedt H, Zasada JC. 1990. *Picea glauca*. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 204–226.

Nikolov N, Helmisaari H. 1992. Silvics of the circumpolar boreal forest tree species. In: Shugart HH, Leemans R, Bonan GB, eds. A systems analysis of the global boreal forest. Cambridge, UK: Cambridge University Press: 13–84.

Owens JN. 1986. Cone and seed biology. In: Shearer RC, comp. Proceedings, Conifer Tree Seed in the Inland Mountain West Symposium; 1985 August 5–6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 14–31.

Owens JN, Molder M. 1976. Bud development in Sitka spruce: 2. Cone differentiation and early development. Canadian Journal of Botany 54: 766–779.

Owens JN, Molder M. 1977. Bud development in *Picea glauca*: 2. Cone differentiation and early development. Canadian Journal of Botany 55: 2746–2760.

Owens JN, Molder M. 1984. The reproductive cycle of interior spruce. Victoria: British Columbia Ministry of Forestry, Information Services Branch. 30 p.

Park YS, Fowler DP. 1988. Geographic variation of black spruce tested in the Maritimes. Canadian Journal of Forest Research 18: 106–114.

Parker WH, Knowles P, Bennett F, Gray A, Krickl T. 1983. Habitat-dependent morphological and chemical variation in *Picea mariana* from northwestern Ontario. Canadian Journal of Botany 61: 1573–1579.

Patterson TE. 1988. A new species of *Picea* (Pinaceae) from Nuevo León, Mexico. SIDA 13(2): 131–135.

Payandeh B, Haavisto VF. 1982. Prediction equations for black spruce seed production and dispersal in northern Ontario. Forestry Chronicle 58: 96–99.

Pharis RP, Tomchuk D, Beall FD, Rauter RM, Kiss G. 1986. Promotion of flowering in white spruce (*Picea glauca*) by gibberellin $A_{4/7}$, auxin (naphthaleneacetic acid), and the adjunct cultural treatments of girdling and $Ca(NO_3)_2$ fertilization. Canadian Journal of Forest Research 16: 340–345.

Philipson JJ. 1985a. The promotion of flowering in large field-grown Sitka spruce by girdling and stem injections of gibberellin $A_{4/7}$. Canadian Journal of Forest Research 15: 166–170.

Philipson JJ. 1985b. The effect of top pruning, girdling, and gibberellin $A_{4/7}$ application on the production and distribution of pollen and seed cones in Sitka spruce. Canadian Journal of Forest Research 15: 1125–1128.

Philipson JJ. 1992. Optimal conditions for inducing coning of container-grown *Picea sitchensis* grafts: effects of applying different quantities of $GA_{4/7}$, timing and duration of heat and drought treatment, and girdling. Forest Ecology and Management 53: 39–52.

Radvanyi A. 1980. Germination of R-55 repellent treated and non-treated seeds of white spruce following prolonged cold storage. Forestry Chronicle 56: 60–63.

Ross SD. 1985. Promotion of flowering in potted *Picea engelmannii* (Perry) grafts: effects of heat, drought, gibberellin $A_{4/7}$, and their timing. Canadian Journal of Forest Research 15: 618–624.

Ross SD. 1988a. Effects of temperature, drought, and gibberellin $A_{4/7}$, and timing of treatment, on flowering in potted *Picea engelmannii* and *Picea glauca* grafts. Canadian Journal of Forest Research 18: 163–171.

Ross SD. 1988b. Pre- and post-pollination polyhouse environment effects on pollen and seed development in potted *Picea engelmannii* grafts. Canadian Journal of Forest Research 18: 623–627.

Ross SD. 1991. Effect of heat sums and of heat applied separately to shoot and roots on flowering in potted *Picea glauca* grafts. Canadian Journal of Forest Research 21: 672–679.

Ross SD. 1992. Promotion of flowering in Engelmann–white spruce seed orchards by GA$_{4/7}$ stem injection: effects of site, clonal fecundity, girdling and NAA, and treatment carry-over effects. Forest Ecology and Management 50: 43–55.

Rushforth K. 1986. Mexico's spruces: rare members of an important genus. Kew Magazine 3: 119-124.

Safford LO. 1974. *Picea*, spruce. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 587–597.

Schmid JM, Mitchell JC, Stevens RE. 1981. *Cydia youngana* (Kearfott) (Lepidoptera: Tortricidae) and associates in Engelmann spruce cones, Fraser Experimental Forest, Colorado 1974–1977. Res. Note RM-394. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 5 p.

Shepperd WD. 1995. Personal communication. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station.

Shepperd WD, Jeffers RM, Ronco F, II. 1981. An Engelmann spruce seed source study in the central Rockies. Res. Pap. RM-231. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 5 p.

Stein WI, Danielson R, Shaw N, Wolff S, Gerdes D. 1986. Users guide for seeds of western trees and shrubs. Gen. Tech. Rep. PNW-193. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 45 p.

Stiell WM. 1976. White spruce: artificial regeneration in Canada. Info. Rep. FMR-X-85. Ottawa: Forest Management Institute. 275 p.

Stone EL, McKittrick RC. 1976. On the layering of white spruce. Tree Planters' Notes 27: 14.

Summers D, Sutherland JR, Woods TAD. 1986. Inland spruce rust (*Chrysomyxa pirolata*) control: relation of ferbam application to basidiospore production, rainfall, and cone phenology. Canadian Journal of Forest Research 16: 360–362.

Sutherland RJ. 1990. Cone and seed diseases of conifers in Canada. In: West RJ, ed. Proceedings, Cone and Seed Pest Workshop; 1990 October 4; St. John's, NF. Info. Rep. N-X-274. St. John's, NF: Forestry Canada, Newfoundland and Labrador Region: 24–36.

Sutherland JR, Woods TAD. 1978. The fungus *Geniculodendron pyriforme* in stored Sitka spruce seeds: effects of seed extraction and cone collection method on disease incidence. Phytopathology 68: 747–750.

Sutherland JR, Lock W, Farris SH. 1981. *Sirococcus* blight: a seed-borne disease of container-grown spruce seedlings in coastal British Columbia forest nurseries. Canadian Journal of Botany 59: 559–562.

Sutherland JR, Woods TAD, Lock W, Hamilton MR, Braulin RR. 1978. Dusting seeds with aluminum powder. Tree Planters' Notes 29: 14–16.

Sutton BCS, Pritchard SC, Gawley JR, Newton CH. 1994. Analysis of Sitka spruce–interior spruce introgression in British Columbia using cytoplasmic and nuclear DNA probes. Canadian Journal of Forest Research 24: 278–285.

Tanaka Y, Kleyn NJ, Harper LM. 1986. Seed stratification of Engelmann spruce and lodgepole pine: the effect of stratification duration and timing of surface drying. Forestry Chronicle 62: 147–151.

Thomson J, Matthes-Sears U, Peterson RL. 1990. Effects of seed provenance and mycorrhizal fungi on early seedling growth in *Picea mariana*. Canadian Journal of Forest Research 20: 1739–1745.

Tompsett PB, Fletcher AM, Arnold GM. 1980. Promotion of cone and seed production on Sitka spruce by gibberellin application. Annals of Applied Biology 94: 421–429.

Thornburgh D. 1990. *Picea breweriana*. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 181–186.

Tyszkiewics S. 1968. Population studies of Norway spruce in Poland. Warsaw: Forest Research Institute. 180 p.

USDA ARS [USDA Agriculture Research Service]. 2002. Germplasm Resources Information Network (GRIN) [database available at http://www.ars-grin.gov]. Beltsville, MD: USDA ARS National Germplasm Resources Laboratory.

USDA NRCS [USDA Natural Resources Service]. 2001. PLANTS, Version 3.1 [database available at http://plants.usda.gov]. Baton Rouge, LA: USDA NRCS National Plant Data Center.

Viereck LA, Johnston WF. 1990. *Picea mariana*. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 227–237.

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

Wang ZM, MacDonald SE. 1992. Peatland and upland black spruce populations in Alberta, Canada: isozyme variation and seed germination ecology. Silvae Genetica 41: 117–122.

Werner RA. 1964. White spruce seed loss caused by insects in interior Alaska. Canadian Entomologist 96: 1462–1464.

West RJ. 1989. Cone depredations by the red squirrel in black spruce stands in Newfoundland: implications for commercial cone collection. Canadian Journal of Forest Research 19: 1207–1210.

West RJ, deGroot P. 1990. Red squirrels and cone crops: damage and management. In: West RJ, ed. Proceedings, Cone and Seed Pest Workshop; 1990 October 4; St. John's, NF. Info. Rep. N-X-274. St. John's, NF: Forestry Canada, Newfoundland and Labrador Region: 118–128.

West RJ, Sundaram KMS. 1992. First- and second-year effects of ACECAPS® implants against cone insects of black spruce. Canadian Entomologist 124: 577-585.

West SD, Ford RG, Zasada JC. 1980. Population response of the northern red-backed vole (*Clethrionomys rutilus*) to differentially cut white spruce forest. Res. Note PNW-362. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 15 p.

Willan RL, comp. 1985. A guide to forest seed handling, with special reference to the tropics. For. Pap. 20/2. Rome: FAO. 379 p.

Winston DA, Haddon BD. 1981. Effects of early cone collection and artificial ripening on white spruce and red pine. Canadian Journal of Forest Research 11: 817–826.

Wright JW. 1955. Species crossability in spruce in relation to distribution and taxonomy. Forest Science 1: 319–349.

Yeh FC, Khalil MAK, El-Kassaby YA, Trust DC. 1986. Allozyme variation in *Picea mariana* from Newfoundland: genetic diversity, population structure, and analysis of differentiation. Canadian Journal of Forest Research 16: 713–720.

Young E, Hanover JW. 1978. Effects of temperature, nutrient, and moisture stresses on dormancy of blue spruce seedlings under continuous light. Forest Science 24: 458–467.

Youngberg CT. 1951. Effect of origin and growth conditions of Norway spruce (*Picea excelsa*) on the chemical composition of seed and physiological characteristics of nursery stock. Soil Science Society of America Proceedings 15: 376–379.

Youngblood A, Max TA. 1992. Dispersal of white spruce seed on Willow Island in interior Alaska. Res. Pap. PNW-443. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 17 p.

Zasada J [C]. 1980. Some considerations in the natural regeneration of white spruce in interior Alaska. In: Murray M, VanVeldhuizen RM, eds. Proceedings, International Workshop on Forest Regeneration at High Latitudes; 1979 November 15–17; Fairbanks, AK. Gen. Tech. Rep. PNW-107. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station: 25–29.

Zasada JC. 1971. Frost damage to white spruce cones in interior Alaska. Res. Note PNW-149. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 7 p.

Zasada JC. 1973. Effect of cone storage method and collection date on Alaskan white spruce (*Picea glauca*) seed quality. In: Proceedings, International Symposium on Seed Processing; IUFRO, working party S2.01.06; Bergen, Norway. Volume 1, Pap. 19. 10 p.

Zasada JC. 1988. Embryo growth in Alaskan white spruce seeds. Canadian Journal of Forest Research 18: 64–67.

Zasada JC, Lovig D. 1983. Observations on primary dispersal of white spruce, *Picea glauca*, seed. Canadian Field-Naturalist 97: 104–106.

Zasada JC, Viereck LA. 1970. White spruce cone and seed production in interior Alaska, 1957–68. Res. Note PNW-129. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 11 p.

Zasada JC, Foote MJ, Deneke FJ, Parkerson RH. 1978. Case history of an excellent white spruce cone and seed crop in interior Alaska: cone and seed production, germination, and seedling survival. Gen. Tech. Rep. PNW-65. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 53 p.

Ericaceae–Heath family

# *Pieris floribunda* (Pursh) Benth. & Hook.

## mountain andromeda

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**Synonym.** *Andromeda floribunda* Pursh.

**Other common names.** mountain pieris, fetterbush, mountain fetterbush.

**Growth habit, occurrence, and uses.** Mountain andromeda—*Pieris floribunda* (Pursh) Benth. & Hook.—is a broadleaf, evergreen, erect shrub 1 to 2 m in height and of equal or greater spread (Kruse 1987). The plant forms a rounded or flat-topped shape when mature and is covered with dense medium green foliage (Sabuco 1990). This species is indigenous to the Appalachian Mountains of the United States, extending from West Virginia southward into northern Georgia (Judd 1982). Mountain andromeda has a limited and scattered distribution along the Blue Ridge Mountains in the southern Appalachians (Spongberg 1990). It is typically found on mountain balds at high elevations and is hardy to USDA Zone 4 (Dirr 1990; Radford and others 1968).

The species is rare in cultivation, due in part to difficulties in propagation. This handsome, evergreen shrub has several desirable landscape attributes: a dense, compact growth habit; white, upright inflorescences; a tolerance of higher soil pH (pH 7.5) than typical for species in the Ericaceae; a greater cold tolerance than shown by other species in *Pieris* D. Don; and resistance to leaf damage by lacebug—*Stephanitis takeyai* Drake and Maa. (Kruse 1987; Sabuco 1990). The plant is best suited for landscape use in lightly shaded sites with a well-drained soil high in organic matter (Kruse 1987).

**Geographic races and hybrids.** There is only 1 known interspecific hybrid of mountain andromeda—*Pieris* × 'Brouwer's Beauty'. The hybrid resulted spontaneously when a plant of *Pieris floribunda* was pollinated by nearby plants of Japanese andromeda—*Pieris japonica* (Thunb.) D. Don ex G. Don (Jaynes and Dunbar 1976). The resultant hybrid has morphological characteristics that are intermediate between both parents (Jaynes 1975). The interspecific hybrid has an increased numbers of flowers that may be attributed to the sterility of the plant (Jaynes 1975). Lack of

seed-set apparently gives the cultivar added vigor, as well as improved flowering over mountain andromeda (Jaynes 1975).

**Flowering and fruiting.** Fragrant, white flowers are borne on upright panicles that open beginning in late March and last until early May. Inflorescences are held well above the leaves at the top of the shrub, where they can be seen easily (Sabuco 1990). The floral display will last from 4 to 6 weeks. After flowering and a flush of new vegetative growth, the plant develops the inflorescences for the next year. Decorative, greenish white flower buds are produced in midsummer and stand out from the foliage during the fall and winter (Hillier Nurseries 1994). These panicles of buds serve to extend the period of landscape interest of this shrub. Flowers are pollinated by small bees (Gibson 1901). Fruits are globular, dry, 5-chambered, dehiscent, capsules borne in clusters, each 1 about 3 mm in diameter (Bailey 1977). Seeds are 3 mm long and 1.5 mm wide, are flattened with 2 inconspicuous wings, and have a dark golden-yellow color (figures 1 and 2).

**Collection of fruits, seed extraction, cleaning, and storage.** Capsules and seeds ripen in mid- to late autumn and can be collected at that time (Kruse 1987). Capsules are removed from the plant, lightly beaten and rubbed to open them completely (Dirr and Heuser 1987), and then shaken to loosen the seeds. Viability can be poor if seeds are not graded rigorously. Use of an air column blower is recommended to remove chaff and empty seeds (Starrett and others 1992). When dried to a moisture content of 6% and cleaned, the number of pure seeds was 7,500/g (210,000/oz) (Starrett and others 1992).

Seeds of mountain andromeda are orthodox in storage behavior. They can be stored at room temperature if used within a year but can remain viable for several years if stored in a sealed container at 4.5 °C (Blazich and Starrett 1996).

**Germination tests.** There are no test methods prescribed for official seed tests of mountain andromeda, but

**Figure 1**—*Pieris floribunda*, mountain andromeda:   seeds.
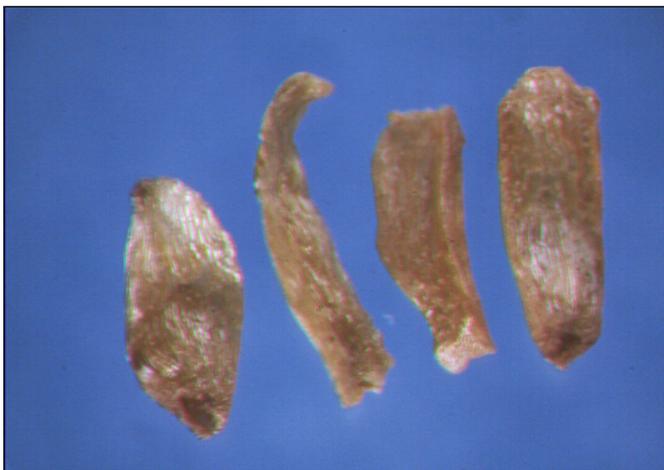


**Figure 2**—*Pieris floribunda*, mountain andromeda: longitudinal section of a seed.
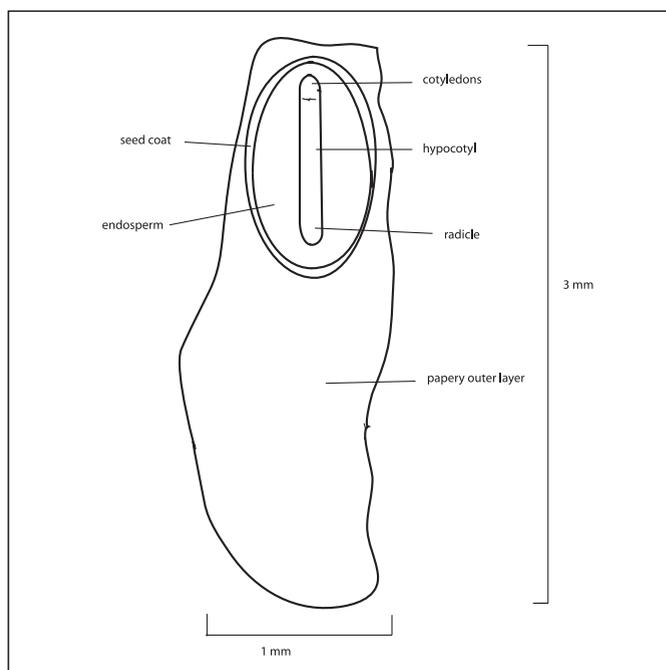


the seeds germinate readily without pretreatment (Kruse 1987). Seeds do not require light for germination, but daily photoperiods as short as $1/_2$ hour will maximize germination (Starrett and others 1992). A 30-day test of seeds from a source in the Blue Ridge Mountains of western North Carolina demonstrated that a daily photoperiod as short as 1/2 hour at 25 °C or an 8/16-hour thermoperiod of 25/15 °C resulted in 90% germination (Starrett and others 1992). Photoperiods of longer duration did not significantly improve germination of seeds from this source, regardless of temperature (Starrett and others 1992). The germination study of Starrett and others (1992) utilized cool-white fluo-rescent lamps as the light source, which provided a photo-synthetic photon flux (400 to 700 nm) of 69 $\mu$mol/m$^2$/sec (5.3 klux). Germination is epigeal.

**Nursery practice.**    Typically, a germination medium is warmed to 24 °C via bottom heat (Bir 1987). Seeds are sown on the surface of a steam-pasteurized medium such as pine bark sifted through a 6-mm ($1/_4$-in)-mesh screen and irrigated slightly. The surface of the germinating medium should never be allowed to dry completely (Bir 1987). Once seeds have germinated, seedlings have very slow initial growth. The authors have observed that seedlings will often produce 1 true leaf above the cotyledons and then fail to exhibit any further growth for several weeks. Current prac-tice is to fertilize seedlings at the first-true-leaf stage with a half-strength solution of a 15-45-5 (N:P$_2$O$_5$:K$_2$O) complete fertilizer (Bir 1987). After 2 weeks, nursery workers then shift the seedlings to a full-strength fertilizer with weekly application until they transplant the seedlings into liner flats or pots (Bir 1987).

Mountain andromeda can also be propagated vegetative-ly by rooting stem cuttings (Dirr and Heuser 1987) and by micropropagation (Starrett and others 1993). However, stem cuttings are reportedly difficult to root (Leach 1976).

## References

Bailey LH. 1977.    Manual of cultivated plants. New York: Macmillan. 1116 p.
Bir RE. 1987.    Native plant production using a multidisciplinary approach. American Nurseryman 166(12): 74–83.
Blazich FA, Starrett MC. 1996.    Unpublished data. Raleigh: North Carolina State University.
Dirr MA. 1990.    Manual of woody landscape plants: their identification, ornamental characteristics, culture, propagation and uses. 4th ed. Champaign, IL: Stipes Publishing. 1007 p.
Dirr MA, Heuser CW Jr. 1987.    The reference manual of woody plant prop-agation: from seed to tissue culture. Athens, GA: Varsity Press. 239 p.
Gibson WH. 1901.    Blossom hosts and insect guests. New York: Newson and Co. 197 p.
Hillier Nurseries. 1994.    The Hillier manual of trees and shrubs. 6th ed. Newton Abbot, Devon, UK: David and Charles. 704 p.
Jaynes RA. 1975.    'Brouwer's Beauty' pieris, a new interspecific hybrid. HortScience 10(2): 185–186.
Jaynes RA, Dunbar D. 1976.    Pieris 'Brouwer's Beauty', a spontaneous hybrid of P. floribunda and P. japonica. American Nurseryman 143(2):15, 54–55.
Judd WS. 1982.    A taxonomic revision of *Pieris* (Ericaceae). Journal of the Arnold Arboretum 63(2): 103–144.
Kruse K. 1987.    Field note: *Pieris floribunda*. American Nurseryman 166(12): 126.
Leach DG. 1976.    Successful rooting of cuttings of *Pieris floribunda*. Plant Propagator 22(2): 13–14.
Radford AE, Ahles HE, Bell CR. 1968.    Manual of the vascular flora of the Carolinas. Chapel Hill: University of North Carolina Press. 1183 p.
Sabuco JJ. 1990.    Mid-sized models: Part 11. American Nurseryman 172(11): 42–44, 46–51.
Spongberg SA. 1990.    A reunion of trees. Cambridge, MA: Harvard University Press. 270 p.
Starrett MC, Blazich FA, Acedo JR, Warren SL. 1993.    Micropropagation of *Pieris floribunda*. Journal of Environmental Horticulture 11(4): 191–195.
Starrett MC, Blazich FA, Warren  SL. 1992.    Seed germination of *Pieris flori-bunda*: influence of light and temperature. Journal of Environmental Horticulture 10(2): 121–124.

Pinaceae—Pine family

# *Pinus* L.
## pine

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**Growth habit, occurrence, and use.** The genus *Pinus* comprises about 100 species and numerous varieties and hybrids. It is one of the largest of the conifer genera, and one of the most important and widely distributed genera of forest trees in the Northern Hemisphere. Globally, the genus spans latitudes from Alaska to Nicaragua, Scandinavia to North Africa, and Siberia to Sumatra and inhabits a diversity of sites at altitudes ranging from sea level to timberline (Critchfield and Little 1966). Various pines exemplify the extremes of coastal and subalpine habitats in different regions of the world, including shore and whitebark pines in western North America; Italian stone and Swiss stone pines in Europe; and Japanese black and Siberian stone pines in Asia (table 1).

Some of the pines occur naturally over vast geographic ranges; others occur only in narrow or highly restricted ones. Those of limited natural range include Canary Island pine in the Canary Islands off the western coast of North Africa; Monterey pine in 3 distinct but quite small coastal areas of central California; and Torrey pine, with its total population of a few thousand trees, in 2 isolated island and coastal areas of southern California. The natural range of Scots pine, the most widespread of all the pines, crosses Eurasia, extending from Scotland and the Iberian Peninsula to eastern Siberia and northern Mongolia.

Evergreens of diverse heights, the pines supply major amounts of the world's most valuable timber and wood fiber, continue to yield the bulk of naval stores, and produce seeds that are valuable food sources for humans and wildlife. Pines are widely planted to protect watersheds, form shelterbelts and windbreaks, and provide wildlife habitats; they also are being increasingly planted to improve environments in rural and urban areas.

Sixty-seven species and varieties of pines are planted in or are known to have potential in the United States (table 1). Forty-three of these pines are native to the United States, and at least 13 of them are native to Mexico. Two are native solely to Mexico; one is native to the Caribbean region; 12

are indigenous to Europe, North Africa, and the Near East; and 12 are native to Asia.

Most of these pines grow tall, but some do not, and a few are shrubby in form (table 2). Eastern white, ponderosa, and sugar pines often surpass 61 m in height at maturity; Parry and Mexican piñyons and Japanese stone pines, by contrast, rarely attain 9, 8, and 2.5 m in height, respectively.

Pines are widely planted in the United States. Most survive and grow well in plantations within their areas of seed origin but largely fail outside their ranges. Nevertheless, successful plantations outside the native range have extended the geographic distributions of many pines in the United States, particularly those of jack, slash, Rocky Mountain ponderosa, Monterey, red, eastern white, loblolly, and Virginia pines (Fowells 1965; Harris and Harrar 1946; Wright 1962). Still, abundant plantation experience has also shown that the eastern pines, and especially the southern ones, survive and grow poorly in the western United States, and reciprocally, that western pines perform poorly in the eastern United States (Krugman and Jenkinson 1974; Schmitt and Namkoong 1965).

Many exotic pines have been introduced into the United States and, depending on region, have survived and grown well. Some have regenerated extensively and at least 4—namely Japanese red and Japanese black pines from Asia and Austrian and Scots pine from Europe—have naturalized in parts of New England and the Great Lakes region (Krugman and Jenkinson 1974; York and Littlefield 1942).

Many pine species have been successfully planted outside their native range, in various regions and on other continents around the world. The best of a host of known thriving introductions include the following species: Canary Island pine in North Africa and South Africa; Caribbean pine in Australia, Fiji, and South Africa; lodgepole, Austrian, eastern white, and Scots pines in Europe; slash, longleaf, maritime, and loblolly pines in Australia, New Zealand, China, and South Africa; Aleppo pine in South America; Khasi pine in East Africa; Merkus pine in Borneo and Java; bishop and

## Table 1— *Pinus,* pine: nomenclature and occurrence

| Scientific name & synonym(s) | Common name(s) | Occurrence |
| --- | --- | --- |
| **P. albicaulis Engelm.** | **whitebark pine** | Subalpine; Sierra Nevada–Cascade Ranges; coastal ranges & Rocky Mtns; S British Columbia, adjacent Alberta S to central California, N Nevada; Idaho, Montana, to NE Oregon, W Wyoming |
| **P. aristata Engelm.**<br>P. balfouriana var. aristata (Engelm.) Engelm. | **bristlecone pine,** foxtail pine, hickory pine | Subalpine; E central California, Nevada, Utah, N Arizona; central Colorado & N New Mexico |
| **P. arizonica Engelm.**<br>P. ponderosa var. arizonica (Engelm.) Shaw | **Arizona pine,** Arizona ponderosa pine, Arizona yellow pine | Sierra Madre Occidental; NW Durango, central Mexico, N into SE Arizona, SW corner New Mexico |
| **P. armandii Franch.** | **Armand pine** | Mid-high elevations of mtns in central China to SW China, N Burma, E Tibet; Hainan, Taiwan; Japan (N Ryuku Islands) |
| **P. attenuata Lemmon**<br>P. tuberculata Gord. | **knobcone pine** | Rocky slopes & ridges of Klamath Mtns, coastal ranges & Sierra Nevada in SW Oregon & California; Baja California Norte |
| **P. balfouriana Grev. & Balf.** | **foxtail pine,** Balfour pine | Subalpine California; central, S Klamath Mtns, S Sierra Nevada |
| **P. banksiana Lamb.**<br>P. divaricata (Ait.) Dum.-Cours. | **jack pine,** scrub pine, banksiana pine, black/gray pine, Hudson Bay pine | Canada, NE US: S Mackenzie to central Alberta, E through Ontario to Nova Scotia, S through Great Lakes region to SW Wisconsin, Michigan to NW Indiana; upstate New York, New Hampshire, Maine |
| **P. brutia Tenore**<br>P. halepensis var. brutia (Ten.) Elwes & Henry | **Calabrian pine** | Crete, Cyprus, Lebanon, W Syria, Turkey to NE Greece, Black Sea; Caucasus Mtns; N Iraq |
| **P. canariensis C. Smith** | **Canary Island pine,** Canary pine | Dry slopes of Canary Islands (Hierro, La Palma, Tenerife, Gomera, & Gran Canaria), Spain |
| **P. caribaea Morelet**<br>P. bahamensia Griseb.<br>P. hondurensis Loock | **Caribbean pine** | W Bahamas; W Cuba, Isle of Pines; Caribbean Central America, Belize S to Nicaragua |
| **P. cembra L.**<br>P. montana Lam. | **Swiss stone pine,** cembrian pine, arolla pine | High elevations in Alps & Carpathian Mtns; N Italy, SE France, Switzerland, Austria, W tip of Yugoslavia; Romania, SW Ukraine, NW [Czecho]slovakia |
| **P. cembroides Zucc.** | **Mexican piñyon,** nut pine, pinyon | Semiarid, low elevations of Sierra Madre Oriental & Occidental; Puebla, Tlaxcala N in E, W Mexico to SE Arizona, SW New Mexico, SW Texas; S Baja California Sur, Mexico |
| **P. clausa (Chapman ex Engelm.) Vasey ex Sarg.** | **sand pine,** scrub pine, spruce pine | Sandy plains; throughout central Florida to coastal NE & S Florida; also W Florida Panhandle W into Baldwin Co., coastal Alabama |
| **P. contorta var. bolanderi (Parl.) Vasey** | **Bolander pine** | Coastal N California: acid podsol soils of Mendocino White Plains in Mendocino Co. |
| **P. contorta var. contorta Dougl. ex Loud.** | **shore pine,** coast pine, beach pine, lodgepole pine | Pacific Coast mtns, low elevations down to sea level; California north coastal ranges N to Yakutat Bay, SE Alaska |
| **P. contorta var. latifolia Engelm. ex S. Wats.** | **Rocky Mountain lodgepole pine,** black pine | Rocky Mtns & intermountain region; Colorado & Utah N through W Canada to central Yukon; Black Hills, South Dakota |
| **P. contorta var. murrayana (Grev. & Balf.) Engelm.** | **Sierra Nevada lodgepole pine,** tamarack pine | Subalpine; Sierra Nevada–Cascade Ranges, transverse–peninsular ranges; California to Baja California Norte, W Nevada, Oregon N to SW Washington |
| **P. coulteri D. Don**<br>P. ponderosa ssp. coulteri (D. Don) E. Murr | **Coulter pine,** nut pine, big-cone pine | Mtns; California south coastal ranges S through transverse–peninsular ranges to N Baja California Norte |
| **P. densiflora Sieb. & Zucc.** | **Japanese red pine** | Mtns, low-mid elevations in Japan (Honshu to Kyushu), South Korea, E North Korea to SE Manchuria, adjoining Chabarovsk, Siberia |
| **P. echinata P. Mill** | **shortleaf pine,** southern yellow pine, oldfield pine | Coastal plains, Piedmont, Appalachian Mtns, Ozark Plateau; tip SE New York S to NW Florida, W to E Texas, E Oklahoma, SE Missouri, S Ohio |
| **P. edulis Engelm.**<br>P. cembroides var. edulis (Engelm.) Voss | **piñyon,** Colorado pinyon, nut pine, two-needle pinyon | Semiarid regions; Arizona, Utah, Colorado, New Mexico; crosses into W Oklahoma, SW Texas, & SE California |

| Table 1— *Pinus,* pine: nomenclature and occurrence (continued) | | |
| --- | --- | --- |
| **Scientific name & synonym(s)** | **Common name(s)** | **Occurrence** |
| **P. elliottii var. densa Little & Dorman** | **South Florida slash pine** | Sandy plains of central to S Florida, E & W Florida coasts; lower Florida Keys |
| **P. elliottii var. elliottii Engelm.** <br> *P. caribaeu* Morelet | **slash pine,** pitch pine, swamp pine, yellow slash pine, Honduras pine | Coastal plains of lower South Carolina S to central Florida, W to S Mississippi, SE Louisiana |
| **P. engelmannii Carr.** <br> *P. latifolia* Sarg. <br> *P. apacheca* Lemmon | **Apache pine,** <br> Arizona longleaf pine | Sierra Madre Occidental; Aguascalientes, SW Zacatecas N through W Mexico into SE Arizona, SW corner of New Mexico |
| **P. flexilis James** | **limber pine,** Rocky Mountain white pine | Subalpine; Sierra Nevada, Great Basin ranges, Rocky Mtns; New Mexico N to Alberta, Canada; W in Idaho, Utah, Nevada, into S California |
| **P. gerardiana D. Don** <br> *P. aucklandii* Lodd. <br> *P. chilghoza* Ehh. | **chilgoza pine,** <br> Gerard pine | Himalayas, dry valleys; E Afghanistan, contiguous N Pakistan, N India |
| **P. glabra Walt.** | **spruce pine,** cedar pine, bottom white pine | Coastal plains of E South Carolina to N Florida, W to S Mississippi, SE Louisiana |
| **P. halepensis P. Mill.** <br> *P. alepensis* Poir. | **Aleppo pine,** <br> Jerusalem pine | Mediterranean region: E Spain, SE France, Italy, S Adriatic Coast to Greece; NE Libya; Israel, Morocco to N Tunisia; Pantalleria, Sicily; W Jordan N to extreme S central Turkey |
| **P. heldreichii Christ** <br> *P. heldreichii* var. *leucodermis* (Ant.) Markgr. <br> *P. eucodermis* Ant. <br> *P. nigra* var. *leucodermis* (Ant.) Rehd. | **Heldreich pine,** <br> Balkan pine, Bosnian pine, graybark pine | High elevations of Balkan Peninsula, Albania to SW Yugoslavia, extreme N Greece, SW to SW Bulgaria, & SW Italy |
| **P. jeffreyi Grev. & Balf.** <br> *P. ponderosa* var. *jeffreyi* (Grev. & Balf.) E. Murr. | **Jeffrey pine** | Sierra Nevada–Cascade & Klamath Mtns, coastal & transverse–peninsular ranges of California to SW Oregon, Baja California Norte, W Nevada |
| **P. kesiya Royle & Gordon** <br> *P. khasya* Royle <br> *P. insularis* Endl. | **Khasi pine,** <br> Benguet pine | High elevations of E India, SE Tibet, Burma, SW Yunnan to N Thailand, Laos, S Vietnam, W Luzon, Philippines |
| **P. koraiensis Sieb. & Zucc.** | **Korean pine,** <br> cedar pine | Mtns of South Korea to North Korea through E Manchuria, S Chabarovsk, Siberia; Japan (central Honshu & Shikoku) |
| **P. lambertiana Dougl.** | **sugar pine,** <br> *piño real* | Sierra Nevada–Cascade & Klamath Mtns, coastal & transverse–peninsular ranges of California to N Oregon, Baja California Norte, W Nevada |
| **P. leiophylla var. chihuahuana (Engelm.) Shaw** <br> *P. chihuahuana* Engelm. | **Chihuahua pine,** <br> yellow pine, <br> *piño real* | Sierra Madre del Sur, trans–Mexico volcanic belt, Sierra Madre Occidental; Oaxaca, Vera Cruz W to Michoacán; N in W Mexico to SE Arizona, SW New Mexico |
| **P. merkusii Junghuhn & Vriese ex Vriese** | **Merkus pine,** <br> Tenasserim pine | Mtns, low elevations of SE Burma, N Thailand, Cambodia, Laos, Vietnam, Hainan, N Sumatra, Philippines (W Luzon & N Mindoro) |
| **P. monophylla Torr. & Frém.** <br> *P. cembroides* var. *monophylla* (Torr. & Frém.) Voss | **singleleaf piñyon,** <br> nut pine, <br> pinyon, piñon | Semiarid mtns of NW Arizona, W Utah to SE Idaho, W through Nevada to E California, S to Baja California Norte |
| **P. monticola Dougl. ex D. Don** | **western white pine,** <br> Idaho white pine, <br> silver pine | Sierra Nevada, Cascade & coastal ranges; Klamath & Rocky Mtns; California, W Nevada, Oregon through Washington, N Idaho, NW Montana, Vancouver Island, S British Columbia, SW corner Alberta |
| **P. mugo Turra** <br> *P. montana* Miller | **Swiss mountain pine,** mugho (or mugo) pine, dwarf mountain pine | Subalpine areas in central & S Europe: Pyrenees, Alps, Carpathian Mtns, Balkan Mtns; Austria, Switzerland, N Italy, E France; N to Germany, Czech Republic & Slovakia into S Poland, E into W Ukraine, Romania; Yugoslavia to N Albania, W Bulgaria; central Italy; S France, NE Spain |
| **P. muricata D. Don** <br> *P. remorata* Mason | **bishop pine,** <br> prickle-cone pine, <br> Santa Cruz Island pine | Coastal mtns; California Coast Ranges, Santa Rosa & Santa Cruz Islands; Baja California Norte, Cedros Island, Mexico |
| **P. nigra Arnold** <br> *P. nigra* var. *austriaca* (Hoess) Aschers. & Graebn. | **Austrian pine,** <br> European black pine, black pine | S Europe, Mediterranean, Asia Minor; Spain to Corsica, Italy, Sicily; Yugoslavia to E Austria, SW Romania, Bulgaria, Albania, Greece, Turkey; Black Sea Coast in Ukraine, Russia; Cyprus; NE Morocco; N Algeria |

**Table 1—** *Pinus,* pine: nomenclature and occurrence (continued)

| Scientific name & synonym(s) | Common name(s) | Occurrence |
|---|---|---|
| *P. palustris* **P. Mill.**<br>*P. australis* Michx. f. | **longleaf pine,**<br>southern pine,<br>longstraw pine | Coastal plains of SE Virginia to central Florida,<br>W to N Louisiana, E Texas |
| *P. parviflora* **Sieb. & Zucc.**<br>*P. pentaphylla* Mayr<br>*P. himekomatsu* Miyabe & Kudo | **Japanese white pine** | Mtns of Japan (Kyushu, Tsushima, Shikoku, Honshu,<br>Sado, & S Hokkaido); South Korea (Ullung Island) |
| *P. patula* **Schiede ex Schtdl.**<br>**& Cham.** | **Mexican weeping pine** | Sierra Madre Oriental, Mexico; central Oaxaca N to<br>Querétaro, SW Tamaulipas; Guatemala, El Salvador,<br>Honduras, Nicaragua |
| *P. peuce* **Griseb.**<br>*P. excelsa* var. *peuce* (Griseb.) Beissn. | **Balkan pine,**<br>Macedonian pine,<br>Greek stone pine | High elevations of Balkan Peninsula: SW<br>Yugoslavia, E Albania, SW Bulgaria, extreme N Greece |
| *P. pinaster* **Aiton**<br>*P. maritima* Poir. | **maritime pine,**<br>cluster pine, pinaster pine | SW Europe & Mediterranean Basin: Iberian Peninsula,<br>SE France + Corsica; W Italy + Sardinia & Pantalleria;<br>Morocco, coastal E Algeria |
| *P. pinea* **L.** | **Italian stone pine,**<br>umbrella pine,<br>stone pine | Iberian Peninsula& Mediterranean Coast of France,<br>W Italy, Albania, Greece, Turkey; NE Turkey; Lebanon;<br>Ibiza, Majorca; Sardinia, Sicily; Corfu, Crete, & Cyprus |
| *P. ponderosa* var. *ponderosa*<br>**P. & C. Lawson.** | **Pacific ponderosa**<br>**pine,** western yellow<br>pine, bull pine, rock<br>pine, blackjack pine | Sierra Nevada–Cascade Mtns, coastal & transverse–<br>peninsular ranges, Klamath Mtns; California to W<br>Nevada, N through Oregon, Washington, Idaho,<br>W Montana, to S British Columbia |
| *P. ponderosa* var. *scopulorum*<br>**Engelm.** | **Rocky Mountain**<br>**ponderosa pine,**<br>western yellow pine,<br>blackjack pine | Rocky Mtns, Sierra Madre Oriental; Montana, SW<br>North Dakota S in Wyoming, Colorado, New Mexico,<br>trans–Pecos Texas to Coahuila, San Luis Potosi; E<br>to central Nebraska; W in Utah, Arizona to Nevada |
| *P. pumila* **Regel**<br>*P. cembra* var. *pumila* Pall. | **Japanese stone pine**,<br>dwarf Siberian pine | NE Asia; E Siberia, Lake Baikal, Lena River regions<br>E to Bering Sea & Sea of Okhotsk; N Mongolia;<br>E Manchuria to South Korea; Sakhalin; Kamchatka,<br>Kuril Islands to central Honshu, Japan |
| *P. pungens* **Lamb.** | **Table Mountain pine,**<br>hickory pine, mountain<br>pine, prickly pine | Appalachian Mtns of SW Pennsylvania, W<br>Maryland through E West Virginia, W Virginia to E<br>Tennessee, W North Carolina, extreme NE Georgia |
| *P. quadrifolia* **Parl. ex Sudworth** | **Parry piñyon,**<br>nut pine, pinyon | Semiarid, low elevations of San Jacinto Mtns, SW<br>California, S to Sierra San Pedro Mártir, Baja |
| *P. radiata* **D. Don**<br>*P. insignis* Dougl. | **Monterey pine,**<br>radiata pine,<br>insignis pine | Coastal central California, in Año Nuevo Point,<br>Monterey, & Cambria areas; Cedros Island<br>& N Guadalupe Island, Mexico |
| *P. resinosa* **Soland.** | **red pine,** Norway<br>pine, hard pine,<br>pitch pine | Great Lakes region, Appalachian Mtns; SE Manitoba<br>E to Nova Scotia, N Newfoundland; S to Wisconsin,<br>N Illinois, Pennsylvania, New Jersey; NE West Virginia |
| *P. rigida* **P. Mill.** | **pitch pine,**<br>hard pine, bull pine | Appalachian Mtns in N Georgia, Kentucky, E Tennessee<br>N through Pennsylvania, Delaware to SE Ontario, &<br>central Maine |
| *P. roxburghii* **Sarg.**<br>*P. longifolia* Roxb. | **Chir pine,**<br>longleaf Indian pine | Himalayas, monsoon belt; N Pakistan E through N<br>India, Nepal, Sikkim, Bhutan |
| *P. sabiniana* **Dougl. ex Dougl.** | **Digger pine,** bull pine,<br>gray pine | Dry slopes, low-mid elevations; California, in S<br>Klamath Mtns, coastal ranges, Cascade<br>Mtns–Sierra Nevada |
| *P. serotina* **Michx.**<br>*P. rigida* var. *serotina* (Michx.) Clausen | **pond pine,** marsh<br>bay pine, pocosin pine | SE US, coastal plains of central & N Florida N to<br>lower New Jersey, W to central & SE Alabama |
| *P. sibirica* **Du Tour**<br>*P. cembra* var. *sibirica* Loud. | **Siberian stone pine** | Ural Mtns of Russia, E across central Siberia to<br>Stanovoy Mtns, S through Sayan Mtns, Lake Baikal<br>region to N Mongolia |
| *P. strobiformis* **Engelm.**<br>*P. flexilis* var. *reflexa* Engelm.<br>*P. reflexa* (Engelm.) Engelm.<br>*P. ayacahuite* var. *brachyptera* Shaw | **southwestern white**<br>**pine,** border limber<br>pine, Mexican white pine | Sierra Madre Occidental & Oriental; S Rocky Mtns;<br>Durango, central Mexico N to E Arizona, SW San<br>Luis Potosi N to extreme W Texas,<br>N through New Mexico to SW Colorado |

**Table 1**— *Pinus,* pine: nomenclature and occurrence (continued)

| Scientific name & synonym(s) | Common name(s) | Occurrence |
|---|---|---|
| *P. strobus* var. *chiapensis* **Martínez** | **Chiapas white pine** | Mtns of S Mexico (Chiapis) & Guatemala |
| *P. sylvestris* **L.** | **Scots pine,** Scotch pine | Eurasia: Scotland, Scandinavia, Germany, France, & Spain E to Turkey, Caucasus Mtns; Central & E Europe through Ural Mtns, N Kazakhstan, Siberia to Sea of Okhotsk, N Mongolia, N Manchuria |
| *P. taeda* **L.** | **loblolly pine,** Arkansas pine, North Carolina pine, oldfield pine | Coastal Plains, Piedmont; Delaware S to central Florida; W through Georgia, S Tennessee, Gulf Coast states to SE corner Oklahoma, E Texas |
| *P. thunbergiana* **Franco** <br> *P. thunbergii* Parl. | **Japanese black pine** | Maritime Japan (Honshu to N Ryukyu Islands), South Korea (Cheju Island) |
| *P. torreyana* **Parry ex Carr.** | **Torrey pine,** Soledad pine, Del Mar pine | Maritime S California (NE Santa Rosa Island) & coastal bluffs of San Diego County |
| *P. virginiana* **P. Mill** | **Virginia pine,** scrub pine, Jersey pine, spruce pine | Piedmont & Appalachian Mtns; Long Island, New York to Chesapeake Bay, S to N Georgia, central Alabama; W to Ohio, S Indiana, W Kentucky, Tennessee, NE Mississippi |
| *P. wallichiana* **A.B. Jacks.** <br> *P. excelsa* Wall. <br> *P. griffithii* McClelland <br> *P. nepalensis* de Chambr. | **blue pine,** Bhutan pine, Himalayan pine | Himalayas, mid-high elevations: NE Afghanistan, N Pakistan, N India E through Nepal, Bhutan, NE India, S Tibet to N Burma, NW Yunnan |
| *P. washoensis* **Mason & Stockwell** | **Washoe pine** | W edge of Great Basin; E slope Mt Rose, W Nevada; Bald Mtn Range in N Sierra Nevada; S Warner Mtns, NE California |

**Sources:** Critchfield and Little (1966), Gardner and Berenson (1987), Griffin and Critchfield (1976).

ponderosa pines in Australia and New Zealand; Mexican weeping pine in South Africa; and Monterey pine in Australia, New Zealand, Spain, South Africa, and South America. Nine of these 17 pines are native to North America (Leloup 1956; Magini and Tulstrup 1955; Mirov 1967; Wright 1962).

**Geographic races.** Abundant field experience and provenance research have shown that genetic adaptation mandates sowing seeds and outplanting seedlings grown from seeds from the proper source. Seed origin critically controls a species' ability to survive and grow in a particular environment. Pines that have extensive natural ranges (and even some with highly restricted ones) have evolved geographic races that are distinct both morphologically and physiologically (Callaham 1963). The resultant genetic—that is, seed-source—differences make each race the best suited for growth and survival in a particular environment.

As a general rule, seeds from pines growing in moist regions are smaller than those from sources in dry regions and seeds from moist regions normally produce seedlings that are faster growing and less deeply rooted than those from dry regions. Seeds from southern sources differ from those from northern sources. Seeds from northern sources often require longer moist chilling times than seeds from southern ones to release seed dormancy and enable germination. Trees from southern sources grow faster, are able to

grow for a longer time during the growing season, and are more prone to winter freezing damage and less prone to damage from hard frosts in late spring and early autumn than are trees from northern sources (Krugman and Jenkinson 1974; Squillace and Silen 1962; Wells 1969; Wright 1962).

Detailed data on geographic races are ample for some pines and still lacking for many others. In some cases, our knowledge of races in pines native to the United States derives from species introduction trials and provenance tests in other countries. We have recapped the knowledge on geographic variation for the following 52 pines, all of those for which sufficient information was available.

*Pinus aristata*—Bristlecone pines in western and eastern parts of the range differ sufficiently in chemical composition and morphological traits that some suggest calling western populations *P. longaeva* D.K. Bailey and eastern populations *P. aristata* (Bailey 1970; Zavarin and Snajberk 1973). This very low crossing ability between western and eastern populations supports the naming of 2 distinct species (Critchfield 1977).

*Pinus attenuata*—For knobcone pine, differences in nursery and morphological traits tend to define 2 major groups, 1 north and 1 south of the Monterey County–San Luis Obispo County line in California. Seed weight generally increases from north to south. Seeds with northern origins

**Table 2** —*Pinus,* pine:   mature tree height, earliest cultivation, seed bearing age, and interval between large cone crops

| Species | Mature tree height (m) | Year first cultivated | Age at onset seed bearing (yr) | Years between cone crops |
|---|---|---|---|---|
| P. albicaulis | 6–33 | 1852 | 20–30 | 3–5 |
| P. aristata | 6–15 | 1861 | 20 | 102 |
| P. arizonica | 23–27 | — | 15–20 | 2–3 |
| P. armandii | 18–37 | 1895 | 20 | — |
| P. attenuata | 5–15 | 1847 | 5–8 | 1 |
| P. balfouriana | 11–18 | 1852 | 20 | 5–6 |
| P. banksiana | 17–30 | 1783, earlier | 3–15 | 3–4 |
| P. brutia | 20–30 | — | 7–10 | 1 |
| P. canariensis | 30 | — | 15–20 | 3–4 |
| P. caribaea | 18–30 | | — | — |
| P. cembra | 10–23 | 1746 | 25–30 | 6–10 |
| P. cembroides | 5–8 | 1830 | — | 5–8 |
| P. clausa | 5–24 | 1832 | 5 | 1–2 |
| P. contorta | | | | |
|   var. contorta | 6–12 | 1855 | 4–8 | 1 |
|   var. latifolia | 8–46 | 1853 | 5–10 | 1 |
|   var. murrayana | 15–30 | — | 4–8 | 1 |
| P. coulteri | 9–23 | 1832 | 8–20 | 3–6 |
| P. densiflora | 21–37 | 1854 | 20–30 | 2 |
| P. echinata | 2–30 | 1726 | 5–20 | 3–10 |
| P. edulis | 3–12 | 1848 | 25–75 | 2–5 |
| P. elliottii | | | | |
|   var. densa | 8–26 | — | 8–12 | 1–5 |
|   var. elliottii | 24–30 | — | 7–10 | 3 |
| P. engelmannii | 15–21 | — | 28–30 | 3–4 |
| P. flexilis | 6–24 | 1861 | 20–40 | 2–4 |
| P. gerardiana | 15–24 | 1839 | — | — |
| P. glabra | 24–27 | — | 10 | — |
| P. halepensis | 15–24 | 1683 | 15–20 | 1 |
| P. heldreichii | 18–30 | 1865 | — | — |
| P. jeffreyi | 18–55 | 1853 | 8 | 2–4 |
| P. kesiya | 30–46 | — | 5–10 | 1 |
| P. koraiensis | 27–46 | 1861 | 15–40 | 1–5 |
| P. lambertiana | 30–69 | 1827 | 40–80 | 3–5 |
| P. leiophylla var. chihuahuana | 9–24 | — | 28–30 | 3–4 |
| P. merkusii | 18–30 | — | 10–20 | 1–2 |
| P. monophylla | 6–15 | 1848 | 20–25 | 1–2 |
| P. monticola | 27–61 | 1851 | 7–20 | 3–7 |
| P. mugo | 2–12 | 1779 | 10 | 1 |
| P. muricata | 12–27 | 1846 | 5–6 | 2–3 |
| P. nigra | 20–50 | 1759 | 15–40 | 2–5 |
| P. palustris | 24–37 | 1727 | 20 | 5–7 |
| P. patula | 18–34 | — | 12–15 | — |
| P. parviflora | 5–30 | 1861 | — | 4–5 |
| P. peuce | 10–30 | 1863 | 12–30 | 3–4 |
| P. pinaster | 27–37 | 1660, earlier | 10–15 | 3–5 |
| P. pinea | 14–23 | Long history | — | — |
| P. ponderosa | | | | |
|   var. ponderosa | 18–70 | 1826 | 16–20 | 2–5 |
|   var. scopulorum | 15–35 | — | 6–20 | 2–5 |
| P. pumila | 0.3–2.5 | 1807 | — | — |
| P. pungens | 9–18 | 1804 | 5 | — |
| P. quadrifolia | 5–9 | 1885 | — | 1–5 |
| P. radiata | 2–46 | 1833 | 5–10 | 1 |

**Table 2 —**_Pinus,_ pine:  mature tree height, earliest cultivation, seed bearing age, and interval between large cone crops (continued)

| Species | Mature tree height (m) | Year first cultivated | Age at onset seed bearing | Years between cone crops |
|---|---|---|---|---|
| P. resinosa | 21–46 | 1756 | 20–25 | 3–7 |
| P. rigida | 6–30 | 1759, earlier | 3–4 | 4–9 |
| P. roxburghii | 46–55 | 1807 | 15–40 | 2–4 |
| P. sabiniana | 12–24 | 1832 | 10–25 | 2–4 |
| P. serotina | 12–24 | 1713 | 4–10 | 1 |
| P. sibirica | 40 | 1837 | 25–35 | 3–8 |
| P. strobiformis | 8–38 | 1840 | 15 | 3–4 |
| P. strobus | 24–67 | 1705 | 5–10 | 3–10 |
| P. sylvestris | 24–40 | Long history | 5–15 | 4–6 |
| P. taeda | 27–34 | 1713 | 5–10 | 3–13 |
| P. thunbergiana | 30–40 | 1855 | 6–40 | — |
| P. torreyana | 8–18 | 1853 | 12–18 | 1 |
| P. virginiana | 15–30 | 1739 | 5 | 1 |
| P. wallichiana | 15–46 | 1827 | 15–20 | 1–2 |
| P. washoensis | 18–46 | — | 15–20 | 2–5 |

**Sources:**  Altman and Dittmer (1962), Bailey (1970), Bates (1930), Britton and Shafer (1908), Carlisle and Brown (1968), Cooling (1968), Dallimore and Jackson (1967), Day (1967), den Ouden and Boom (1965), Dimitroff (1926), Duff (1928), Fowells (1965), Fritts (1969), Goor (1955), Harlow and Harrar (1950), Iroshnikov (1963), Iroshnikov and others (1963), Jacaline and Lizardo (1958), Krugman and Jenkinson (1974), Little EL (1941a, 1950), Loock (1950), Luckhoff (1964), Magini and Tulstrip (1955), McIntyre (1929), Mirov (1956), NBV (1946), Otter (1933), Pearson (1931), Poynton (1961), Pravdin (1963), Rehder (1940), Rohmeder and Loebel (1940), Rossi (1929), Sargent (1905, 1965), Sudworth (1908), Troup (1921), Veracion (1966), Wahlenberg (1946), Wakeley (1954), Wakeley and Barnett (1968), Wappes (1932), Wellner (1962).
**Note:**   See table 3 for cone ripening and seed dispersal dates and table 4 for cone ripeness criteria.

require longer stratification times (3 weeks or more) than seeds with southern origins (less than 3 weeks). Seedlings from northern sources tend to be more frost resistant than seedlings from southern sources. Trees in the northern part of the species' range are somewhat larger than those in the southern part. The source differences appear to be clinal and largely reflect the species' latitudinal distribution (Brown and Donan 1985; Newcomb 1962).

*Pinus balfouriana*—Foxtail pine seeds of northern origin in California (Lake Mountain, in the eastern Klamath Mountains) are longer than those of southern origin (Mineral King, in the southern Sierra Nevada). Seeds of northern origin have persistent wings, and seeds of southern origin have detachable wings (Mastrogiuseppe 1968).

*Pinus banksiana*—Jack pine seeds from various sources differ in seed size, cone traits, seedling and tree growth, tree form, and susceptibility to insect and disease damage (King 1971; Yeatman 1974). Cone serotiny in Minnesota changes from closed cones in the north to chiefly open cones in the south (Rudolph and others 1959). Seeds tend to be larger from trees growing in warmer parts of the range (Fowells 1965), and seedlings from lower latitudes show less winter needle coloration than those from higher latitudes (Stoeckeler and Rudolf 1956). In Canada, height growth was greater for seeds from areas with longer growing seasons; height growth of selections moved north was better than that of those moved south (Holst 1962). Growth in provenance

tests follows a largely clinal pattern that is linked to environmental gradients of latitude and length and temperature of the growing season at seed origin (Rudolph and Laidly 1990; Rudolph and Yeatman 1982).

*Pinus brutia*—Calabrian pine has 2 known varieties, both in the northernmost parts of its range. The var. *pithyusa* Stev. occurs along the north central and northeast shores of the Black Sea and var. *eldarica* Medw. occurs in the central Caucasus Mountains (Magini and Tulstrup 1955). Trees from an Afghanistan source related to var. *eldarica* outgrew trees of var. *pithyusa*, had good form, and were both frost and drought hardy in California (Harris and others 1970; Krugman and Jenkinson 1974). Altitudinal variation in a number of seed and seedling traits is manifested in Greece and in Turkey (Isik 1986; Panetsos 1986).

*Pinus canariensis*—Canary Island pine is native only to the Canary Islands, where it is found at 640 to 2,195 m above sea level (Magini and Tulstrup 1955). Seedlings grown from seeds from the various islands and an array of elevations showed marked differences in winter cold hardiness when grown at the USDA Forest Service's Institute of Forest Genetics nursery near Placerville, California. Seedlings from a seed source at 1,220 m on Tenerife Island showed more cold damage than those from a source at 1,890 m there. Seedlings from a source from 1,890 m on Palma Island, however, were badly damaged, suggesting that

sources on different islands differ in their susceptibility to cold (Krugman and Jenkinson 1974).

*Pinus caribaea*—Caribbean pine has 3 geographic variants. The var. *caribaea*, native to Cuba and the Isle of Pines, has persistent seed wings. The others do not. The var. *bahamensis* Barr. & Golf., in the Bahama Islands, has the smallest seeds, and var. *hondurensis* (Seneclauze) W.H.G. Barret & Golfari has the largest. In tests in South Africa, var. *caribaea* outgrew var. *hondurensis* from mainland Central America (Luckhoff 1964; Styles and Huges 1983).

*Pinus cembra*—Swiss stone pine has several recognized cultivars (Dallimore and Jackson 1967; den Ouden and Boom 1965). No distinct geographic races have been described, but there is genetic variation in needle width and in height growth (Holzer 1975)

*Pinus cembroides*—Mexican piñyon has 2 known varieties at the species' northernmost limits. The var. *bicolor* Little occurs in southeastern Arizona and southwestern New Mexico. The var. *remota* occurs on the Edwards Plateau of southwestern Texas and has very thin seedcoats (Little 1968).

*Pinus clausa*—Sand pine has 2 geographic races that are distinguished primarily on the basis of cone characteristics (Brendemuehl 1990). The wider ranging var. *clausa* (Ocala sand pine) occurs in central and eastern Florida and bears closed cones. The var. *immuginata* Ward (Choctawhatchee sand pine) occurs in the western Florida Panhandle and bears cones that ripen in September and shed seeds in October (Krugman and Jenkinson 1974; Little and Dorman 1952a). The varieties differ in important physiological traits. Seedlings grown from Choctawhatchee seed sources show higher survival rates after planting, better growth form, and greater resistance to root rot (Burns 1975).

*Pinus contorta*—Lodgepole pine has 5 highly differentiated geographic races that differ morphologically and ecologically (Critchfield 1980; Lotan and Critchfield 1990). The races include 4 recognized varieties—*bolanderi, contorta, latifolia, and murrayana*—and 1 poorly known race (not named). The var. *bolanderi* (Bolander pine) is restricted to the narrow strip of highly acid podsol soils (the Mendocino White Plains) that parallels the coast in Mendocino County in northern California and bears serotinous cones similar to those of the interior var. *latifolia* (Rocky Mountain lodgepole pine). Both the var. *contorta* (shore pine) and the var. *murrayana* (Sierra Nevada lodgepole pine) bear cones that open at maturity or shortly thereafter. The open cones of var. *contorta* persist indefinitely, whereas those of var. *murrayana* do not. The fifth race is endemic to ultramafic soils in the low coastal mountains in Del Norte County in northern-most California. Its cones are heavier and more reflexed than those of any other race and often are serotinous. The var. *murrayana* produces the largest seeds, and var. *latifolia* has seeds that germinate twice as fast at 10 to 20 °C as those of coastal origins (Critchfield 1957). In provenance tests in northern Europe, seedlings of var. *contorta* grew faster but were less winter hardy and more branchy than those of var. *latifolia* from the Rocky Mountains and interior British Columbia (Edwards 1954–55).

Seed-source differences exist within varieties. Seeds from high-elevation populations in central British Columbia germinated fastest at 20 °C; those low-elevation populations germinated faster at temperatures above 20 °C (Haasis and Thrupp 1931). Trees from southern seed sources commonly grow faster than those from northern sources (Critchfield 1980).

*Pinus coulteri*—Coulter pine has no known races but grows in isolated stands on fertile to very poor soils at altitudes ranging from 152 to 2,134 m in central California to northern Baja California. Seeds from the species' northernmost populations, at Mount Diablo, the north end of the southern coastal range, are judged to have the poorest form, with greater branching than those from any other source (Zobel 1953).

*Pinus densifloria*—Japanese red pine is widely planted and shows hardy growth in the Great Lakes region, New England, and southern Ontario (Krugman and Jenkinson 1974). Cultivars have been described (Ouden and Boom 1965).

*Pinus echinata*—Shortleaf pine shows wide geographic and racial variation (Dorman 1976; Lawson 1990). Tree growth and survival in a rangewide seed source test in the southern United States showed that seeds from sources east of the Mississippi River were superior to northern sources and that those from northern sources should be planted in the northernmost parts of the species' range (Little 1969; Wells 1969, 1973, 1979; Wells and Wakeley 1970). Important differences in tree height, bole diameter at breast height, and stem volume were found among the various sources planted in Oklahoma (Tauer and McNew 1985). An Arkansas source performed the best in an Oklahoma test, surpassing even a local source (Posey and McCullough 1969).

*Pinus edulis*—Piñyon has 2 forms (Ronco 1990). The single-needle form, var. *fallax* Little, ranges near 1,830 m in the mountains of central and eastern Arizona, in the Grand Canyon, and in parts of New Mexico. Seeds of var. *fallax* tend to be larger and have a thicker seedcoat than seeds of

the 2-needle form, var. *edulis*. Moreover, the var. *fallax,* unlike the more widespread var. *edulis*, seldom produces seeds in quantity (Little 1968).

*Pinus elliottii*—Slash pine has 2 distinct varieties (Lohrey and Kossuth 1990). Geographic variation in the widespread var. *elliottii* is clinal in numerous form and growth traits (Dorman 1976; Frampton and Rockwood 1983; Gansel and Squillace 1976). Seeds from northeast Florida sources are susceptible to ice damage and are less resistant to drought than those from northern and western sources. The var. *densa* (Little & Dorman) Gaussen in south Florida germinates faster than the var. *elliottii*, shows a grasslike seedling stage with crowded needles, and has heavy wood with wide summer growth rings (Kraus 11963; Little and Dorman 1952b, 1954; Squillace 1966, Wells 1969).

*Pinus flexilis*—Limber pine generally shows genetic variation in a north–south pattern, but the overall variability for any one trait is small (Steele 1990; Steinhoff and Andresen 1971). Seedlings of southern origins grow faster than those of northern origins (Steinhoff 1964).

*Pinus halepensis*—Aleppo pine is distributed extensively around the Mediterranean basin and shows broad geographic variation in seed germination, seedling growth, trunk straightness, branch size and angle, and cone shape (Falusi and others 1983; Giordano 1960). Two elevational ecotypes are known in Israel, and others are expected in other parts of the species' range (Karschon 1961; Magini and Tulstrup 1955).

*Pinus heldreichii*—Heldreich pine is viewed as a timberline tree by some and has 4 varieties. The var. *leucodermis* (Ant.) Markgr. ex Fitschen, the main variety, grows on drier sites and on soils formed on limestones (Dallimore and Jackson 1967). The var. *heldreichii* forms open forests in mountains at 915 to 1,524 m of elevation (Ouden and Boom 1965). The other, minor varieties are var. *longiseminis* and var. *pancici* (Vidacovic 1991).

*Pinus jeffreyi*—Jeffrey pine has 2 distinct distributions, one linked to climatic and altitudinal factors and the other to ultramafic soils, edaphic factors that signal geographic races (Jenkinson 1990). Seedlings from sources from east of the crest of the Sierra Nevada grow more slowly and are more drought resistant and cold hardy than those from sources west of the Sierra crest (Haller 1957). Seeds from high-elevation sources in the Sierra Nevada grew more slowly than those from lower elevations when planted in the western Sierra Nevada but showed ranking changes when planted in the northern California coastal range (Callaham and Liddicoet 1961; Callaham and Metcalf 1959). Seasonal pat-

terns of seedling top and root growth capacity (RGC) vary with region and altitude of seed origin (Jenkinson 1980). Allele frequencies in populations on ultramafic soils in the Klamath Mountains of southwest Oregon and northwest California differ from those in the Sierra Nevada and transverse–peninsular ranges (Furnier and Adams 1986). Trees derived from populations on ultramafic soil in the Sierra Nevada, with allele frequencies similar to those of Klamath Mountains sources, show resistance to dwarf mistletoe (Scharpf and others 1992). New Zealand provenance tests showed that trees grown from a seed source at 514 m in the northern California coastal range—at low altitude, undoubtedly one on ultramafic soil—were distinct from those from a Sierra Nevada source in having higher resistance to needle blight, faster tree growth on moister sites, and higher wood density (Burdon and Low 1991).

*Pinus kesiya*—Khasi pines of Philippine seed origin had greater vigor and better form than those of Burmese, Indian, or Vietnamese origins in tests in what is now northern Zimbabwe (Magini and Tulstrup 1955; Savory 1962).

*Pinus koraiensis*—Korean pines from Siberia, mainland China, and Korea should likely be considered a geographic race distinct from those of Japanese origins (Krugman and Jenkinson 1974). Several horticultural cultivars have been identified (Vidacovic 1991).

*Pinus lambertiana*—Sugar pine, the tallest and largest of all pines, grows on diverse sites at altitudes from near sea level to more than 3,000 m and ranges through California into north central Oregon, west Nevada, and Baja California Norte. It is one of the more genetically variable pines (Kinloch and others 1996; Kinloch and Scheuner 1990). Pronounced differences among rangewide seed sources in seedling growth and in tree growth and survival were demonstrated in common garden tests in nurseries in the western Sierra Nevada and on cleared sites at low and high altitudes in the western Sierra Nevada and sites in coastal and inland regions of southwest Oregon. Genetic variation in adaptive traits is associated with altitude, latitude, and geographic region of seed origin (Harry and others 1983; Jenkinson 1996; Jenkinson and McCain 1993, 1996). Differences in xylem resin monoterpenes distinguish stands in the Cascade Range–Sierra Nevada from stands in the transverse–peninsular ranges of southern California (Smith and Green 1996). Gametic frequency of the dominant allele for resistance to white pine blister rust increases clinally from zero in the Oregon Cascade Range to 0.08 in the southern Sierra Nevada, then declines in the transverse–peninsular ranges to zero in the Sierra San Pedro Mártir in Baja California Norte (Kinloch 1992).

*Pinus leiophylla* var. *chihuahuana*—Chihuahua pine shows both good and poor growth forms. Trees of good form grow up to 24 m in height. Trees of poor form have short, crooked boles and many branches (Magini and Tulstrup 1955).

*Pinus merkusii*—Merkus pine shows distinct races on the Asian mainland and on Sumatra. Seeds of mainland origins are larger than seeds of Sumatra origins. Trees of mainland origins pass through a grasslike stage and tend to develop a straight, cylindrical bole, but they do not grow so tall as trees of Sumatran origins. Sumatran origins tend to sinuous growth and may reach 61 m in height (Cooling 1968). Some classify these races as 2 distinct species, placing *P. merkusiana* Jungh & Vriese on the Asian mainland and *P. merkusii* on Sumatra (Cooling and Gaussen 1970).

*Pinus monophylla*—Singleleaf piñyon grows over a wide geographic and altitudinal range, and differences in growth form, foliage color, and cone production are commonly observed among trees on identical sites (Meeuwig and others 1990). No variety has been named, but variants have partly or mostly 2 needles per fascicle, rather than the typical 1 needle per fascicle (Little 1968).

*Pinus monticola*—Western white pine varies by geographic region and elevation of seed origin. Seeds of northern Idaho sources are smaller than seeds of Washington and California sources, and progenies of high-elevation sources grow faster at high elevation than those of low-elevation sources (Squillace and Bingham 1958; USDA Forest Service 1948). Idaho populations differ from California populations, but populations in northern Idaho differ little from those in coastal Washington and western British Columbia (Rehfeldt and others 1984; Steinhoff 1981). Adaptation to different geographic, climatic, topographic, and edaphic conditions reflects phenotypic plasticity more than selective genetic differentiation (Graham 1990; Rehfeldt 1979; Steinhoff 1979).

*Pinus mugo*—Swiss mountain pine has many horticultural varieties, with growth forms ranging from the sprawling shrubs of var. *pumilio* (Haenke) Zenari to the small trees of var. *rostrata* (Antoine) Hoopes (den Ouden and Boom 1965; Vidacovic 1991). Varieties differ in seed size and germination capacity (Rafn 1915), and seedlings of sources from low elevations are not cold hardy at high elevations (Wappes 1932).

*Pinus muricata*—Bishop pine populations north of Fort Ross in the northern coastal range of California differ from those south of Fort Ross in tree growth form, foliage color, and cone shape. Trees of northern sources tend to grow larger and have fuller, more compact crowns than trees of southern sources (Duffield 1951). In tests in Australia, trees of northern sources maintained better growth rate and form than trees of southern sources (Fielding 1961).

*Pinus nigra*—Austrian pine has an extensive, disjunct distribution; the species encompasses a host of recognized varieties and cultivars (Magini and Tulstrup 1955; Rafn 1915; Van Haverbeke 1990; Vidacovic 1991). The var. *caramanica* (Loudon) Rehder in Cyprus, Turkey, and the Crimea tends to have the largest seeds, 38,500 to 45,760/kg (17,500 to 20,800/lb); var. *corsicana* (Loudon) Hyl. in Corsica has the smallest seeds, 61,600 to 79,000/kg (28,000 to 36,000/lb). The Corsican variety has notably better wood than typical Austrian pine, the var. *austriaca* (Hoess) Aschers. & Graebn. in the eastern Alps and on the Balkan Peninsula. Planted stands of the var. *calabrica* C.K. Schneid. in Belgium are believed to represent one of the more cold-hardy varieties. Other distinct varieties include the var. *cebennensis* (Godr.) Rehder in the Pyrenees of France, the var. *hispanica* in Spain, and the ssp. *mauritanica* (Maire & Peyerimh.) Heywood in Morocco and Algeria. Physiological traits delimit 3 regional seed source groups (Magini and Tulstrup 1955): (1) Western sources in France and Spain have often proved to be both drought resistant and indifferent to soil type. (2) Central sources in Corsica and Italy grow well and have good form, but all need high humidity and grow poorly on limestone soils. (3) Eastern sources in the Balkan and Crimean regions appear to grow well on poorer limestone soils.

In provenance tests in the north central United States, trees grown from seed sources in the eastern half of the species' natural range were the fastest growing and most winter hardy, but those from western Europe were more susceptible to frost damage (Wheeler and others 1976). A disease-resistant seed source from Yugoslavia had the fastest growing trees in a provenance test in eastern Nebraska (Read 1976; Van Haverbeke 1986b).

*Pinus palustris*—Longleaf pines of different geographic origins differ in seedling survival, height growth, and cold resistance. Southeastern and central Louisiana seed sources performed poorly and southern Florida sources failed outside their area of seed origin. Trees from central Gulf Coast seed sources grow well throughout the Gulf Coast region and are expected to outgrow those from other sources on coastal plains sites from Louisiana to northern Florida and Georgia (Boyer 1990; Fowells 1965; Snyder and others 1977; Wells 1969). Longleaf pines grown from seed sources west of the Mississippi River are more susceptible to brown spot needle blight than are those from Gulf Coast sources east of the Mississippi River (Dorman 1976; Lantz and Kraus 1987).

*Pinus parviflora*—Japanese white pine is thought to consist of 2 geographical varieties that merge in central Honshu (Critchfield and Little 1966). Several horticultural forms of the species are cultivated (Krüssmann 1960).

*Pinus patula*—Mexican weeping pine grows rapidly and has been widely introduced. It grows well in Australia, New Zealand, and East Africa and has become an important source of wood in the summer-rainfall areas of South Africa (Leloup 1956; Loock 1950; Magini and Tulstrup 1955). Two varieties are known. The typical var. *patula* bears closed cones and has entirely black seeds. The var. *longepedunculata* ssp. *tecumumanii* Loock, found in the Mexican states of Oaxaca and Chiapas, opens cones quickly at maturity and yields seeds that are black with brown marks (Loock 1950).

*Pinus peuce*—Balkan pine of the best quality in Europe is believed to come from seed sources in the Rila and Pirin Mountains of Bulgaria (Müller 1932). Two distinct varieties have been identified, one in the mountains near Rodopes, Bulgaria, and the other in the western part of the species' range near Prokletije, Albania (Vidacovic 1991).

*Pinus pinaster*—Maritime pine has 5 major races. The highly variable French or Atlantic race typically inhabits coastal sands. The Portuguese race also inhabits coastal sands, but surpasses the French race in tree form, growth rate, and drought resistance. It grew well in tests in South Africa and western Australia and appears to have dormant seeds (Hopkins 1960; Wright 1962). The Iberian Mountains race is continental and slow growing (Resch 1974). The Corsican race occurs mainly in the mountains. In the Moroccan race, trees grown from seeds of mountain origins differ from near-coastal ones, as trees grown from seeds of mountain origins fail when they are planted in coastal areas. Trees of more southern origins are highly susceptible to frost damage. Trees of mountain origins are believed to be frost resistant (Magini and Tulstrup 1955).

*Pinus ponderosa*—Ponderosa pine, one of the most widely ranging pines in North America, has 2 distinct varieties: Pacific (var. *ponderosa*) and Rocky Mountain (var. *scopulorum*) Engelm. (Oliver and Ryker 1990). The varieties differ in a host of traits, including needle length and number per fascicle, xylem resin monoterpenes, cone and seed size, seed isozymes, seed dormancy and germination rate, seasonal patterns of seedling top and root growth capacity (RGC), seedling and tree survival, growth rate, stem form, drought tolerance, cold hardiness, disease resistance, and susceptibility to hail (Callaham 1962; Conkle and Critchfield 1988; Eldridge and Dowden 1980; Fowells 1965; Hoff 1988; Jenkinson 1976, 1980; Larson 1966; Read 1980, 1983; Read and Sprackling 1981; Rehfeldt 1986a&b; Smith 1977;

Squillace and Silen 1962; Van Haverbeke 1986a; Wang 1977; Weidman 1939; Wells 1964).

Interpretation of this vast genetic diversity suggests that there are 5 major geographic races, including 3 in var. *ponderosa* and 2 in var. *scopulorum* (Conkle and Critchfield 1988). In var. *ponderosa,* the Pacific race occurs west of the crest of the Cascade Range–Sierra Nevada from northern Oregon to the transverse ranges in southern California; the southern California race ranges through the transverse–peninsular ranges; and the North Plateau race ranges along the east side of the Cascade Range–Sierra Nevada and extends east to the Continental Divide in Montana. In var. *scopulorum*, the Rocky Mountain race occurs in the northeast part of the species' range and joins the southwest race along a broad and ill-defined front in southern Colorado, Utah, and Nevada.

Provenances within varieties and races differ in a host of traits. Seeds from sources in the Pacific Northwest, Rocky Mountain, and Southwest differed in germination rate at different temperatures (Callaham 1962). In Oregon and Washington, growth rate generally increased with seed origin from east to west, and from south to north in eastern parts of the range. Seeds from sources from eastern and southeastern parts of the range produced seedlings showing the slowest growth (Squillace and Silen 1962). In northern Arizona, seedlings from eastern and southeastern sources grew well, but those from northern and western sources and the southernmost one failed (Larson 1966). Northern sources of var. *scopulorum* showed comparatively good growth and frost resistance, while southern sources were slower growing but also frost resistant (Weidman 1939). In California, seedlings of var. *ponderosa* from sources west of the crest of the Cascade Range–Sierra Nevada grow faster but are more subject to frost injury than those from east of the crest (Krugman and Jenkinson 1974). Important differences exist between sources in adaptation to ultramafic soils on the west slope (Jenkinson 1974, 1977), and the seasonal pattern of seedling RGC in the nursery depends on climatic region and altitude of seed origin in the Cascade Range–Sierra Nevada and transverse–peninsular ranges (Jenkinson 1976, 1980).

Tree growth rate increased with decrease in source elevation in early years in plantations at low, middle, and high elevations in the western Sierra Nevada, but in later years, performances of high-elevation sources at high elevation overtook those of low-elevation sources and neared those of mid-elevation sources. Wind and snow damage reduced the superiority of mid- and low-elevation sources. Wood specific gravity increased with decrease in source elevation in all

plantations (Callaham and Liddicoet 1961; Conkle 1973; Echols and Conkle 1971; Namkoong and Conkle 1976). Elevational differentiation in growth also exists in Idaho populations (Rehfeldt 1986a). New Zealand provenance tests confirm and elaborate the complex combination of differences between discrete races and clinal variation, particularly for the Pacific and North Plateau races and show that the patterns of differentiation vary according to the traits assessed (Burdon and Low 1991).

*Pinus pungens*—Table Mountain pine has no distinct races. Seed weight and cone length and width appear to decrease with increase in seed source elevation and decrease in source latitude. Stands in which most cones open the first and second year after they ripen are found in the northern end of the species range. Cone serotiny is commonest in the southern part of the range (Della-Bianca 1990; Zobel 1969).

*Pinus radiata*—Monterey pine, native to just 5 limited areas, is the most widely introduced of all pines (Critchfield and Little 1966; McDonald and Laacke 1990). Rapid growth and valuable timber and pulp qualities have made it a major timber species in plantation forestry in Australia, New Zealand, Chile, Argentina, Uruguay, Spain, South Africa, and Kenya. The varieties from native mainland sources—Año Nuevo, Monterey, and Cambria—situated on the central California coast are faster growing than the 2-needled var. *binata* (S. Wats.) Lemm., isolated on Cedros and Guadalupe Islands, Mexico, in the Pacific Ocean west of Baja California Norte.

Cambria populations have the largest cones and seeds, and Monterey populations the smallest ones (Forde 1964). Seedlings from Año Nuevo and Monterey seed sources grew better than those from Cambria sources in Australia (Fielding 1961). Moran and others (1988) found little genetic differentiation among the native populations, which indicates that most of the genetic variation occurs within stands. Cedros and Guadalupe Island populations are more resistant to western gall rust than those on the mainland, and Año Nuevo populations are more resistant than the Monterey and Cambria ones (Old and others 1986).

*Pinus resinosa*—Red pine is one of the least variable pines and one of the most widely planted species in the northern United States and Canada. It has no described varieties or subspecies, yet northern and southern races may exist (Rudolf 1990; Wright and others 1972). Differences in height growth, tree form, and wood quality appear among sources in the Great Lakes region, New England, and West Virginia. Seeds usually are smaller, lammas frequency is less, and frost resistance is higher in northern sources than in southern ones (Fowler and Lester 1970; Wright 1962).

*Pinus rigida*—Pitch pine lacks distinct races but exhibits differences between populations in cone serotiny, tree growth, and form (Kuser and Ledig 1987; Ledig and Fryer 1974; Little and Garrett 1990). In a test of Atlantic Coastal Plain provenances, trees from southern seed sources grew faster than trees of northern sources, but adaptation of all sources decreased with distance from seed origin. Throughout most of the species' range, pitch pine promptly opens cones and sheds seeds at maturity, but in southern New Jersey, pitch pine mostly bears closed cones that open only at irregular intervals. The latter populations developed in areas that have a history of wild fire (Andresen 1963; Fowells 1965).

*Pinus roxburghii*—Chir pine has no reported varieties, but seeds from sources in different regions of India show differences in tree growth, wood quality, and oleoresin yield and quality (Dogra 1987).

*Pinus sabiniana*—Digger pine has no distinct races or varieties but shows genetic differences between populations and geographic regions in cone shape and size, seed size and germination traits, seedling growth traits, and adaptation to highly infertile (serpentinite) soil (Griffin 1962; Powers 1990). Larger cones are more frequent in the northern coastal ranges and Klamath Mountains than in the Sierra Nevada. Seeds from stands in milder climates germinate faster after cold, moist stratification than seeds from stands in colder climates. Seedlings of southern origins grow for a longer time during the growing season than those of northern origins (Griffin 1964, 1965, 1971).

*Pinus serotina*—Pond pine has no distinct races (Bramlett 1990). Slight differences were found between trees from the coastal plain and trees from drier inland areas. Cone serotiny is greater in southern and coastal populations than in northern and Piedmont populations (Smouse 1970).

*Pinus sibirica*—Siberian stone pine showed important growth and morphological differences in a series of seed-source studies in Russia (Pravdin and Iroshnikov 1982). Differences in growth rate, branching habit, and seed fat content between certain populations have also been reported. No varieties are recognized, but distinct forms exist: the form *coronans* has a wide, dense crown, is fairly drought resistant, and extends from sea level to 2,012 m; the form *humistrata* is a dwarf form found on mountain summits and ridges; and the form *turfosa* grows on peat (Pravdin 1963).

*Pinus strobus*—Eastern white pine in Canada and the United States is the typical var. *strobus*. One of the more wide ranging and widely planted American trees, it is geographically variable and is separated by a discontinuity of more than 1,932 km from its variant in southern Mexico and

Guatemala, the var. *chiapensis* Martinez (Chiapas white pine) (Critchfield and Little 1966; Wendel and Smith 1990). Within the var. *strobus,* seeds from western sources are lighter than those from eastern sources, and seeds from southern sources require longer times in stratification than seeds from northern ones (Fowler and Dwight 1964; Krugman and Jenkinson 1974; Mergen 1963). Seedlings grown from eastern seed sources had blue-green foliage in fall; seedlings of northwestern sources had yellow-green foliage (Wright and others 1963). Trees from sources in the southern Appalachian Mountains tend to grow faster and continue shoot elongation longer in autumn than trees from northern seed sources (Fowler and Heimburger 1969; Wright 1970). Artificial freezing studies and field observations in the northern Great Lakes region showed that seedlings from northern sources are less sensitive to cold than seedlings from southern sources (Krugman and Jenkinson 1974; Mergen 1963). Geographic differences in flower production, winter injury, susceptibility to blister rust, and sensitivity to air pollution are also known (Wendel and Smith 1990; Wright and others 1979). Horticultural varieties have been described (Waxman 1977).

*Pinus sylvestris*—Scots pine is the most widely planted introduced pine species in the United States, especially in the Northeast, Great Lakes region, central states, and the Pacific Northwest. It is now is naturalized in parts of New England and the Great Lakes region (Skilling 1990). The pine with the greatest natural range of all the pines, it grows in a host of different ecological situations, was involved in the first comparative seed source trials of pine, and is likely the most intensively studied of all pines. Its geographic varieties conservatively number from 21 to 52, and numerous forms and ecotypes have been described. Abundant variation exists within varieties, and seed sources differ in many traits, including flowering; needle, cone, and seed color; seed size, dormancy, and germination rate; root system structure, seedling and tree growth rate and form, and susceptibility to heat, cold, and drought (Brown 1969; Genys 1976; Giertych 1976; Pravdin 1964; Read 1971; Steven and Carlisle 1959; Wright 1962; Wright and others 1966). Seed size decreases from south to north, ranging from 97,240 seeds/kg (44,200/lb) in Spain to 279,400/kg (127,000/lb) in Lapland (Heit 1969). Seeds from sources in the extreme northern parts of the range and certain areas in Greece and Turkey show the highest seed dormancy (Heit 1969). Incompletely developed embryos explain part of the dormancy of northern sources (Kamra 1969). Growth rate typically decreases and cold hardiness increases from south to north. Trees from Finnish and Russian sources survived

better in prairie conditions in Canada than did trees from more southern sources (Cram and Brack 1953). In Michigan, trees from certain French sources grew 3 times taller than trees from northern sources from Finland and Siberia, but northern sources were more cold hardy than southern ones (Wright 1962; Wright and others 1966). Needles of trees with origins in Asia Minor, the Balkans, southern France, and Spain remained green in winter, whereas those with Siberian and Scandinavian origins turned yellow. In Sweden, seeds from sources at north latitudes or high elevations germinated well over a wider range of temperatures than did seeds from sources at south latitudes or low elevations, and seedlings trees of southern sources grew faster and later in autumn than trees of northern sources (Kamra and Simak 1968). Trees from introduced sources produced better trees than did local sources in some European localities (Vidacovic 1991).

*Pinus taeda*—Loblolly pine, commercially the most important forest tree in the southern United States, has repeatedly demonstrated important geographic variation in seedling and tree survival, growth rate, cold hardiness, drought hardiness, and disease resistance (Baker and Langdon 1990; Dorman 1976; Dorman and Zobel 1973). Local seed sources have often proved to be the best. Seedlings from southern sources are more prone to cold damage than those from northern ones, and seedlings grown from seeds from west of the Mississippi River are more drought tolerant and disease resistant than those from most sources east of the Mississippi. Seedlings from Maryland sources tend to grow less than those from other sources when planted in different areas (Wells 1969; Wells and Wakeley 1966). Trees of southern sources outgrew trees of northern sources in South Africa (Sherry 1947).

*Pinus thunbergiana*—Japanese black pine of inland origin show better growth form than those of coastal origin (Krugman and Jenkinson 1974).

*Pinus torreyana*—Torrey pines with mainland California origins in a planting on the California mainland had a single trunk and grew taller than trees with a Santa Rosa Island origin, which were bushy and branched freely. Trees from the Santa Rosa Island source produced larger cones (Haller 1967). The populations differ morphologically and biochemically as well (Ledig and Conkle 1983).

*Pinus virginiana*—Virginia pine has no known varieties or races, but populations in the Talledega Mountains of central Alabama and on deep sands of the mid-Atlantic Coast conceivably are distinct ecotypes (Carter and Snow 1990; Dorman 1976; Kellison and Zobel 1974). Seeds from local sources or sources from locations with climate similar to

that of the planting site generally yield the best survival and growth rates. Southern seed sources produce fast-growing trees on southern sites but on northern sites these trees grow slowly and suffer winter injury (Dorman 1976; Genys 1966; Genys and others 1974). Genetic variation in growth rate, stem form, wood traits, and monoterpene content in Kentucky and Tennessee occurs mainly among and within stands, rather than among geographic origins (Carter and Snow 1990).

*Pinus wallichiana*—Blue pine ranges through the Himalayan region in discontinuous distribution from eastern Afghanistan to eastern-most India, north Burma, and adjoining China. Although no distinct varieties have been reported, at least 7 broad provenances have been proposed, including 4 in the western Himalayas and 3 in the eastern Himalayas (Dogra 1987).

*Pinus washoensis*—Washoe pine ranges in limited areas along the western edge of the Great Basin in western Nevada and northern California, notably on the east slope of Mount Rose in the Carson Range in Nevada, in the Bald Mountain Range in the northern Sierra Nevada, and in the South Warner Mountains and several intervening areas in northeastern California (Critchfield 1984; Critchfield and Allenbaugh 1965; Niebling and Conkle 1990; Smith 1981). Closely related in appearance to and often wrongly identified as Pacific ponderosa pine, this rare pine ranges at higher altitudes than ponderosa pine, the same as Jeffrey pine. Washoe pine flowers in July, and its male and developing second-year female cones are purple to purplish black. The latter mature in August–September, turn to a dull purple, purplish brown, or light brown, and open in September. Cones are assessed and processed like those of Pacific ponderosa pine. Stored seeds germinate quickly after 60 days of moist, cold stratification (Jenkinson 1980; Krugman and Jenkinson 1974).

**Hybrids.** Pine hybrids are myriad. More than 260 first- and second-generation hybrids—as well as backcrosses, crosses between varieties of the same species, and crosses that involve 3 or more different species—either occur naturally or have been produced artificially (Critchfield 1963, 1966a, 1977, 1984; Critchfield and Krugman 1967; Krugman and Jenkinson 1974; Little and Righter 1965; Mirov 1967; Vidacovic 1991; Wright 1962). We provide no yield statistics for hybrids because such data are highly variable. Yields of sound seeds depend on species and individual trees, as well as on the environmental conditions under which the cross is made.

Natural hybrids are common, and we list but few of the many known. *P. palustris × taeda* (Sonderegger pine) occurs

frequently in Louisiana and east Texas and is the best-known southern pine hybrid (Baker and Langdon 1990; Chapman 1922). Most natural hybrids occur infrequently in the overlaps of their parent species' ranges. Some of the better-known examples include the following:

- *P. contorta* var. *murrayana × banksiana* in western Canada (Zavarin and others 1969)
- *P. ponderosa × jeffreyi*, *P. jeffreyi × coulteri*, and *P. radiata × attenuata in California* (Critchfield and Krugman 1967; Mirov 1967)
- *P. flexilis × strobiformis* in north central Arizona and north central New Mexico (Steinhoff and Andresen 1971)
- *P. taeda × echinata* in east Texas
- *P. taeda × serotina* throughout the species' common range in southern United States (Critchfield 1963; Smouse 1970; Wright 1962)

The hybrid *P. densiflora × thunbergiana*, natural in Japan, has formed spontaneously in plantations of its parent species in Michigan (Krugman and Jenkinson 1974). In Europe, Scots pine crosses occasionally with Austrian pine and with mugo pine where the species are planted near one another (Wright 1962), and Austrian pine crosses with Heldreich pine var. *leucodermis* where they overlap in Herzegovina (Vidacovic 1991).

Several pine hybrids have been produced in relatively large numbers by controlled pollination methods. They include *P. rigida × taeda* in Korea where the hybrid is important in plantation forestry (Hyun 1962), and *P. attenuata × radiata*, tested in California and Oregon (Griffin and Conkle 1967). Many other pine hybrids have been produced in small numbers and tested for fitness in various parts of the United States (Burns and Honkala 1990).

**Flowering and fruiting.** Reproductive structures in certain pines first form when the trees are 5 to 10 years old, as in knobcone, jack, sand, lodgepole, and Monterey pines, among others (table 2). In other pines, reproductive structures form when the trees are 25 to 30 years old (as in Swiss stone and Siberian stone pines; piñyon; and Apache and Chihuahua pines) or 40 years old (as in sugar pine).

Pines are monoecious. Male and female "flowers"—properly strobili (microsporangiate and megasporangiate strobili)—are borne separately on the same tree. Male strobili predominate on the basal part of new shoots, mostly those on older lateral branches in the lower crown. Female strobili occur most often in the upper crown, chiefly at the apical ends of main branches in the position of subterminal

**Table 3**—*Pinus*, pine:   phenology of flowering and fruiting

| Species | Location | Flowering | Cone ripening | Seed dispersal |
|---|---|---|---|---|
| *P. albicaulis* | California | July | Aug–Sept | Not shed † |
| *P. aristata* | Arizona | July–Aug | Sept–Oct | Sept–Oct |
| *P. arizonica* | Arizona | May | Sept–Oct | Oct |
| *P. armandii* | California | Apr–May | Aug | Aug–Sept |
| *P. attenuata* | California | Apr | Jan–Feb | Closed cone‡ |
| *P. balfouriana* | California | July–Aug | Sept–Oct | Sept–Oct |
| *P. banksiana* | Great Lakes | May–June | Sept | Sept§ |
| *P. brutia* | California | Mar–May | Jan–Mar | Closed cone‡ |
| *P. canariensis* | California | Apr–May | Sept | Sept–Oct |
| *P. caribaea* | Cuba | Jan–Feb | July–Aug | Sept |
| *P. cembra* | Germany | May | Aug–Oct | Not shed† |
| *P. cembroides* | California | May–June | Nov–Dec | Nov–Dec |
| *P. clausa* | Florida | Sept–Dec | Sept | Sept§ |
| *P. contorta* | | | | |
|   var. *contorta* | California | May–June | Sept–Oct | Fall§ |
|   var. *latifolia* | Rocky Mtns | June–July | Aug–Sept | Sept–Oct § |
|   var. *murrayana* | California | May–June | Sept–Oct | Sept–Oct |
| *P. coulteri* | California | May–June | Aug–Sept | Octê |
| *P. densiflora* | California | Apr | Aug–Sept | Sept–Oct |
| *P. echinata* | South Carolina | Mar–Apr | Oct–Nov | Oct–Nov |
| *P. edulis* | Arizona | June | Sept | Sept–Oct |
| *P. elliottii* | | | | |
|   var. *densa* | Florida | Jan–Apr | Aug–Sept | Sept–Nov |
|   var. *elliottii* | Florida | Jan–Feb | Sept–Oct | Oct |
| *P. engelmannii* | Arizona | May | Nov–Dec | Nov–Feb |
| *P. flexilis* | California, Montana | June–July | Aug–Sept | Sept–Oct |
| *P. gerardiana* | India, California | May–June | Sept–Oct | Nov |
| *P. glabra* | Mississippi | Feb–Mar | Oct | Oct–Nov |
| *P. halepensis* | France | May–June | Sept | Fall § |
| *P. heldreichii* | Italy, California | May–July | Aug–Sept | Sept–Oct |
| *P. jeffreyi* | California | June–July | Aug–Sept | Sept–Oct |
| *P. kesiya* | Philippines | Jan–Mar | Oct–Jan | Feb–Mar |
| *P. koraiensis* | Japan | May–June | Sept | Oct |
| *P. lambertiana* | California | June–July | Aug–Sept | Aug–Oct |
| *P. leiophylla* var. | | | | |
|   *chihuahuana* | California | May–June | Nov* | Dec–Jan |
| *P. merkusii* | Thailand | Jan | Apr–Jun | May–Jul |
| *P. monophylla* | California, Nevada | May | Aug | Sept–Oct |
| *P. monticola* | Idaho | June–July | Aug | Aug–Sept |
| *P. mugo* | Europe | May–June | Oct | Nov–Dec |
| *P. muricata* | California | Apr–June | Sept | Midwinter § |
| *P. nigra* | Ontario, Canada | May–June | Sept–Nov | Oct–Nov |
| *P. palustris* | SE US | Feb–Mar | Sept–Oct | Oct–Nov |
| *P. parviflora* | Japan | May–June | Sept | Nov |
| *P. patula* | Mexico, California | Feb–Apr | Dec | Midwinter § |
| *P. peuce* | Europe | May | Fall | Fall |
| *P. pinaster* | Europe, California | Apr | Nov–Dec | Dec–Jan § |
| *P. pinea* | Europe | May–June | Late summer* | Late summer |
| *P. ponderosa* | | | | |
|   var. *ponderosa* | California | Apr–June | Aug–Sept | Aug–Sept |
|   var. *scopulorum* | South Dakota, Colorado | May–June | Aug–Sept | Sept–Jan |
| *P. pumila* | Russia | July | — | Fall or not shed † |
| *P. pungens* | West Virginia, California | Mar–Apr | Fall | Fall § |
| *P. quadrifolia* | California | June | Sept | Sept–Oct |
| *P. radiata* | California | Jan–Feb | Nov | Midwinter § |

| **Table 3**—*Pinus,* pine:   phenology of flowering and fruiting (continued) | | | | |
|---|---|---|---|---|
| **Species** | **Location** | **Flowering** | **Cone ripening** | **Seed dispersal** |
| *P. resinosa* | Great Lakes, California | Apr–June | Aug–Oct | Oct–Nov |
| *P. rigida* | New Jersey | May | Sept | Fall § |
| *P. roxburghii* | India | Feb–Apr | Winter | Apr–May§ |
| *P. sabiniana* | California | Mar–Apr | Oct | Oct II |
| *P. serotina* | SE US | Mar–Apr | Sept | Spring § |
| *P. sibirica* | Russia | May | Aug–Sept | Not shed † |
| *P. strobiformis* | Arizona | June | Sep | Sept–Oct |
| *P. strobus* | NE US | May–June | Aug–Sept | Aug–Sept |
| *P. sylvestris* | Great Britain, California | May–June | Sept–Oct | Dec–Mar |
| *P. taeda* | SE US | Feb–Apr | Sept–Oct | Oct–Dec |
| *P. thunbergiana* | Japan, Long Island | Apr–May | Oct–Nov | Nov–Dec |
| *P. torreyana* | California | Feb–Mar | Jun–Jul* | Sept II |
| *P. virginiana* | E US | Mar–May | Sept–Nov | Oct–Nov § |
| *P. wallichiana* | India | Apr–June | Aug–Oct | Sept–Nov |
| *P. washoensis* | Nevada, California | July | Aug–Sept | Sept |

**Sources:** Andreev (1925), Britton and Shafer (1908), Carlisle and Brown (1968), Cocozza (1961), Cooling (1968), Critchfield (1966b), Dallimore and Jackson (1967), Dimitroff (1926), Dorman and Barber (1956), Duffield (1953), Fowells (1965), Goor (1955), Jacaline and Lizardo (1958), Krugman and Jenkinson (1974), Lamb (1915), Letourneux (1957), Little EL (1938a & b, 1940), Little S (1941, 1959); Loiseau (1945), Loock (1950), Luckhoff (1964), Mikhalevskaya (1960), Mirov (1962), NBV (1946), Ohmasa (1956), Pearson (1931), Rehder (1940), Rohmeder and Loebel (1940), Sargent (1905), Snow (1960), Sudworth (1908), Tkachenko (1939), Troup (1921), Veracion (1964), Vines (1960), Wahlenberg (1946).

\* Cones and seeds mature in the third year.
† Seeds are dispersed when the detached cones disintegrate.
‡ Cones open after several years, if at all. Seed dispersal normally requires fire.
§ Many cones remain closed for several months or years.
II Cones are massive, open slowly, and shed seeds over several months.

or lateral buds. Exceptions to this general scheme are common. Trees of knobcone, jack, sand, and Monterey pines are multinodal in the bud, and female strobili occasionally arise in secondary whorl positions. Trees of knobcone, Monterey, and Virginia pines usually produce female strobili in all parts of the crown. In temperate climates, the earliest stages of male and female strobili can be detected in the developing buds in summer or fall. Male strobili appear from 1 to several weeks before the female strobili (Fowells 1965; Gifford and Mirov 1960; Krugman and Jenkinson 1974; Mirov 1967).

Male and female strobili of the southern and tropical pines emerge from buds in late winter, as in slash pine × var. *densa* and var. *elliottii)* and spruce and longleaf pines (table 3). Strobili of other pines emerge from the winter bud in early spring or in late spring and early summer.

Male strobili are arrayed in indistinct spirals in clusters that range from 13 to 51 mm in length (Dallimore and Jackson 1967; Pearson 1931; Shaw 1914; Sudworth 1908). Immature male strobili are green or yellow to reddish purple; mature male strobili at the time of pollen shed are light brown to brown. In most pines, male strobili fall soon after ripening.

Female strobili emerge from the winter bud shortly after the male strobili and are green or red to purple (Dallimore and Jackson 1967; Fowells 1965; Pearson 1931; Sudworth 1908). At the time of pollination, they are nearly erect and range from 10 to 38 mm long and sometimes longer. After pollination, the female strobili close their scales, begin a slow development, and grow to nearly one-eighth to one-fifth the length of mature cones at the end of their first growing season. Cone development continues through the winter where temperatures are favorable, as in knobcone and ponderosa pines at low elevations in the Sierra Nevada of California and south Florida slash pine (Krugman and Jenkinson 1974; Wakeley 1954).

Fertilization occurs in spring or early summer, about 13 months after pollination, and the young cones begin to grow rapidly. New shoot growth leaves the developing cones in a lateral position. As they mature, the developing cones gradually change color from green or purple to yellow, light brown, reddish brown, or dark brown (table 4).

Cones and seeds of most pines mature rapidly in late summer or fall of the second year (table 3). Cones of a few pines mature in late winter of the second year or in early spring of the third year, as in knobcone, Calabrian, and Merkus pines (Boskok 1970; Cooling 1968; Krugman and Jenkinson 1974). Seeds of knobcone and Calabrian pines mature in fall, about 16 to 18 months after pollination, but their cones do not develop fully until late winter (Boskok

## Table 4—*Pinus,* pine: cone ripeness criteria

| Species | Pre-ripe color | Ripe color |
|---|---|---|
| *P. albicaulis* | Dark purple | Dull purple to brown |
| *P. aristata* | Green to brown-purple | Deep chocolate brown |
| *P. arizonica* | Green | Green-brown to dull yellowish buff or brown |
| *P. armandii* | Green | Yellowish brown |
| *P. attenuata* | Greenish brown | Lustrous tawny yellow to light brown |
| *P. balfouriana* | Deep purple | Dark brown, red-brown, or russet-brown |
| *P. banksiana* | Green | Lustrous tawny yellow to brown |
| *P. brutia* | Green | Yellow to reddish brown |
| *P. canariensis* | Yellow-green | Nut brown |
| *P. caribaea* | Green | Yellow-tan, light brown to reddish brown |
| *P. cembra* | Greenish violet | Purplish brown |
| *P. cembroides* | Green | Yellowish to reddish brown or lustrous brown |
| *P. clausa* | Green | Dark yellow-brown |
| *P. contorta* | | |
|   var. *contorta* | Purple-green | Lustrous light yellowish brown to yellow-brown |
|   var. *latifolia* | Purple-green | Light brown |
|   var. *murrayana* | Purple-green | Clay brown |
| *P. coulteri* | Green | Shiny brown to yellowish brown |
| *P. densiflora* | Green | Dull tawny yellow to brown |
| *P. echinata* | Green | Green to light brown or dull brown |
| *P. edulis* | Green | Light yellow-brown |
| *P. elliottii* | | |
|   var. *densa* | Green | Brown |
|   var. *elliottii* | Green | Brown-yellow to brown |
| *P. engelmannii* | Brownish purple-green | Light brown |
| *P. flexilis* | Green | Lustrous yellowish brown to light brown |
| *P. gerardiana* | Green | Brown |
| *P. glabra* | Green | Green |
| *P. halepensis* | Green | Lustrous yellowish brown or reddish brown |
| *P. heldreichii* | Yellow-green | Yellowish or light brown to dull brown |
| *P. jeffreyi* | Dark purple to black | Dull purple to light brown |
| *P. kesiya* | Green | Bright brown to dark brown |
| *P. koraiensis* | Green | Yellowish brown |
| *P. lambertiana* | Green | Lustrous greenish brown to light brown |
| *P. leiophylla* | | |
|   var. *chihuahuana* | Green | Light brown |
| *P. merkusii* | Green | Light brown |
| *P. monophylla* | Green | Shiny deep russet brown |
| *P. monticola* | Green to purple-black | Yellowish beige-brown to reddish, dark brown |
| *P. mugo* | Violet purple | Lustrous tawny yellow to dark brown or cinnamon brown |
| *P. muricata* | Green to purple | Shiny light chestnut brown |
| *P. nigra* | Yellowish green | Shiny yellow brown to light brown |
| *P. palustris* | Green | Green to dull brown |
| *P. patula* | Green | Yellow ochre to nut brown |
| *P. parviflora* | Yellow-green | Leathery-woody brownish red to reddish brown |
| *P. peuce* | Green to yellow | Tawny yellow to light brown |
| *P. pinaster* | Purplish | Lustrous light brown |
| *P. pinea* | Green | Shiny nut brown |
| *P. ponderosa* | | |
|   var. *ponderosa* | Green to yellow-green, rarely purple | Lustrous brownish green or yellow-brown to russet brown |
|   var. *scopulorum* | Green | Purplish brown |
| *P. pumila* | Green to violet-purple | Dull reddish or yellowish brown |
| *P. pungens* | Deep green to brown | Lustrous light brown |
| *P. quadrifolia* | Green | Yellowish or reddish brown |
| *P. radiata* | Green | Lustrous nut brown to light brown |
| *P. resinosa* | Green | Purple with reddish-brown scale tips to nut brown |
| *P. rigida* | Green | Lustrous brown or light yellow-brown |
| *P. roxburghii* | Green to brown | Light brown |
| *P. sabiniana* | Green to light brown | Reddish to red-brown or chestnut brown |

| Table 4—*Pinus,* pine: cone ripeness criteria (continued) | | |
|---|---|---|
| **Species** | **Pre-ripe color** | **Ripe color** |
| *P. serotina* | Green to yellow | Lustrous light yellow to brown |
| *P. sibirica* | Green | Violet to light gray or brown |
| *P. strobiformis* | Green | Greenish brown to dark brown |
| *P. strobus* | Green | Yellow green to light brown |
| *P. sylvestris* | Green | Dull tawny yellow, greyish or dull brown, or cinnamon brown |
| *P. taeda* | Green | Green, shiny light or dull pale reddish brown |
| *P. thunbergiana* | Deep lustrous purple | Nut brown or reddish brown |
| *P. torreyana* | Green to dark violet | Shiny deep chestnut brown to chocolate brown |
| *P. virginiana* | Green | Lustrous dark purple to reddish and dark brown |
| *P. wallichiana* | Green | Tawny yellow to light brown |
| *P. washoensis* | Purple to purplish black | Dull purple to purplish brown or light brown |

**Sources:** Bailey (1939), Barnett and McLemore (1967b), Britton and Shafer (1908), Cerepnin (1964), Cooling (1968), Dallimore and Jackson (1967), den Ouden and Boom (1965), Fowells (1965), Jacaline and Lizardo (1958), Krugman and Jenkinson (1974), Little EL (1940, 1950), Lizardo (1950), Loock (1950), Luckhoff (1964), McIntyre (1929), McLemore (1961a&b), Pravdin (1963), Rehder (1940), Sargent (1965), Sudworth (1908), Troup (1921), Wahlenberg (1946), Wakeley (1954).

**Note:** See table 2 for intervals between large cone crops and table 3 for cone ripening and seed dispersal dates.

**Figure 1A** —*Pinus,* pine: mature cones, collected before seed dispersal, of *P. albicaulis,* whitebark pine (**upper left**); *P. aristata,* bristlecone pine (**upper center**); *P. attenuata,* knobcone pine (**upper right**); *P. banksiana,* jack pine (**center left**); *P. cembroides,* Mexican piñyon (**center middle**); *P. clausa,* sand pine (**center right**); *P. engelmannii,* Apache pine (**bottom left**); *P. flexilis,* limber pine (**bottom center**); *P. leiophylla* var. *chihuahuana,* Chihuahua pine (**bottom right**).
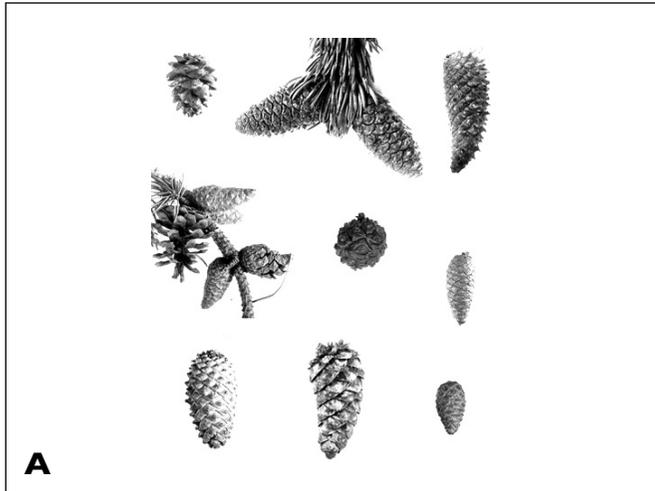
**Figure 1B** —*Pinus,* pine: mature cones, collected before seed dispersal, of *P. monophylla,* singleleaf piñyon (**upper left**); *P. arizonica,* Arizona pine (**upper center**); *P. ponderosa* var. *scopoulorum,* Rocky Mountain ponderosa pine (**upper right**); *P. rigida,* pitch pine (**center left**); *P. pungens,* Table Mountain pine (**center middle**), *P. serotina,* pond pine (**center right**); *P. strobiformus,* southwestern white pine (**bottom left**); *P. sylvestris,* Scots pine (**bottom center**); *P. virginiana,* Virginia pine (**bottom right**).

A

B
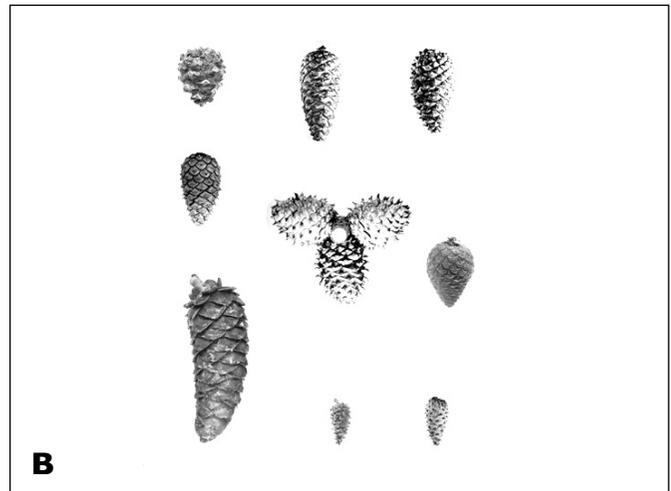
1970; Krugman and Jenkinson 1974). Seeds and cones of Italian stone and Chihuahua pines require 3 years to ripen (Dallimore and Jackson 1967; Little 1950). Seeds of Torrey pine are said to take 3 years to mature, but evidence suggests that the seeds of this pine mature in 2 years, whereas the cones require 3 years (Krugman and Jenkinson 1974).

Intervals between large cone crops vary and apparently depend on species and environment (table 2). Some pines consistently produce large cone crops. Others show cyclic or erratic patterns of 2 to 10 years between large crops.

Mature cones of pines vary greatly in size (figure 1). At one extreme, cones of mugo pine range from 2.5 to 5.1 cm in length and weigh about 1.7 g. At the opposite extreme, cones of sugar pine range from 30 to 64 cm in length and weigh from about 0.45 to 0.91 kg. Cones of Digger and Coulter pines, the California big-cone pines, often weigh more than 0.91 kg (Dallimore and Jackson 1967; den Ouden and Boom 1965; Sudworth 1908).

Mature cones consist of overlapping woody scales, each bearing 2 seeds at the base on its upper surface. In most

**Figure 2A**—*Pinus*, pine:  seeds (although most are shed naturally from their cones, some are shed wingless) of **ROW 1, left to right**:  *P. albicaulis*, whitebark pine; *P. aristata*, bristlecone pine; *P. armandii*, Armand pine; *P. attenuata*, knobcone pine; *P. balfouriana*, foxtail pine. **ROW 2, left to right**:  *P. banksiana*, jack pine; *P. brutia*, Calabrian pine; *P. cembroides*, Mexican piñyon; *P. clausa*, sand pine. **ROW 3, left to right**:  *P. contorta* var. *murrayana*, Sierra Nevada lodgepole pine; *P. coulteri*, Coulter pine; *P. densiflora*, Japanese red pine; *P. echinata*, shortleaf pine. **ROW 4, left to right**:  *P. edulis*, piñyon; *P. elliottii* var. *elliottii*, slash pine; *P. engelmannii*, Apache pine; *P. flexilis*, limber pine; *P. gerardiana*, chilgoza pine. **ROW 5, left to right**:  *P. glabra*, spruce pine; *P. halepensis*, Aleppo pine; *P. heldreichii*, Heldrich pine; *P. kesiya*, Khasi pine; *P. jeffreyi*, Jeffrey pine. **ROW 6, left to right**:  *P. koraiensis*, Korean pine; *P. lambertiana*, sugar pine; *P. leiophylla* var. *chihuahuana*, Chihuahua pine; *P. merkusii*, Merkus pine; *P. monophylla*, singleleaf piñyon.
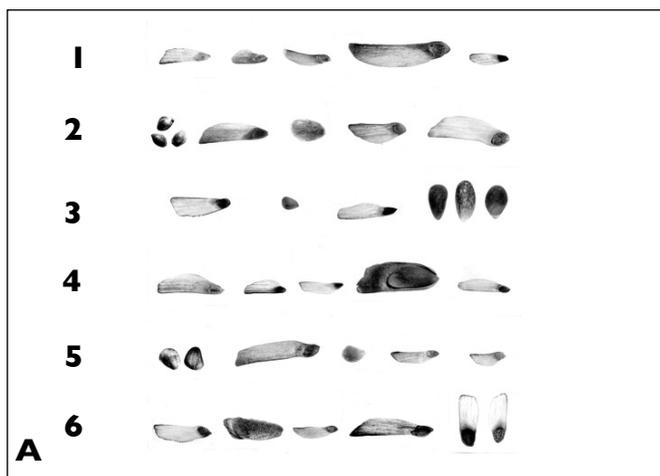


pines, cones open on the tree shortly after ripening and seeds are rapidly dispersed (table 3). As the cone dries, the cone scales separate by differential contraction of 2 tissue systems. One system consists of woody strands of short, thick-walled, tracheid-like cells that extend from the cone axis to the scale tip, and the other has thick-walled sclerenchyma cells in the abaxial zone of the scale (Allen and Wardrop 1964; Thompson 1968). In species with massive cones—Coulter, Chir, Digger, and Torrey pines—the scales separate slowly and seeds are shed over a period of several months (Sudworth 1908; Troup 1921).

In pines with serotinous cones—including knobcone, jack, Calabrian, sand, Rocky Mountain lodgepole, Aleppo, bishop, maritime, Table Mountain, and Monterey pines— some or all of the mature cones remain closed for several to many years, or they open on the tree only at irregular intervals (Dallimore and Jackson 1967; Fowells 1965; Sudworth 1908). Besides their closed-cone habit, jack, sand, lodgepole/shore, and pitch pines have forms whose cones open promptly at maturity (Fowells 1965;, Krugman and

Jenkinson 1974; Rudolph and others 1959). The closed-cone habit results from 3 factors: an extremely strong adhesion between adjacent, overlapping cone scales beyond the ends of the winged seeds (LeBarron and Roe 1945, Little and Dorman 1952a); cone structure; and the nature of the scale tissue systems described. The scales appear to be bonded by a resinous substance. The melting point of this resin seal is between 45 and 50 °C for Rocky Mountain lodgepole pine (Critchfield 1957). Heat, especially that of fire, melts the resin so that the cones open. Still other pines, such as whitebark, Japanese stone, Swiss stone, and Siberian pines, shed partly opened or unopened cones, and their seeds are dispersed only when the cones disintegrate on the ground (Dallimore and Jackson 1967; Mirov 1967; Pravdin 1963; Sudworth 1908).

Cones that open on the tree are usually shed within a few months to a year after the seeds are shed. Pines such as knobcone, Rocky Mountain lodgepole, and pitch pine, how-

**Figure 2B**—*Pinus*, pine:  seeds (although most are shed naturally from their cones, some are shed wingless) of **ROW 1, left to right:**  *P. monticola*, western white pine; *P. muricata*, bishop pine; *P. nigra*, Austrian pine; *P. palustris*, longleaf pine; *P. patula*, Mexican weeping pine. **ROW 2, left to right:**  *P. peuce*, Balkan pine; *P. pinaster*, maritime pine; *P. pinea*, Italian stone pine; *P. arizonica*, Arizona pine; *P. ponderosa* var. *ponderosa*, ponderosa pine. **ROW 3, left to right:**  *P. ponderosa* var. *scopulorum*, Rocky Mountain ponderosa pine; *P. pumila*, Japanese stone pine; *P. pungens*, Table Mountain pine; *P. quadrifolia*, Parry piñyon. **ROW 4, left to right:**  *P. radiata*, Monterey pine; *P. resinosa*, red pine; *P. rigida*, pitch pine; *P. sabiniana*, Digger pine; *P. serotina*, pond pine. **ROW 5, left to right:**  *S. sibirica*, Siberian stone pine; *P.* × *sondereggeri*, Sonderegger pine; *P. strobiformis*, southwestern white pine; *P. strobus* var. *strobus*, eastern white pine; *P. sylvestris*, Scots pine. **ROW 6, left to right:**  *P. taeda*, loblolly pine; *P. torreyana*, Torrey pine; *P. virginiana*, Virginia pine; *P. wallichiana*, blue pine; *P. washoensis*, Washoe pine.
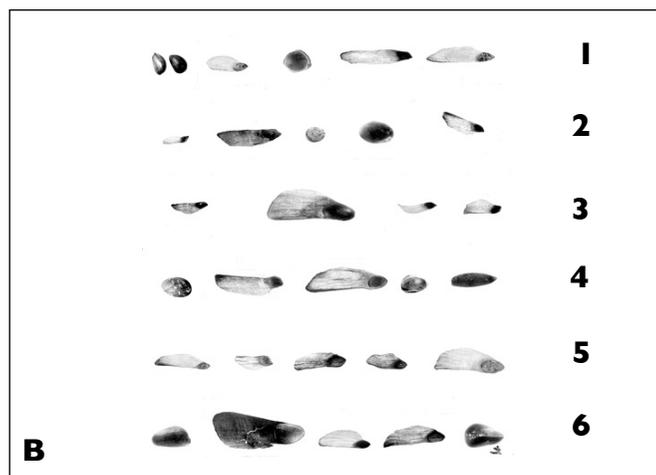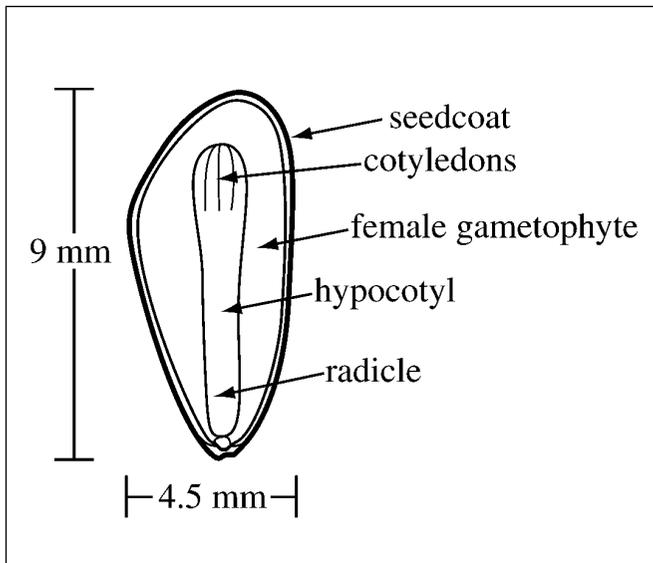
**Figure 3**—*Pinus ponderosa,* ponderosa pine:    longitudinal section through a mature seed.



ever, may retain opened cones on the trees for up to 5 years or indefinitely (Fowells 1965; Sudworth 1908).

Mature seeds vary widely in size, shape, and color (figure 2). De-winged seeds vary from 1.6 to 2.5 mm in length for jack pine and range up to more than 19 mm long for Digger pine.  Seeds are cylindric in shape for chilgoza pine, ovoid for Balkan pine, convex on the inner side and flat on the outer side for Italian stone pine, pear-shaped for Japanese stone pine, variously triangular for Table Mountain pine, and ellipsoid for Monterey pine (Dallimore and Jackson 1967; den Ouden and Boom 1965; Uyeki 1927). Mature seedcoats may be reddish, purplish, grayish brown, or black, and are often mottled. Depending on species, the seedcoats can be thin and papery, or thick and hard, or even stony (Dallimore and Jackson 1967; Shaw 1914; Sudworth 1908).

The seedcoat of the mature seed encloses a whitish food-storage tissue—female gametophyte tissue, the conifer analog of endosperm—which in turn encases the embryo (figure 3). A brown papery cap, the remnant of the nucellus, is attached to the micropylar end of the food-storage tissue. A thin, brown, membranous skin, the remnant inner layer of the ovules integument, covers the papery cap and the food-storage tissue.

Seeds of most pines have a membranous seedwing (figure 2). Seedwings detach readily in the hard pines (except for Canary Island, Italian stone, and Chir pines) but adhere firmly in the soft pines (except bristlecone and certain sources of foxtail pine). In nut pines such as Mexican, single-leaf, and Parry piñyons and chilgoza pine, the wings or

modified wings may stay attached to the cone scale when the seeds are shed. In pines such as whitebark, Armand, Swiss stone, limber, chilgoza, Korean, Japanese stone, Siberian, and southwestern white pines, seedwings are rudimentary or nonexistent (Mirov 1967; Shaw 1914; Sudworth 1908; Troup 1921; Uyeki 1927).

**Cone collection.**   Cones should be collected from trees that are free of disease and have superior growth and form characteristics. Larger cones generally contain more seeds, but normally all cones are collected except those with obvious disease and insect damage. Dominant, widely spaced trees with full crowns produce the most seeds per cone, given that other trees supply sufficient amounts of viable pollen. Seed yields tend to be low when trees are isolated and incur limited amounts of pollen from other trees. Spacing among trees in seed orchards is regulated to produce large crowns and plenty of pollen. With proper irrigation and fertilization, 20-year-old loblolly pine orchards in the South can average around 100 kg of seeds/ha (88 lb/ac) of orchard (Bonner 1991). Most pines growing in dense, young stands produce few or no seeds. Pines that commonly form fire thickets, such as knobcone, jack, sand, pitch, and pond pines, are prominent exceptions (Fowells 1965).

Ripe cones can be collected from standing trees, newly felled trees, and animal caches. To avoid large yields of immature seeds, collections from animal caches should be made in late fall, after seeds have matured (Schubert and others 1970). Because the mature cones of most pines open and shed seeds promptly, collections from standing trees should begin when cones are ripe and just cracking. Collections from closed-cone pines can be safely delayed, and such delay is often desirable. Although the seeds may be mature, closed cones are difficult to open and added maturation on the tree facilitates both cone opening and seed extraction (Boskok 1970; Krugman and Jenkinson 1974).

To avoid extensive collections of immature or empty seeds, it is wise to check seed ripeness in small samples of cones from a number of typical individual trees. Mature seeds have a firm, white to yellow or cream-colored "endosperm," or female gametophyte tissue, and a white to yellow embryo that nearly fills the endosperm cavity (figure 3). This simple visual check is useful for most pines, and critical for some.

Cone ripeness in some pines can be usefully estimated by change in cone color (table 4). In Pacific ponderosa pine, for example, cones are mature when their color changes from green or yellow-green to brownish green, yellow-brown, or russet brown. In red pine, cones are mature when they turn from green to purplish with reddish brown on the

**Table 5**—*Pinus*, pine:  specific gravity of ripe cones and flotation liquids used to assess cone ripeness*

| Species | Specific gravity of ripe cones | Flotation liquid † |
|---|---|---|
| *P. aristata* | 0.59–.80 | Kerosene |
| *P. arizonica* | .88–.97 | — |
| *P. contorta* var. *latifolia* | .43–.89 | — |
| *P. densiflora* | 1.10 | — |
| *P. echinata* | .88 | SAE 20 oil ‡ |
| *P. edulis* | .80–.86 | Kerosene |
| *P. elliottii* | | |
|   var. *densa* | <.89 | SAE 20 oil |
|   var. *elliottii* | <.95 | SAE 20 oil |
| *P. glabra* | .88 | SAE 20 oil |
| *P. jeffreyi* | .81–.86 | SAE 30 oil |
| *P. lambertiana* | .70–.80 | Kerosene |
| *P. merkusii* | 1.00 | — |
| *P. palustris* | .80–.89 | SAE 20 oil |
| *P. ponderosa* | | |
|   var. *ponderosa* | .80–.89 | Kerosene |
| | .84–.86 | SAE 30 oil |
|   var. *scopulorum* | <.85–.86 | Kerosene |
| *P. radiata* | <1.00 | Water |
| *P. resinosa* | .80–.94 | Kerosene § |
| *P. serotina* | .88 | — |
| *P. strobiformis* | .85–.95 | 95% ethanol |
| *P. strobus* | .90–.97 | Linseed oil |
| *P. sylvestris* | .88–1.00 | — |
| *P. taeda* | .88–.90 | SAE 20 oil‡ |
| *P. virginiana* | <1.00 | — |

**Sources:** Barnett (1976), Barnett and McLemore (1967b), Bonner (1986a&b), Bonner and others (1994), Eliason and Hill (1954), Fenton and Sucoff (1965), Fowells (1965), Krugman and Jenkinson (1974), Lindquist (1962), Schubert (1955), Schubert and Adams (1971), Stoeckeler and Slabaugh (1965), Wakeley (1954), Yanagisawa (1965).

\* Test sample cones promptly after picking to avoid excessive drying. Five or more cones should float before the crop is considered ripe.
† Specific gravity of kerosene is 0.80; 95% ethanol, 0.82; SAE 20 motor oil, 0.88; and  linseed oil, 0.93.
‡ Alternatively, use a 1:4 kerosene–linseed oil mix.
§ Cones that float in a 1:1 kerosene–linseed oil mix should be ripe within 10 days

ples of newly picked cones are floated in liquids of known specific gravity. Thus, seeds of ponderosa pine are mature if the cones float in kerosene; seeds of eastern white pine, if the cones just float in linseed oil; and seeds of spruce pine, if the cones just float in SAE 20 motor oil. A very simple, workable method uses water displacement in a graduated cylinder (Barnett 1979). Cone weight equals the volume displaced when the cone is floated, cone volume equals the displacement of the fully immersed cone, and the cone's specific gravity is its weight divided by its volume. Sampled cones should be assessed immediately, as drying results in false conclusions about seed ripeness.

Oils and other organic liquids are seldom used on cones of the southern pines anymore; if measurements of specific gravity are required, the water flotation and volume method is used. In large-scale collections of loblolly pine in seed orchards, cones are typically picked when sample cones float in water, indicating a specific gravity of <1.0. The scale of the operations is so large that every tree cannot be harvested at the ideal time. Proper storage of the cones, however, ensures complete ripening of the seeds without damage. Good orchard managers keep records of the ripening sequence and dates for all families to aid in scheduling of collections.

To avoid risks of harvesting immature seeds, cones should not be collected from felled trees until the seeds are mature. Nearly mature cones ripen in the crowns of felled trees of some pines, such as loblolly and shortleaf pines, but not in others (Wakeley 1954). Slightly immature seeds can be ripened successfully in harvested cones of some pines, including after picking for slash pine  (Bevege 1965; Wakeley 1954); in moist cold storage for sugar pine (Krugman 1966); and in dry cold storage in closed containers for Virginia pine (Church and Sucoff 1960). Ripening by such methods should be attempted only if mature seeds cannot be collected.

Cones usually are hand-picked from ladders and hydraulic lifts or by climbing the trees. In a typical loblolly pine seed orchard, it has been estimated that 9 bucket trucks and 14 workers can harvest 40 ha (100 ac) of trees with a "good" cone crop in 20 days (Edwards 1986). Less often, helicopters may be used where the trees are difficult to reach (Tanaka 1984). For some pines, hand-cutters or a cutting hook must be used to detach the cones, and hooks may be needed to pull the cone-laden branches to the picker. Mechanical tree shakers are used to harvest cones rapidly from species such as slash and longleaf pines (Kmecza 1970). Good shaker operation should remove 80% or more of the cones (Edwards 1986).

scale tips, and in eastern white pine, when they turn from green to yellow-green with brown on the scale tips, or to light brown. In certain other pines, however, cone color changes too late to be a useful index to ripeness. In longleaf pine, for example, ripe cones are still green in color and may have already started to open before turning brown (Wakeley 1954).

In species for which cone color changes may not be useful, seed maturity may be assessed by flotation tests of the cone's specific gravity (table 5). Although the crucial factor in cone ripening is moisture content, not specific gravity, measuring specific gravity is the quickest and easiest way to estimate cone moisture content (Bonner 1991). To determine whether cones have reached a desired specific gravity, sam-

# Table 6—*Pinus,* pine: cone processing schedules and safe times to cold- or freeze-store dry, mature seeds

| Species | Boiling water dip (sec) | Air-drying (day) | Kiln-drying (hr) | Kiln temp (°C) | Seed storage (yr)† |
|---|---|---|---|---|---|
| | | | **Cone processing schedule\*** | | |
| *P. albicaulis‡* | 0 | 15–30 | 0 | — | 8 |
| *P. aristata* | 0 | 2–8 | 0 | — | 9 |
| *P. arizonica* | 0 | — | 60 | 43 | — |
| *P. armandii* | 0 | 15 | 0 | — | — |
| *P. attenuata* | 15–30 | 1–3 | 48 | 49 | 16 |
| *P. balfouriana* | 0 | 2–8 | 0 | — | 16 |
| *P. banksiana* | 0 | — | 2–4 | 66 | 17–18 |
| | 10–30 | 3–10 | 0 | — | — |
| *P. brutia* | 0 | 3–20 | 0 | — | 3 |
| | 0 | — | 10 | 54 | — |
| *P. canariensis* | 0 | 2–10 | 0 | — | 18 |
| *P. caribaea* | — | — | — | — | 3 |
| *P. cembra‡* | — | — | — | — | >1 |
| *P. cembroides§* | 0 | 2–8 | 0 | — | — |
| *P. clausa* | 10–30 | 1 | 2–4 | 63 | 5 |
| *P. contorta* | | | | | |
|   var. *contorta* | 0 | 2–20 | 0 | — | 17 |
| | 0 | — | 96 | 49 | — |
|   var. *latifolia II* | 30–60 | 2–30 | 0 | — | 20 |
| | 0 | — | 6–8 | 60 | — |
|   var. *murrayana* | 0 | 2–20 | 0 | — | 17 |
| *P. coulteri* | 0–120 | 3–15 | 0 | — | 5 |
| | 0 | — | 72 | 49 | — |
| *P. densiflora* | 0–30 | 3–4 | 0 | — | 2–5 |
| *P. echinata* | 0 | — | 48 | 41 | 35 |
| *P. edulis §* | 0 | 2 | 0 | — | — |
| *P. elliottii* | | | | | |
|   var. *densa* | 0 | — | 8–10 | 49 | — |
| | 0 | 4 | 0 | — | — |
|   var. *elliottii* | 0 | — | 8–10 | 49 | 50 |
| | 0 | 42 | 0 | — | — |
| *P. engelmannii* | 0 | — | 60 | 43 | — |
| *P. flexilis* | 0 | 15–30 | 0 | — | 5 |
| *P. gerardiana* | 0 | 15 | 0 | — | — |
| *P. glabra* | 0 | — | 48 | 38 | >1 |
| *P. halepensis* | 0 | — | 10 | 54 | 10 |
| | 0 | 3–10 | 0 | — | — |
| *P. heldreichii* | 0 | 5–20 | 0 | — | — |
| *P. kesiya* | 0 | 5–20 | 0 | — | — |
| *P. jeffreyi* | 0 | — | 24 | 49 | 18 |
| | 0 | 5–7 | 0 | — | — |
| *P. lambertiana* | 0 | — | 24 | 49 | 21 |
| | 0 | 5–7 | 0 | — | — |
| *P. merkusii* | 0 | 5–7 | 0 | — | 7 |
| *P. monophylla §* | 0 | 2–3 | 0 | — | — |
| *P. monticola* | 0 | — | 4 | 43 | 20 |
| | 0 | 5–7 | 0 | — | — |
| *P. mugo* | 0 | — | 48 | 49 | 5 |
| *P. muricata* | 0 | — | 48 | 49 | — |
| *P. nigra* | 0 | — | 24 | 46 | >10 |
| | 0 | 3–10 | 0 | — | — |
| *P. palustris* | 0 | — | 48 | 38 | 5–10 |
| *P. parviflora* | 0 | 5–15 | 0 | — | — |
| *P. patula* | 15–30 | 1–2 | 48 | 46 | 21 |
| *P. pinaster* | 0 | — | — | 46 | 11 |
| | 0 | 4–10 | 0 | — | — |

| Table 6—*Pinus*, pine: cone processing schedules and safe times to cold- or freeze-store dry, mature seeds (continued) | | | | | |
|---|---|---|---|---|---|
| | **Cone processing schedule\*** | | | | |
| **Species** | **Boiling water dip (sec)** | **Air-drying (day)** | **Kiln-drying (hr)** | **Kiln temp (°C)** | **Seed storage (yr)†** |
| *P. pinea* | — | — | — | — | 18 |
| *P. ponderosa* | | | | | |
|   var. *ponderosa* | 0 | — | 3 | 49 | 18 |
| | 0 | 4–12 | 0 | — | — |
|   var. *scopulorum* | 0 | — | 2 | 74 | >15 |
| | 0 | 4–12 | 0 | — | — |
| *P. pumila‡* | — | — | — | — | — |
| *P. pungens* | 0 | — | 72 | 49 | 9 |
| | 0 | 30 | 0 | — | — |
| *P. quadrifolia§* | 0 | 2–8 | 0 | — | — |
| *P. radiata* | 60–120 | 0 | 48–72 | 49 | 21 |
| | 60–120 | 3–7 | 0 | — | — |
| *P. resinosa* | 0 | — | 13–20 | 54 | 30 |
| *P. rigida¶* | — | — | — | — | 11 |
| *P. roxburghii* | 0 | — | — | — | >4 |
| *P. sabiniana* | 0 | — | 48 | 49 | 5 |
| *P. serotina* | 0 | — | 48 | 41 | — |
| *P. sibirica‡* | — | — | — | — | >2 |
| *P. strobiformis* | 0 | 14 | 0 | — | — |
| *P. strobus* | 0 | — | 15–20 | 54 | 10 |
| *P. sylvestris* | 0 | — | 10–16 | 49 | 15 |
| | 0 | 3–7 | 0 | — | — |
| *P. taeda* | 0 | — | 48 | 41 | >9 |
| *P. thunbergiana* | 0–30 | 5–20 | 0 | — | 11 |
| *P. torreyana* | 0 | 5–20 | 0 | — | 6 |
| *P. virginiana* | 0 | — | 2 | 77 | >5 |
| *P. washoensis* | 0 | 4–12 | 0 | — | 8 |

**Sources:** Barnett (1969, 1970), Barnett and McLemore (1967a&b), Bonner (1990), Church and Sucoff (1960), Dent (1947), FAO (1993), Goor and Barney (1968), Heit (1967b), Jones (1962, 1966), Kamra (1967), Karschon (1961), Krugman and Jenkinson (1974), LeBarron and Roe (1945), Little and Dorman (1952a), Lizardo (1950), Luckhoff (1964), McLemore (1961b), Mirov (1946), Nather (1958), NBV (1946), Nyman (1963), Ohmasa (1956), Schubert (1952), Schubert and Adams (1971), Simak and others (1961), Steinhoff (1964), Stoeckeler and Jones (1957), Swingle (1939), Troup (1921), Wakeley (1954), Wakeley and Barnett (1968).

\* Air drying temperatures are 15.6 to 32.2 °C. Kiln drying, if used, should follow air drying. Recommended air drying time is 3 to 7 days, where none is listed.
† Seed germination was at least 50% after storage. Seeds of most pines were stored at 0.5 to 5 °C or −15.6 to −18.8 °C. Freezing is preferred. Seed moisture contents were between 5 and 10%.
‡ Cones of *P. albicaulis*, *P. cembra*, *P. pumila*, and *P. sibirica* must be broken up to free and extract the seeds.
§ An alternate extraction method for *P. cembroides*, *P. edulis*, *P. monophylla*, and *P. quadrifolia* is to shake the trees mechanically and collect shed seeds from cloths spread on the ground.
‖ Time needed in boiling water is estimated. Reported treatment was 5 to 10 minutes in water at 64 °C or higher.
¶ Cones were soaked in water overnight and dried in a warm room.

Large numbers of seeds of certain other pines, such as piñyon and singleleaf and Parry piñyons, are harvested by shaking or beating the tree crowns and gathering extracted seeds from the ground (Krugman and Jenkinson 1974). This technique has been expanded with the net retrieval system that is used in many seed orchards of loblolly, Virginia, and eastern white pines (Bonner 1991). The system, originated in the early 1970s by the Georgia Forestry Commission (Wynens and Brooks 1979), employs large rolls of polypropylene netting (carpet backing) spread out beneath the trees. As the cones open naturally on the trees, seeds fall onto the netting, usually aided by light mechanical shaking.

When most of the crop is on the netting, it is rolled up and the seeds recovered. The recovered seeds are usually very moist and trashy, so they must be carefully dried and cleaned. If this is properly done, the seed quality is not damaged (Bonner and Vozzo 1986a). The net retrieval system can be used only where an orchard mix of families is desired for seedling production. If families are to be kept separate for site-specific planting, as is becoming increasingly common for loblolly pine, cones must be collected by hand from each tree.

**Cone processing and seed extraction.** In general, cones should be dried quickly after collection to avoid inter-

nal heating, mold development, and rapid seed deterioration (table 6). Cones may be dried in 2 to 60 days by immediately spreading them in thin layers on dry surfaces in the sun or on trays in well-ventilated buildings, or by hanging them in sacks from overhead racks protected against rain (Schubert and others 1970; Stoeckeler and Jones 1957; Stoeckeler and Slabaugh 1965; Wakeley 1954). Cones should be dried slowly to avoid "case hardening." After initial drying, cones can be stored temporarily in well-ventilated bags or trays. Ripe cones of many pines open quickly under such conditions, but those of others may require additional drying in either a heated shed or a cone-drying kiln.

In large-scale collections of cones of the southern pines, cones are frequently stored in burlap bags or 704-liter (20-bu) wire-bound boxes for as long as several months before going into heated kilns to complete drying. During this storage period, significant amounts of cone moisture are lost (thereby reducing fuel costs in later drying) and seeds in cones that were picked a little early complete the maturation process (Bonner 1991). There are species with "sensitive" seeds, such as longleaf and eastern white pines, that are more easily damaged during cone storage, and a maximum of 1 week is suggested for bulk storage of these cones. For loblolly, slash, shortleaf, and Virginia pines, cone storage in bags or boxes for 3 to 5 weeks appears to benefit seed yield and quality (Bonner 1991).

Properly air-dried cones may open amply after just a few hours in a kiln, or they may take several days, depending on species. With the exception of the white pines and perhaps others, cones must reach moisture contents of 10% for maximum seed release (Belcher and Lowman 1982). Seeds of most trees are killed at temperatures around 66 °C. Many kilns operate at temperatures of 32 to 60 °C. Maximums of 43 °C and lower have been recommended for most species (Tanaka 1984), but such temperatures are not always effective. Cones of most pines open at a kiln temperature of 54 °C or lower and relative humidity near 20% (table 6). Cones of a few pine species, including jack, sand, and Rocky Mountain ponderosa pines, need temperatures higher than 54 °C to open (Schubert and others 1970; Stoeckeler and Jones 1957; Stoeckeler and Slabaugh 1965). For all species, however, kiln temperatures will depend on initial cone moisture content, relative humidity, kiln load, and the type of kiln in use. The common types of cone kilns are rotating tumbler driers, progressive kilns, and tray kilns (Bonner 1991). For additional information on kilns, see chapter 3.

Cones that have been stored in containers long enough to dry without opening and cones that have been dried under cool conditions may not open properly during kiln drying. Such cones first should be soaked in water for 12 to 24 hours and then kiln-dried to open satisfactorily (Stoeckeler and Slabaugh 1965). In the South, most producers place their storage containers in the open, where the alternating wetting and drying in natural weather patterns facilitates cone opening (Bonner 1991).

Serotinous cones normally can be opened by dipping them in boiling water for 10 seconds to 2 minutes (table 6). Immersion times of up to 10 minutes in boiling water have been needed to open some lots of serotinous cones (Krugman and Jenkinson 1974). This procedure melts the resins bonding the cone scales, fully wets the woody cone, and causes maximum scale reflexing (LeBarron and Roe 1945; Little and Dorman 1952a). If serotinous cones are partially open, dipping them in boiling water may damage the seeds (Belcher 1984). To avoid this, the cones should be sprayed with water to close the scales, then dipped. Cones of sand pine are sometimes opened by quick exposure to live steam, a process that may be safer than dipping in boiling water (Bonner 1997).

Once opened, cones are shaken to extract the seeds. Most seeds are extracted by placing the opened cones in a large mechanical tumbler or shaker for large lots, or in a small manual shaker for small lots. Seeds from the extractor still must be separated from cone fragments, dirt, and other debris. Seeds are cleaned by rapid air movement, vibration, or screening or by a combination of these methods (Tanaka 1984). Extracted seeds are de-winged by using machines of various types, by flailing them in a sack, or by rubbing.

**Table 7—***Pinus*, pine: flotation liquids used to separate empty seeds from full seeds

| Species | Flotation liquid for empty seeds |
|---|---|
| *P. brutia* | Water |
| *P. coulteri* | Water |
| *P. echinata* | 95% ethanol |
| *P. echinata* | Water |
| *P. elliottii* var. *elliottii* | Water |
| *P. glabra* | 95% ethanol |
| *P. halepensis* | 95% ethanol |
| *P. nigra* | 95% ethanol |
| *P. palustris* | Pentane |
| *P. pinaster* | 95% ethanol |
| *P. pinea* | Water |
| *P. sabiniana* | Water |
| *P. strobus* | 100% ethanol |
| *P. sylvestris* | Petroleum ether |
| *P. taeda* | Water |

**Sources:** Barnett (1970), Goor (1955), Karschon (1961), Krugman and Jenkinson (1974), Lebrun (1967), McLemore (1965), NBV (1946), Stoeckeler and Jones (1957), Wakeley (1954).

**Table 8—**_Pinus_, pine: cone and seed yields

| Species | Place collected | Seed weight | | | | Clean seeds (x1,000)/wt | | | | Lot |
| | | /cone wt | | /cone vol | | Range | | Avg | | |
| | | g/kg | oz/lb | kg/hl | lb/bu | /kg | /lb | /kg | /lb | |
|---|---|---|---|---|---|---|---|---|---|---|
| P. albicaulis | Idaho | — | — | — | — | 4.8–6.6 | 2.2–3.0 | 5.7 | 2.6 | 3 |
| P. aristata | Arizona | 40 | 0.6 | 1.42 | 1.1 | 39–42 | 17–19 | 40 | 18 | 4 |
| P. arizonica | Arizona | 9–23 | .14–.35 | .90–1.3 | .7–1.0 | 24–26 | 11–19 | 25 | 11 | 10 |
| P. armandii | France | — | — | — | — | 2.6–4.1 | 1.2–1.9 | 3.5 | 1.6 | 2 |
| P. attenuata | California & Oregon | — | — | 0.13 | .1 | 33–71 | 15–32 | 56 | 25.4 | 6 |
| P. balfouriana | California | — | — | — | — | 31–49 | 14–22 | 37 | 17 | 3 |
| P. banksiana | Great Lakes | 10 | .15 | .26–.9 | .2–.7 | 156–551 | 71–250 | 289 | 131 | 423 |
| P. brutia | Europe | — | — | — | — | 17–26 | 7.6–11.6 | 20.1 | 9.1 | 5 |
| P. canariensis | South Africa | — | — | — | 8.8–9.9 | 4.0–4.5 | 9.3 | 4.2 | 10 | |
| P. caribaea | — | — | — | — | — | 52–81 | 24–37 | 68.3 | 31 | >10 |
| P. cembra | Germany | — | — | — | — | 3.5–5.1 | 1.6–2.3 | 4.4 | 2.0 | >10 |
| P. cembroides | — | — | — | — | — | 1.4–4.6 | 0.6–2.1 | 2.4 | 1.1 | 5 |
| P. clausa | Florida | 35 | .52 | .77–1.2 | .6–.9 | 143–187 | 65–85 | 165 | 75 | >10 |
| P. contorta | | | | | | | | | | |
| var. contorta | California | — | — | .64–1.5 | .5–1.2 | 245–364 | 111–165 | 298 | 135 | 28 |
| var. latifolia | Montana to Colorado | 8–10 | .1–.15 | .26–1.0 | .2–.8 | 174–251 | 79–114 | 207 | 94 | 39 |
| var. murrayana | California | 5.5 | .1 | .26 | .2 | 256–262 | 116–119 | 258 | 117 | 4 |
| P. coulteri | California | 22 | .33 | 1.03 | .8 | 2.6–3.5 | 1.2–1.6 | 3.1 | 1.4 | 8 |
| P. densiflora | Japan | 20 | .3 | .64–1.0 | .5–.8 | 79–141 | 36–64 | 115 | 52 | 26 |
| P. echinata | — | 20–30 | .3–.45 | .52–1.4 | .4–11.1 | 71–161 | 32–73 | 102 | 46 | 144 |
| P. edulis | Arizona | 28 | .4 | 3.3 | 4.25 | 3.3–5.5 | 1.5–2.5 | 4.2 | 1.9 | 9 |
| P. elliottii | | | | | | | | | | |
| var. densa | S Florida | — | — | .64–1.3 | .5–1.0 | 31–37 | 14–17 | 34 | 15 | 30 |
| var. elliottii | — | 10–20 | .15–.3 | .77–1.0 | .6–.8 | 21–43 | 10–19 | 30 | 13 | 404 |
| P. engelmanni | Arizona | 11 | .16 | .52 | .4 | — | — | 22 | 10 | 1 |
| P. flexilis | — | — | — | — | — | 7.1–15.0 | 3.2–6.8 | 10.8 | 10.0 | 44 |
| P. gerardiana | India | — | — | — | — | 2.4–2.9 | 1.1–1.3 | 2.4 | 4.9 | 10 |
| P. glabra | Louisiana | — | — | .13–1.3 | .1–1.3 | 88–115 | 40–52 | 101 | 1.1 | 8 |
| P. halepensis | Italy | — | — | — | — | 48–88 | 22–40 | 62 | 46 | >10 |
| P. heldreichii | — | — | — | — | — | 35–71 | 16–32 | 46 | 28 | 18 |
| P. jeffreyi | California | 35 | .52 | 1.2–2.6 | .9–2.0 | 5.8–11.7 | 2.6–5.3 | 8.2 | 3.7 | 26 |
| P. keisya | SE Asia | — | — | — | — | 44–76 | 20–34 | 59.5 | 27 | >5 |
| P. koraiensis | Korea | — | — | — | — | 1.6–2.0 | 0.7–0.9 | 1.8 | 3.7 | 3 |
| P. lambertiana | California | 37 | .56 | 1.9–2.6 | 1.5–2.0 | 3.3–6.0 | 1.5–2.7 | 4.6 | 2.1 | 27 |
| P. leiophylla var. chihuahuana | — | — | — | .90–1.2 | .7–.9 | — | — | 88 | 40 | >1 |
| P. merkussi | — | — | — | — | — | 28–59 | 13–27 | 40 | 18.2 | 11 |
| P. monophylla | Nevada | — | — | 2.2–6.0 | 1.7–4.7 | 2.3–2.6 | 1.0–1.2 | 2.4 | 1.1 | 2 |
| P. monticola | Utah | 10 | .15 | .4–1.03 | .3–.8 | 31–71 | 14–32 | 59 | 27 | >99 |
| P. mugo | Germany | — | — | 1.03 | .8 | 126–201 | 57–91 | 152 | 69 | 10 |
| P. muricata | California | 4 | | .26 | .2 | 86–112 | 40–50 | 103 | 46.8 | 3 |
| P. nigra | — | 20–40 | .3–.6 | .52–1.5 | .4–1.2 | 31–86 | 14–39 | 57 | 26 | >159 |
| P. palustris | Louisiana | 21 | .32 | 1.03 | .8 | 6.6–15.4 | 3–7 | 10.8 | 4.9 | 220 |
| P. parviflora | — | — | — | — | — | 6.8–10.1 | 3.1–4.6 | 8.6 | 3.9 | >3 |
| P. patula | South Africa & Mexico | — | — | — | — | 88–132 | 40–60 | 116 | 53 | >3 |
| P. peuce | — | — | — | — | — | 22–31 | 10–14 | 24 | 11 | 6 |
| P. pinaster | — | 35–55 | .53–.82 | — | — | 15–29 | 7–13 | 22 | 10 | 16 |
| P. pinea | Europe | — | — | — | — | 1.1–1.6 | 0.5–0.7 | 1.3 | 0.6 | 4 |

Southern species, except for longleaf pine, are de-winged in mechanical de-wingers that spray a fine mist of water on the seeds as they slowly tumble; capacities are about 90 kg/hr. The seeds and wing fragments must be dried for separation, and if seed moisture goes above 10% during the process, additional drying may be necessary (Bonner 1991).

Longleaf pine must be de-winged dry. In a few pines, de-winging can be simplified by first wetting the seeds and then drying them. Proper redrying precludes loss in seed quality (Wang 1973). The loose seedwings can be fanned out (Stoeckeler and Slabaugh 1965; Wakeley 1954). Mechanical

**Table 8**—*Pinus,* pine:   cone and seed yields   (continued)

| Species | Place collected | Seed weight /cone wt g/kg | oz/lb | /cone vol kg/hl | lb/bu | Clean seeds (x1,000)/wt Range /kg | /lb | Avg /kg | /lb | Lot |
|---|---|---|---|---|---|---|---|---|---|---|
| *P. ponderosa* | | | | | | | | | | |
| var. *ponderosa* | — | 20–70 | .3–1.0 | .8–2.6 | .6–2.0 | 15–51 | 7–23 | 26 | 12 | 185 |
| var. *scopulorum* | Black Hills | 39 | .6 | 1.93 | 1.5 | 22–34 | 10–15 | 29 | 13 | 74 |
| *P. pumila* | — | — | — | — | — | — | — | 24 | 11 | 11 |
| *P. pungens* | West Virginia | 30 | .45 | .52 | .4 | 68–84 | 31–38 | 75 | 34 | 3 |
| *P. quadrifolia* | California | — | — | — | — | 1.8–2.6 | 0.8–1.2 | 2.1 | 1.0 | 3 |
| *P. radiata* | California | 9 | .14 | .39 | .3 | 23–35 | 10–16 | 29 | 13 | 7 |
| *P. resinosa* | Lake States | 10–20 | 1.5–.3 | .64–1.0 | .5–.8 | 66–166 | 30–76 | 115 | 52 | 529 |
| *P. rigida* | Pennsylvania/ New York | 20–30 | .3–.45 | 1.03 | .8 | 94–181 | 42–82 | 136 | 62 | 10 |
| *P. roxburghii* | India | — | — | — | — | 6.8–25 | 3–11 | 12 | 25 | 36 |
| *P. sabiniana* | California | — | — | — | — | 1.2–1.4 | 0.5–0.6 | 1.3 | 0.6 | 3 |
| *P. serotina* | SE US | — | — | .52 | .4 | 104–139 | 47–63 | 119 | 54 | 4 |
| *P. sibirica* | Siberia | — | — | — | — | 3.5–4.6 | 1.6–2.1 | 4.0 | 1.8 | >10 |
| *P. strobiformis* | Arizona | 80 | 11.2 | 3.5 | 2.7 | 5.5–6.4 | 2.5–2.9 | 6.0 | 2.7 | 10 |
| *P. strobus* | — | 20–30 | .3–.45 | .4–2.2 | .3–1.7 | 39–117 | 17.5–53 | 58 | 26 | 300 |
| *P. sylvestris* | Europe, E US | 20 | .3 | .5–0.8 | .4–.6 | 74–245 | 33.8–111 | 165 | 75 | >346 |
| *P. taeda* | — | 20–30 | .3–.45 | .8–1.7 | .6–.63 | 27–58 | 12–26 | 40 | 18 | 652 |
| *P. thunbergiana* | Japan, Korea, NE US | — | — | .26–1.0 | .2–.8 | 57–110 | 26–50 | 75.0 | 34 | 50 |
| *P. torreyana* | California | — | — | — | — | 8.8–17.6 | .4–.8 | 11.0 | 0.5 | 7 |
| *P. virginiana* | — | 30 | .45 | .64–1.2 | .5–.9 | 101–201 | 46–91 | 122 | 55 | 30 |
| *P. wallichiana* | India | — | — | — | — | 16–23 | 7–10 | 20 | 9 | 163 |

**Sources:** Barnett and McLemore (1967b), Cooling (1968), Curtis (1955), Debazac (1964), Delevoy (1935), Eliason (1942), Heit (1963, 1969), Karschon (1961), Krugman and Jenkinson (1974), Letourneux (1957), Luckhoff (1964), Magini and Tulstrup (1955), Miller and Lemmon (1943), Mirov (1936), Nather (1958), NBV (1946), Ohmasa (1956), Poynton (1961), Pravdin (1963), Rafn (1915), Read (1932), Sen Gupta (1936), Steinhoff (1964), Stoeckeler and Jones (1957), Sudworth (1908), Swingle (1939), Takayama (1966), Troup (1921), Wappes (1932).

de-wingers can cause severe damage to seeds if they are not used properly. Seeds of 3 pines—bristlecone (Krugman and Jenkinson 1974), longleaf (Wakeley 1954), and Scots pine (Kamra 1967)—are highly susceptible to such damage and demand careful de-winging. De-winged seeds are cleaned by using air-screen cleaners, aspirators, or fanning mills to remove the broken wings, pieces of cone scale, and other impurities. The increasing use of family lots of known genetic identity has increased the use of small tumblers, de-wingers, and cleaners and decreased the use of large equipment for many species.

After de-winging and cleaning are completed, empty seeds of many pines can be separated from the filled ones with gravity tables or aspirators (see chapter 3). This separation can also be done by simple flotation in water for many species, such as loblolly, Coulter, and Italian stone pines. It is also possible to use organic liquids of suitable specific gravity on small lots of other species (table 7), but immersing seeds in an organic liquid like ethanol, pentane, or petroleum ether may reduce seed viability. Such reduction can be minimized by using a short immersion time and evaporating all traces of the organic liquid from the seeds retained before use (Barnett 1970). Seeds sorted in organic solvents should be used right away and not stored, as the potential for dam-

age increases in storage (Bonner 1997). If plain water is used to float off empty seeds, the retained seeds should be dried to moisture contents between 5 and 10% before they are stored. Seedlots of some pines, notably lodgepole pine, can be upgraded with the IDS (incubation-drying-separation) method developed in Sweden (Simak 1984) (see chapter 3). Cleaned seeds per weight are known for 65 species and varieties, and cone and seed yields are available for many of them (table 8).

**Seed storage.**    Pine seeds are orthodox in storage behavior, and seeds of most species can be stored easily for extended periods of time without serious losses in viability (table 6). Seeds of red pine that had been stored for 30 years still produced vigorous seedlings in the nursery, as did seeds of shortleaf and slash pines that were stored for 35 years (Krugman and Jenkinson 1974; Wakeley and Barnett 1968). Lots of slash and shortleaf pine seeds stored for 50 years still germinated at 66 and 25%, respectively (Barnett and Vozzo 1985). Seeds of many pines are now routinely stored for 5 to 10 years and more. They should be dried to a moisture content between 5 and 10% and stored in containers that prevent absorption of ambient moisture. For long-term storage of most pine seeds, temperatures of –18 to –15 °C or

**Table 9—***Pinus*, pine:  recommended moist seed chilling times, stratification at 0.5 to 5 °C

| Species | Seed chilling (days) | |
| | Fresh | Stored |
| --- | --- | --- |
| P. muricata | 0 | 20–30 |
| P. nigra | 0 | 0–60 |
| P. palustris | 0 | 0–30 |
| P. parviflora † | 90 | 90 |
| P. patula | 60 | 60 |
| P. peuce § | 0–60 | 60–180 |
| P. pinaster ‡ | 0 | 60 |
| P. pinea ‡ | 0 | 0 |
| P. ponderosa | | |
|   var. ponderosa | 0 | 30–60 |
|   var. scopulorum | 0 | 0–60 |
| P. pumila | 120–150 | 120–150 |
| P. pungens | 0 | 0 |
| P. quadrifolia | 0 | 0–30 |
| P. radiata | 0–7 | 7–20 |
| P. resinosa | 0 | 60 |
| P. rigida | 0 | 0–30 |
| P. roxburghii | 0 | 0 |
| P. sabiniana ‖ | 60–120 | 60–120 |
| P. serotina | 0 | 0–30 |
| P. sibirica † | 60–90 | 60–90 |
| P. strobiformis | 60–120 | 60–120 |
| P. strobus | 30–60 | 60 |
| P. sylvestris | 0 | 15–90 |
| P. taeda | 30–60 | 30–60 |
| P. thunbergiana | 0 | 30–60 |
| P. torreyana | 30–90 | 30–90 |
| P. virginiana | 0–30 | 30 |
| P. wallichiana | 0–15 | 15–90 |
| P. washoensis | 60 | 60 |

**Sources:**  Andresen (1965), Asakawa (1957), Barnett (1970), Barton (1930), Bonner (1991), Dent (1947), Goor and Barney (1968), Hartmann and Hester (1968), Heit (1963, 1967a, 1968b, 1969), Hopkins (1960), ISTA (1966), Jones (1962), Krugman and Jenkinson (1974), Luckhoff (1964), Magini and Tulstrup (1955), Malac (1960), McLemore and Barnett (1967), McLemore and Czabator (1961), Mirov (1936), Rohmeder and Loebel (1940), Shafiq and Omer (1969), Swingle (1939), Swofford (1958), Wakeley (1954).

\* Chilling time can be held to 90 days if seeds first are scarified mechanically or soaked for 3 to 5 hours in sulfuric acid.  Acid soaks are not advised.
† Seeds of *P. cembra*, *P. koraiensis*, *P. parviflora*, and *P. sibirica* with immature embryos may need a warm, moist treatment, 60 days at 21 to 26 °C, before the cold one.
‡ Good germination of *P. edulis*, *P. pinaster*, and *P. pinea* can be obtained by soaking the seeds in cold water for 24 hours at 5 °C.
§ A 60-day moist chilling treatment was sufficient when the seeds first were soaked 30 minutes in sulfuric acid.  Acid soaks are not advised.
‖ Seed germination is faster if the seedcoats are cracked before the moist chilling treatment.

–6 to –5 °C are preferred (Krugman and Jenkinson 1974; Wakeley and Barnett 1968), but those of 0.5 to 5 °C are sufficient for 2 to 3 years (Bonner 1991). Seeds of Khasi and blue pines have remained viable at ordinary room temperatures for several years (Claveria 1953; Dent 1947), but such ambient storage is risky and not recommended. Seeds deteriorate rapidly if they are held long at room temperature after cold storage. Seeds in cold storage should be pulled within

days of cold, moist stratification, sowing, or testing (Wakeley 1954).

Liquid nitrogen at –196 °C has been used to store seeds of several pines in research studies with no loss of viability for short periods, including shortleaf pine seeds for 4 months and ponderosa seeds for 6 months (Bonner 1990). This method is under study for germplasm conservation purposes, however, and not for routine storage.

**Pregermination treatments.**    Seeds of most pines in temperate climates are shed in the autumn and germinate promptly the next spring. Seeds of certain others, such as Swiss stone and Balkan pines, may not germinate until the second or even third year after seed dispersal. Pine seeds display highly variable germination behavior when sown after extraction or after storage. Seed dormancy varies in type and degree among species, among geographic sources within species, and among seedlots of the same source. Secondary dormancy may result from prolonged extraction at too-high temperatures and may increase with extended time in cold storage (Heit 1967a; Krugman and Jenkinson 1974). Seeds of many pines germinate without pretreatment, but germination rates and amounts are greatly increased by pretreating the seeds, and especially stored seeds, using moist, cold stratification. Recommended moist chilling times for fresh and stored seeds are available for 65 species and varieties (table 9).

Air-dried and stored seeds of most pines are effectively readied for rapid, complete germination by first soaking them in clean, constantly aerated water at temperatures of 20 to 25 °C for 36 to 40 hours, or until they sink (Jenkinson and McCain 1993; Jenkinson and others 1993). The soaked seeds are promptly drained of free water, placed naked in polybags, and chilled at 0 to 1 °C for the times shown (table 9). Both the development of molds on and visible germination of seeds in the polybags are prevented by surface drying the seeds after their first 4 weeks of chilling.

Seeds of some pines show strong dormancy, that is, they require 60 to 90 days or more of moist chilling to attain rapid and complete germination (table 9). Such dormancy may be caused by physiological or physical factors. Pretreatment may be needed to overcome a physiological block in the embryo, as in sugar pine (Krugman 1966), or to effect a physical change in the seedcoat to make it more permeable to water, as in Digger pine (Griffin 1962; Krugman 1966).  Seed dormancy can be even more complex. An anatomically immature embryo with a physiological block may be coupled with an impermeable seedcoat, as in Swiss stone pine. Acid scarification of seedcoats has been used for a few pines, including Swiss stone, Balkan, and Digger

**Table 10**—*Pinus,* pine: seed germination test conditions and results

| Species | Seeds treated | Daily light (hr) | Seed medium | Temp (°C)* Light | Dark | Days | Rate amt (%) | Time (days) | Total (mean %) | Samples |
|---|---|---|---|---|---|---|---|---|---|---|
| *P. albicaulis* | + | 8 | A, P | 30 | 20 | 28 | — | — | — | — |
| | + | 0 | pe, s | 21 | 10 | 365 | — | — | 30 | 2 |
| *P. aristata* | | 0 | A, P | 30 | 20 | 14 | — | — | — | — |
| | | 24 | P | 32 | 21 | 22 | 75 | 7 | 91 | 74 |
| | | 0 | pe, s | 35 | 20 | 30 | — | — | 86 | >7 |
| *P. arizonica* | | 0 | P, pl | — | 24 | 20 | 52 | 10 | 75 | 8 |
| *P. attenuata* | + | 24 | A, P | 22 | 26 | 30 | 79 | 5 | 92 | 1 |
| | | 8 | s | 30 | 20 | 120 | 69 | 10 | 85 | 4 |
| *P. banksiana* | | 8 | A, P | 30 | 20 | 14 | 86 | 10 | 87 | 14 |
| | + † | 8 | s | 30 | 20 | 8 | 54 | 5 | 69 | 29 |
| | | 8 | s | 30 | 20 | 23 | 72 | 9 | 75 | 6 |
| *P. canariensis* | + | 0 | A | — | 20 | 28 | 58 | 20 | 74 | 9 |
| | | 8 | A | 20 | 20 | 21 | 63 | 7 | 76 | 4 |
| *P. caribaea* | | >8 | P | 30 | 20 | 21 | — | — | 72 | 3 |
| *P. cembra* | + | 0 | P, s | 30 | 20 | 28 | — | — | — | — |
| | + | 0 | A | 30 | 20 | 90 | 21–42 | 17–37 | 37 | 8 |
| | + | 0 | s | 22 | 20 | 60 | 55 | 28 | 62 | 1 |
| *P. cembroides* | | 0 | B, P | — | 20 | 28 | — | — | — | — |
| *P. clausa* | | 8 | K | 20 | 20 | 21 | 86 | 14 | 90 | 19 |
| | | 8 | s + v | 21 | 16–18 | 30 | 85 | 20 | 90 | — |
| *P. contorta* | | | | | | | | | | |
|   var. *contorta* | + | >8 | A, P, v | 30 | 20 | 28 | — | — | 60 | 3 |
| | | 0 | pe, s | 30 | 20 | 50 | — | — | 80 | 29 |
|   var. *latifolia* | + | 8 | A, P | 30 | 20 | 21 | 73 | 10 | 80 | 10 |
| | + | 0 | s | 28 | 14 | 62 | — | — | 73 | 9 |
| | – † | 0 | s | 28 | 14 | 62 | — | — | 65 | 12 |
|   var. *murrayana* | | 10 | s | 26 | 26 | 30 | — | — | 75 | 3 |
| *P. coulteri* | + | 0 | P, s | 30 | 20 | 28 | — | — | — | — |
| | + | 8 | s, v | 30 | 20 | 28 | — | — | 37 | 7 |
| *P. densiflora* | | 8 | A, P | 30 | 20 | 21 | — | — | — | — |
| | | 0 | s | 30 | 20 | 30 | 75 | 15 | 87 | 3 |
| | + | 0 | s | 30 | 20 | 24–60 | 54 | 15 | 83 | 4 |
| | | 0 | A | — | 24 | 30 | — | — | 74 | 20 |
| *P. echinata* | | >8 | A, P | 30 | 20 | 28 | — | — | — | — |
| | | 8 | s + v | 22 | 22 | 28 | 88 | 14 | 90 | 139 |
| | + | 8 | pl + s | 22 | 22 | 27 | 81 | 10 | 90 | 148 |
| *P. edulis* | + | 0 | A | 30 | 20 | 28 | — | — | — | — |
| | + | 0 | P | 32 | 21 | 16 | 80 | 7 | 96 | 4 |
| *P. elliottii* | | | | | | | | | | |
|   var. *densa* | | >8 | s + v | 22 | 22 | 32 | 30–79 | 7–11 | 32–82 | 30 |
| | | 16 | K | 22 | 22 | 28 | 86 | 7 | 87 | 28 |
|   var. *elliotti* | | >8 | A, P | 30 | 20 | 28 | — | — | — | — |
| | | 16 | K | 22 | 22 | 26 | 80 | 10 | 89 | 392 |
| | + | 16 | K | 22 | 22 | 26 | 75 | 9 | 84 | 83 |
| *P. engelmannii* | | 0 | P | 32 | 21 | 16 | 70 | 4 | 88 | 4 |
| *P. flexilis* | + | 0 | B, P | 30 | 20 | 21 | — | — | — | — |
| | + | 8 | A | 30 | 20 | 21 | — | — | — | — |
| | | 8 | s + v | 22 | 22 | 27 | — | — | 42 | 1 |
| | + | 8 | A | 30 | 20 | 30 | 69 | 14 | 82 | 1 |
| *P. gerardiana* | | 0 | A | — | 21 | 30–60 | — | — | 47 | 2 |
| *P. glabra* | + | 8 | A, P | 30 | 20 | 21 | — | — | — | — |
| | + | 16 | s + v | 22 | 22 | 30 | 85 | 13 | 98 | 25 |
| | | 16 | s + v | 22 | 22 | 30 | 46 | 30 | 98 | 30 |
| *P. halepensis* | | 0 | A, P | — | 20 | 28 | — | — | — | — |
| | | 0 | A | — | 20–22 | 30 | 50–66 | 20 | 79 | 5 |
| | | 0 | A | — | 18–19 | 30 | 65–80 | 16–20 | 89 | 12 |

**Table 10—***Pinus*, pine: seed germination test conditions and results (continued)

| Species | Seeds treated | Daily light (hr) | Seed medium | Temp (°C)* Light | Dark | Days | Rate amt (%) | Time (days) | Total (mean %) | Samples |
|---|---|---|---|---|---|---|---|---|---|---|
| *P. heldreichii* | + | 8 | A, P | 30 | 20 | 28 | — | — | — | — |
|  | + | 8 | A | 30 | 20 | 40 | — | — | 72 | 14 |
|  |  | — | A | — | 21 | 40 | — | — | 69 | 1 |
| *P. jeffreyi* | + | 8 | A, P, s | 30 | 20 | 28 | — | — | — | — |
|  | + | 24 | P | 22 | 26 | 30 | 95 | 5 | 99 | 1 |
|  |  | 0 | v | 30 | 20 | 21 | — | — | 79 | 5 |
| *P. kesiya* |  | 8 | A | 30 | 20 | 28 | 82 | 14 | 86 | 1 |
| *P. koraiensis* | + | 0 | s | 30 | 20 | 60 | 14 | 25 | 18 | 1 |
|  | + | >8 | P | 30 | 20 | 28 | — | — | 85–95 | 4 |
| *P. lambertiana* | + | 0 | P, s | 30 | 20 | 28 | — | — | — | — |
|  | + | — | v | 30 | 20 | 28 | — | — | 59 | 5 |
|  | + | 24 | P, s | 22 | 26 | 30 | 49 | 21 | 55 | 1 |
| *P. leiophylla* var. chihuahuana |  | 0 | pl | — | 24 | 22 | 60 | 6 | 70 | 3 |
| *P. merkusii* |  | 8 | A | 30 | 20 | 21 | — | — | 59 | 1 |
|  |  | 8 | A | 20 | 20 | 21 | — | — | 67 | 1 |
| *P. monophylla* |  | 24 | pl | 75 | 21 | 35 | 39–50 | 7 | 86–90 | 2 |
| *P. monticola* | + | 0 | P, s | 30 | 20 | 28 | — | — | — | — |
|  | + | 8 | pl + s | 22 | 22 | 71 | 39 | 11 | 44 | 11 |
| *P. mugo* |  | 8 | A, P | 30 | 20 | 14–21 | — | — | — | — |
|  |  | 0 | A | — | 20 | 30 | 25 | 10 | 45 | 30 |
|  |  | 8 | A | 30 | 20 | 20 | 76 | 10 | 80 | 30 |
| *P. muricata* |  | 0 | A | 30 | 20 | 35 | — | — | — | — |
|  | + | 0 | v | 30 | 20 | 21 | — | — | 38 | 5 |
|  | + | 24 | P | 22–26 | — | 30 | 70 | 7 | 85 | 1 |
| *P. nigra* |  | 8 | A, P | 30 | 20 | 14 | 91 | 10 | 92 | 49 |
|  |  | 0 | A | 30 | 20 | 30 | 54 | 10 | 86 | 49 |
| *P. palustris* |  | 16 | P | 20 | 20 | 21 | — | — | — | — |
|  |  | 16 | s + v | 22 | 22 | 30 | 90 | 10 | 95 | 100 |
| *P. parviflora* |  | 0 | P | 22 | 18 | 10–14 | — | — | — | — |
|  | + | 8 | s | 30 | 20 | 28 | 71 | 35 | — | — |
|  | + | >8 | A | 25 | 25 | 28 | — | — | 80 | 1 |
| *P. peuce* | + | 0 | s | 30 | 20 | 28 | — | — | — | — |
|  |  | 0 | A | 20 | 22 | 30 | — | — | 69 | 4 |
| *P. pinaster* |  | 8 | A | 20 | 20 | 35 | — | — | — | — |
|  | + | 8 | A, P | 20 | 20 | 28 | 41 | 7 | 79 | 8 |
|  | + | 0 | A | — | 20 | 30 | 70 | 20 | 83 | 5 |
| *P. pinea* | + | 0 | s | — | 20 | 21 | — | — | — | — |
|  | + | 8 | A | 20 | 20 | 21 | 30 | 7 | 81 | 4 |
|  |  | 0 | A | — | 18 | 22 | 88 | 14 | 98 | 3 |
| *P. ponderosa* var. *ponderosa* | + | 8 | A | 30 | 20 | 21 | — | — | — | — |
|  | + | >8 | A | 30 | 20 | 21 | — | — | 67 | 100 |
|  |  | 0 | pe, s | 29 | 18 | 30–60 | 14–87 | 7–29 | 59 | 186 |
| var. *scopulorum* |  | 16 | K | 22 | 22 | 30 | 84 | 11 | 86 | 4 |
|  |  | 0 | s | 20 | 30 | 30–60 | 50 | 19 | 64 | 40 |
| *P. pumila* | + | >8 | A | 30 | 20 | 21 | — | — | 77 | 9 |
| *P. pungens* |  | 0 | pe + s | — | 21–29 | 45–60 | — | — | 55 | 3 |
|  |  | 0 | pe, s | — | 24 | 40 | — | — | 65 | 9 |
| *P. quadrifolia* | + | 24 | A | 22–26 | — | 30 | 46 | 9 | 69 | 1 |
| *P. radiata* | + | 8 | A | 30 | 20 | 28 | — | — | — | — |
|  |  | >8 | P | 20 | 20 | 25 | 16 | 7 | 81 | 9 |
|  |  | >8 | v | 30 | 20 | 28 | — | — | 67 | 15 |
| *P. resinosa* |  | 0 | A, P | 30 | 20 | 14 | 69 | 10 | 83 | 23 |
|  |  | 0 | s | 30 | 20 | 30 | 25–75 | 7–25 | 75 | 551 |
| *P. rigida* |  | 8 | A, P | 30 | 20 | 14 | 77 | 10 | 86 | 6 |
|  | + | 0 | A | 30 | 20 | 30 | 24 | 10 | 47 | 6 |
|  |  | 8 | A | 30 | 20 | 45 | 60 | 18 | 70 | 19 |

**Table 10—*Pinus*, pine:  seed germination test conditions and results (continued)**

| Species | Seeds treated | Daily light (hr) | Seed medium | Temp (°C)* Light | Temp (°C)* Dark | Days | Rate amt (%) | Time (days) | Total (mean %) | Samples |
|---|---|---|---|---|---|---|---|---|---|---|
| *P. roxburghii* | | 0 | A | — | 20–22 | 30 | — | — | 83 | 5 |
| | | 0 | s | — | — | 30 | 79 | 10 | 81 | 135 |
| *P. sabiniana* | + | 0 | s | — | 22 | 30 | — | — | 76 | 3 |
| | + | 24 | A | 22–26 | — | 30 | — | — | 13 | 1 |
| *P. serotina* | | 8 | pl + s | 22 | 22 | 21 | 90 | 10 | 73 | 1 |
| *P. sibirica* | + | 0 | s | 20 | 30 | 60 | — | — | 7 | 1 |
| | | 0 | A | 20 | 22 | >60 | — | — | 40 | 4 |
| *P. strobiformis* | | 0 | A | 30 | 20 | 35 | — | — | 94 | 8 |
| | | 0 | pl | — | 24 | 46 | — | — | 39 | 31 |
| *P. strobus* | + | >8 | A, P | 30 | 20 | 21 | — | — | — | — |
| | + | >8 | K | 30 | 20 | 40 | 33 | 8 | 100 | 20 |
| | + | >8 | K | 22 | 22 | 40 | — | — | 93 | 28 |
| *P. sylvestris* | | 8 | A, P | 30 | 20 | 14 | 78 | 10 | 81 | 99 |
| | | 8 | A | 30 | 20 | 30 | 46 | 10 | 59 | 99 |
| | | 24 | s | 22–25 | — | 50 | — | — | 89–99 | 36 |
| | | 8 | A | 20 | 20 | 30 | 18–99 | 14 | 21–99 | 18 |
| *P. taeda* | | >8 | A, P | 30 | 20 | 28 | — | — | — | — |
| | | 16 | pl + s | 22 | 22 | 30 | 90 | 17 | 90 | 481 |
| *P. thunbergiana* | | >8 | A, P | 30 | 20 | 21 | 50 | 10 | 75 | 4 |
| | | >8 | A | 24 | 24 | 30 | 69 | 10 | 76 | 19 |
| | + | 0 | A | 25 | 21 | 28 | — | — | 85 | 100 |
| *P. torreyana* | + | 0 | pe, s | 27 | 18 | 60 | — | — | 81 | 21 |
| *P. virginiana* | | >8 | A | 30 | 20 | 21 | — | — | — | — |
| | | >8 | K | 22 | 22 | 28 | 87 | 10 | 90 | 29 |
| | | 0 | pe, s | 30 | 20 | 30 | — | — | 65 | 5 |
| *P. wallichiana* | | >8 | A, P | 30 | 20 | 28 | — | — | — | — |
| | | 0 | A | 24 | 21 | 60 | 44 | 20 | 64 | 12 |

**Sources:**  Andresen (1965), Asakawa (1957), AOSA (1965, 1996), Graber (1965), Heit (1958, 1963), Heit and Eliason (1940), ISTA (1966), Kamra (1969), Krugman and Jenkinson (1974), Luckhoff (1964), Magini (1955), McIntyre (1929), McLemore (1961a), Nather (1958), Ohmasa (1956), Rafn (1915), Rohmeder and Loebel (1940), Rossi (1929), Sen Gupta (1936), Simak and others (1961).

**Note:**  The + symbol shows that the seeds were pretreated, usually by moist chilling. Letters show the seed germination media that were used, as follows:  A = absorbent paper (filter, blotter), B = blotters supporting and covering seeds, K = Kimpak, P = absorbent medium in covered petri dish, pe = peat, pl = perlite, s = sand or soil, v = vermiculite.

\* Alternating periods of high and low temperatures typically were 8 and 16 hours (8/16). The light period normally coincided with the warmer temperature. Temperatures of 10, 15, 20, 25, 30, and 35 °C equal 50, 59, 68, 77, 86, and 95 °F, respectively.

† Seeds were extracted from old cones.

pines, but extended cold stratification, 6 to 9 months of moist chilling, is much more effective (Heit 1968b; Krugman 1966). In any case, acid scarification is not recommended for pine seeds (Krugman and Jenkinson 1974).

Seeds of some pines, including Swiss stone pine, Korean, Japanese white, and Siberian pine, may have immature embryos at the time of cone collection. Seed germination has been increased by placing seeds first in moist, warm stratification for several months and then in cold stratification for several more months (Asakawa 1957; Krugman and Jenkinson 1974).

**Germination tests.**    For reliable tests of seed viability, seeds are germinated in near-optimum conditions of aeration, moisture, temperature, and light. Standardized tests for many of the pines have been established by the Association of Official Seed Analysts (AOSA 1996), International Seed Testing Association (ISTA 1996), and regional organizations such as the Western Forest Tree Seed Council (WFTSC 1966). Extensive research and abundant practical experience have developed reliable test conditions and germination data for seeds of 61 species and varieties (table 10).

Seed germination can be effectively tested in any medium or container that provides adequate aeration and moisture. Seeds of a few pine species need light for reliable tests. Light, when used, usually is supplied by cool white fluorescent lamps operated for 8 or 16 hours in each 24-hour period. Several different temperature regimes are employed, but the commonest are a constant 20 °C and an alternating 30/20 °C. Alternating regimes typically maintain the higher temperature for 8 hours and the lower one for 16 hours.

**Figure 4**—*Pinus resinosa*, red pine:   seedling development at 1, 7, and 30 days after emergence.
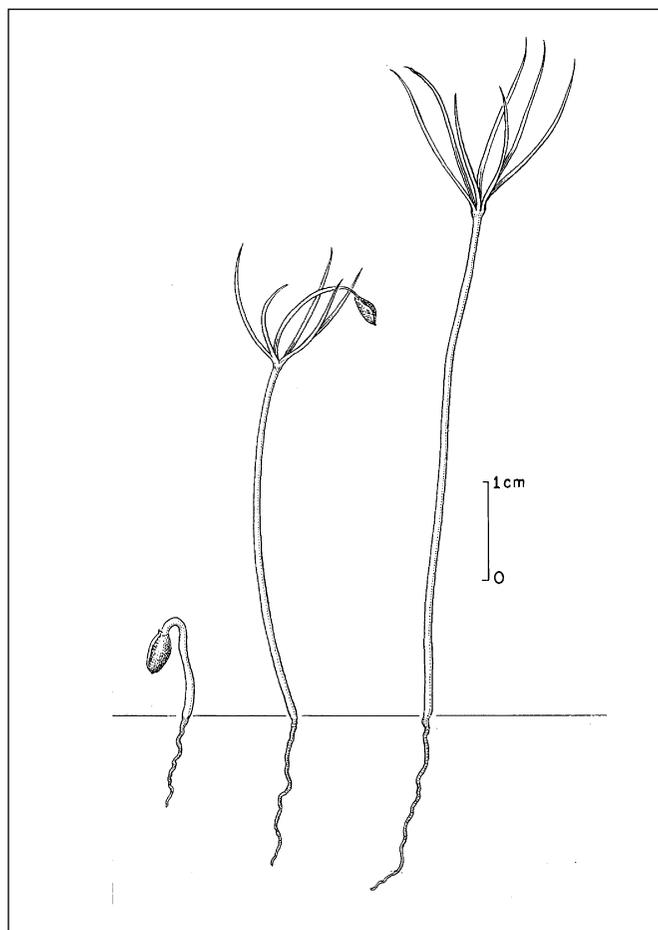


Most tests of viable seeds are clear within 2 weeks and ended within 3 to 4 weeks. Sample sizes of 400 seeds per lot (4 replications of 100) are ample for most pines, but in some cases, up to 1,000 per lot may be used. Germination is epigeal (figure 4).

Cutting methods are often used to obtain fast, rough assessments of seed quality. Cutting seeds provides a visible check of seed soundness, and serves to guide fall-sowings of fresh seeds that have embryo dormancy. It is a surprisingly accurate method with fresh seeds. X-radiography can also provide visible estimates of seed soundness without destroying the seeds. Another rapid estimate of viability is the leachate conductivity test (Bonner and Vozzo 1986b). Because no seeds are actually germinated, cutting, x-ray, and conductivity tests provide only estimates of viability and are somewhat prone to error (Stoeckeler and Jones 1957; Stoeckeler and Slabaugh 1965; Wakeley 1954).

Biochemical methods, such as staining with tetrazolium chloride to indicate viability, are recommended in official testing for the very dormant stone pines (ISTA 1996), but they are used on other species for rapid tests only. Tetrazolium test estimates are highly dependent on the analyst's experience and seed age, and too often exceed the percentages attained in standard germination tests (Stoeckeler and Slabaugh 1965; Tanaka 1984).

**Nursery and field practices.**   Pines are grown successfully in diverse soil types in most regions of the United States. Various regional handbooks, manuals, and reports on forest tree nursery and reforestation practices describe bare-root seedling production, illustrate typical nursery equipment and facilities, and provide critical guides on soil management, bed preparation, seed treatment, seed sowing, seedling cultural regimes and pest control, undercutting, wrenching, lifting, packing, transplanting, cold and freeze storage, shipping, field handling, and safe planting times (Cleary and others 1978; Duryea and Landis 1984; Heit 1964; ICIA 1963; Jenkinson 1980; Jenkinson and others 1993; Lowman and others 1992; Schubert and Adams 1971; Schubert and others 1970; Stoeckeler and Jones 1957; Stoeckeler and Slabaugh 1965; Wakeley 1954). Together, these references and work cited therein capture the bulk of knowledge and practical experience gained on pine seedling production and planting in the United States.

Productive nursery soils are invariably deep, arable, fertile, and drain rapidly to ensure root aeration. Most of the large mechanized nurseries fumigate their soils (in late summer–early fall) to control soil-borne diseases, insects, nematodes, and weeds before the scheduled sowing in fall or spring (Thompson 1984). Nursery climates, soils, seed sources, and their interactions have resulted in a wide range of cultural regimes and practices. Recommended practices for 35 different species and varieties show the wide ranges encountered in seed chilling time, in sowing time, density, and depth, in bed mulches, and in yields and types of planting stock produced (table 11).

In temperate regions, seeds can be sown in fall or spring. Seeds with embryo dormancy can be sown in fall without pretreatment. Normally, both dormant seeds and nondormant seeds are sown in spring more often than in fall. Dormant seeds in spring-sowings must be pretreated to enable rapid and complete germination. Applying the same treatment to the dormant seeds of all pines is inadvisable. Success of the treatment applied depends on species and seed source, and the one applied should be the one that achieves the highest germination and seedling emergence for the particular seedlot. Seedlings produced in fall-sowings after 1 growing season are often larger and better developed than those produced in spring-sowings. But fall-sowings are inherently risky. They typically incur excessive overwinter

**P**

## Table 11—*Pinus,* pine:  nursery practices

| Species | Seed chill (days) | Seed sowing Season | Density† (/ft²) | Seedbed mulch Depth‡ (mm) | Material | Planting stock Depth (mm) | Yield (%) | Type§ |
|---|---|---|---|---|---|---|---|---|
| *P. attenuata* | 60 | Spring | 25 | 10 | None | — | 80 | 1+0 |
| *P. banksiana* | 0 | Fall or spring | 30 | 6 | None | — | 50–60 | 1+0, 2+0, ¹/₂+1¹/₂, 1+1, 1+2 |
| *P. canariensis* | 0 | Spring | — | 6 | Sponge Rok® | 6–13 | 35–50 | 1+0, 2+0, ¹/₂+1¹/₂ |
| *P. clausa* | 0 | Spring | — | 6–13 | None | — | 70 | 1+0 |
| *P. contorta* | | | | | | | | |
| var. *contorta* | 28 | Spring | 30 | 3 | None | — | 48 | 1+0 |
| var. *latifolia* | 28–35 | Spring | 48 | 3 | Sawdust | 13 | 60 | 2+0 |
| var. *murrayana* | 30–60 | Spring | 25–60 | 10 | Peat mossll | 6–13 | 70–75 | 1+0, 2+0 |
| *P. coulteri* | 60 | Spring | 25 | 13 | None | — | 80 | 1+0 |
| *P. densiflora* | 0 | Spring | 50 | 3–6 | Sand | — | — | 2+0, 3+0, 1+1 |
| *P. echinata* | 15–60 | Spring | 40 | Press | Pine straw | — | 60 | 1+0 |
| *P. edulis* | 60 | Spring | 30 | 6 | Sawdust | 13 | 80 | 2+0 |
| *P. elliottii* | | | | | | | | |
| var. *densa* | 0 | Spring | 35 | Press | Pine straw | 13 | 80 | 1+0 |
| var. *elliotti* | 0 | Spring | 30–35 | Press | Sawdust or pine straw | — | 58–74 | 1+0 |
| *P. jeffreyi* | 28–60 | Spring | 25–30 | 6–10 | None | — | 58–80 | 1+0, 2+0, 1+1 |
| *P. kesiya* | 0 | Spring | 30 | 10 | None | — | 50 | 1+0 |
| *P. lambertiana* | 90 | Spring | 30–35 | 10–13 | None | — | 21–80 | 1+0, 2+0, 1+1 |
| *P. monophylla* | 90 | Spring | 25–30 | 13 | Sawdust | 6–13 | 33 | 2+0 |
| *P. monticola* | 42–90 | Spring | 35–120 | 6–10 | Sawdust ll | 6–13 | 32–90 | 2+0, 3+0 |
| *P. mugo* | 40–50 | Spring | 50 | 10 | Peat moss | 6–13 | 55 | 3+0 |
| *P. muricata* | 28–40 | Spring | 30–75 | 3–19 | Peat moss ll | 6–13 | 37–60 | 1+0 |
| *P. nigra* | 0 | Fall | 50–60 | 13–19 | Peat moss | 6–13 | 60–65 | 2+0, 2+1, 2+2 |
|  | 35–45 | Spring | — | — | — | — | — | — |
| *P. palustris* | 0 | Spring | 15 | Press | Pine straw | — | 75 | 1+0 |
| *P. pinaster* | 0 | Spring | 30 | 6–13 | — | — | — | 1+0 |
| *P. ponderosa* | | | | | | | | |
| var. *ponderosa* | 28–60 | Spring | 25–46 | 6–10 | None | — | 48–80 | 1+0, 2+0, 3+0, 1+1, 1+2 |
| var. *scopulorum* | 20–30 | Spring | 35–40 | 3–6 | None | — | 70 | 1+0, 2+0 |
|  | 0 | Fall or spring | 50–65 | 13 | None | — | 70 | 1+2, 2+1, 2+2 |
| *P. pungens* | 0 | Fall or spring | 20–33 | 6–13 | Straw | — | 19–28 | 1+0, 2+0 |
| *P. radiata* | 35–45 | Spring | 25–75 | 3–19 | Peat moss ll | 6–13 | 34–70 | 1+0 |
| *P. resinosa* | 0 | Fall or spring | 30–50 | 6–10 | None | — | 65–80 | 2+0, 3+0, 2+1, 2+2 |
| *P. rigida* | 0 | Spring | 30–35 | Press | Sand | 3 | — | 2+0 |
| *P. roxburghii* | 0 | Spring | — | 3–13 | — | — | 30–35 | 1+1, 2+1 |
| *P. strobus* | 0 | Fall | 20–50 | 16, or | Sawdust, or | 3–6 | 55–85 | 2+0, 3+0, 2+1, 2+2 |
|  | 30 | Spring | — | Press | wood fiber | — | — |  |
| *P. sylvestris* | 0 | Fall | 30–60 | 3–13 | Peat moss ll | 6–13 | 25–70 | 1+0, 2+0, 2+1, 2+2 |
|  | 2–60 | Spring | — | — | — | — | — |  |
| *P. taeda* | 30–60 | Spring | 40 | Press | Pine straw | — | 60 | 1+0 |
| *P. thunbergiana* | 0 | Fall or spring | 50–100 | 3 | Burlap or straw in winter | — | 31 | 2+0, 1+1 |
| *P. virginiana* | 0 | Fall | 30–35 | 6 or | Sand, pine | 6–13 | 63–90 | 1+0, 2+0 |
|  | 14 | Spring |  | press | Needles or sawdust | — | — | — |
| *P. wallichiana* | 0 | Fall | cast | 13 | None | — | 46 | 1+1, 1+1+1 |
|  | 15–20 | Spring | — | — | — | — | — | — |
| *P. washoensis* | 60 | Spring | 25–30 | 6–10 | None | — | 50–80 | 1+0, 2+0 |

**Sources:** Claveria (1953), Derr (1955), Goor (1955), Heit (1968a), Krugman and Jenkinson (1974), Letourneux (1957), Magini and Tulstrup (1955), NBV (1946), Schubert and Adams (1971), Shoulders (1961), Stoeckeler and Jones (1957), Stoeckeler and Rudolf (1956), Stoeckeler and Slabaugh (1965), Troup (1921), Veracion (1964, 1966).

* Seeds were chilled in a moist medium at 0.5 to 5 °C.
† Multiply number per square foot by 10.758 to convert to number per square meter.
‡ The word "press" indicates that seeds were pressed flush to the soil surface.
§ Type of planting stock codes the number of growing seasons and transplant operations for seedlings in the nursery: 1+0 stock is lifted and shipped to the field for outplanting after 1 nursery growing season, and 2+0 stock, after 2 seasons; 1+1 stock is transplanted after its first growing season and shipped to the field after its second season.
ll Mulch was not always used.

losses to birds and rodents, and they must be delayed until the soils are cold enough to prevent germination in fall and avoid winter freeze damage and mortality of germinants.

Seeds can be drill-sown or broadcast by hand or machine, but mechanized nurseries drill-sow in prepared seedbeds because it is most efficient and economical (Thompson 1984). Quantity of seeds sown per unit area of nursery bed varies with species, seed size, expected germination and emergence percentages, and the target seedling density, that is, stems per unit bed area. Sowing density controls seedling density, which markedly affects both the size and vigor of seedlings and transplants. Target density depends on species and stock type, on when seedlings are to be lifted and on whether they are to be transplanted.

Seeds are sown at rates that are selected to produce from 160 to 800 seedlings/m$^2$ (15 to 75/ft$^2$). Higher seedling survivals are obtained when medium and lower densities are used. Most nurseries sow seeds at slightly higher densities if the seedlings are to be grown in transplant beds for 1 or 2 additional years, and higher sowing densities are used for 1+0 than for 2+0 seedlings. Sowing densities range from 61 to 610 g of seeds/10 m$^2$ (2 to 20 oz/100 ft$^2$) of bed, depending on species, nursery, and seedlot. To produce 2+0 planting stock of western white pine, for example (Krugman and Jenkinson 1974), one western nursery drill-sows 115 seeds/m (35/ft) in rows spaced 9 cm (3 $^1/_4$ in) apart to get 1,290 seedlings/m$^2$ (120/ft$^2$), whereas another drill-sows 60 seeds/m (18/ft) in rows spaced 15 cm (6 in) apart to get 375 seedlings/m$^2$ (35/ft$^2$). Experience is the ultimate guide to sowing density for a given species and seed source in a particular nursery situation. Seed germination in the nursery has varied from just 20 to 85% of that obtained in laboratory tests. On average, 55% of the seeds germinated in nursery beds, with a range of 19 to 90%, have yielded acceptable seedlings.

At sowing time, seeds are drilled or pressed firmly into the soil and then uniformly covered with 3 to 19 mm ($^1/_8$ to $^3/_4$ inch) of soil, sand, or other mulch, with depth depending on seed size and the nursery (table 11). Fall-sown seeds are set slightly deeper than spring-sown seeds to protect them against frost heaving and wind erosion. For large-seeded pines such as whitebark and sugar pines and singleleaf piñyon, seeds may be covered to a depth of 13 mm ($^1/_2$ inch). Seeds of small-seeded pines require the least covering. Seeds of the southern pines—such as shortleaf, slash, longleaf, loblolly, and Virginia pines—are pressed into the soil surface and covered with burlap or chopped pine straw. Mulching protects seeds against rain displacement, helps protect against predations by birds, and slows evaporative loss of soil moisture. Seeds of shore, Rocky Mountain lodgepole, Japanese red, and Japanese black pines are typi-cally sown 3 mm ($^1/_8$ in) deep, and seeds of jack, Canary Island, and western white pines as well piñyon, 6 mm ($^1/_4$ in) deep. Sowing seeds deeper than advised is to be avoided, because deep sowing at best delays and often disables seedling emergence.

Germination of most pines is completed 10 to 50 days after spring-sowing. Pretreated dormant seeds of certain lots of whitebark, Swiss stone, Balkan, and southwestern white pines, however, have taken from several months to a year to germinate after sowing (Krugman and Jenkinson 1974).

Fungicides are often needed during and after seedling emergence to limit damping-off in most nurseries, and both insecticide and fungicide sprays are needed during the growing season to control insects and foliar diseases. Repeated nursery applications of fungicides are needed to control fusiform rust (*Cronartium quercuum* (Bark.) Miy. ex Shirai f. sp. *fusiforme* Bards. et Snow) on slash and loblolly pines and brown spot (*Scirrhia acicola* (Dearn.) Sigg.) on longleaf pines in southern United States, and to control sweetfern blister rust (*Cronartium comptoniae* Arth.) on jack, ponderosa, and Scots pines in the Great Lakes region (Krugman and Jenkinson 1974).

Transplants and older planting stock types are generally recommended for more difficult planting sites (table 11). In the Great Lakes regions and the prairie-plains, stock types used for jack pine are 1+0 or 1+$^1/_2$ for usual sites; 1+1 or 2+0 for tough sites; and 1+2, 2+1, or 2+2 for windbreaks. Stock types used for most white pines are 2+0 and 3+0, or 2+1 and 2+2 transplants.

Pines are also routinely grown in specialized container nurseries. In general, seeds are sown or new germinants are transplanted in containers filled with a standard rooting medium or soil mix, partial shade is provided during seed germination and seedling establishment phases, and seedlings are cultured for 1 growing season before planting. Care must be taken not to grow pines in too small containers for prolonged times, as they become rootbound and grow poorly after planting. Container-grown longleaf pine has performed exceptionally well in the South (Brissette and others 1991), and this species is now widely regenerated with container stock. A vast literature details every aspect of container stock production which is fully captured in the 6 current volumes in the Container Tree Nursery Manual (Agric. Handbk. 674) (Landis and others 1989, 1990a&b, 1992, 1994, 1999). An updated directory of forest tree nurseries in the United States indicates their ownership (private, industry, state, federal, and other), location by state, stock offered (bareroot, container, rooted cuttings), and amount shipped in fall 1992–spring 1993 (Okholm and Abriel 1994).

All pines can be vegetatively propagated by rooting or grafting (Krugman and Jenkinson 1974; O'Rourke 1961; Ticknor 1969). Rooting success for most pines, however, decreases rapidly when scions are taken from trees older than 5 years. A few, such as Monterey, knobcone, Japanese red, and Japanese black pines, are relatively easy to root, but only Monterey pine is widely propagated by rooting cuttings under nursery and greenhouse conditions (Thulin and Faulds 1968). Considerable progress has been made in the last 20 years, but for many species, production costs for vegetative propagules still cannot compete with seedling production (Greenwood and others 1991). Selected trees of many pines are cloned by rooting cuttings. Grafting is routinely used to propagate rare materials and to clone selected superior forest trees, particularly in orchards designed to supply genetically improved seeds for intensive forest management programs (Krugman and Jenkinson 1974).

## References

Allen R, Wardrop AB. 1964. The opening and shedding mechanism of the female cones of *Pinus radiata*. Australian Journal of Botany 12: 125–134.

Altman PL, Dittmer DS. 1962. Biological handbook of growth. Washington, DC: Federation American Society Experimental Biology. 608 p.

Andreev VN. 1925. *Pinus peuce* Griseb. [in Russian]. In: Dendrology. Volume 1, Gymnosperms. Kiev: Ukraine State Printing Office: 96

Andresen JW. 1963. Germination characteristics of *Pinus rigida* seed borne in serotinous cones. Broteria 32(3/4): 151–178.

Andresen JW. 1965. Stratification of seed of *Pinus strobiformis*. Tree Planters' Notes 72: 5–7.

Asakawa S. 1957. Studies on hastening germination of the seeds of five-leaved pines [in Japanese]. Government Forest Experiment Station, Meguro (Tokyo) Bulletin 100: 41–54.

AOSA [Association of Official Seed Analysts]. 1965. Rules for testing seeds. Proceedings Association of Official Seed Analysts 54(2): 12–112.

AOSA [Association of Official Seed Analysts]. 1996. Rules for testing seeds. Journal of Seed Technology 16(3): 1–113.

Bailey DK. 1970. Phytogeography and taxonomy of *Pinus* subsection Balfourianae. Annals Missouri Botanical Garden 57: 210–249.

Bailey LH. 1939. The standard cyclopedia of horticulture. New York: Macmillan. 3 vol., 3639 p.

Baker JB, Langdon OG. 1990. *Pinus taeda* L., loblolly pine. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 497–512.

Barnett JP. 1969. Long-term storage of longleaf pine seeds. Tree Planters' Notes 20(2): 22–25.

Barnett JP. 1970. Flotation in ethanol affects storability of spruce pine seeds. Tree Planters' Notes 21(4): 18–19.

Barnett JP. 1976. Cone and seed maturation of southern pines. Res. Pap. SO-122. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 11 p.

Barnett JP. 1979. An easy way to measure cone specific gravity. In: Karrfalt RP, comp. Proceedings, Seed Collection Workshop; 1979 May 16–18; Macon, GA. SA-TP-8. Atlanta: USDA Forest Service, State and Private Forestry: 21–23.

Barnett JP, McLemore BF. 1967a. Improving storage of spruce pine seed. Tree Planters' Notes 18(2): 16.

Barnett JP, McLemore BF. 1967b. Study of spruce pine cone maturity and seed yield. Tree Planters' Notes 18(2): 18.

Barnett JP, Vozzo JA. 1985. Viability and vigor of slash and shortleaf pine seeds after 50 years of storage. Forest Science 31: 316–320.

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

Bates CG. 1930. The production, extraction, and germination of lodgepole pine seed. Tech. Bull. 191. Washington, DC: USDA. 92 p.

Belcher EW Jr. 1984. Seed handling. In: Southern pine nursery handbook. Atlanta: USDA Forest Service, Region 8: 5.1–5.29.

Belcher EW Jr, Loman BJ. 1982. Energy considerations in cone drying. Tree Planters' Notes 33(4): 31–34.

Bevege DI. 1965. An investigation of cone and seed maturity of slash pine in southern Queensland. Australian Forests 29(3): 135–148.

Bonner FT. 1986. Cone storage and seed quality in eastern white pine (*Pinus strobus* L.). Tree Planters' Notes 37(4): 3–6.

Bonner FT. 1990. Storage of seeds: potential and limitations for germplasm conservation. Forest Ecology and Management 35: 35–43.

Bonner FT. 1991. Seed management. In: Duryea ML, Dougherty PM, eds. Forest regeneration manual. Dordrecht, The Netherlands: Kluwer Academic Publishers: 51-53.

Bonner FT. 1997. Personal communication. Starkville, MS: USDA Forest Service, Southern Research Station.

Bonner FT, Vozzo JA. 1986a. Seed quality of loblolly pine in the net collection system [unpublished report, FS-SO-1108-1.4]. Starkville, MS: USDA Forest Service, Southern Forest Experiment Station.

Bonner FT, Vozzo JA. 1986b. Evaluation of tree seeds by electrical conductivity of their leachate. Journal of Seed Technology 10: 142–150.

Bonner FT, Vozzo JA, Elam WW, Land SB Jr. 1994. Tree seed technology training course. Instructor's manual. Gen. Tech. Rep. SO–106. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 40 p.

Boskok TE. 1970. Seed maturation period in *Pinus brutia, Picea orientalis* and *Abies bornmuelleriana* [in Turkish]. Orman Arastirma Enstitusa Tek. Bulteria 42: 11–64.

Boyer WD. 1990. *Pinus palustris* Mill., longleaf pine. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 405–412.

Bramlett DL. 1990. *Pinus serotina* Michx., pond pine. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 470–475.

Brendemuehl RH. 1990. *Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sarg., sand pine. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 294–301.

Brissette JC, Barnett JP, Landis TD. 1991. Container seedlings. In: Duryea ML, Dougherty PM, eds. Forest regeneration manual. Dordrecht, The Netherlands: Kluwer Academic Publishers: 117–141.

Britton NL, Shafer JA. 1908. North American trees. New York: Henry Holt. 849 p.

Brown AG, Donan JC. 1985. Variation in growth and branching characteristics of *Pinus attenuata*. Silvae Genetica 34(2/3): 100–104.

Brown JH. 1969. Variation in roots of greenhouse grown seedlings of different Scotch pine provenances. Silvae Genetica 4(4): 111–117.

Burdon RD, Low CB. 1991. Performance of *Pinus ponderosa* and *Pinus jeffreyi* provenances in New Zealand. Canadian Journal of Forest Research 21: 1401–1414.

Burns RM. 1975. Sand pine: fifth-year survival and height on prepared and unprepared sandhill sites. Res. Note SE–217. Asheville, NC: USDA Forest Service, Southeastern Forest Experiment Station. 5 p.

Burns RM, Honkala BH, tech. coords. 1990. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service. 675 p.

Callaham RZ. 1962. Geographic variability in growth of forest trees. In: Kozlowski TT, ed. Tree growth. New York: Ronald Press: 311–325.

Callaham RZ. 1963. Provenance research: investigation of genetic diversity associated with geography. Unasylva 18(2/3): 73–74.

Callaham RZ, Liddicoet AR. 1961. Altitudinal variation at 20 years in ponderosa and Jeffrey pines. Journal of Forestry 59(11): 814–820.

Callaham RZ, Metcalf W. 1959. Altitudinal races of *Pinus ponderosa* confirmed. Journal of Forestry 57: 500–502.

Carlisle H, Brown AHF. 1968. Biological flora of the British Isles: *Pinus sylvestris* L. Journal of Ecology 56(1): 269–307.

Carter KK, Snow AG Jr. 1990. *Pinus virginiana* Mill., Virginia pine. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 513–519.

Cerepnin VL. 1964. The importance of *Pinus sylvestris* seed origin, weight, and colour in selection [in Russian]. Sel. Drev. Porod v Vost. Sibiri. p.: 58–68.

Chapman HH. 1922. A new hybrid pine (*Pinus palustris* × *Pinus taeda*). Journal of Forestry 20: 729–734.

Church TW Jr, Sucoff EI. 1960. Virginia pine seed viable two months before natural cone opening. Res. Note 102. Radnor, PA: USDA Forest Service, Northeastern Forest Experiment Station. 4 p.

Claveria JR. 1953. Growing Benguet pine (*Pinus insularis*) in Cebu Province. Philippine Journal of Forestry 9: 57–76.

Cleary BD, Greaves RD, Hermann RK, comp. 1978. Regenerating Oregon's forests. Corvallis: Oregon State University Extension Service. 287 p.

Cocozza MA. 1961. Osservazioni sul circlo riproduttivo di *Pinus heldreichii* Christ. var. *leucodermis* Ant. del monte pollino [in Italian]. Accademia Italiana di Scienze Forestalia 10: 97–110.

Conkle MT. 1973. Growth data for 29 years from the California elevational transect study of ponderosa pine. Forest Science 19(1): 31–39.

Conkle MT, Critchfield WB. 1988. Genetic variation and hybridization of ponderosa pine. In: Ponderosa pine: the species and its management. Pullman: Washington State University Cooperative Extension: 27–43.

Cooling ENG. 1968. Fast growing timber trees of the lowland tropics. Volume 4, *Pinus merkusii*. Oxford, UK: Commonwealth Forestry Institute, Department of Forestry. 169 p.

Cooling ENG, Gaussen H. 1970. In Indo China: *Pinus merkusiana* sp. nov. et non *P. merkusii* Jungh. et de Vriese. Travaux du Laboratoirer Forestier de Toulouse Tome 18(7): 1–8.

Cram WH, Brack CGE. 1953. Performance of Scotch pine races under prairie conditions. Forestry Chronicles 29(4): 334–342.

Critchfield WB. 1957. Geographic variation in *Pinus contorta*. Pub. 3. [Cambridge, MA]: Harvard University, Maria Moors Cabot Foundation. 118 p.

Critchfield WB. 1963. Hybridization of the southern pines in California. Pub. 22. Macon, GA: Southern Forest Tree Improvement Committee: 40–48.

Critchfield WB. 1966a. Crossability and relationships of the California big-cone pines. Res. Pap. NC-6. St. Paul: USDA Forest Service, North Central Forest Experiment Station; 36–44.

Critchfield WB. 1966b. Phenological notes on Latin American *Pinus* and *Abies*. Journal of the Arnold Arboretum 47(4): 313–318.

Critchfield WB. 1977. Hybridization of foxtail and bristlecone pines. Madroño 24(4): 193–211.

Critchfield WB. 1980. Genetics of lodgepole pine. Res. Pap. WO-37. Washington, DC: USDA Forest Service. 57 p.

Critchfield WB. 1984. Crossability and relationships of Washoe pine. Madroño 31(3): 144–170.

Critchfield WB, Allenbaugh GL. 1965. Washoe pine on the Bald Mountain Range, California. Madroño 18(2): 63–64.

Critchfield WB, Krugman SL. 1967. Crossing the western pines at Placerville, California. University of Washington Arboretum Bulletin 30(4): 78–81, 92.

Critchfield WB, Little EL Jr. 1966. Geographic distribution of the pines of the world. Misc. Pub. 991. Washington, DC: UDSDA Forest Service. 97 p.

Curtis JD. 1955. Effects of origin and storage method on the germinative capacity of ponderosa pine seed. Res. Note 26. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 5 p.

Dallimore W, Jackson AB. 1967. A handbook of Coniferae and Gingkoaceae. 4th ed. Harrison SG, rev. New York: St. Martin's Press. 729 p.

Day RJ. 1967. Whitebark pine in the Rocky Mountains of Alberta. Forestry Chronicles 43(3): 278–282.

Debazac EF. 1964. Manuel des conifères [in French]. Nancy: Ecole Naturel Èaux Forêts. 172 p.

Delevoy G. 1935. Note preliminaire sur l'influence de l'origine des graines chez le pin maritime [in French]. Bulletin de la Societe Centre Forestier Belge 42(3): 97–105.

Della-Bianca L. 1990. *Pinus pungens* Lamb., Table Mountain pine. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 425–432.

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

Dent TV. 1947. Seed storage with particular reference to the storage of seed of Indian forest plants. Indian Forest Record (N.S.) Silviculture 7(1): 1–134.

Derr HJ. 1955. Seedbed density affects longleaf pine survival and growth. Tree Planters' Notes 20: 28–29.

Dimitroff I. 1926. Study of the seed material of *Pinus peuce* [in Bulgarian]. Annales de l'Universite de Sofia Faculte Agricultra 4: 259-306.

Dogra PD. 1987. Forestry, environmental and tree breeding potential of Himalayan conifers. In: Pangtey YPS, Joshi SC, eds. Western Himalaya Nainital, India. Gyanodaya Prakashan 1/2: 99–120.

Dorman KW. 1976. The genetics and breeding of southern pines. Agric. Handbk. 471. Washington, DC: USDA Forest Service. 407 p.

Dorman KW, Barber JC. 1956. Time of flowering and seed ripening in southern pines. Pap. 72. Asheville, NC: USDA Forest Service, Southeastern Forest Experiment Station. 15 p.

Dorman KW, Zobel, BJ. 1973. Genetics of loblolly pine. Res. Pap. WO–19. Washington, DC: USDA Forest Service. 21 p.

Duff CE. 1928. The varieties and geographical forms of *Pinus pinaster* Soland., in Europe and South Africa, with notes on the silviculture of the species. South Africa Department of Forestry Bulletin 22-a: 1–55.

Duffield JW. 1951. Interrelationships of the California closed-cone pines with reference to *Pinus muricata* D. Don. [PhD thesis]. Berkeley: University of California. 114 p.

Duffield JW. 1953. Pine pollen collections dates: annual and geographic variation. Res. Note 85. Berkeley, CA: USDA Forest Service, California Forest and Range Experiment Station. 9 p.

Duryea ML, Landis TD, eds. 1984. Forest nursery manual: production of bareroot seedlings. The Hague: Martinus Nihoff/Dr. W. Junk Publishers. 386 p.

Echols RM, Conkle MT. 1971. The influence of plantation and seed-source elevation on wood specific gravity of 20-year-old ponderosa pines. Forest Science 17(3): 388–394.

Edwards JL. 1986. Mechanical tree shakers [unpublished paper presented at Mississippi State University/Forest Service Forest Tree Seed Shortcourse; 1986 August 12–14; Starkville, MS].

Edwards MU. 1954–55. A summary of information on *Pinus contorta*. Forestry Abstracts 15: 389–396 and 16: 3–13.

Eldridge RH, Dowden H. 1980. Susceptibility of five provenances of ponderosa pine to *Dothistroma* needle blight. Plant Disease 64(4): 400–401.

Eliason EJ. 1942. Data from cone collections of various species in New York. Notes For. Invest. 39. Albany: New York Conservation Department. 1 p.

Eliason EJ, Hill J. 1954. Specific gravity as a test for cone ripeness with red pine. Tree Planters' Notes 17: 1–4.

Falusi M, Calamassi R, Tocci A. 1983. Sensitivity of seed germination and seedling root growth to moisture stress in four provenances of *Pinus halepensis* Mill. Silvae Genetica 32(1/2): 4–9.

Fenton RH, Sucoff EI. 1965. Effects of storage treatments on the ripening and viability of Virginia pine seed. Res. Note NE–31. Radnor, PA: USDA Forest Service, Northeastern Forest Experiment Station. 6 p.

Fielding JM. 1961. Provenances of Monterey and Bishop pines. Commonwealth Forestry Bureau Bulletin 38: 1–30.

FAO [Food and Agriculture Organization]. 1993. *Ex situ* storage of seeds, pollen and *in vitro* culture of perennial woody plant species. For. Pap. 113. Rome: FAO. 84 p.

Forde MB. 1964. Variation in natural population of *Pinus radiata* in California: Part 3, cone characters and Part 4, discussion. New Zealand Journal of Botany 2(4): 459–485.

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

Fowler DP, Dwight TW. 1964. Provenance differences in the stratification requirements of white pine. Canadian Journal of Botany 42: 669–673.

Fowler DP, Heimburger C. 1969. Geographic variation in eastern white pine 7-year results in Ontario. Silvae Genetica 18(4): 123–129.

Fowler DP, Lester DT. 1970. Genetics of red pine. Res. Pap. WO-8. Washington, DC: USDA Forest Service. 13 p.

Frampton LJ, Rockwood DL. 1983. Genetic variation in traits important for energy utilization of sand and slash pines. Silvae Genetica 32(1/2): 18–23.

Fritts HC. 1969. Bristlecone pine in the White Mountains of California: growth and ring-width characteristics. Tree-Ring Pap. 4. Tucson: University of Arizona Press. 44 p.

Furnier GR, Adams WT. 1986. Geographic patterns of allozyme variation in Jeffrey pine. American Journal of Botany 73(7): 1009–1015.

Gansel CR, Squillace AE. 1976. Geographic variation of monoterpene in cortical oleoresin of slash pine. Silvae Genetica 25(5/6): 150–154.

Gardner JL, Berenson RJ. 1987. Reader's Digest atlas of the world. Pleasantville, NY: Reader's Digest Association. 240 p.

Genys JB. 1966. Geographic variation in Virginia pine. Silvae Genetica 15: 72–75.

Genys JB. 1976. Growth rates of eighty Scotch pine populations at fourteen year results in Maryland. In: Proceedings, 23rd Northeastern Forest Tree Improvement Conference. Upper Darby, PA: USDA Forest Service, Northeastern Forest Experiment Station; 108–120.

Genys JB, Wright JW, Forbes DC. 1974. Intraspecific variation in Virginia pine: results of a provenance trial in Maryland, Michigan, and Tennessee. Silvae Genetica 23: 99–104.

Giertych M. 1976. Racial variation: genetics of Scots pine (*Pinus sylvestris* L.). Annales des Sciences Forestieres 7(3): 59–105.

Gifford EM, Mirov NT. 1960. Initiation and ontogeny of the ovulate strobilus in ponderosa pine. Forest Science 6(1): 19–25.

Giordano E. 1960. Osservazion: su alcuna provenienze italiane di *Pinus halepensis* [in Italian]. Centro di Sperimentale Agrie. Forest. 5: 13–43.

Goor AY. 1955. Tree planting practices for arid areas. For. Dev. Pap. 6. Rome: FAO. 126 p.

Goor AY, Barney CW. 1968. Forest tree planting in arid zones. New York: Ronald Press. 409 p.

Graber RE. 1965. Germination of eastern white pine seed as influenced by stratification. Res. Pap. NE-36. Radnor, PA: USDA Forest Service, Northeastern Forest Experiment Station. 9 p.

Graham RT. 1990. *Pinus monticola* Dougl. ex D. Don., western white pine. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 385–394.

Greenwood MS, Foster GS, Amerson HV. 1991. Vegetative propagation of southern pines. In: Duryea ML, Dougherty PM, eds. Forest regeneration manual. Dordrecht, The Netherlands: Kluwer Academic Publishers: 75–86.

Griffin JR. 1962. Intraspecific variation in *Pinus sabiniana* Dougl. [PhD thesis]. Berkeley: University of California. 274 p.

Griffin JR. 1964. Cone morphology in *Pinus sabiniana*. Journal of the Arnold Arboretum 45(2): 260–273.

Griffin JR. 1965. Digger pine seedling response to serpentinite and non-serpentinite soil. Ecology 46(6): 801–807.

Griffin JR. 1971. Variability of germination in Digger pine in California. Res. Note PSW-248. Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. 5 p.

Griffin JR, Conkle MT. 1967. Early performance of knobcone and Monterey pine hybrids on marginal timber sites. Res. Note PSW-156. Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. 10 p.

Griffin JR, Critchfield WB. 1976. The distribution of forest trees in California. Res. Pap. PSW–82 (reprinted with supplement). Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. 118 p.

Haasis FW, Thrupp AC. 1931. Temperature relations of lodgepole pine seed germination. Ecology 12: 728–744.

Haller JR. 1957. Taxonomy, hybridization and evolution in *Pinus ponderosa* and *Pinus jeffreyi* [PhD thesis]. Los Angeles: University of California. 169 p.

Haller JR. 1967. A comparison of the mainland and island populations of Torrey pine. In: Philbrick RN, ed. Symposium proceedings, Biology of the California Islands. Santa Barbara, CA: Santa Barbara Botanic Garden.

Harlow WM, Harrar ES. 1950. Textbook of dendrology. 3rd ed. New York: McGraw-Hill. 555 p.

Harrar ES, Harrar JG. 1946. Guide to southern trees. New York: Whittlesey House, McGraw-Hill. 712 p.

Harris RW, Leiser AT, Chan FJ. 1970. Vegetation management on reservoir recreation sites [annual report]. Rep. Davis: University of California, Department of Environmental Horticulture. 17 p.

Harry DE, Jenkinson JL, Kinloch BB. 1983. Early growth of sugar pine from an elevational transect. Forest Science 29: 660–669.

Hartmann HT, Hester DE. 1968. Plant propagation: principles and practices. 2nd ed. Englewood Cliffs, NJ: Prentice-Hall. 702 p.

Heit CE. 1958. The effect of light and temperature on germination of certain hard pines and suggested methods for laboratory testing. Proceedings of the Association of Official Seed Analysts 48: 111–117.

Heit CE. 1963. Balkan pine: promising new exotic conifer. American Nurseryman 118(12): 10–11, 32, 34, 36.

Heit CE. 1964. Tips on growing healthy, vigorous conifer seedlings and transplants. New York Christmas Tree Growers Bulletin 2(1). 5 p.

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

Heit CE. 1967b. Propagation from seed: 10. Storage method for conifer seeds. American Nurseryman 126(8): 14–54 (not inclusive).

Heit CE. 1968a. Propagation from seed: 12. Growing choice, less common pines. American Nurseryman 127(2): 14–15, 112–120.

Heit CE. 1968b. Thirty-five year's testing of tree and shrub seeds. Journal of Forestry 66(8): 632–634.

Heit CE. 1969. Propagation from seed: 19. Testing and growing Scotch pine seeds from different sources. American Nurseryman 129(7): 10–15, 110–118.

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

Hoff RJ. 1988. Susceptibility of ponderosa pine to the needle cast fungus *Lophodermium baculiferum*. Res. Pap. INT-386. Ogden, UT: USDA Forest Service, Intermountain Research Station. 6 p.

Holst M. 1962. Seed selection and tree breeding in Canada. Tech. Note 115. Petawawa, ON: Canadian Department of Forestry, Forest Research Branch. 20 p.

Holzer K. 1975. Genetics of *Pinus cembra* L. Annales Forestiere 6/5:139–158.

Hopkins ER. 1960. Germination stimulation in *Pinus pinaster*. Bull. 66. Perth: Western Australia Forestry Department. 10 p.

Hyun SH. 1962. Improvement of pines through hybridization. 13th IUFRO Proceedings, Volume 1(2): 1–2.

ICIA [International Crop Improvement Association]. 1963. Minimum seed certification standards. International Crop Improvement Association 20: 1–128.

ISTA [International Seed Testing Association]. 1966. International rules for seed testing. Proceedings of the International Seed Testing Association 1966: 1–152.

Iroshnikov AI. 1963. Fruit bearing of stone pine forests in the northwestern part of the eastern Sayan. In: Shimanyuk AP, ed. Fruiting of the Siberian stone pine in east Siberia. Akad. Nauk SSSR Sibirskoe Otdel 62: 98–109 [English translation TT65-50123, Springfield, VA: USDC CFSTI].

Iroshnikov AI, Lebkov VF, Cherednikova YuS. 1963. Fruit bearing of stone pine forests of the Lena-Ilim interfluvial area. In: Shimanyuk AP, ed. Fruiting of the Siberian stone pine in east Siberia. Akad. Nauk SSSR Sibirskoe Otdel 62: 35–79 [English translation TT65-50123, Springfield, VA: USDC CFSTI].

Isik K. 1986. Altitudinal variation in *Pinus brutia* Ten.: seed and seedling characteristics. Silvae Genetica 35(2/3): 58–67.

Jacaline DV, Lizardo L. 1958. Silvical characteristics of Benguet pine (*Pinus insularis* Endl.). Silv. Leaflet 2. Manila: Philippines Bureau of Forestry 32 p.

Jenkinson JL. 1974. Ponderosa pine progenies: differential response to ultramafic and granitic soils. Res. Pap. PSW-101. Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. 14 p.

Jenkinson JL. 1976. Seasonal patterns of root growth capacity in western yellow pines. In: America's renewable resource potential—1975: the turning point. Proceedings, Society of American Foresters National Convention. Washington, DC: Society of American Foresters: 445–453.

Jenkinson JL. 1977. Edaphic interactions in first-year growth of California ponderosa pine. Res. Pap. PSW-127. Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. 16 p.

Jenkinson JL. 1980. Improving plantation establishment by optimizing growth capacity and planting time of western yellow pines. Res. Pap. PSW-154. Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. 22 p.

Jenkinson JL. 1990. *Pinus jeffreyi* Grev. & Balf., Jeffrey pine. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 359–369.

Jenkinson JL. 1996. Genotype–environment interaction in common garden tests of sugar pine. In: Kinloch BB Jr, Marosy M, Huddleston ME, eds. Sugar pine: status, values, and roles in ecosystems. Pub. 3362. Davis: University of California, Division of Agriculture and Natural Resources: 5474.

Jenkinson JL, McCain AH. 1993. Winter sowings produce 1–0 sugar pine planting stock in the Sierra Nevada. Res. Pap. PSW-219. Albany, CA: USDA Forest Service, Pacific Southwest Research Station. 10 p.

Jenkinson JL, McCain AH. 1996. Improving nursery management of sugar pine in the Sierra Nevada. In: Kinloch BB Jr, Marosy M, Huddleston ME, eds. Sugar pine: status, values, and roles in ecosystems. Pub. 3362. Davis: University of California, Division of Agriculture and Natural Resources: 152–161.

Jenkinson JL, Nelson JA, Huddleston ME. 1993. Improving planting stock quality: the Humboldt experience. Gen. Tech. Rep. PSW-143. Albany, CA: USDA Forest Service, Pacific Southwest Research Station. 219 p.

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

Jones L. 1966. Storing pine seed: what are best moisture and temperature conditions? Res. Pap. 42. Macon, GA: Georgia Forest Research Council. 8 p.

Kamra SH. 1967. Studies on storage of mechanically damaged seed of Scots pine (*Pinus sylvestris* L.). Studia Forestalia Suecica 42: 1–19.

Kamra SH. 1969. Investigations on the suitable germination duration for *Pinus sylvestris* and *Pinus abies* seed. Studia Forestalia Suecica 73: 1–16.

Kamra SH, Simak M. 1968. Germination studies on Scots pine (*Pinus sylvestris* L.) seed of different provenances under alternating and constant temperatures. Studia Forestalia Suecica 62. 14 p.

Karschon R. 1961. Studies in nursery practice for pines. La-Yaaran 11(1): 1–12.

Kellison RC, Zobel BJ. 1974. Genetics of Virginia pine. Res. Pap. WO-21. Washington, DC: USDA Forest Service. 10 p.

King JP. 1971. Pest susceptibility variation in Lake States jack pine seed sources. Res. Pap. NC-53. St Paul: USDA Forest Service, North Central Forest Experiment Station. 10 p.

Kinloch BB Jr. 1992. Distribution and frequency of a gene for resistance to white pine blister rust in natural populations of sugar pine. Canadian Journal of Botany 70: 1319–1323.

Kinloch BB Jr, Marosy M, Huddleston ME, eds. 1996. Sugar pine: status, values, and roles in ecosystems. Pub. 3362. Davis: University of California, Division of Agriculture and Natural Resource. 225 p.

Kinloch BB Jr, Scheuner WH. 1990. *Pinus lambertiana* Dougl., sugar pine. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 370–379.

Kmecza NS. 1970. Using tree shakers for pine cone collections in Region 5. Tree Planters' Notes 21(1): 9–11.

Kraus JF. 1963. The Olustee arboretum. Res. Pap. SE-4. Asheville, NC: USDA Forest Service, Southeastern Forest Experiment Station. 47 p.

Krugman SL. 1966. Artificial ripening of sugar pine seeds. Res. Pap. PSW-32. Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. 7 p.

Krugman SL, Jenkinson JL. 1974. *Pinus* L., pine. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 598–638.

Krüssmann G. 1960. Die Nadelgehölze. 2nd ed. Berlin: Paul Parey. 335 p.

Kuser JE, Ledig FT. 1987. Provenance and progeny variation in pitch pine from the Atlantic Coastal Plain. Forest Science 33(2): 558–564.

**P**

Lamb GN. 1915. A calendar of the leafing, flowering and seeding of the common trees of the eastern United States. US Monthly Weather Review (Suppl.) 2: 3–19.

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 Forest Service. 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 Forest Service. 88 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 Forest Service. 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 Forest Service. 145 p.

Landis TD, Tinus RW, McDonald SE, Barnett JP. 1994. The container tree nursery manual. Volume 1, Nursery planning, development, and management. Agric. Handbk. 674. Washington, DC: USDA Forest Service. 188 p.

Landis TD, Tinus RW, McDonald SE, Barnett JP. 1999. The container tree nursery manual. Volume 6, Seedling propagation. Agric. Handbk. 674. Washington, DC: USDA Forest Service. 167 p.

Lantz CW, Kraus JF. 1987. A guide to southern pine seed sources. Gen. Tech. Rep. SE–43. Asheville, NC: USDA Forest Service, Southeastern Forest Experiment Station. 34 p.

Larson MM. 1966. Racial variation in ponderosa pine at Fort Valley, Arizona. Res. Note RM–73. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 7 p.

Lawson RE. 1990. *Pinus echinata* Mill., shortleaf pine. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 316–326.

LeBarron RH, Roe EI. 1945. Hastening the extraction of jack pine seeds. Journal of Forestry 43: 820–821.

Lebrun C. 1967. Separation of (full and empty) seeds by specific gravity measurement through immersion in liquids [in French]. Revue Forestiere Francaise 19(11): 786–789.

Ledig FT, Conkle MT. 1983. Gene diversity and genetic structure in a narrow endemic, Torrey pine (*Pinus torreyana* Parry ex Carr.). Evolution 37: 79–85.

Ledig FT, Fryer JH. 1974. Genetics of pitch pine. Res. Pap. WO-27. Washington, DC: USDA Forest Service. 14 p.

Leloup M. 1956. Tree planting practices in tropical Africa. For. Dev. Pap. 8. Rome: FAO. 306 p.

Letourneux C. 1957. Tree planting practices in tropical Asia. For. Dev. Pap. 11. Rome: FAO. 172 p.

Lindquist CH. 1962. Maturity of Scots pine seeds: summary report for the Forest Nursery Station. Indian Head, SK: Canadian Department of Agriculture, Research Branch: 20–21.

Little EL Jr. 1938a. The earliest stages of piñyon cones. Res. Note 46. USDA Forest Service, Southwestern Forest and Range Experiment Station. 4 p.

Little EL Jr. 1938b. Stages of growth of piñyons in 1938. Res. Note 50. USDA Forest Service, Southwestern Forest and Range Experiment Station. 4 p.

Little EL Jr. 1940. Suggestions for selection cutting of piñyon trees. Res. Note 90. USDA Forest Service, Southwestern Forest and Range Experiment Station. 3 p.

Little EL Jr. 1941. Managing woodlands for piñyon nuts. Chronicles of Botany 16: 348–349.

Little EL Jr. 1950. Southwestern trees: a guide to the native species of New Mexico and Arizona. Agric. Handbk. 9. Washington, DC: USDA Forest Service. 109 p.

Little EL Jr. 1968. Two new pinyon varieties from Arizona. Phytologia 17(4): 329–342.

Little EL Jr, Dorman KW. 1952a. Geographic differences in cone opening in sand pine. Journal of Forestry 50(3): 204–205.

Little EL Jr, Dorman KW. 1952b. Slash pine (*Pinus elliottii*), its nomenclature and varieties. Journal of Forestry 50: 918–923.

Little EL Jr, Dorman KW. 1954. Slash pine (*Pinus elliottii*) including South Florida slash pine. Pap. 36. Asheville, NC: USDA Forest Service, Southeastern Forest Experiment Station. 82 p.

Little EL Jr, Righter FI. 1965. Botanical descriptions of forty artificial pine hybrids. Tech. Bull. 1345. Washington, DC: USDA Forest Service. 47 p.

Little S. 1941. Calendar of seasonal aspects for New Jersey forest trees. Forest Leaves 31(4): 1–2, 13–14.

Little S. 1959. Silvical characteristics of pitch pine (*Pinus rigida*). Pap. 119. Radnor, PA: USDA Forest Service, Northeastern Forest Experiment Station. 22 p.

Little S. 1969. Local seed sources recommended for loblolly pine in Maryland and shortleaf pine in New Jersey and Pennsylvania. Res. Pap. NE–134. Radnor, PA: USDA Forest Service, Northeastern Forest Experiment Station. 16 p.

Little S, Garrett PW. 1990. *Pinus rigida* Mill. pitch pine. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 456–462.

Lizardo L. 1950. Benguet pine (*Pinus insularis* Endl.) as a reforestation crop. Philippine Journal of Forestry 7(1/4): 43–60.

Lohrey RE, Kossuth SV. 1990. *Pinus elliottii* Engelm., slash pine. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 338–347.

Loiseau J. 1945. Les arbres et la forêt [in French]. Volume 1. Paris: Vigot Freres. 204 p.

Loock EEM. 1950. The pines of Mexico and British Honduras. Bull. 35. Pretoria: Union of South Africa, Department of Forestry. 244 p.

Lotan JE, Critchfield WB. 1990. *Pinus contorta* Dougl. ex Loud., lodgepole pine. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 302–315.

Lowman BJ, Landis TD, Zensen F, Holland BJ. 1992. Bareroot nursery equipment catalog. Proj. Rep. 9224-2839-MTDC. Missoula, MT: USDA Forest Service, Missoula Technology and Development Center. 198 p.

Luckhoff HA. 1964. Natural distribution, growth, and botanical variation of *Pinus caribaea* and its cultivation in South Africa. Annals of the University of Stellinbosch (A) 39(1): 1–160.

Magini E. 1955. Conditions of germination of Aleppo and Italian stone pines [in Italian]. Italia Forestale e Montana 10(3): 106–124.

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

Malac BF. 1960. More on stratification of pine seed in polyethylene bags. Tree Planters' Notes 42: 7–9.

Mastrogiuseppe RJ. 1968. Geographic variation in foxtail pine. Prog. Rep. Placerville, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Institute of Forest Genetics. 15 p.

McDonald PM, Laacke RJ. 1990. *Pinus radiata* D. Don, Monterey pine. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 433–441.

McIntyre AC. 1929. A cone and seed study of the mountain pine (*Pinus pungens* Lambert). American Journal of Botany 16: 402–406.

McLemore BF. 1961a. Hila of full and empty longleaf pine seeds are distinguishable. Forest Science 7: 246.

McLemore BF. 1961b. Storage of longleaf pine seed. Tree Planters' Notes 47: 15–19.

McLemore BF. 1965. Pentane flotation for separating full and empty longleaf pine seeds. Forest Science 11: 242–243.

McLemore BF, Barnett JP. 1967. Effective stratification of spruce pine seed. Tree Planters' Notes 18(2): 17–18.

McLemore BF, Czabator FJ. 1961. Length of stratification and germination of loblolly pine seed. Journal of Forestry 58: 267–269.

Meeuwig RO, Budy JD, Everett RL. 1990. *Pinus monophylla* Torr. & Frem., singleleaf pinyon. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 380–384.

Mergen F. 1963. Ecotypic variation in *Pinus strobus* L. Ecology 44: 716–727.

Mikhalevskaya OB. 1960. The biology of *Pinus pumila* Rgl. in Kamchatka [in Russian]. Nauchnye Doklady Vysshei Shkoly, Biologicheskie Nauki 3: 136–141.

Miller H, Lemmon PE. 1943. Processing cones of ponderosa pine to extract, dewing, and clean seed. Journal of Forestry 41(12): 889–894.

Mirov NT. 1936. A note on germination methods for coniferous species. Journal of Forestry 34(7): 719–723.

Mirov NT. 1946. Viability of pine seed after prolonged cold storage. Journal of Forestry 44(3): 193–195.

Mirov NT. 1956. Photoperiod and flowering of pine. Forest Science 2: 328–332.

Mirov NT. 1962. Phenology of tropical pines. Journal of the Arnold Arboretum 43(2): 218–219.

Mirov NT. 1967. The genus Pinus. New York: Ronald Press. 602 p.

Moran GF, Bell JC, Eldridge KG. 1988. The genetic structure and the conservation of the five natural populations of *Pinus radiata*. Canadian Journal of Forest Research 18: 506–514.

Müller KM. 1932. *Pinus peuce*, the Macedonian white pine as a substitute for *Pinus strobus*. Blister Rust News 16(3) Suppl.: 62–70.

Namkoong G, Conkle MT. 1976. Time trends in genetic control of height growth in ponderosa pine. Forest Science 22(1): 2–12.

Nather H. 1958. Germination of Swiss stone pine seed [in German]. Centralblatt für das Gesamte Forstwesen 75(1): 161–170.

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

Newcomb GB. 1962. Geographic variation in *Pinus attenuata* Lem. [PhD thesis]. Berkeley: University of California. 190 p.

Niebling CR, Conkle MT. 1990. Diversity of Washoe pine and comparisons with allozymes of ponderosa pine races. Canadian Journal of Forest Research 20: 298–308.

Nyman B. 1963. Studies on the germination in seeds of Scots pine. Studia Forestalia Suecica 2: 1–164.

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

Okholm DJ, Abriel RD. 1994. Directory of forest and conservation tree nurseries in the United States. R6-CP-TP-02-94. Portland, OR: USDA Forest Service, Pacific Northwest Region, State and Private Forestry. 99 p.

Old KM, Libby WJ, Russell JH, Eldridge KG. 1986. Genetic variability in susceptibility of *Pinus radiata* to western gall rust. Silvae Genetica 35(4): 145–149.

Oliver WW, Ryker RA. 1990. *Pinus ponderosa* Dougl. ex Laws., ponderosa pine. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 413–424.

O'Rourke FLS. 1961. The propagation of pines. Proceedings of the International Plant Propagator's Society 11: 16–22.

Otter FL. 1933. Idaho's record trees. Idaho Forester 15: 37–39.

Panetsos KP. 1986. Genetics and breeding in the group halepensis. Foret Mediteranienne 7(1): 5–13.

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

Posey CE, McCullough RB. 1969. Tenth year results of a shortleaf pine seed source study in Oklahoma. Oklahoma Agricultural Experiment Station Bulletin B-668: 1–14.

Powers RF. 1990. *Pinus sabiniana* Dougl., Digger pine. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 463–469.

Poynton RJ. 1961. A guide to the characteristics and uses of trees and shrubs quoted in the price list of the Forest Department. Republic of South Africa Bulletin 39: 1–50.

Pravdin LF. 1963. Selection and seed production of the Siberian stone pine. In: Shimanyuk AP, ed. Fruiting of the Siberian stone pine in east Siberia. Akad. Nauk SSSR Sibirskoe Otdel 62: 1-20 [English translation TT65-50123. Springfiled, VA: USDC CFSTI].

Pravdin LF. 1964. Scots pine variation, intraspecific taxonomy and selection. Acad. Nauk SSSR. 208 p. [English translation TT69-55066. Springfield, VA: USDC CFSTI].

Pravdin LF, Iroshnikov AI. 1982. Genetics of *Pinus sibirica* Du Tour, *P. koraiensis* Sieb et Zucc., and *P. pumila* Regel. Annales Forestieres 9/3: 79–123.

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

Read AD. 1932. Notes on Arizona pine and Apache pine. Journal of Forestry 30: 1013–1014.

Read RA. 1971. Scots pine in eastern Nebraska: a provenance study. Res. Pap. RM-78. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 13 p.

Read RA. 1976. Austrian (European black) pine in eastern Nebraska: a provenance test. Res. Pap. RM–180. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 8 p.

Read RA. 1980. Genetic variation in seedling progeny of ponderosa pine provenances. For. Sci. Monogr. 23. Washington, DC: Society of American Foresters. 59 p.

Read RA. 1983. Ten-year performance of ponderosa pine provenances in the Great Plains of North America. Res. Pap. RM–250. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 17 p.

Read RA, Sprackling JA. 1981. Hail damage variation by seed source in a ponderosa pine plantation. Res. Note RM–410. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 6 p.

Rehder A. 1940. Manual of cultivated trees and shrubs hardy in North America. 2nd ed. New York: Macmillan. 996 p.

Rehfeldt GE. 1979. Ecotypic differentiation in populations of *Pinus monticola* in north Idaho: myth or reality? American Naturalist 114: 627–636.

Rehfeldt GE. 1986a. Adaptive variation in *Pinus ponderosa* from Intermountain regions: 1. Snake and Salmon River basins. Forest Science 32(1): 79–92.

Rehfeldt GE. 1986b. Adaptive variation in *Pinus ponderosa* from Intermountain regions: 2. Middle Columbia River system. Res. Pap. INT–373. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 9 p.

Rehfeldt GE, Hoff RJ, Steinhoff RJ. 1984. Geographic patterns of genetic variation in *Pinus monticola*. Botanical Gazette 145: 229–239.

Resch T. 1974. Essai de description morphologique des races majeours de *Pinus pinaster* [in French]. Annales de Recherche Forestiere du Maroc 1–4.

Rohmeder E, Loebel H. 1940. Keimversuche mit Zirbelkiefer [in German]. Forstwissenschaft Centralblatt 62: 25–366.

Ronco FP Jr. 1990. *Pinus edulis* Engelm., pinyon. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 327–337.

Rossi E. 1929. Sulla germinabilita de seme di *Pinus maritima* in rapporto alla temperatura [in Italian]. Istituto Botanica R. Univ. Pavia Atti., Series IV 1: 107–115.

Rudolf PO. 1990. *Pinus resinosa* Ait., red pine. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 442–455.

Rudolph TD, Laidly PR. 1990. *Pinus banksiana* Lamb., jack pine. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 280–293.

Rudolph TD, Schoenike RE, Schantz-Hansen T. 1959. Results of one-parent progeny tests relating to the inheritance of open and closed cones in jack pine. For. Note 78. St. Paul: University of Minnesota. 2 p.

Rudolph TD, Yeatman CW. 1982. Genetics of jack pine. Res. Pap. WO-38. Washington, DC: USDA Forest Service. 60 p.

Sargent CS. 1905. Manual of the trees of North America. New York: Houghton Mifflin. 826 p.

Sargent CS. 1965. Manual of trees of North America (exclusive of Mexico). 2nd ed. New York: Dover. 934 p.

Savory BH. 1962. The taxonomy of *Pinus khasya* (Royle) and *Pinus insularis* (Endlicher). Empire Forestry Review 41(1): 67–80.

Scharpf RF, Kinloch BB, Jenkinson JL. 1992. One seed source of Jeffrey pine shows resistance to dwarf mistletoe. Res. Pap. PSW-207. Berkeley, CA: USDA Forest Service, Pacific Southwest Research Station. 8 p.

Schmitt D, Namkoong G. 1965. Pine species in the Harrison Experimental Forest Arboretum. Res. Pap. SO-18. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 18 p.

Schubert GH. 1952. Germination of various coniferous seeds after cold storage. Res. Note 83. Berkeley, CA: USDA Forest Service, California Forest and Range Experiment Station. 7 p.

Schubert GH. 1955. Effect of ripeness on the viability of sugar, Jeffrey, and ponderosa pine seed. Society of American Foresters Proceedings 55: 67–69.

Schubert GH, Adams RS. 1971. Reforestation practices for conifers in California. Sacramento: California Department of Conservation, Division of Forestry. 359 p.

Schubert GH, Heidmann LJ, Larson MM. 1970. Artificial reforestation practices for the Southwest. Agric. Handbk. 370. Washington, DC: USDA Forest Service. 25 p.

Sen Gupta JN. 1936. Seed weights, plant percents, etc., for forest plants in India. Indian Forest Records Silviculture 2(5): 175–221.

Shafiq Y, Omer H. 1969. The effect of stratification on germination of *Pinus brutia* seed. Mesopotamian Agriculture 4: 96–99.

Shaw GR. 1914. The genus *Pinus*. Pub. 5. Boston: Arnold Arboretum. 96 p.

Sherry SP. 1947. The potentialities of genetic research in South African forestry. Pretoria: Department of Forestry. 11 p.

Shoulders E. 1961. Effect of nurserybed density on loblolly and slash pine seedlings. Journal of Forestry 59: 576–579.

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

Simak M, Ohba K, Suszka B. 1961. Effect of X-irradiation on seeds of different weight from individual trees of Scots pine (*Pinus sylvestris* L.). Botaniska Notiser 114(3): 300–312.

Skilling DD. 1990. *Pinus sylvestris* L., Scotch pine. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 489–496.

Smith RH. 1977. Monoterpenes of ponderosa pine xylem resin in western United States. Tech. Bull. 1532. Washington, DC: USDA Forest Service. 48 p.

Smith RH. 1981. Variation in immature cone color of ponderosa pine (Pinaceae) in northern California and southern Oregon. Madroño 28(4): 272–275.

Smith RH, Greene LE. 1996. Xylem monoterpenes of *Pinus lambertiana*. In: Kinloch BB Jr, Marosy M, Huddleston ME, eds. Sugar pine: status, values, and roles in ecosystems. Pub. 3362. Davis: University of California, Division of Agriculture and Natural Resources: 100–108.

Smouse PE. 1970. Population studies in the genus *Pinus* L. [PhD thesis]. Raleigh: North Carolina State University. 126 p.

Snow AG Jr. 1960. Silvical characteristics of Virginia pine. Stn. Pap. 131. Radnor, PA: USDA Forest Service, Northeastern Forest Experiment Station. 22 p.

Snyder EB, Dinus RJ, Derr HJ. 1977. Genetics of longleaf pine. Res. Pap. WO–33. Washington, DC: USDA Forest Service. 24 p.

Squillace AE. 1966. Geographic variation in slash pine. For. Sci. Monogr. 10. Washington, DC: Society of American Foresters. 56 p.

Squillace AE, Bingham RT. 1958. Localized ecotypic variation in western white pine. Forest Science 4(1): 20–33.

Squillace AE, Silen RR. 1962. Racial variation in ponderosa pine. For. Sci. Monogr. 2. Washington, DC: Society of American Foresters. 27 p.

Steele R. 1990. *Pinus flexilis* James., limber pine. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 348–354.

Steinhoff RJ. 1964.　Taxonomy, nomenclature, and variation within the *Pinus flexilis* complex [PhD thesis]. Ann Arbor: Michigan State University. 81 p.

Steinhoff RJ. 1979.　Variation in early growth of western white pine in north Idaho. Res. Pap. INT–222. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 22 p.

Steinhoff RJ. 1981.　Survival and height growth of coastal and interior western white pine saplings in north Idaho. Res. Note INT-303. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 3 p.

Steinhoff RJ, Andresen JW. 1971.　Geographic variation in *Pinus flexilis* and *Pinus strobiformis* and its bearing on their taxonomic status. Silvae Genetica 20(5/6): 159–167.

Steven HM, Carlisle A. 1959.　The native pinewoods of Scotland. Edinburgh: Oliver and Boyd. 368 p.

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

Stoeckeler JH, Rudolf PO. 1956.　Winter coloration and growth of jack pine in the nursery as affected by seed source. Zeitschrift für Forstgenetika und Forstpflanzenzücht 5: 161–165.

Stoeckeler JH, Slabaugh PE. 1965.　Conifer nursery practice in the prairie-plains. Agric. Handbk. 279. Washington, DC: USDA forest Service. 93 p.

Styles BT, Hughes CE. 1983.　Studies of variation in Central American pines: 3. Notes on the taxonomy and nomenclature of the pines and related gymnosperms in Honduras and adjacent Latin American republics. Brenesia 21: 269–291.

Sudworth GB. 1908.　Forest trees of the Pacific slope. Washington, DC: USDA Forest Service. 441 p.

Swingle CF, comp. 1939.　Seed propagation of trees, shrubs, and forbs for conservation planting. SCS–TP–27. Washington, DC: USDA Soil Conservation Service. 198 p.

Swofford TF. 1958.　Stratification harmful to some loblolly and slash pine seed. Tree Planter's Notes 32: 5–6.

Takayama Y. 1966. Studies on the seed orchard of Japanese red pine (*Pinus densiflora* Sieb. & Zucc.): 1. On the 1000-seed weight of the crops from the grafted clones of Japanese red pine [in Japanese]. Journal of the Japanese Forestry Society 48(5): 199–208.

Tanaka Y. 1984.　Assuring seed quality for seedling production: cone collection and seed processing, testing, storage, and stratification. In: Duryea ML, Landis TD, eds. Forest nursery manual: production of bareroot seedlings. The Hague: Martinus Nijhoff/Dr. W. Junk Publishers: 27–39.

Tauer CG, McNew RW. 1985.　Inheritance and correlation of growth of shortleaf pine in two environments. Silvae Genetica 34(1): 5–11.

Thompson BE. 1984.　Establishing a vigorous nursery crop: bed preparation, seed sowing, and early seedling growth. In: Duryea ML, Landis TD, eds. Forest nursery manual: production of bareroot seedlings. The Hague: Martinus Nijhoff/Dr. W. Junk Publishers: 41–49.

Thompson NS. 1968.　The response of pine cone scales to changes in moisture content. Holzforschung 22(4): 124–125.

Thulin IJ, Faulds T. 1968.　The use of cuttings in the breeding and afforestation of *Pinus radiata*. New Zealand Forestry Science 13(1): 66–77.

Ticknor RL. 1969.　Review of the rating of pines. Proceedings of the International Plant Propagator's Society 19: 132–137.

Tkachenko, ME. 1939.　General forestry [in Russian]. Leningrad: Goslestekhizdat. 745 p.

Troup RS. 1921.　The silviculture of Indian trees. Volume 3. Oxford, UK: Clarendon Press: 1013–1095.

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

Uyeki H. 1927.　The seeds of the genus *Pinus* as an aid to the identification of species [in Korean]. Suigen Agriculture and Forestry College Bulletin 2: 1–129.

Van Haverbeke DF. 1986a.　Genetic variation in ponderosa pine: a 15-year test of provenances in the Great Plains. Res. Pap. RM-265. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 16 p.

Van Haverbeke DF. 1986b.　Twenty-year performance of Scotch, European black (Austrian), red, and jack pines in eastern Nebraska. Res. Pap. RM–267. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 14 p.

Van Haverbeke DF. 1990.　*Pinus nigra* Arnold., European black pine. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 395–404.

Veracion VP. 1964.　Correlation of cone size and weight with the numbers, size and weight of seeds of Benguet pine (*Pinus insularis* Endl.). Occ. Pap. 16. Manila: Philippines Bureau of Forestry. 11 p.

Veracion VP. 1966.　Correlation of the size of seeds to the germination and early growth of Benguet pine (*Pinus insularis* Endl.). Occ. Pap. 26. Manila: Philippines Bureau of Forestry. 7 p.

Vidacovic M. 1991.　Conifers: morphology and variation. Zagreb, Croatia: Graficki Zavod Hrvatske. 755 p.

Vines RA. 1960.　Trees, shrubs, and woody vines of the Southwest. Austin: University of Texas Press. 1104 p.

Wahlenberg WG. 1946.　Longleaf pine. Washington, DC: Charles Lathrop Park Forestry Foundation. 429 p.

Wakeley PC. 1954.　Planting the southern pines. Agric. Monogr. 18. Washington, DC: USDA Forest Service. 233 p.

Wakeley PC, Barnett JP. 1968.　Viability of slash and shortleaf pine seed stored for 35 years. Journal of Forestry 66: 840–841.

Wang BSP. 1973.　Collecting, processing, and storing tree seed for research use. In: Proceedings, IUFRO Symposium on Seed Processing; Bergen, Norway. Volume 1, paper 17. 12 p.

Wang CW. 1977.　Genetics of ponderosa pine. Res. Pap. WO-34. Washington, DC: USDA Forest Service. 24 p.

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

Waxman S. 1977.　Four white pine introductions from the University of Connecticut. Bull. 445. Storrs: University of Connecticut Agricultural Experiment Station. 4 p.

Weidman RH. 1939.　Evidence of racial influences in a 25-year test of ponderosa pine. Journal of Agricultural Research 59: 855–888.

Wellner CA. 1962.　Silvics of western white pine. Misc. Pub. 26. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 24 p.

Wells OO. 1964.　Geographic variation in ponderosa pine: 1. The ecotypes and their distribution. Silvae Genetica 13(4): 89–103.

Wells OO. 1969.　Results of the Southwide pine seed source study through 1968–69. In: Proceedings, 10th Southern Conference Forest Tree Improvement: 117–129.

Wells OO. 1973.　Variation among shortleaf pines in a Mississippi seed source planting. Res. Note SO-162. New Orleans: USDA Forest Service, Southern Forest Experiment Statio. 8 p.

Wells OO. 1979.　Geographic seed source affects performance of planted shortleaf pine. In: Proceedings, Symposium for the Management of Pines of the Interior South. Tech. Pub. SA-2. Atlanta: USDA Forest Service, Southeastern Area State and Private Forestry: 48–57.

Wells OO, Wakeley PC. 1966.　Geographic variation in survival, growth and fusiform-rust infection of planted loblolly pine. Forest Science Monograph 11: 1–40.

Wells OO, Wakeley PC. 1970.　Variation in shortleaf pine from several geographic sources. Forest Science 16(4): 415–423.

Wendel GW, Smith HC. 1990.　*Pinus strobus* L., eastern white pine. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 476–488.

WFTSC [Western Forest Tree Seed Council]. 1966.　Sampling and service testing western conifer seeds. Portland, OR: WFTSC. 36 p.

Wheeler NC, Kriebel HB, Lee CH, Read RA, Wright JW. 1976.　15-year performance of European black pine in provenance tests in North Central United States. Silvae Genetica 25(1): 1–6.

Wright JW. 1962.　Genetics of forest tree improvement. Forestry & Forest Prod. Studies 16. Rome: FAO. 399 p.

Wright JW. 1970.　Genetics of eastern white pine. Res. Pap. WO-9. Washington, DC: USDA Forest Service. 16 p.

Wright JW, Amiel RJ, Cech FC, and others. 1979.　Performance of eastern white pine from the southern Appalachians in eastern United States, New Zealand, and Australia. In: Proceedings, 26th Northeastern Forest Tree Improvement Conference: 203–217.

Wright JW, Lemmien WL, Bright J. 1963.　Geographic variation in eastern white pine: 6 year results. Michigan Agricultural Experiment Station Quarterly Bulletin 45(4): 691–697.

Wright JW, Pauley SS, Polk RB, Jokela JJ, Read RA. 1966.　Performance of Scotch pine varieties in the North Central Region. Silvae Genetica 15(4): 101–110.

Wright JW, Read RA, Lester DT, Merritt C, Mohn C. 1972.　Geographic variation in red pine. Silvae Genetica 21(6): 205–210.

Wynens J, Brooks T. 1979.　Seed collection from loblolly pine. Res. Pap. 3. Macon: Georgia Forestry Commission. 3 p.

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

Yeatman CW. 1974.　The jack pine genetics program in Petawawa Forest Experiment Station 1950–1970. Pub. 1331. Ottawa: Canadian Forest Service, Department of the Environment. 30 p.

York HH, Littlefield EW. 1942.　The naturalization of Scotch pine, northeastern Oneida County. Journal of Forestry 40(7): 552–559.

Zavarin E, Critchfield WB, Snajberk K. 1969.　Turpentine composition of *Pinus contorta* × *Pinus banksiana* hybrids and hybrid derivatives. Canadian Journal of Botany 47(9): 1443–1453.

Zavarin E, Snajberk K. 1973.　Variability of the wood monoterpenes from *Pinus aristata*. Biochemical Systematics and Ecology 1: 39-44.

Zobel B. 1953.　Geographic range and intraspecific variation of Coulter pine. Madroño 12: 1–7.

Zobel DB. 1969.　Factors affecting the distribution of *Pinus pungens*, an Appalachian endemic. Ecological Monographs 39(3): 303–333.

Fabaceae—Pea family

# *Pithecellobium dulce* (Roxb.) Benth.

## *guamúchil*

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**Nomenclature.** *Pithecellobium* is a genus of about 110 species, mostly native to Asia and tropical America. The taxonomy of this genus has been changed in recent years, and the names of some species are still in debate. *Pithecellobium saman* (Jacq.) Benth., which was included in the 1974 edition of this work (Walters and others 1974), became *Albizia saman* (Jacq.) F. Muell., then *Samanea saman* (Jacq.) Merr. In the current book, it is included in *Albizia*. Texas ebony (*P. flexicaule* (Benth.) Coult.) is now *Ebenopsis ebano* (Berl.) Barneby & Grimes and appears under that name in this book.

**Growth habit, occurrence, and use.** *Guamúchil*, also known as Madras thorn and monkeypod, is valued primarily for its fuelwood, fodder, and ornamental properties (Parrotta 1991). It is found on the Pacific slopes of Mexico and southern California, south to Colombia and Venezuela. Guamúchil has been planted in Florida, Puerto Rico, and Hawaii (Little and Wadsworth 1964) and has been introduced to India and Pakistan as a hedge plant (Khatra and others 1994). The species has become naturalized where planted and is now considered a pest in Florida (Morton 1976). It is a medium-sized tree that reaches heights of 22 m.

**Flowering and fruiting.** Guamúchil's white flowers are umbels, about 3 cm in length, that are borne in paniculate clusters on branch ends (figure 1). The species flowers primarily from December to May but is known to fruit throughout the year in Puerto Rico (Parrotta 1991). Fruits are linear, curved legumes (pods) that range in length from 10 to 13 cm (figure 1). They turn from green to brown or black when they ripen in February to August. The legumes may contain 5 to 12 seeds each, and they are dehiscent (Parrotta 1991). The seeds are reddish brown to black, elliptical, beanlike, and about 1 cm in length. As the legumes split open, the seeds often hang down partially enclosed in a pulpy aril that may be 2 cm long (figure 2). Seeds vary widely in size, ranging from 6,000 to 26,000/kg (2,720 to 11,800/lb) (Little and Skolmen 1989; Parrotta 1991).

**Collection, extraction, and storage.** Legumes may be picked from the trees or from the ground, and air-dried in the sun. Seeds can be removed by hand-flailing or by use of a macerator, and pod fragments can be removed with screens. There are no long-term seed storage data for guamúchil, but these are typical hardseeded legumes with orthodox storage behavior. The seeds should be easy to store at low moisture contents (<10%) and low temperatures (any refrigeration) for a number of years.

**Germination.** Official seed testing organizations do not include guamúchil in their prescriptions for testing, but tests with a single seedlot in Costa Rica found that germina-

**Figure 1**—*Pithecellobium dulce,* guamúchil:    flowering twig, leafy twig, legumes, and seeds (from Little and Wadsworth 1964).
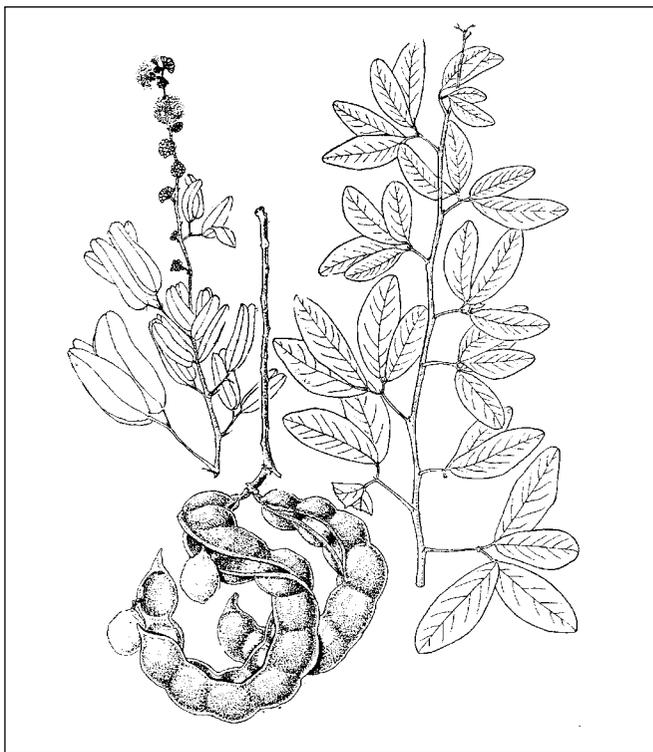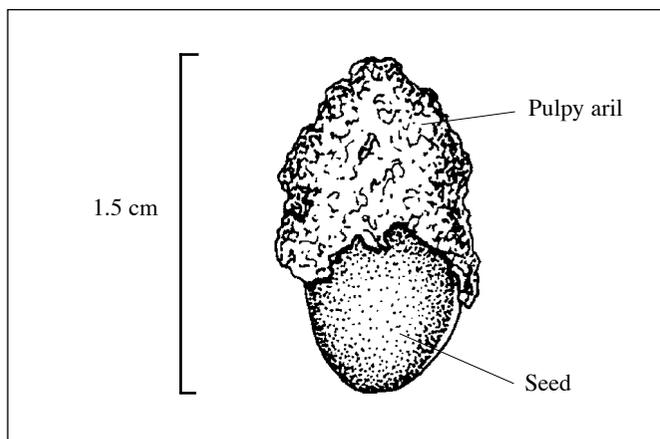
**Figure 2**—*Pithecellobium dulce*, guamúchil: seed partially enclosed in the pulpy aril (from Gunn 1984).



tion averaged 93% over a wide range of conditions (Castro 2000). Temperatures of 24, 27, 30, and 32 °C were equally good, and light from 0 to 24 hours made no difference either. Scarification with sulfuric acid or by clipping the seedcoats gave germination above 90%, but hot water treatments and long soaks at room temperature were not as successful. Good germination of this species without pretreatment has also been reported (Parrotta 1991).

**Nursery practice.** Guamúchil seeds germinate 1 to 2 days after sowing without treatment in Puerto Rico. Seedlings reach a good outplanting height of 40 cm about 3 months after sowing. This species can also be grown from cuttings (Parrotta 1991).

## References

Castro KL. 2000. Estudios de germinación en Jaúly Cenízaro. Boletín-Mejoramiento Genético y Semillas Forestales. 24: 1–5 [Seed Abstracts 24:3606, 2001].

Gunn CR. 1984. Fruits and seeds of genera in the subfamily Mimosoideae (Fabaceae). Tech. Bull. 1681. Washington, DC: USDA Agricultural Research Service. 194 p.

Khatra LM, Nasir MKA, Saleem R, Valhari MU. 1994. The fatty acid composition of *Pithecellobium dulce* seed oil. Pakistan Journal of Scientific and Industrial Research 37: 216. (Seed Abstracts 18(11): 3554. 1995).

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, Wadsworth FH. 1964. Common trees and shrubs of Puerto Rico and the Virgin Islands. Agric. Handbk. 249. Washington, DC: USDA Forest Service. 548 p.

Morton JF. 1976. Pestiferous spread of many ornamental and fruit species in South Florida. Proceedings, Florida State Horticultural Society 89: 348–353 [Weed Abstracts 28(5): 1618; 1979].

Parrotta JA. 1991. *Pithecellobium dulce* (Roxb.) Benth, Guamúchil, Madras thorn. SO-ITF-SM-40. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 5 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.

Platanaceae—Planetree family

# *Platanus* L.

## sycamore

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**Growth habit, occurrence, and uses**.    Sycamores— genus *Platanus*—are deciduous trees that range from 24 to 43 m in height at maturity. Two native and 1 introduced species are included in this manual (table 1). American sycamore is a large and valuable timber species in the eastern United States and has been widely planted in the Southeast for fiber production, wetlands restoration, and mine spoil reclamation (Haynes and others 1988; Wells and Schmidtling 1990). California sycamore is valued for watershed protection and wildlife food, whereas oriental planetree is primarily planted for ornamental purposes. London plane—*P.* × *aceriolia* (Ait.) Willd.—a hybrid between sycamore and oriental planetree, is also widely planted as an ornamental in the United States because of its tolerance of air pollution and alkali (Little 1961; Dirr and Heuser 1987). No geographic races of these species are recognized, but there is sufficient variation within American sycamore for

growth (Ferguson and others 1977) and disease resistance (Cooper and others 1977) to justify tree improvement programs.

**Flowering and fruiting.**    The minute monoecious flowers of sycamores appear in the spring (table 2). The dark red staminate flower clusters are borne on branchlets of the previous year's growth, and the light green pistillate flowers are found on older branchlets (Vines 1960; Wells and Schmidtling 1990). Sycamore fruiting heads are usually solitary, but California sycamore may have 2 to 7 heads grouped on a single stem (Bonner 1974) (figure 1).

Fruit heads are greenish brown to brown at maturity in the autumn (table 2). Those of sycamore are 25 to 40 mm in diameter, and those of the other species are closer to 25 mm. The true fruits are elongated, chestnut-brown, single-seeded achenes with a hairy tuft at the base (figure 2). They are closely packed, with their bases anchored in a hard central

**Table 1**—*Platanus,* sycamore:   nomenclature and occurrence

| Scientific name & synonym(s) | Common name(s) | Occurrence |
|---|---|---|
| **P. occidentalis L.**<br>*P. occidentalis* var. Sarg. *glabrata* (Fern.) | **American sycamore,** American planetree, buttonwood, planetree, buttonball-tree | Maine to Iowa, S to central Texas & NW Florida; also in NW Mexico; planted in South Dakota, Colorado, Nebraska, & Kansas |
| **P. orientalis L.** | **oriental planetree** | SE Europe, W Asia to India; planted in US as an ornamental |
| **P. racemosa Nutt.** | **California sycamore,** California planetree, western sycamore, *aliso* | Central to S California & into NW Mexico; below 1,200 m elevation |

**Sources:**   Little (1961, 1979).

**Table 2**—*Platanus,* sycamore:   phenology of flowering and fruiting

| Species | Location | Flowering | Fruit ripening | Seed dispersal |
|---|---|---|---|---|
| *P. occidentalis* | E US | Mar–May | Sept–Nov | Jan–Apr |
| *P. orientalis* | NE US | May | Sept–Oct | — |
| *P. racemosa* | — | — | June–Aug | June–Dec |

**Sources:**   Bonner (1974), Wells and Schmidtling (1990).

core. The elongated embryo is surrounded by a thin endosperm (figure 3). Sycamore usually bears good seed-crops every 1 to 2 years and light crops in the intervening years. Open-grown trees of this species as young as 6 years have produced seeds, but trees in dense natural stands are usually much older (25 years) before large crops are evident (Briscoe 1969; Wells and Schmidtling 1990). Fruit heads persist on the trees through the winter and break up the following spring. The hairy tufts at the base of the fruits act as parachutes for dissemination by wind. Sycamore fruits float easily and are therefore widely distributed by moving water (Wells and Schmidtling 1990).

**Collection of fruits.** Fruit heads of sycamore can be collected any time after they turn brown, but the job is easiest if done after leaf-fall. Because the heads are persistent, collections can be made into the next spring, usually making

**Figure 1**—*Platanus*, sycamore: fruiting heads of *P. occidentalis,* American sycamore (**top**) and *P. racemosa*, California sycamore (**bottom**).
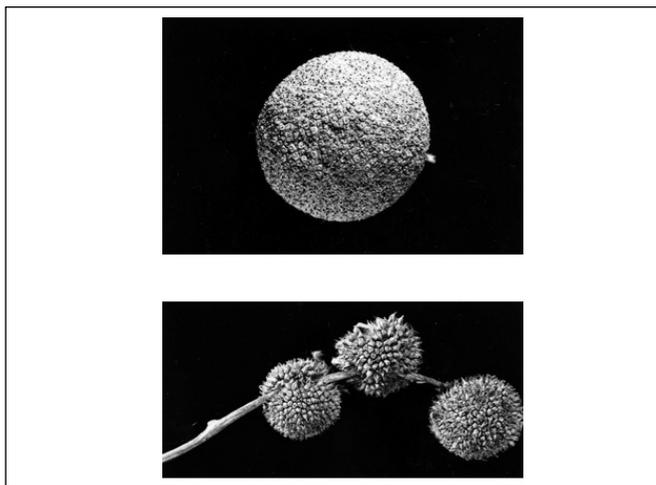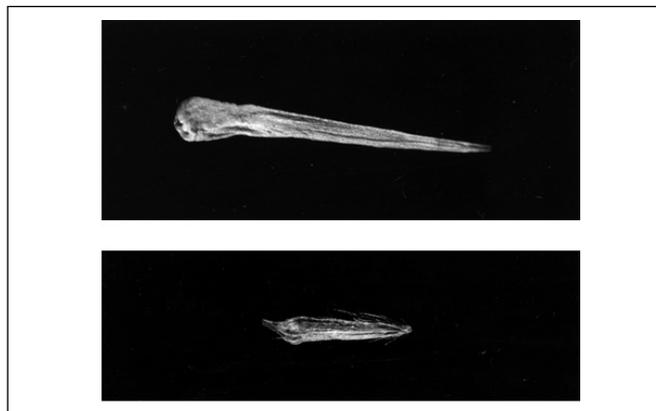


**Figure 2**—*Platanus*, sycamore: single achenes of *P. occidentalis,* American sycamore (**top**) and *P. racemosa*, California sycamore (**bottom**).



**Figure 3**—*Platanus occidentalis,* American sycamore: longitudinal section through a seed.



sycamore the last fall-maturing species to be collected in the East. This additional time on the tree after full maturity apparently does not harm seed quality (Briscoe 1969). Picking fruit heads by hand from the tree is the most common method of collection. At the northern and western limits of the range of sycamore, intact heads can sometimes be collected from the ground late in the season. As fruit heads begin to fall apart in the early spring, the seeds may sometimes be shaken loose by tapping the branches (Briscoe 1969). Once collected, fruit heads should be spread in single layers and dried in well-ventilated trays until they can be broken apart, no matter how dry they look at collection. This step is essential with fruit heads collected early in the season, as their moisture contents can be as high as 70% (Bonner 1972b).

**Extraction and cleaning of seeds.** Seeds should be extracted by crushing the dried fruit heads and removing the dust and fine hairs that are attached to the individual achenes. Small lots can be broken up in small mechanical scarifiers or by hand-rubbing through hardware cloth (2 to 4 wires/cm) (Briscoe 1969). Medium-sized lots of up to 2 hl can be quickly broken up in mechanical macerators. Larger lots can be broken up in fertilizer distributors, hammermills, or centrifugal disks (Briscoe 1969; Bonner 1979). No matter which method is used, some method of dust removal should be provided and dust masks should be worn by workers! The fine hairs that are dislodged during extraction and cleaning are a danger to respiratory systems. The fertilizer distributor method is widely used, and the dust problem is

lessened when the operation is carried out in the open. The distributor can be loaded with fruits and pulled along with ejection gates closed, or a powered belt can be attached to a jacked-up wheel. With the jacked-up wheel arrangement, clean seeds will work out through the gates, while fruit cores and fluffs of the hairs will collect at the top.

Dust, fine hairs, and large trash can also be removed from seedlots with air-screen cleaners or aspirators. Studies with sycamore have shown that a 3 × 19 mm ($^{7}/_{64}$ × $^{3}/_{4}$ in) oblong-hole screen will remove twigs, leaves, and fruit cores, while dust, hairs, and small trash can be removed with 1.2 mm (1/21) round-hole screens (Bonner 1979). If the seedlot is especially trashy, 2 runs through the air-screen cleaner may be needed. The smaller cleaners can clean 5 to 7 kg of seeds/hour, and purities of greater than 99% are possible. Electrostatic seed cleaners can also do a good job cleaning sycamore. In a test by Karrfalt and Helmuth (1984), purity was increased from 88 to 99%. Louisiana and Mississippi collections of sycamore yielded 9 to 14 kg of seed/hl of fruitheads, and 55 to 66 kg of seeds/100 kg of fruitheads (Briscoe 1969). Some representative seed weight data for sycamore are listed in table 3.

Sycamore is noted for its low proportion of filled seeds, a condition due to poor cross-pollination and self-incompatibility in isolated trees (Beland and Jones 1967). Effective control of bed density in nurseries can be severely hampered by this condition, so upgrading of seedlots by mechanical means is highly desirable. Such operations are possible with gravity separators, aspirators, and electrostatic separators (Bonner 1979; Karrfalt and Helmuth 1984). For exmaple, a single pass on a gravity separator upgraded a sycamore seedlot from 27% filled seeds to 56% (Bonner and Switzer 1974).

**Storage of seeds.** Seeds of all sycamore species are orthodox in storage behavior and can be easily stored for long periods in cold, dry conditions. Storage tests with sycamore have shown that seed moisture contents of 5 to 10% and temperatures of 0 to 5 °C are suitable for short-term storage of up to 5 years. For longer storage periods, sub-freezing temperatures (–18 °C) at the same moisture content are recommended (Bonner 1979). The upper limit of storage potential for sycamore is not yet known, but current research suggests that it will be far beyond 10 years under optimum conditions (Bonner 1994). To maintain low seed moisture in moist surroundings, the dried seeds must be stored in moisture-proof containers, such as polyethylene bags or fiber drums with plastic liners (Bonner 1979). Several species of *Aspergillus* fungi have been identified as pathogens that harm viability of sycamore seeds in storage (Fakir and others 1971), but they have never been a major problem.

**Pregermination treatments.** Moist stratification for 60 to 90 days at 5 °C in sand, peat, or sandy loam has been reported as beneficial for germination of California sycamore (Bonner 1974). The other sycamores have no dormancy, and pregermination treatments are usually not required for prompt germination (Bonner 1972a; Webb and Farmer 1968). Germination rate of sycamore can be increased by treating with gibberellin (GA$_3$) at 100 to 1,000 mg/liter, but this increase seems to be simple growth stimulation that is not involved in seed dormancy (Bonner 1976).

**Germination tests.** Germination can be easily tested on wet paper or sand or even in shallow dishes of water (table 4). Official testing prescriptions call for alternating day/night temperatures of 30/20 °C on the top of moist blotters for 14 days (AOSA 1993). A large percentage of the sound seeds will usually germinate, but the great variation in number of sound seeds among lots will result in varied germination percentages. Surface sterilization of the seeds with a 30-second dip in a 1% commercial bleach solution is often beneficial to laboratory germination (Mullins 1976). Rapid viability tests can also be made on sycamore with tetrazolium staining and x-radiography (Bonner 1974).

**Table 3**—*Platanus,* sycamore: seed data

| Species | Place of collection | Range /kg | Range /lb | Average /kg | Average /lb | Samples |
|---|---|---|---|---|---|---|
| *P. occidentalis* | Louisiana–Mississippi* | 294,370–589,620 | 133,500–267,400 | 426,160 | 193,270 | 100+ |
| | SE US | 192,340–500,100 | 87,2330–226,800 | 330,530 | 149,900 | 28 |
| *P. orientalis* | Denmark | 178,600–357,200 | 81,000–162,000 | 282,240 | 128,000 | 8 |
| | United States | 249,160–370,440 | 113,000–168,000 | 308,700 | 140,000 | 2+ |

**Sources:** Bonner (1974), Briscoe (1969), Swingle (1939).
* Seedlots from these sources averaged 1,765 seeds/fruit (range from 804 to 3,050).

**Nursery practice.** Sycamores are usually sown in the spring by broadcasting or by mechanically drilling. For drilling, seeds should be placed no deeper than 3 mm ($^1/_8$ in) in rows 15 to 20 cm (6 to 8 in) apart. If sown on the surface of the beds, they should be covered with no more than 6 mm ($^1/_4$ in) of light mulch (Williams and Hanks 1976). Seedling density will depend on the intended use of the stock. For those wanting small seedlings, 110 seedlings/m² (10/ft²) is recommended; for larger stock, 55/m² (5/ft²) (Vande Linde 1960; Williams and Hanks 1976).

Bed surfaces must be kept moist through germination, and shading, while not necessary, can be helpful for the first month (Briscoe 1969; Engstrom and Stoeckler 1941). On neutral to slightly alkaline soils, damping-off may be a problem. Root pruning in midsummer is recommended to promote growth of smaller roots, and some nurseries prune seedling tops in late July or August to reduce size. Seedlings should not be both root- and top-pruned during the growing season (Briscoe 1969). Sycamore is usually outplanted as 1+0 stock, and oriental planetree is often planted as 1+1 or 2+0 seedlings in Europe (Bonner 1974). The sycamores are easy to propagate vegetatively by dormant or greenwood cuttings (Dirr and Heuser 1987), and many plantations of sycamore have been established in the South by these techniques. Some tests show no difference in growth after 1 year between seedlings and cuttings (Garrett 1975).

## References

AOSA [Association of Official Seed Analysts]. 1993. Rules for testing seeds. Journal of Seed Technology 16(3): 1–113.

Beland JW, Jones L. 1967. Self-incompatibility in sycamore. In: Proceedings, 9th Southern Conference on Forest Tree Improvement; 1967 June 8–9; Knoxville, TN. Spons. Publ. 28. Macon, GA: USDA Forest Service, Eastern Tree Seed Laboratory: 56–58.

Bonner FT. 1972a. Laboratory germination testing of American sycamore. Proceedings of the Association of Official Seed Analysts 62: 84–87.

Bonner FT. 1972b. Maturation of sweetgum and American sycamore seeds. Forest Science 18: 223–231.

Bonner FT. 1974. *Platanus* L., sycamore. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 641–644.

Bonner FT. 1976. Effects of gibberellin on germination of forest tree seeds with shallow dormancy. In: Hatano K, Asakawa S, Katsuta M, Sasaki S, Yokoyama T, eds. Proceedings, Second International Symposium on Physiology of Seed Germination; 1976 October 18–30; Fuji, Japan. Tokyo: Government Forest Experiment Station: 21–32.

Bonner FT. 1979. Collection and care of sycamore seeds. Southern Journal of Applied Forestry 3(1): 23–25.

Bonner FT. 1994. Predicting seed longevity for four forest tree species with orthodox seeds. Seed Science and Technology 22: 361–370.

Bonner FT, Switzer GL. 1974. Mechanical separation of full and empty sycamore seeds. In: 1974 Southeastern Nurserymen's Conferences; 1974 July 17–18; Nacogdoches, TX and August 6–8; Gainesville, FL. Atlanta: USDA Forest Service, Southeastern Area State & Private Forestry: 95–100.

Briscoe CB. 1969. Establishment and early care of sycamore plantations. Res. Pap. SO-50. New Orleans: USDA Forest Service. Southern Forest Experiment Station. 18 p.

Cooper DT, Filer TH Jr, Wells OO. 1977. Geographic variation in disease susceptibility of American sycamore. Southern Journal of Applied Forestry 1(4): 21–24.

Dirr MA, Heuser CW Jr. 1987. The reference manual of woody plant propagation: from seed to tissue culture. Athens, GA: Varsity Press. 239 p.

Engstrom HE, Stoeckeler JH. 1941. Nursery practice for trees and shrubs. Misc. Pub. 434. Washington, DC: USDA. 159 p.

Fakir GA, Welty RE, Cowling EB. 1971. Prevalence and pathogenicity of fungi associated with achenes of sycamore in the field and in storage. Phytopathology 61: 660–668.

Ferguson RB, Land SB Jr, Cooper DT. 1977. Inheritance of growth and crown characters in American sycamore. Silvae Genetica 26: 180–182.

Garrett HE. 1975. Root initiation and development in sycamore seedlings and cuttings. Tree Planters' Notes 26(3): 19–20, 29.

Haynes RJ, Allen JA, Pendleton EC, Grau GA. 1988. Reestablishment of bottomland hardwood forests on disturbed sites: an annotated bibliography. Biol. Rep. 88(42). Washington, DC: USDI Fish and Wildlife Service, Research and Development. 104 p.

Karrfalt RP, Helmuth RE. 1984. Preliminary trials on upgrading *Platanus occidentalis* with the Helmuth electrostatic seed separator. In: Murphy PM, comp. The challenge of producing native plants for the Intermountain area. Proceedings, Intermountain Nurseryman's Association; 1983 August 8–11; Las Vegas, NV. Gen. Tech. Rep. INT-168. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 79–81.

Little EL Jr. 1961. Sixty trees from foreign lands. Agric. Handbk. 212. Washington, DC: USDA Forest Service. 30 p.

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

Mullins JA. 1976. Variation in seed quality of American sycamore (*Platanus occidentalis* L.) [MSc thesis]. Starkville: Mississippi State University, School of Forest Resources. 57 p.

Swingle CF (comp.). 1939. Seed propagation of trees, shrubs, and forbs for conservation planting. SCS-TP-27. Washington, DC: USDA Soil Conservation Service. 198 p.

Vande Linde F. 1960. Nursery practice for growing sycamore seedlings. Tree Planters' Notes 41: 15–16.

Vines RA. 1960. Trees, shrubs, and woody vines of the Southwest. Austin: University of Texas Press. 1104 p.

Webb CD, Farmer RE Jr. 1968. Sycamore seed germination: the effects of provenance, stratification, temperature, and parent tree. Res. Note SE-100. Asheville, NC: USDA Forest Service, Southeastern Forest Experiment Station. 6 p.

Wells OO, Schmidtling RC. 1990. *Platanus occidentalis* L., sycamore. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 2, Hardwoods. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 511–517.

Williams RD, Hanks SH. 1976. Hardwood nurseryman's guide. Agric. Handbk. 473. Washington, DC: USDA Forest Service. 78 p.

Cupressaceae—Cypress family

# *Platycladus orientalis* (L.) Franco

## oriental arborvitae

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**Synonym.** *Thuja orientalis* L., *T. acuta* Moench., *Platycladus stricta* Spach., *Biota orientalis* (L.) Endl.

**Other common names.** Chinese arborvitae, biota.

**Growth habit, occurrence, and use.** Oriental arborvitae is native to northern and western China and Korea (Vidakovic 1991). This species was previously included in the genus *Thuja* (Schopmeyer 1974), but it has now been placed in *Platycladus,* a monotypic genus. It is a medium-sized tree (approximately 12 m tall) that is widely cultivated as an ornamental in the United States. Many ornamental cultivars have been developed (Dirr and Heuser 1987; LHBH 1976). The foliage of oriental arborvitae is not as aromatic as that of *Thuja* species, and its cones are rather fleshy (Rushforth 1987). It can be planted in many different soils and will tolerate drier soils than northern white-cedar—*Thuja occidentalis* L. Oriental arborvitae should be restricted to regions where the minimum temperature is above –24 °C (Rushforth 1987).

**Flowering and fruiting.** Flowering occurs in the spring, and the cones mature in the fall of the same year. The cones range from 1.5 to 2.5 cm in length and typically have 4 fertile scales. The seeds are dark reddish purple and wingless (figures 1 and 2) (Schopmeyer 1974).

**Extraction, cleaning, and storage of seeds.** Cones are usually collected by hand from the branches after they turn yellow or brown but before they open. Cones will open partially with only air-drying in the sun or inside at room temperature, but auxiliary heating is needed for complete extraction. Most cones should open in 24 to 36 hours when heated at 30 °C (Dirr and Heuser 1987). Seeds can be shaken from the cones with small cone tumblers or similar devices, then scales and trash can be removed with screens or seed blowers. If large numbers of empty seeds are present, seedlots can be upgraded with the careful use of seed blowers. Oriental arborvitae seeds range from 44,100 to 55,125/kg (20,000 to 25,000/lb) (Schopmeyer 1974).

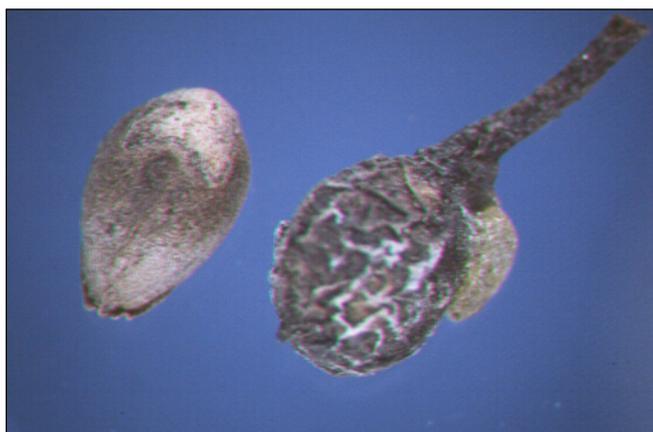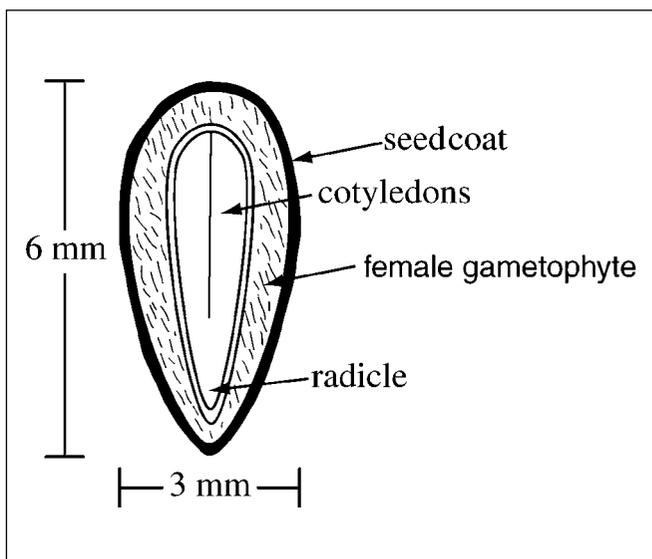**Figure 1**—*Platycladus* orientalis, oriental arborvitae: seeds.



**Figure 2**—*Platycladus orientalis*, oriental arborvitae: longitudinal section through a seed.



Seeds of this species are orthodox in storage behavior. If dried to moisture contents of 5 to 10% and stored at near-freezing (0 to 5 °C) temperatures, viability should be main-

tained for at least 5 years. For longer storage periods, sub-freezing temperatures of about –18 °C are recommended (Bonner 1991).

**Germination tests.**   For most seedlots, pretreatments are not needed for germination tests, although beneficial effects have been reported for cold stratification for 1 to 1 $1/2$ months and for short soaks in weak solutions of gibberellic acid (Dirr and Heuser 1987; Schopmeyer 1974). Both AOSA (1993) and ISTA (1993) recommend testing oriental arborvitae on the top of moist paper media at a constant 20 °C for 21 days; no pretreatments are prescribed. Germination is epigeal.

**Nursery practice.**   Sowing outdoor nursery beds should take place in the spring at a depth of 6 to 9 mm ($1/4$ to $3/8$ in) and no mulch. A bed density of 375 to 430/m² (35 to 40/ft²) has been recommended (Schopmeyer 1974). Under most conditions, seedlings are grown for 2 years before outplanting, although this may vary according to individual nursery practices. Container production in greenhouses is also possible, using techniques that are successful with the closely related *Thuja* species.

Vegetative reproduction, while more difficult than it is with *Thuja* species, is possible with oriental arborvitae and is widely used for ornamental cultivars. Dirr and Heuser (1987) recommend taking cuttings from June to August, treating with indole-butyric acid (IBA) in talc and Benlate®, then rooting with mist and bottom heat in a peat and perlite mixture (2:1, v/v).

## References

AOSA [Association of Official Seed Analysts]. 1993.    Rules for testing seeds. Journal of Seed Technology 16(3): 1–59.
Bonner FT. 1991.    Seed storage. In: Gordon AG, Gosling P, Wang BSP, eds. Tree and shrub seed handbook. Zurich: International Seed Testing Association: 13: 1–4.
Dirr MA, Heuser CW Jr. 1987.    The reference manual of woody plant propagation: from seed to tissue culture. Athens, GA: Varsity Press. 239 p.
ISTA [International Seed Testing Association]. 1993.    Rules for testing seeds: rules 1993. Seed Science and Technology 21 (Suppl.): 1–259.
LHBH [Liberty Hyde Bailey Hortorium]. 1976.    Hortus third: a concise dictionary of plants cultivated in the United States and Canada. New York: Macmillan. 1290 p.
Rushforth KD. 1987.    Conifers. New York: Facts on File. 232 p.
Schopmeyer CS. 1974.    *Thuja,* arborvitae. In: Schopmeyer CS, tech. Coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 805–809.
Vidakovic M. 1991.    Conifers: morphology and variation. Zagreb, Croatia: Graficki zavod Hrvatske. 754 p.

Salicaceae—Willow family

# *Populus* L.

## poplar, cottonwood, aspen

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**Growth habit, occurrence, and use.** The Salicaceae, the family that includes poplars, cottonwoods, and aspens (*Populus* spp.) and willows (*Salix* spp.), is the most widespread group of woody plants in North America. The poplar genus—*Populus*—is subdivided into 5 sections (Aigeros, Leucoides, Leuce, Tacamahaca, and Turanga) and comprises 30 species, under the common names of poplar, cottonwood, and aspen. The taxonomy of the genus is complex because natural variation and hybridization are common among some sympatric species. In addition, species have been introduced from Europe, and both planned and natural hybrids have been produced for use in forestry and horticulture (Barnes 1961; Brayshaw 1966; Ceulemans 1990; Dickmann and Stuart 1983; Eckenwalder 1977, 1980; Einspahr and Benson 1964; Little and others 1957; Pregitzer and Barnes 1980; Rehder 1940; Schreiner and Stout 1934; Spies and Barnes 1982; Stettler and others 1996; Viereck and Foote 1970). The nomenclature and occurrence of the North American species and some of the exotic species and cultivars are presented in table 1. A thorough coverage of the nomenclature, distribution, genetics, evolution, hybridization, biology, and ecology of the genus can be found in Burns and Honkala (1990), Ceulemans (1990), Dickmann and Stuart (1983), Dickmann and others (2001), Einspahr and Winton (1977), FAO (1980), Hyun and others (1984), Schreiner (1971), Smith (1943), Stettler and others (1996), and Stout and Schreiner (1933).

The genus is wide ranging in North America (Burns and Honkala 1990). There are some unique aspects to the distribution of the poplar genus. Balsam poplar has the northernmost (and westernmost) range of any tree in North America, as it grows in the foothills transition from the Brooks Range to the Arctic coastal plain in northern Alaska and in the Mackenzie River delta in the Yukon (Viereck and Little 1972). These northernmost stands are associated with riparian areas. The distribution of poplar species within their natural ranges varies considerably. Quaking aspen, which has

the most widespread range of any North American tree species, can form large monospecific stands of 40 to 50 ha consisting of only one clone. In fact, an aspen clone in Colorado is reputed to be the largest living organism known (Mitton and Grant 1996). Quaking aspen clones in the Great Lakes region, Alaska, and adjacent Canadian provinces, however, are generally small, seldom greater than .03 to 1.5 ha (Barnes 1966, 1969; Kemperman 1976; Kemperman and Barnes 1976; Parkerson 1977; Steneker 1973). Aspen in pure and mixed stands covers thousands of hectares in north temperate and boreal forests. Although some poplar species may have fairly large geographic ranges, they are restricted in occurrence and often exhibit their best development in (or are restricted to) riparian areas. Plains cottonwood, for example, occurs primarily in riparian areas in the Great Plains and occupies little of the dry upland area (Burns and Honkala 1990; Friedman and others 1997; Rood and others 1995; Stromberg 1993).

Species of the poplar genus occur mainly in early successional plant communities. They can quickly colonize after natural or human disturbances and grow rapidly where light, exposed mineral soil, and moisture are readily available. Depending on the species and site, they are usually replaced by more shade-tolerant species in 60 to 100 years. However, stands of some species have remained intact for more than 200 years in boreal forest environments in the Rocky Mountains. In areas with fire return intervals of 50 to 100 years, single clones of a species like aspen may persist for many centuries or, as some theorize, thousands of years (Barnes 1966; Burns and Honkala 1990; Mitton and Grant 1996). Although poplars are often viewed as being replaced by more tolerant trees, stands in the western Great Plains are replaced by grassland communities if they are not disturbed by periodic flooding (Friedman and others 1997).

Utilization and value of the genus can be considered in relation to their use in intensive culture and agroforestry plantations and in naturally occurring forests. Natural stands

**Table 1**—*Populus*, poplar, cottonwood, aspen:   nomenclature and occurrence

| Scientific name & synonym(s) | Common name(s) | Occurrence |
|---|---|---|
| ***P. x acuminata* Rydb. (pro sp.)**<br>*P. accuminata* var. *rehderi* (Sarg.) | **lanceleaf cottonwood,** lanceleaf poplar, smooth-bark cottonwood, & Andrews poplar | S Alberta, Montana, W North Dakota, Wyoming, W Nebraska, E Colorado, & New Mexico |
| ***P. alba* L.** | **white poplar**, abele | Central & S Europe to W Siberia & Central Asia |
| ***P. angustifolia* James** | **narrowleaf cottonwood,** narrowleaf poplar, black cottonwood, mountain cottonwood, *álamo* | S Saskatchewan & Alberta S to Arizona, W Nebraska, & trans-Pecos Texas; also in N Mexico (Chihuahua) |
| ***P. balsamifera* L.** | **balsam poplar,** tacamahac poplar, cottonwood, hackmatack, tacamahac | Alaska to Labrador, S to New York & Oregon |
| ***P. balsamifera* L. spp. *trichocarpa* (Torr. & Gray ex Hook.) Brayshaw**<br>*P. trichocarpa* Torr. & Gray | **black cottonwood**, California poplar, cottonwood, balsam cottonwood, western balsam poplar | S Alaska & S Yukon to S California & W Nevada; local in Wyoming, SW North Dakota, & Lower California |
| ***P.* x *canescens* (Ait.) Sm. (pro sp.)** | **gray poplar** | Europe & W Asia |
| ***P. deltoides* Bartr. ex Marsh.** | **eastern cottonwood**, eastern poplar | Quebec to North Dakota, S to Texas & Florida |
| ***P. deltoides* Bartr. ex Marsh. ssp. *monilifera* (Ait.)**<br>*P. deltoides* var. *occidentalis* Ryb. | **plains cottonwood,** plains poplar, cottonwood, Texas cottonwood | SW Utah, Nevada, to N California, S to Arizona & New Mexico, NW Mexico |
| ***P. deltoides* Bartr. ex Marsh. ssp. *wislizeni* S. Wats.**<br>*P. fremontii* var. *wislizeni* S. Wats. | **Rio Grande cottonwood**, Rio Grande poplar, cottonwood, valley cottonwood, Wislizenus cottonwood, álamo | S Colorado, S Utah, New Mexico, W Texas, & N Mexico |
| ***P. euphratica* Olivier** | **Euphrates poplar**, bahan, Gharab-Palk-Saf-Saf | Spain & W Morocco to Kenya, E to Central Asia |
| ***P. fremontii* S. Wats.** | **Fremont cottonwood**, Fremont poplar, cottonwood, Arizona cottonwood, Macdougal cottonwood, *álamo* | SW Utah, Nevada, to N California, S to Arizona & New Mexico, NW Mexico |
| ***P. grandidentata* Michx.** | **bigtooth aspen**, largetooth aspen, aspen, poplar, popple | Nova Scotia to NE North Dakota, S to Iowa & Pennsylvania, & along Appalachian Mtns to North Carolina |
| ***P. heterophylla* L**. | **swamp cottonwood,** swamp poplar, cottonwood, black cottonwood, river cottonwood, downy poplar | Coastal plain from Connecticut & SE New York to Georgia & NW Florida, W to Louisiana, N in Mississippi Valley to Indiana, Ohio, & S Michigan |
| ***P. laurifolia* Lebed.** | **laurel poplar** | Siberia |
| ***P. maximowiczii* A. Henry** | **Japanese poplar** | NE Asia & Japan |
| ***P. nigra* L.** | **black poplar**, European black poplar | Europe & W Asia |
| ***P.* x *petrowskiana* R.I. Schrod. ex Regel** | **Petrowsky poplar,** Russian poplar | Europe |
| ***P. sieboldii* Miq.** | **Siebold aspen,** Japanese aspen | Japan |
| ***P. simonii* Carriere** | **Simon poplar** | NW China to Korea |
| ***P. tremula* L.** | **European aspen**, tremble, Zitterpappel | Europe, North Africa, & NE Asia |
| ***P. tremuloides* Michx.** | **quaking aspen**, quaking asp, aspen, golden aspen, mountain aspen, trembling aspen, Vancouver aspen poplar, popple, *alamo blanco* | Labrador to Alaska, S to Pennsylvania, Missouri, N Mexico, & Lower California |

**Source:** Schreiner (1974).

of aspen, in particular, but other species too, are the basis for the pulp and paper industry in the north central United States and western Canada (Einspahr and Wyckoff 1990). Their ability to rapidly reoccupy a site by root suckering following harvest makes management of the species relatively easy. There is essentially no regeneration cost provided that care is taken to protect the root system of the har-

vested stand. Poplars have provided lumber for various uses and are important in the manufacture of reconstituted board products. Throughout human association with these species, virtually every part of the tree has been used for purposes that range from medicines to livestock feed to providing bark for carving art objects. Pure and mixed forests are important wildlife habitat. In the Great Plains areas of the

western United States and Canada, where they are the only tree cover, cottonwoods provide critical habitat for some species (Friedman and others 1997; Rood and others 1995; Stromberg 1993). They provide bark and male flowerbuds for specialist species such as beaver (*Castor canadensis*) and ruffed grouse (*Bonasa umbellus*) as well as forage for generalist browsers such as moose (*Alcea alcea*), elk (*Cervus elaphus*), and deer (*Odocoileus* spp.) (Burns and Honkala 1990; Dickmann and Stuart 1983; Dickmann and others 2001; Graham and others 1963; MacKinnon and others 1992; Peterson and Peterson 1995; Viereck 1987).

Poplars have long been important as ornamentals and in horticulture (tables 1 and 2). They were commonly used for amenity plantings in urban areas as ornamentals and landscaping. In rural areas, they have been used in shelterbelts and as ornamentals. The most rapidly increasing use of the species today is in intensive culture for wood fiber and biomass for energy in such diverse climates as the lower Mississippi Valley, western and eastern Washington, and western Minnesota. Shortages of fiber due to regulation of harvesting to protect critical wildlife habitat and old-growth forests, declining traditional forest land base, and concerns about effects of carbon dioxide ($CO_2$) from combustion of fossil fuels have renewed interest in intensive culture.

Poplars are ideal for short-rotation, intensive-culture management systems because (a) species and hybrids can be produced easily and propagated vegetatively, (b) juvenile growth is rapid, (c) response to cultural treatments is rapid, and (d) coppicing following harvest is prolific (Mitchell and others 1992; Stettler and others 1996). Poplar species are also readily propagated from tissue culture (Ostry and Ward 1991). Indeed, the first tree derived from tissue culture with both a shoot and attached root was a quaking aspen clone (Winton 1968a). Tree growth models are available for examining and predicting growth of poplar clones under different cultural regimes (Isebrands and others 1990; Stettler and others 1996).

In addition to classic tree breeding, advances have occurred due to the development of new genotypes using molecular genetics techniques (FAO 1980; Mitchell and others 1992; Stettler and others 1996).

Despite the large geographic range of the Salicaceae and the huge variation in growth form, there is remarkable uniformity in many aspects of the seed biology, dispersal, and germination. Thus information for willows, *Salix* spp. (Zasada and others 2005)—particularly those dispersing seeds during the summer—is relevant to poplar, *Populus* spp.

**Table 2**—*Populus,* poplar, cottonwood, aspen:   height at maturity, first cultivation, minimum seed-bearing age, and seed crop frequency

| Species | Height at maturity* (m) | Year first cultivated† | Minimum seed-bearing age (yr) | Years between large seedcrops |
|---|---|---|---|---|
| *P. x acuminata* | 10.7–15.4 (18.5) | 1898 | 5–10 | 1 |
| *P. alba* | 15.4–42.1 | LC | 10–15 | — |
| *P. angustifolia* | 10.7–15.4 (18.5) | 1893 | — | 1 |
| *P. balsamifera* | 18.5–36.3 | Before 1689 | 8–10 | — |
| *P. balsamifera* spp. trichocarpa | 15.4–61.5 | 1892 | 10 | 1 |
| *P. x canescens* | 29.2–30.8 (40) | LC | 8–15 | — |
| *P. deltoides* | 24.6–58.5 | Before 1750 | 10 | 1 |
| spp. *monilifera* | 12.3–30.8 | 1908 | 10 | 1 |
| spp. *wislizeni* | 2.3–30.8 (40) | 1894 | 5 | 1 |
| *P. fremontii* | 15.4–30.8 | 1904 | 5–10 | 1 |
| *P. grandidentata* | 9.2–27.7 (30.8) | 1772 | 10–20 | 4–5 |
| *P. heterophylla* | 24.6–27.3 (30.8) | 1656 | 10 | 1 |
| *P. laurifolia* | to 15.4 | 1830 | 8–10 | — |
| *P. maximowiczii* | to 30.2 | Before 1890 | 10 | 1 |
| *P. nigra* | 18.5–30.8 | LC | 8–12 | 1 |
| *P. simonii* | to 12.3+ | 1862 | 10 | — |
| *P. tremula* | 21.5–38.5 | LC | 8–10 | 4.5 |
| *P. tremuloides* | 15.4–27.7 (30.8) | 1812 | 10–20 | 4–5 |

**Source:**   Schreiner (1974).

* Figures in parentheses indicate occasional heights on favorable sites.

† LC=long cultivated.

**Flowering and fruiting.** Poplars are mostly dioecious (Rehder 1940); but *P. lasiocarpa* Oliver (from China) has been described as a monoecious, self-fertilizing species (FAO 1980). Deviations from strict dioecism have been found in individual trees and catkins (Einspahr 1960a; Lester 1961, 1963; Maini and Coupland 1964; Pauley 1950; Pauley and Mennel 1957; Santamour 1956; Stettler 1971; Spies 1978). In addition, Santamour (1956), Pauley and Mennel (1957), and Lester (1963) reported that quaking aspen had bisexual frequencies of 7, 8.7 and 38%, respectively, and that hermaphroditism was higher among females (10.7, 20.6, and 32.3%) than among males (5.1, 4, and 27.4%). Stettler (1971) reported variation in sex expression among females of black cottonwood but not among males. Year-to-year variation in the frequency of abnormal flowers among individual trees was also reported.

Sex ratios in natural populations are not well-documented in the genus but appear to be male-dominated or equal, at least for quaking aspen (Einspahr 1960b; Einspahr and Benson 1971; Farmer 1964b; Grant and Mitton 1979; Lester 1963; Mitton and Grant 1996 ;Valentine 1975). Grant and Mitton (1979) and Comtois and others (1986) reported that sex ratios in quaking aspen and balsam poplar, respectively, were 1:1 on a regional or landscape basis, but the sexes seemed to be segregated to some extent within the regions studied. Grant and Mitton (1979) found that male quaking aspen trees were more common at higher elevations than females and that male balsam poplar trees tended to be more common on relatively drier and less fertile sites (Comtois and others 1986). Sex ratio reports have been criticized because of the biased sampling technique used in many of the studies. Generally, only flowering trees were sampled. Einspahr (1960b) attempted to eliminate this bias by girdling non-flowering trees within the sample population and returning to record sex the following year. Einspahr and Benson (1971) and Valentine (1975) also recorded the sex of individual trees within test plantings of quaking aspen over a period of years and thus observed flowering over enough years to determine the sex of all individuals in a population.

Aspen ramet growth rate and density, clone size, and rate of clone expansion appear to differ among male and female clones, with female clones surpassing males in the characteristics studied (Mitton and Grant 1996). Farmer (1964b) did not find differences among male and female trees in eastern cottonwood.

Age of first flowering shows considerable inter- and intraspecific variation (table 2). Cottonwoods and balsam poplars generally reach flowering age at 10 to 15 years. Usually, few seeds can be collected from plains and eastern cottonwood trees that are less than 10 inches in diameter or less than 10 years old (Maisenhelder 1951). Precocious flowering of seedlings a few months after germination has been observed in the poplar genus, but it is difficult to keep young seedlings alive to produce mature seeds (Riemenschneider 1996). Genetically engineered aspen that flower within months after germination have been developed (Weigel and Nilsson 1995).

Flowering and seed maturation differ within and among individual species (table 3). For example, aspen in the north temperate and boreal forests flowers in April or early May and seeds begin to disperse 4 to 6 weeks after flowering and finish in a few weeks. Winton (1968b) examined quaking aspen and eastern cottonwood fertilization under greenhouse and growth chamber conditions. Quaking aspen pollen germinated 6.5 hours after pollination and fertilization occurred after 8 to 72 hours, depending upon temperature. At 25 °C, aspen seeds mature in about 2 weeks in a controlled environment (Fechner 1972) and in 3 to 4 weeks in an environment with more variable temperatures (Brown 1989; Wyckoff 1975). By contrast, cottonwood in the lower Mississippi Valley flowers from March to early April; maximum dispersal of seeds occurs 8 to 10 weeks after flowering, with some dispersal occurring after 16 weeks (Farmer 1964a, 1966). In a controlled environment, viable cottonwood seeds are obtained in May to June following pollination in late February to early March (Farmer and Nance 1968). Cottonwood fertilization occurred between 24 to 72 hours after pollination.

Within these general flowering and dispersal patterns, there is significant variation among trees in local populations for most of the species studied. There are also observations of very early flowering and seed dispersal that are well outside the general ranges (table 3) attesting to the temperature controls over flowering. For example, Shafroth (1996) observed flowering in Fremont cottonwood in January and seed dispersal by mid-late February. Quaking aspen flowers have broken bud during warm spells in mid-February in interior Alaska; subsequent temperatures of –30 to –40 °C arrested development, but it resumed with the onset of higher temperatures in April (Barnes 1961; Farmer 1966; Pregitzer and Barnes 1980; Spies and Barnes 1982). Flowering in hybrids may be intermediate between or similar to one of the parents (Pregitzer and Barnes 1980; Spies and Barnes 1982).

Interspecific crossing between desired species or intraspecific crossing of selected individuals of the same species in a controlled environment is a common practice in breeding poplars. The general steps in this process are sum-

**Table 3**—*Populus,* poplar, cottonwood, aspen:   phenology of flowering and fruiting

| Species | Location | Flowering | Seed ripening & dispersal |
|---|---|---|---|
| *P.* x *acuminata* | Nebraska | May | July |
| *P. alba* | Nebraska | Apr–May | Early June |
| | NE US | Apr–May | May–June |
| | S Michigan | Mar–Apr | May–June |
| *P. balsamifera* | Alberta | Late Apr | Early June–early July |
| | Lake States | Apr–May | May–June |
| | Interior Alaska | May–June | July |
| *P. balsamifera* spp. *trichocarpa* | Vancouver Island, British Columbia | Apr–June | Late May–mid-July |
| *P.* x *canescens* | Great Lakes region | Late Apr | Late May |
| *P. deltoides* | Lower Mississippi Valley | Early Mar–early Apr | Mid-May–late Aug |
| | NE US | Apr–early May | May–mid-June |
| spp. monilifera | Alberta | — | late June–early Aug |
| | Lincoln, Nebraska | Apr–May | June |
| spp. *wislizeni* | Albuquerque, New Mexico | Apr–May | June–July |
| *P. fremontii* | Central Arizona | mid-Feb–mid-Mar | Mar–Apr |
| *P. grandidentata* | Syracuse, New York | Mid-Mar–mid-Apr | Mid-May–late May |
| | S Michigan | Late Mar–min-May | early May–late June |
| | New England | Mid-Mar–Apr | May–early June |
| | N Great Lakes region | Late Apr–early May | Late May–early June |
| *P. heterophylla* | Mississippi | Mar–May | Apr–July |
| *P. maximowiczii* | Rochester, New York | Late Apr | Aug |
| *P. nigra* | Rochester. New York | Apr | Late May |
| *P. tremula* | N Great Lakes region | Mid-Apr | Mid-May |
| *P. tremuloides* | Great Lakes region | Late Mar–early May | Mid-May–mid-June |
| | Alberta, Canada | Early Apr–early May | Mid-May–mid-June |
| | New England | Mid-Mar–Apr | May–early June |
| | Interior Alaska | Apr–May | Late May–early June |
| *P. tremula* | N Great Lakes region | Mid-Apr | Mid-May |

**Sources:**   Johnson (1990); Schreiner (1974).

marized below, but for more detail refer to Einspahr and Benson (1964), Farmer and Nance (1968), Gladysz (1983), Johnson (1945), Larsson (1975), Stanton and Villar (1996), Stettler and others (1980, 1996), Wettstein (1933), and Wyckoff (1975).

- Branches with flower buds are collected from male clones in late winter after cold requirements for dormancy have been satisfied. The branches are incubated in a controlled environment in water-filled containers. (Water should be changed 2 to 3 times per week. Before branches are placed in water and each time the water is changed, their ends should be recut. This removes 1 to 2 cm of wood and exposes fresh xylem to maintain water uptake.) Pollen is usually produced in 1 to 2 weeks, depending on species and temperature conditions. Pollen can be collected and stored in a desiccator for 1 to 2 months at about 0 to 1 °C and low humidity. For longer storage, the pollen should be kept under vacuum at –20 °C according to the procedure described by Hermann (1969).

- Branches or grafted material from female clones are brought into a controlled environment after cold requirements have been satisfied. This is usually timed to be several days after male branches are collected or after pollen has been extracted. The best length for cut branches is about 1 m. The cut stems are treated as described above for male branches. Alternatively, grafted or rooted cuttings have been recommended for species with large catkins or with longer flowering and seed maturation periods such as occur in eastern cottonwood.

- As the female flowers begin to elongate, pollen is applied with a brush or atomizer. Pollen is sometimes applied to flowers over several days to ensure good pollination and seed yield. Small quantities of viable, select pollen are often mixed with heat-killed pollen to extend the amount available. To make crosses between individuals with poor compatibility, irradiated or otherwise sterile pollen (mentor pollen) from a compatible source is mixed with the desired viable pollen (Stettler and Guries 1976). It may be necessary to remove a sig-

nificant number of flowers from the branches in order to ensure enough water, nutrition, and carbohydrate for full development of a limited number of catkins. Cooler greenhouse temperatures (15 to 21 °C) are better than warmer temperatures. Seeds are collected as the ripened capsules open. *In vitro* embryo culture has also been used in hybrid breeding programs where seed yield is low or non-existant.

An individual eastern cottonwood tree, measured to be 12.3 m in height with a stem diameter of 0.6 m and a crown spread of 13.8 m, bore about 32,400 catkins. These produced about 27 capsules per catkin and about 32 seeds per capsule. The average weight of 100 seeds (with cotton) was 0.065 g. On this basis, it was estimated that this tree produced nearly 28 million seeds, weighing about 18.2 kg (Bessey 1904). Aspen species also produce seeds in large quantities. Reim (1929) reported the following estimates of seed production for sample trees of European aspen in Estonia and Finland:

| Age of tree (yr) | Catkins (no.) | Seeds (no.) |
| --- | --- | --- |
| 8 | 9 | 8,700 |
| 25 | 1,200 | 1,275,000 |
| 25 | 500 | 205,000 |
| 45 | 10,000 | 3,300,000 |
| 100 | 40,000 | 54,000,000 |

Although poplar seeds seem to be available each year, there have been few studies thoroughly documenting annual periodicity (Burns and Honkala 1990). Cottonwoods and balsam poplar (Figure 1) produce large seedcrops almost every year; aspens produce some seeds almost every year, and bumper crops are produced at intervals of 3 to 5 years. Six-year records for seed shedding by balsam and Petrowsky poplars in Alberta indicated an abundance of seeds in all years; aspen produced heavy seedcrops about 3 of every 7 years and comparatively little or no seeds in the other years (Moss 1938). During a 3-year period in interior Alaska, there was 1 excellent and 2 poor seedcrops (Zasada 1996).

Annual flowering records of 25- to 33-year-old quaking aspen clones (17 female and 16 male) established as grafts in a Wisconsin breeding arboretum indicated that the females flowered in 70% of the years of a 20- to 26-year period; males in 80% of the years and 2 bisexual clones in 78% of the years. (Note: these clones were randomly selected based on superior phenotypic characteristics, with no prior knowledge of tree gender. The male to female ratio for this collection covering a wide geographic area was basical-

ly 1:1 and substantiates studies cited above.) Individual female clones flowered in as few as 41% and as high as 100% of the years; individual male clones flowered in as few as 55% and as high as 100% of the years. Males tended to flower more frequently than females, with 38% of the male clones flowering in at least 95% of the years compared to 18% of the female clones flowering in at least 95% of the years. Eleven grafted clones established in the arboretum flowered 1 year after planting. Years when widespread flowering occurred in a Wisconsin arboretum appeared to be related to below normal rainfall in May of the previous years (Wyckoff 1996).

One clone of quaking aspen was established in the same year as both grafts and rooted root sprouts. The grafted ramets flowered in 70% of the years in a 23-year period; the rooted ramets flowered in 4% of the those years (Wyckoff 1996).

**Figure 1**—*Populus balsamifera*, balsam poplar:   tree at peak stage of seed dispersal.

Flowering of 24- to 36-year-old grafted clones of big-tooth aspen (3 female and 7 male) was also followed in the above-mentioned Wisconsin arboretum. The female clones flowered in 35% of the years in a 20- to 25-year observation period and the males in 18% of the years. Flowering of individual female clones occurred in from 29 to 40% of the years; male clones flowered in 0 to 50% of the years (Wyckoff 1996).

Mature catkins are made up of many capsules, each developed from an individual flower (figures 1 and 2). The number of viable seeds per capsule has been reported to vary from 2 to 7 for quaking aspen (Brown 1989; Henry and Barnes 1977; Nagaraj 1952; Spies 1978); 2 to 10 for big-tooth aspen (Henry and Barnes 1977); 2 to 4 for bigtooth–quaking aspen hybrids (Henry and Barnes 1977); about 1 for white poplar (Spies 1978); 1 to 2 for white poplar hybrids with bigtooth aspen (Spies 1978); and 8 to 15 (Nagaraj 1952), 32 (Bessey 1904), and 40 to 60 for eastern cottonwood (Farmer and Nance 1968). Estimates of seed production per catkin for quaking aspen have varied considerably among studies and locations: 500 in central Alberta (Brown 1989), 77 in northern Wisconsin (Rudolph 1978) 280 to 290 in southern Michigan, (Henry and Barnes 1977; Spies 1978), and 150 to 300 in central Wisconsin (Einspahr and Benson 1964). Henry and Barnes (1977) reported 500 seeds per catkin for bigtooth aspen. Spies (1978) reported about 11 seeds per catkin for white poplar, 281 for quaking aspen, and 102 for the hybrid P. × *rouleauiana* Boivin.

**Figure 2**—*Populus*, poplar:    catkins consisting of mature but unopened capsules.—*P.deltoides* ssp. *monilifera*, plains cottonwood (**top**); *P. fremontii*, freemont cottonwood (**middle**); *P. freemontii* ssp. *wislizeni*, Rio Grande cottonwood (**bottom**).



The distance traveled by poplar seeds during primary dispersal equals or exceeds that for any tree species in North America. If seeds should land in a river, the distance of secondary dispersal can also be great. Aspen seed rain and seedling establishment have been observed in significant quantities at distances of 5 to 10 km from the nearest seed source (Dyrness and others 1988; Zasada 1996; Zasada and Densmore 1979). Large quantities of seeds are deposited in the parent stand too. The dispersal unit—seed plus hairs, also referred to as "cotton" and "coma" (Fechner 1972; Fechner and others 1981; Roe and McCain 1962)—is very buoyant and ideally suited for both vertical and horizontal long distance movement by wind and air turbulence. The hairs are an outgrowth of epidermal cells of the ovule and are attached to the seed near the radicle (Fechner 1972). The deployment of these hairs has been described by Lautenschlager (1984) and Lautenschlager and Lautenschlager (1994) for Willow and briefly summarized by Zasada and others (2005).

Estimating seed rain in the Salicaceae is more difficult than in other trees because of the small size and short life of seeds and the type of dispersal unit. Water-filled seed traps and germination seed traps have proved useful (Walker and others 1986; Zasada 1996; Zasada and Densmore 1979), as have traps that use sticky substances. Water is a particularly good medium in which to catch seeds because once the dispersal unit lands on water it remains and because Salicaceae seeds germinate in water, allowing an assessment of viability.

A seed consists of an embryo surrounded by a thin transparent seedcoat. Seeds are very small, measuring but a few millimeters in length and width (figures 3, 4, and 5). There may be a rudimentary endosperm, but it apparently contributes nothing to the vigor of seeds during germination (Simak 1980). Nagaraj (1952) reports that the endosperm is completely consumed by the developing embryo in both quaking aspen and eastern cottonwood. The dry seeds tend to be tan to straw-colored in some species and green in others. Seed weights can vary substantially within a species and among sympatric species. For example, quaking aspen seeds were reported to weigh 0.127 g/1,000 seeds (223,200/oz) (Spies 1978), 0.133 g/1,000 seeds (212,000/oz) (Benson 1972), and 0.035 g/1,000 seeds (818,000/oz) (Henry and Barnes 1977) and bigtooth aspen, 0.091 g/1,000 seeds (312,000/oz), 0.093 g/1,000 seeds (306,000/oz), and 0.021 g/1,000 seeds (1,350,000/oz), respectively, for seeds of the 2 species collected in different years. The seed size of hybrids may be intermediate or smaller than that of their parents (Henry and Barnes 1977; Spies 1978). Tables 4 and

Figure 3—*Populus balsamifera*, balsam poplar: catkins in different stages of capsule opening. Capsules on the catkin in the foreground are unopened whereas those on the catkin in the background, and on the same branch as catkin in foreground, are fully opened and their cotton is fully expanded. The small dark dots in the cotton mass are individual seeds.



Figure 4—*Populus*, poplar: cleaned seeds of quaking aspen, *P. tremuloides* (**left**); cottonwood, *P. deltoides* (**center**); and bigtooth aspen, *P. grandidentata* (**right**); units on the scale at right are millimeters.



5 provide seed weight information for several poplar species and their hybrids (Wyckoff and Harder 1996). These seed weights are in agreement with other published information (Schreiner 1974) and support the reports of intermediate seed weight of hybrids. Section Leuce poplars tend to have smaller and lighter weight seeds than do species of other sections.

**Collection, extraction, and cleaning of seeds.** Seeds can be safely collected when a small percentage of capsules begin to open (Brown 1989; Fung and Hamel 1993; Johnson 1946; Maisenhelder 1951; Moss 1938; Wyckoff 1975). For aspen, it has been suggested that catkins should be picked from the trees when the seeds are a light straw color; those collected before reaching this stage do not ripen completely, reducing the yield of viable seeds (Brown 1989; Faust 1936). Branches with attached, immature catkins can be collected, placed in water, and ripened in a greenhouse. Seeds are collected as open capsules.

Care must be taken in handling catkins after they have been removed from the tree. They should be transported in a container, for example a large paper bag, that allows some air circulation and from which water can evaporate; this is particularly true if the catkins are to be kept in the container for several days during transport. For rapid drying, catkins should be spread out in thin layers in pans or on screens at room temperatures as soon as possible. Seeds will be shed in 1 to 5 days, depending on the ripeness of the catkin. Eastern cottonwood seeds also have been extracted by putting the ripe catkins through a standard seed macerator with the cylinder teeth 1.3 cm ($^1/_2$ inch) apart and running the macerated catkins over a clipper fanning mill (Engstrom 1948).

If the catkins are permitted to mature on cut branches in water culture, the seeds can be collected with a shop vacuum cleaner using a clean cloth bag substituted for the dust bag (Harder 1970; Roe and McCain 1962). Seeds from detached catkins spread out to dry in a thin layer can also be collected with this machine.

The most efficient method for freeing poplar seeds from the cotton is by tumbling them in a rotating drum or stream of relatively high pressure air. For small quantities of seeds, separation can be done by placing the seeds with cotton in a container over a nest of soil sieves or between 2 soil sieves and applying a stream of air at high velocity to tumble the seeds in the container. The seeds fall through to the lower screen of smaller sieve openings (Einspahr and Schlafke 1957; Fung and Hamel 1993; Roe and McCain 1962). Compressed air from any source or air from a vacuum cleaner exhaust can be used. Screen mesh size (openings per inch) will depend on seed size (table 4); a larger-seeded

**Table 4**—*Populus,* poplar, cottonwood, aspen:   seed weights by soil sieve size (20 to 50 mesh)*

| Species | 20-mesh /g | /oz | 28-mesh /g | /oz | 40-mesh /g | /oz | 50-mesh /g | /oz |
|---|---|---|---|---|---|---|---|---|
| | | | **Seeds (millions)/weight** | | | | | |
| *P. alba* | 5.09 | 2.31 | 8.89 | 4.03 | 19.71 | 8.94 | — | — |
| *P. balsamifera* | — | — | 7.90 | 3.58 | 8.69 | 3.94 | — | — |
| spp. *trichocarpa* | 2.71 | 1.23 | 4.54 | 2.06 | — | — | — | — |
| *P. x canescens* | — | — | 7.50 | 3.40 | 13.87 | 6.29 | — | — |
| *P. deltoides* | 2.93 | 1.33 | 4.92 | 2.23 | — | — | — | — |
| *P. grandidentata* | — | — | — | — | 21.52 | 9.76 | 39.58 | 17.95 |
| *P. tremula* | — | — | — | — | 17.46 | 7.92 | — | — |
| *P. tremuloides* | — | — | 13.19 | 5.98 | 18.46 | 8.37 | 23.62 | 10.70 |
| **Some hybrid crosses†** | | | | | | | | |
| *P tremuloides x P. tremula* | — | — | 10.61 | 4.81 | 17.68 | 8.02 | 38.68 | 17.54 |
| *P. tremula x P. tremuloides* | — | — | 18.43 | 8.36 | 44.10 | 20.00 | — | — |
| *P. tremuloides x P. canescens* | — | — | — | — | 16.27 | 7.38 | — | — |
| *P. canescens x P. tremuloides* | — | — | 7.74 | 3.51 | 13.38 | 6.07 | 35.57 | 16.13 |
| *P. grandidentata x P. alba* | — | — | — | — | 23.09 | 10.47 | 47.83 | 21.69 |
| *P. alba x P. grandidentata* | 4.81 | 2.18 | 10.52 | 4.77 | 15.79 | 7.16 | 35.10 | 15.92 |
| *P. grandidentata x P. canescens* | — | — | — | — | 19.45 | 8.82 | 30.96 | 14.04 |
| *P. canescens x P. grandidentata* | — | — | 7.08 | 3.21 | 10.36 | 4.70 | 31.00 | 14.06 |
| *P. deltoides x P. balsamifera* | 4.34 | 1.97 | 5.18 | 2.35 | — | — | — | — |
| *P. deltoides x P. nigra* | 4.43 | 2.01 | 6.90 | 3.13 | 60.86 | 27.60 | — | — |
| *P. deltoides x P. trichocarpa* | 3.00 | 1.36 | 4.54 | 2.06 | — | — | — | — |
| *P. trichocarpax  P. balsamifera* | 3.20 | 1.45 | 4.83 | 2.19 | — | — | — | — |

**Source:**  Wyckoff (1999).
\* Sieve=standard soil screen sieve openings per square inch.
† In hybrid crosses, the female parent is listed first.

species, for example cottonwood, requires larger mesh screens (Einspahr and Schlafke 1957). Nests of sieves recommended for aspen are 20-, 28-, 40-, and 50-mesh soil screens from top to bottom  (Harder 1970). Seeds were collected on the 40- and 50-mesh screens, with the best seeds on the 28- and 40-mesh screens for aspen and 20- to 28 mesh screens for cottonwood (Fung and Hamel 1993; Harder 1970; Rudolph 1978). Larger quantities of seeds may be cleaned efficiently in a rotating drum with or without a fan to blow the seeds through the wire seed screen; the cotton will remain in the drum. Small quantities of seeds can be separated from the cotton by rubbing them over a wire soil screen with suitably small mesh, by hand, or with a heavy brush (Faust 1936; Maisenhelder 1951). However, only about 20% of the seedlot can be extracted by this method (Maisenhelder 1951). Simak (1980) stresses that dried seeds can be brittle and damaged with rough handling during the extraction process.

Debris can be partially removed from poplar seedlots by carefully applying low-pressure air to seeds placed in a 500-ml Erlenmeyer flask held at a 30 to 45% angle. A highly efficient technique used routinely by the University of
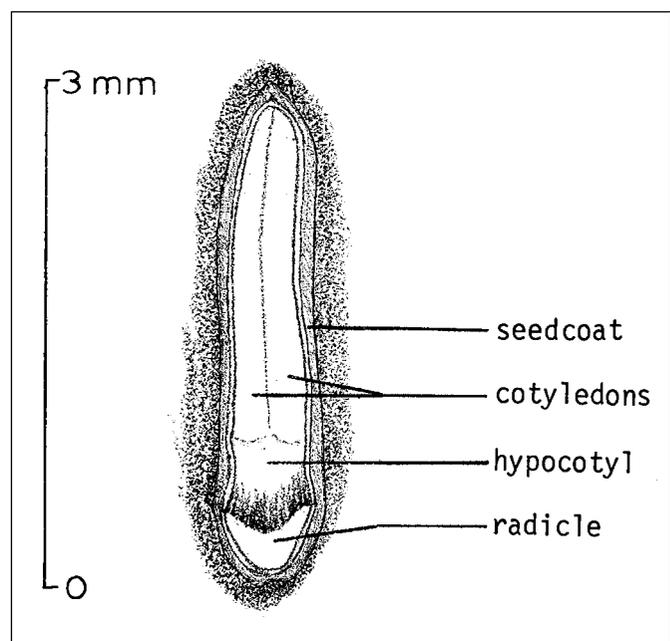
**Figure 5**—*Populus*, poplar:    longitudinal section through the embryo of a seed.

**Table 5**—*Populus*, poplar, cottonwood, aspen:   seed weights of non-screened samples

| | Seeds (x million)/weight | | | | |
| | Range | | Average | | |
| Species | /kg | /lb | kg | /lb | Samples |
| --- | --- | --- | --- | --- | --- |
| *P. deltoides* | 0.44–3.31 | 0.20–1.50 | 0.77 | 0.425 | 6+ |
| *P. deltoides* spp. *monilifera* | 0.55–1.06 | 0.25–0.48 | — | — | 4+ |
| *P. grandidentata* | — | — | 6.62 | 3.00 | 1 |
| *P. heterophylla* | 0.31–0.36 | 0.14–0.16 | 0.34 | 0.15 | 4 |
| *P. tremula* | 5.89–16.65 | 2.66–7.55 | 8.09 | 3.67 | 30 |
| *P. tremuloides* | 5.51–6.62 | 2.5–3.0 | 6.00 | 2.75 | — |

**Source:**   adapted from Schreiner (1974).

Minnesota's Aspen and Larch Genetics Cooperative employs a vacuum seed sorter built after the one described by Edwards (1979). Seedlots cleaned by this technique are virtually free of contamination, an important consideration when seeds are to be sown mechanically in containers.

**Storage of seeds.**    Under natural conditions, poplar seeds have been reported to maintain viability from 2 weeks to a month, varying with species, season, and microenvironment. There is some evidence that poplar seeds may have a longer lifespan under apparently adverse conditions such as in colder soils (Graham and others 1963; McDonough 1979; Moss 1938; Trappe 1964; Zasada and Densmore 1977).

Poplar seeds are one of the best examples of seeds with a short life-span (microbiotic seeds) among tree species. However, with proper drying and storage at subfreezing temperatures in sealed containers, the viability of seeds of eastern cottonwood (Tauer 1979, 1995; Wang 1982), and quaking and bigtooth aspen (Benson and Harder 1972, 1996; Wang 1982) have been maintained at fairly high levels for 10 to 12 years. Loss in viability during these relatively long storage periods varies among species and trees within species (Asakawa 1980; Benson and Harder unpublished data; Fechner and others 1981; Simak 1980; Tauer 1979, 1995; Wang 1982; Zasada and Densmore 1977, 1980). For example, Tauer (1995) found that percentage germination varied from 3 to 53% among individual trees after 12 years of storage, whereas initial germination ranged from 47 to 100%.

There is no single method of storage found to be generally acceptable for all species (Simak 1980). There are several elements that are important for maintaining long-term viability.  Prestorage drying during capsule opening and immediately after extraction is essential for successful storage (Simak 1980). The desired moisture content for several species seems to lie between 6 and 10% (dry weight basis) (Simak 1980; Tauer 1979; Zasada and Densmore 1977,

1980), although Wang (1982) reported good long-term storage at 11 to 15% moisture content (dry-weight basis). Seed viability is maintained at lower moisture contents, but there is an indication that seedling vigor is reduced under these conditions (Simak 1980). Recommendations for drying time to achieve these approximate moisture contents have varied: for example, 2 to 3 days at 21 °C (Moss 1938); 3 to 8 days at 24 °C  (Faust 1936); air-drying for 7 days (Tauer 1979); 1 day at 35 to 40 °C, and 1 day of drying over calcium chloride ($CaCl_2$) (Simak 1980). If achieving a specified moisture content is important, a method should be used that attains the desired content as quickly as possible while not affecting seed viability.

A number of research trials have compared storage under vacuum and with various desiccants to storage in sealed containers; unfortunately, the results are not definitive. In some cases, they work and in others they seem to be of no benefit or may even have a negative effect on viability.

Benson and Harder (1972) compared 4-year germination results from 40-mesh aspen and aspen hybrid seeds stored over calcium chloride in a desiccator at 4.4 °C and –24 °C. Freezer storage maintained higher levels of viability in each of the 4 years with the exception of 2 hybrids of bigtooth aspen during the first year. By year 4, all seedlots stored at 4.4 °C were either nonviable or had considerably reduced germination. Freezer-stored seeds maintained a high level of germinative ability at the end of 4 years, with the exception of gray poplar hybrids. Benson and Harder's study (1977, 1996) indicates that germination of freezer-stored seed of quaking aspen dropped from an average of 98% to 65% over a 10-year period. Hybrid seeds and 50-mesh seeds generally had lower germination than quaking aspen and 40-mesh seeds after 10 years of freezer storage. Seed viability of 3 of 4 open-pollinated cottonwood seedlots stored at –24 °C over calcium chloride did not decrease during 8 years of storage.

Hellum (1973) found that balsam poplar seedlots stored in sealed containers without desiccant at 7 °C and 21 to 24 °C rapidly lost viability after 130 days at both temperatures. Cold-stored seedlots retained viability longer (40 vs 5% at 200 days) but viability dropped to 5% at 245 days.

Simak (1980) reported that storage of European aspen seeds with a desiccant reduced viability because it dried seeds to a sub-optimal moisture content. Simak (1980) concluded that, when using desiccants, the desired moisture content of the seeds should be known and the type and quantity of desiccant should be selected to achieve the desired conditions. For example, seeds will equilibrate at the desired moisture content in an atmosphere of 10 to 30% relative humidity, and thus the desiccant should be selected that provides these conditions (Simak 1980). The optimum rate of drying is not known. Tauer (1979, 1995) reported that there was no difference in viability between cottonwood seeds stored with and without a vacuum at –22 °C after about 6 years. However, after 12 years, seeds from different families stored in a vacuum germinated at 10 to 99%, whereas those without vacuum germinated at 3 to 53%.

The one aspect of storage about which there seems to be no question is temperature conditions for long-term storage. Seeds should be extracted and placed in subfreezing storage as soon as possible. Seeds from boreal and Arctic species and those from warm climate species all seem to have the same general requirements. Temperatures from –5 to –24 °C seem acceptable and easy to achieve and maintain (Benson and Harder 1972; Fechner and others 1981; Moss 1938; Simak 1980; Tauer 1979; Wang 1982; Zasada and Densmore 1977, 1980). Seeds can be stored at 0 to 5 °C, but longevity is shorter and high levels of abnormal germination may occur sooner than at sub-freezing temperatures.

**Germination tests.** The criteria used to define germination are important when evaluating germination in the Salicaceae. The standards proposed by Simak (1980) for *Salix* and *Populus* germination provide a basis for assessing germination (figure 6). The work of Simak (1980) illustrates convincingly that use of criteria that do not include all of the stages leading up to appearance of a "normal" seedling may be suspect. Development of the hypocotyl hairs—or "coronet" as described by Fechner and others (1981)—and attachment of these hairs to the substrate is a departure from the usual pattern of epigeal germination (other species do not have these specialized hairs) and should be an assessment criteria for germination. The average time elapsed to achieve the various stages of development under greenhouse conditions are shown in figure 6; they will, however, vary depending on temperature and water availability (McDonough

1979; Schreiner 1974; Simak 1980).

Poplar seeds do not exhibit dormancy; they germinate at temperatures ranging from 2 to 40 °C (figure 7). Simak (1980) provides a thorough description of abnormal germination in Salicaceae. Average time required for aspen seeds to achieve various stages of germination under greenhouse conditions are indicated in hours and days (Wyckoff 1996). Optimum temperatures for germination may vary with species and possibly within widely distributed species like quaking aspen, but they appear to be in the range of 20 to 30 °C. Germination rate increases with temperature but appears to be fairly uniform above 15 to 20 °C and may decline slightly above 30 to 35 °C (figure 7). Temperatures above 35 °C caused a large decline in germination in aspen but had little effect on eastern cottonwood (Farmer and Bonner 1967; Faust 1936; Moss 1938; McDonough 1979; Zasada and Densmore 1980; Zasada and Viereck 1975). Seeds germinate fully in complete darkness, but rate of germination may be less than in light (Asakawa 1980; McDonough 1979).

Germination occurs on a wide variety of substrates. Some *Populus* species appear to have fairly exacting requirements for germination whereas others are less affected. Substrates with a steady supply of water during germination and early seedling development and a neutral or slightly acidic to slightly basic pH provide conditions for maximum germination (Dickmann and Stuart 1983; Farmer and Bonner 1967; Faust 1936; Fechner and others 1981; McDonough 1979; Segelquist and others 1993). Seeds germinate while floating in water or when fully submerged (Hosner 1957; Krasny and others 1988). Substrates with high salt concentrations appear to reduce germination potential (Faust 1936; Krasny and others 1988; McDonough 1979; Shafroth and others 1995).

At the University of Minnesota's Aspen and Larch Genetics Cooperative, seeds are germinated on damp filter paper in petri dishes for viability checks. However, for estimates of germination and vigor of seedlots to be used in nursery beds and containers, seeds are sown in clay saucers filled with commercial soil-less mix. This technique is more important for seedlots with germination less than 70 to 80% because it gives a more accurate prediction of cell occupancy in containers and seedlings per area in seedbeds (Wyckoff 1996).

Aspects of germination outlined above apply to newly collected seeds. Results may vary for the following reasons:

• Seeds stored for varying lengths of time may germinate slowly and exhibit poorer germination than would be

**Figure 6**—*Populus*, poplar:  stages in the normal germination of a seed (adapted from Simak (1980) and McDonough (1979).
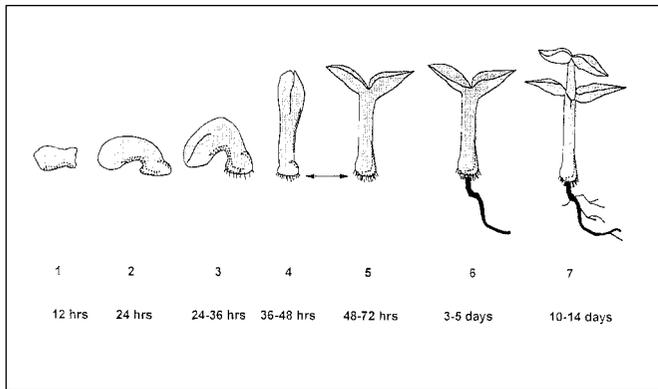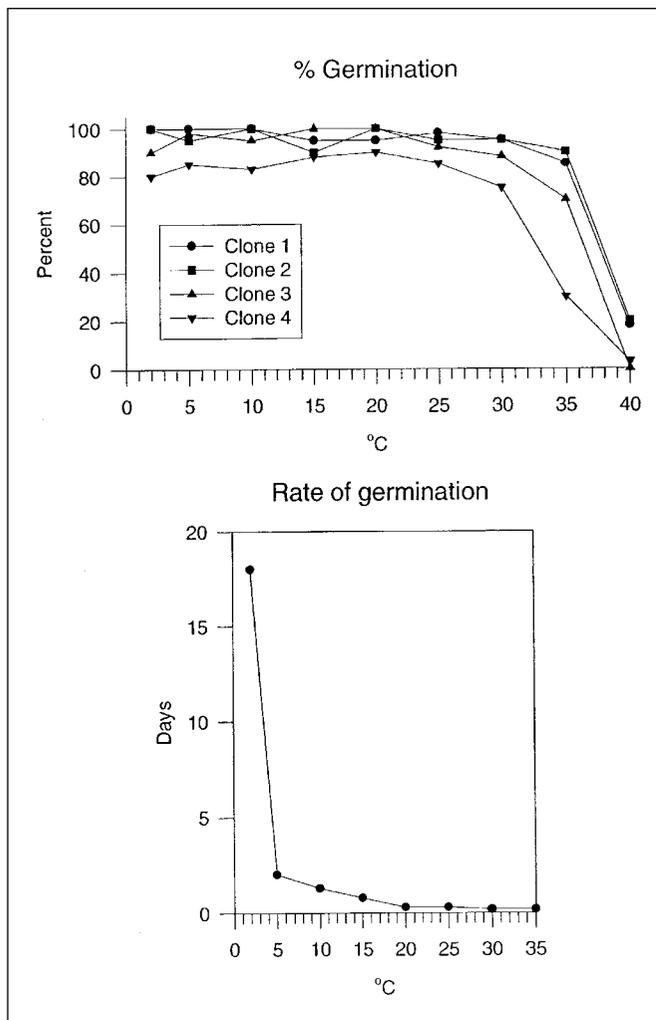


**Figure 7**—*Populus tremuloides*, quaking aspen:  effects of temperature on percentage germination and germination rate in seeds (from McDonough 1979); rate is expressed as time for 10% of seeds to germinate.



expected for fresh seeds; this may be particularly true when germinating outside the optimum temperature range (Farmer and Bonner 1967; McDonough 1979).

- Small seeds may not germinate as well as large seeds. For example, Faust (1936) found that seeds graded to a 40-mesh soil screen showed a germination percentage of less than half that of seeds graded to a 30-mesh soil screen. The same relation holds true for seeds from 40- and 50-mesh soil screens (Rudolph 1978).
- Germination of stored seeds of white poplar was reduced due to too rapid imbibition of water (Polya 1961).

Seed testing rules (ISTA 1993) recommend that germination tests consist of four 100-seed replications and that tests be conducted at temperatures between 20 and 30 °C, with initial counts after 3 days. The results of the research summarized above suggest that using temperatures of 20 to 25 °C might be best for all seeds, including those tested following storage. Because of the rapid rate of germination and germinant development, there will be instances where evaluation would be desirable after 1 or 2 days, particularly when comparing germination rates of stored vs. newly collected seeds. Earlier versions of seed testing rules (ISTA 1966) called for using 0.25 g of seeds per replicate. Because of the small size of poplar seeds (table 4), this is an unmanageable number of seeds for most species.

**Nursery practice.**  Poplar, aspen, and cottonwood seedlings can be produced in containers or as bareroot stock. High-quality seedlings can be grown under either system or a combination of the two (for example, plug+1 stock). The choice of a seedling production system will be determined by climate, economics, the method/system of planting, available facilities and equipment, and the type of seedling (diameter and root system characteristics) that will best meet management objectives. Containerized production seems to be more common, particularly in northern areas where greenhouse production can provide a longer and warmer growing season.

Early nursery techniques for direct-sowing cottonwood seeds into seedbeds have been described by Bull and Muntz (1943), Einspahr (1959), Engstrom (1948), Gammage and Maisenhelder (1962), Maisenhelder (1951), Peterson and Peterson (1992), Schreiner (1974), and  Wycoff (1960). Currently, both bareroot and container-grown aspen and aspen hybrid seedlings are being produced on a commercial scale. Bareroot seedlings are grown by direct-sowing cleaned seedlots onto seedbeds that are formed with sideboards and watered prior to sowing. Seeds are sown at a

density of 265 viable seeds/m$^2$ (25/ft$^2$) to produce 42 to 63 plantable seedlings/m$^2$ (4 to 6/ft$^2$) at lifting. The beds are lightly watering again after sowing, then covered with 1.3-cm ($^1/_2$-in) mesh hardware cloth and 50% shadecloth (Wyckoff 1996). Sowing is often done by hand: enough seeds to cover a given area of bed space are weighed out and sprinkled from vials with small holes drilled in the caps. Mechanical sowing is used where seeders capable of handling such small seeds are available.

Seedbeds are watered from an overhead irrigation system as needed during the first 3 weeks to maintain a moist surface without runoff or standing water; the seedbed covers are left in place during irrigation. The shadecloth is removed at 3 weeks, having served primarily to reduce surface drying and allowing irrigation without removal of seedbed covers. The hardware cloth is left in place until seedlings begin to reach it, for it can serve as protection against hail. Seedlings are lifted in the fall after leaf drop, then graded and placed in polyethylene lined boxes for storage at –2 to –4 °C. Packing material such as sphagnum moss, shredded wet newsprint, and hydromulch have been used to keep roots from desiccating during storage. The same technique has also been used successfully with cottonwood, balsam poplar, and poplar hybrids (Wyckoff 1996).

Containers of different sizes and shapes have been used to produce aspen seedlings. However, plug-type containers with cavity volumes of 350 to 450 cm$^3$ (21 to 27 in$^3$) provide sufficient growing space to produce a large seedling with 5 to 7 mm (0.2 to 0.3 in) root collar diameters and 60 cm (2 ft) heights in 1 growing season (Burr 1985; Wyckoff and others 1995). The containers are typically sown by hand or with precision mechanical seeders, germinated in a greenhouse, then moved outside for the remainder of the growing season. Seedlings are planted in the same year that they are grown or stored for planting the following year. The time of planting will determine the sowing schedule, provided greenhouses can be heated (Carlson and Fung 1996).

A third technique, using both greenhouse and nursery beds to produce plug+1 bareroot aspen seedlings, combines the advantage of seed-use efficiency of greenhouse containers with the production of a high number of large-diameter seedlings from seedbeds (Wyckoff 1996). Typically, seeds are mechanically sown into horticulture bedding flats with cavity volumes of 15 to 25 cm$^3$ (0.9 to 1.5 in$^3$) and 1,280 cavities/m$^2$ (119/ft$^2$). These are kept under greenhouse conditions for 8 to 9 weeks. At the end of this time, 8- to 10-cm

(3- to 4-inch) tall seedlings are transplanted into seedbeds at densities of 43 to 54 seedlings/m$^2$ (4 to 5 seedlings/ft$^2$) and grown for one season. On average, it requires 1.5 to 2 viable seeds to produce 1 container seedling with a minimum 5-mm (0.2-in) root collar diameter; 5 to 6 viable seeds to produce a bareroot seedling with a minimum 7-mm (0.3-in) root collar diameter; and 2.7 seeds to produce a plug+1 bareroot seedling with a minimum 7-mm (0.3-in) root collar diameter. Seedlings grown in the plug +1 regime attain heights of 1 m (3.2 ft) in a single growing season (Wyckoff 1996).

The following features are common to all growing systems:

- Sowing is most efficient when seeds are separated from the hair, which makes it easier to control seeding density and distribution in nursery beds and containers.
- It is necessary to determine seedlot viability prior to sowing; this is particularly important for seeds that have been stored for several or more years.
- Covering seeds with more than a few millimeters of soil may significantly reduce germination (Maisenhelder 1951; McDonough 1979; Richter 1936).
- Maintaining adequate water content of the seedbed surface is critical for germination and establishment. Application of a fine spray of water causes less flooding of the seedbed and less seed movement, resulting in more rapid seedling establishment and more efficient use of seeds.
- Shading may be beneficial during germination, but seedlings will grow most rapidly in full light (Burns and Honkala 1990).
- Use of a fungicide may be necessary because of the continuous high moisture levels during early development (Shea and Kuntz 1956). This may be more critical in greenhouse production where temperature and relative humidity are more conducive to development of damping-off fungi.

Seedling production is important in breeding and clone development, but once desirable clones have been identified for use in intensively managed biomass and energy plantations they are propagated exclusively by vegetative reproduction. For a discussion of various aspects of vegetative reproduction see Dickmann and Stuart (1983), FAO (1980), Stettler and others (1996), and Dickmann and others (2001).

Andrejak GE, Barnes BV. 1969. A seedling population of aspens in southeastern Michigan. Michigan Botanist 8: 189–202.

Asakawa S. 1980. Storage of *Populus maximowiczii* seeds. In: Proceedings, International Symposium on Forest Tree Seed Storage; 1980 September 23–27; Chalk River, ON. Ottawa: Canadian Forestry Service: 136–141.

Baker S. 1925. Aspen in the central Rocky Mountain Region. Dept. Bull. 1291. Washington, DC: USDA Forest Service. 47 p.

Barnes BV. 1961. Hybrid aspens in the lower peninsula of Michigan. Rhodora 63(775): 311–324.

Barnes BV. 1966. The clonal growth habit of American aspens. Ecology 47(3): 439–447.

Barnes BV. 1969. Natural variation and delineation of clones of *Populus tremuloides* and *P. grandidentata* in northern lower Michigan. Silvae Genetica 18: 130–142.

Benson MK. 1972. Breeding and establishment—and promising hybrids. In Aspen: Symposium Proceedings. Gen. Tech. Rep. NC-1. St. Paul: USDA Forest Service, North Central Forest Experiment Station: 88–96.

Benson MK, Harder ML. 1972. Storage of aspen seed. Genetics and Physiology Notes 11. Institute of Paper Chemistry.

Benson MK, Harder ML. 1996. Unpublished data. Grand Rapids, MN: University of Minnesota Aspen and Larch Genetics Cooperative and USDA Forest Service, North Central Experiment Station.

Bessey CE. 1904. The number and weight of cottonwood seeds. Science 20(499): 118–119.

Brayshaw TC. 1966. Native poplars of southern Alberta and their hybrids. Pub. 1109. Ottawa: Canada Department of Forestry. 40 p.

Brown KR. 1989. Catkin growth, seed production, and development of seed germinability in quaking aspen in central Alberta. Tree Planters' Notes 40(20): 25–29.

Bull H, Muntz HH. 1943. Planting cottonwood on bottomlands. Bull. 391. [Starkville], MS: Mississippi State College Agricultural Experiment Station. 18 p.

Burns RM, Honkala BH, tech. coord. 1990. Silvics of North America. Volume 2, Hardwoods. Agric. Handbk. 654. Washington, DC: USDA Forest Service. 877 p.

Burr KE. 1985. Greenhouse production of quaking aspen seedlings. In: Intermountain Nurseryman's Association Meeting; 1985 August 13–15; Fort Collins, CO: 31–37.

Carlson M, Fung MYP. 1996. Personal communication. Vernon, BC: British Columbia Forest Service, Kalamalka Research Station.

Ceulemans R. 1990. Genetic variation in functional and structural productivity determinants in poplar. Amsterdam: University of Antwerp, Thesis Publishers. 99 p.

Comtois PJ, Simon P, Payette S. 1986. Clonal constitution and sex ratio in northern populations of balsam poplar. Holarctic Ecology 9(4): 251–260.

DeByle NV, Winokur RP, eds. 1985. Aspen: ecology and management in the western United States. Gen. Tech. Rep. RM-119. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 283 p.

Dickmann DI, Stuart KW. 1983. The culture of poplars in eastern North America. East Lansing: Michigan State University, Department of Forestry. 168 p.

Dickmann DI, Isebrands JG, Eckenwalder JE, Richardson J, eds. 2001. Poplar culture: North America. Ottawa: NRC Press.

Dyrness CT, Viereck LA, Foote MJ, Zasada JC. 1988. The effect on vegetation and soil temperature of logging flood-plain white spruce. Res. Pap. PNW-392. Corvallis, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 45 p.

Eckenwalder JE. 1977. North American cottonwoods (*Populus* Salicaceae) of sections Abaso and Aigeros. Journal of the Arnold Arboretum 58: 193–208.

Eckenwalder JE. 1980. Foliar heteromorphism in *Populus* (Salicaceae), a source of confusion in the taxonomy of tertiary leaf remains. Systematic Botany 5: 366–383.

Edwards DGW. 1979. An improved air seed-sorter for laboratory use. BC-X-188. Victoria, BC: Environment Canada, Pacific Forest Research Centre. 11 p.

Einspahr DW, Schlafke D. 1957. A method for aspen and cottonwood seed extraction. Tree Planters' Notes (28): 10.

Einspahr DW. 1959. Nursery production of aspen seedlings. Tree Planters' Notes 35: 22–24.

Einspahr DW. 1960a. Abnormal flowering behavior in aspen. Iowa State Journal of Science 34(4): 623–630.

Einspahr DW. 1960b. Sex ratio in quaking aspen and possible sex-related characteristics. 5th World Forestry Congress Proceedings 2: 747–750.

Einspahr DW, Benson MK. 1964. Production and evaluation of aspen hybrids. Journal of Forestry 62: 806–809.

Einspahr DW, Benson MK. 1971. Sex ratio and flowering in quaking aspen. Annual Report 23. Project 1800, Genetic Improvement of Aspen—Basic and Applied Studies During 1971. Appleton, WI: Institute of Paper Chemistry: 37–41.

Einspahr DW, Winton LW. 1977. Genetics of quaking aspen. Res Pap. WO-25. Washington, DC: USDA Forest Service. 23 p.

Einspahr DW, Wyckoff GW. 1990. North American aspen: timber supply, utilization, and research. Northern Journal of Applied Forestry 7(4): 168–171.

Engstrom A. 1948. Growing cottonwood from seed. Journal of Forestry 46: 130–132.

Farmer RE Jr. 1964a. Cottonwood flowering as related to cold requirement of flower buds. Forest Science 10(3): 296–299.

Farmer RE. 1964b. Sex ratio and sex-related characteristics in eastern cottonwood. Silvae Genetica 13(4): 116–118.

Farmer RE. 1966. Variation in time of flowering and seed dispersal of eastern cottonwood in the lower Mississippi valley. Forest Science 12(3): 343–347.

Farmer RE, Bonner FT. 1967. Germination and initial growth of eastsern cottonwood as influenced by moisture stress, temperature, and storage. Botanical Gazette 128 (3/4): 211–215.

Farmer RE, Nance WL. 1968. Crossing eastern cottonwood in the greenhouse. Proceedings, International Plant Propagator's Society 17th Annual Meeting. 17: 333–338.

Faust ME. 1936. Germination of *Populus grandidentata* and *P. tremuloides*, with particular reference to oxygen consumption. Botanical Gazette 97: 808–821.

Fechner GH. 1972. Development of the pistillate flower of *Populus tremuloides* following controlled pollination. Canadian Journal of Botany 50: 2503–2509.

Fechner GH, Burr KE, Myers JF. 1981. Effects of storage, temperature, and moisture stress on seed germination and early seedling development of trembling aspen. Canadian Journal of Forest Research 11: 718–722.

FAO [Food and Agriculture Organization of the United Nations]. 1980. Poplars and willows in wood production and land use. For. Series 10. Rome: FAO. 328 p.

Friedman JM, Scott ML, Auble GT. 1997. Water management and cottonwood forest dynamics along prairie streams. In: Knopf FL, Samson F, eds. Ecology and conservation of Great Plains vertebrates. Ecological Studies. New York: Springer-Verlag.

Fung MYP, Hamel BA. 1993. Aspen seed collection and extraction. Tree Planters' Notes 44(3): 98–100.

Fung MYP. 1996. Personal communication. Fort McMurray AB: Syncrude Canada Ltd.

Galloway G, Worrall J. 1979. Cladoptsis: a reproductive strategy in black cottonwood. Canadian Journal of Forest Research 9(1): 122–125.

Gammage JL, Maisenhelder LC. 1962. Easy way to sow cottonwood nursery beds. Tree Planters' Notes (51): 19–20.

Gladysz A. 1983. Jakosc nasion osiki produkowanych w warunkach szklarniowych [Quality of aspen seed produced in greenhouse conditions]. Sylwan 127(2): 9–20.

Graham SA, Harrison RP Jr, Westell CE Jr. 1963. Aspens, phoenix trees of the Great Lakes Region. Ann Arbor: University of Michigan Press. 272 p.

Grant MC, Mitton JH. 1979. Elevational gradients in adult sex ratios and sexual differentiation in vegetative growth rates of *Populus tremuloides* Michx. Evolution 33(3): 914–918.

Harder ML. 1970. Procedures for collection and extraction of *Populus* seed. Institute of Paper Chemistry, Genetics and Physiology Notes 9: 1–3.

Hellum AK. 1973. Seed storage and germination of black poplar. Canadian Journal of Plant Science 53: 227–228.

Henry RM, Barnes BV. 1977. Comparative reproductive ability of bigtooth and trembling aspen and their hybrid. Canadian Journal of Forest Research 55: 3093–3098.

Hermann S. 1969. Practical method to conserve pollen of forest trees under vacuum. In: Proceedings, 2nd World Consultation on Forest Tree Breeding; 1969 August 7–16; Washington, DC. Rome: FAO & IUFRO.

Holmes KW. 1982. Natural revegetation of gold dredge tailings at Fox, Alaska [master's thesis]. Fairbanks: University of Alaska. 197 p.

Hosner JF. 1957. Effects of water upon the seed germination of bottomland trees. Forest Science 3(1): 67–70.

Hyun SK, Noh ER, Hyun JO. 1984. A study for the nomenclature and registration for poplar species of the Section Leuce and their hybrids. In: Report to International Poplar Commission, 32nd Session of the Executive Committee, Subcommittee on Poplar Nomenclature and Registration, 1984 October 1; Ottawa. 53 p.

ISTA [International Seed Testing Association]. 1966. International rules for seed testing. Proceedings of the International Seed Testing Association 31(1): 1–152.

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

Isebrands JG, Rauscher HM, Crow TR, Dickmann DI. 1990.   Whole-tree process models based on structural-functional relationships. In: Dixon RK, Meldahl RS, Ruark GA, Warren WG, eds. Process modeling of forest growth responses to environmental stress. Portland, OR: Timber Press: 96–112.

Johnson LPV. 1945.   Development of sexual and vegetative organs on detached forest tree branches cultured in the greenhouse. Forestry Chronicle 21: 130–136.

Johnson LPV. 1946.   Effect of humidity on the longevity of *Populus* and *Ulmus* seeds in storage. Canadian Journal of Research (Sect. C) (24): 298–302.

Johnson RL. 1965.   Regenerating cottonwood from natural seedfall. Journal of Forestry 63(1): 33–36.

Kaszkurewicz A. 1975.   Establishment and early growth of *Poplus deltoides* Bartr. [PhD dissertation]. Baton Rouge: Louisiana State University, School of Forestry and Wildlife Management. 229 p.

Kay CE. 1993.   Aspen seedlings in recently burned areas of Grand Teton and Yellowstone National Parks. Northwest Science 67: 94–104.

Kemperman, JA. 1976.   Aspen clones: development, variability, and identification. For. Res. Info. Pap. 101. Sault Ste. Marie: Ontario Ministry of Natural Resources, Division of Forests, Forest Research Branch. 11 p.

Kemperman JA, Barnes BV. 1976.   Clone size in American aspens. Canadian Journal of Botany 4: 2603–2607.

Krasny ME, Vogt KA, Zasada JC. 1988.   Establishment of four Salicaceae species on river bars in interior Alaska. Holarctic Ecology 11: 210–219.

Larsson HC. 1975.   Techniques of mass-producing Jackii poplar under greenhouse conditions. Proceedings, 23rd Northeastern Tree Improvement Conference. Maple, ON: Ontario Ministry of Natural Resources: 158–164.

Lautenschlager E. 1984.   Keimungsbeobachtungen bei einigen Weidenspecies. Bauhinia 8(1): 31–35.

Lautenschlager FI, Lautenschlager E. 1994.   Die Weiden von Mittel- und Nordeuropa. Berlin: Birkhauser Verlag. 171 p.

Lester DT. 1961.   Observation on flowering in the aspens. Northeastern Forest Tree Improvement Conference 8 (1960): 35–39.

Lester DT. 1963.   Variation in sex expression in *Populus tremuloides* Michx. Silvae Genetiva 12(5): 141–151.

Little EL Jr, Brinkman K, McComb AL. 1957.   Two natural Iowa hybrid poplars. Forest Science 3(3): 253–262.

MacKinnon A, Pojar J, Coupe R, eds. 1992.   Plants of northern British Columbia. Edmonton, AB: Lone Pine Publishers. 351 p.

Maini JS, Coupland RT. 1964.   Anomalous floral organization in *Populus tremuloides*. Canadian Journal of Botany 42: 835–839.

Maisenhelder LC. 1951.   Planting and growing cottonwood on bottomlands. Bull. 485. Mississippi Agricultural Experiment Station. 23 p.

McDonough WT. 1979.   Quaking aspen: seed germination and early seedling growth. Res. Pap. INT-234. Ogden UT: USDA Forest Service. 13 p.

McDonough WT. 1985.   Sexual reproduction, seeds, and seedlings. In: Debyle NV, Winokur RP, eds. Aspen ecology and management in the western United States. Gen. Tech. Rep. RM-119. Fort Collins, CO: USDA Forest Service: 25–28.

Mitchell CP, Ford-Robertson JB, Hinckley T, Sennerby-Forsse L, eds. 1992.   Ecophysiology of short rotation forest crops. New York: Elsevier Applied Science. 308 p.

Mitton JB, Grant MC. 1996.   Genetic variation and the natural history of quaking aspen. Bioscience 46: 25–31.

Moss EH. 1938.   Longevity of seed and establishment of seedlings in species of *Populus*. Botanical Gazette 99(3): 529–542.

Nagaraj M. 1952.   Floral morphology of *Populus deltoides* and *P. tremuloides*. Botanical Gazette 114: 222–243.

Ostry ME, Ward KT. 1991.   Bibliography of *Populus* cell and tissue culture. Gen. Tech. Rep. NC-146. St. Paul: USDA Forest Service, North Central Forest Experiment Station. 26 p.

Parkerson RH. 1977.   The effects of N, P, and K fertilization on the lower stem xylem of quaking aspen in interior Alaska [PhD thesis]. Fairbanks: University of Alaska. 128 p.

Pauley SS. 1950.   Flowering habits in *Populus* [abstract]. Genetics 35: 684.

Pauley SS, Mennel GF. 1957.   Sex ratio and hermaphroditism in a natural population of quaking aspen. [University of Minnesota] Forest Notes 55: 1–2.

Peterson EB, Peterson NM. 1992.   Ecology, management, and use of aspen and balsam poplar in the prairie provinces. Edmonton, AB: Forestry Canada, Northwest Region, Northern Forestry Center. 252 p.

Peterson EB, Peterson NM. 1995.   Aspen managers' handbook for British Columbia: Canada-British Columbia Partnership agreement on forest resource development (FRDA II). Victoria: British Columbia Ministry of Forests. 110 p.

Polya L. 1961.   Injury by soaking of *Populus alba* seeds. Nature 189(4759): 159–160.

Pregitzer KS, Barnes BV. 1980.   Flowering phenology of *Populus tremuloides* and *P. grandidentata* and the potential for hybridization. Canadian Journal of Forest Research 10 (2): 218–223.

Rehder A. 1940.   Manual of cultivated trees and shrubs. 2nd ed. New York: Macmillan. 996 p.

Reim P. 1929.   Die Vermehrung biologie der Aspe auf Grundlage des in Estland und Finnland gesamelten Untersuchungsmaterial [Rudolf PE, trans. 1935. Regeneration biology of aspen on the basis of data collected Esthonia and Finland. Silvic. Transl. 220. Washington, DC: USDA Forest Service. 23 p.]

Richter H. 1936.   Über Pappelsaaten. Forstwissenschaftliche Centralblatt 58: 813–818.

Riemenschneider D. 1996.   Personal communication. Rhinelander, WI: USDA Forest Service, North Central Research Station.

Roe EI, McCain DP. 1962.   A quick method of collecting and cleaning aspen seed. Tree Planters' Notes 51: 17–18.

Rood SB, Mahoney JM, Reid DE, Zilm L. 1995.   Instream flows and the decline of riparian cottonwoods along the St. Mary River, Alberta. Canadian Journal of Botany 73: 1250–1260.

Rudolph TD. 1978.   Seed yield and quality in *Populus tremuloides* with gamma-irradiated pollen. Canadian Journal of Botany 56: 2967–2972.

Santamour FS. 1956.   Hermaphroditism in *Populus*. Northeast. In: Proceedings, Forest Tree Improvement Conference 3(1955): 28–30.

Schreiner EJ, Stout AB. 1934.   Description of ten new hybrid poplars. Bulletin of the Torrey Botanical Club 61: 449–460.

Schreiner EJ. 1971.   Genetics of eastern cottonwood. Res Pap. WO-11. Washington, DC: USDA Forest Service. 19 p.

Schreiner EJ. 1974.   *Populus* L., poplar. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 645–655.

Segelquist CA, Scott ML, Auble GT. 1993.   Establishment of *Populus deltoides* under simulated alluvial groundwater declines. American Midland Naturalist 130: 274–285.

Shafroth PB, Friedman JM, Ischinger LS. 1995.   Effects of salinity on establishment of *Populus fremontii* (cottonwood) and *Tamarix ramosissima* (saltcedar) in southwestern United States. Great Basin Naturalist 55(1): 58–65.

Shafroth PB. 1996.   Personal communication. Tempe: Arizona State University, Center for Environmental Studies.

Shea KR, Kuntz JE. 1956.   Prevention of damping-off of poplar seedlings. Forestry Science 2(1): 54–57.

Simak M. 1980.   Germination and storage of *Salix caprea* L. and *Populus tremuloides* L. seeds. In Proceedings, International Symposium on Forest Tree and Seed Storage; 1980 Sept. 23–27; Chalk River, ON. Ottawa: Canadian Forestry Service: 142–160.

Smith CE. 1943.   A study of cytology and speciation in the genus Populus L. Journal of the Arnold Arboretum 24: 275–305.

Spies TA. 1978.   The occurrence, morphology, and reproductive biology of natural hybrids of *Populus alba* in southeastern Michigan [MS thesis]. Ann Arbor: University of Michigan.

Spies TA, Barnes BV. 1982.   Natural hybridization between *Populus alba* L. and the native aspens in southeastern Michigan. Canadian Journal Forestry Research 12 (3): 653–660.

Stanton BJ, Villar M. 1996.   Controlled reproduction of *Populus*. In: Stettler RF, Bradshaw HD, Heilman PE, Hinckley TM, ed. Biology of *Populus* and its implications for management and conservation. Ottawa: NRC Press: 113–138.

Steneker GA. 1973.   The size of trembling aspen (*Populus tremuloides*) clones in Manitoba. Canadian Journal of Forest Research 3: 472–478.

Stettler RF. 1971.   Variation in sex expression in black cottonwood and related hybrids. Silvae Genetica 20: 42–46.

Stettler RF, Guries RP. 1976.   The mentor pollen phenomenon in black cottonwood. Canadian Journal of Botany 54(9): 820–830.

Stettler RF, Koster R, Steenackers V. 1980.   Interspecific crossability studies in poplars. Theoretical and Applied Genetics 58: 273–292.

Stettler RF, Bradshaw HD, Heilman PE, Hinckley TM, ed. 1996.   Biology of *Populus* and its implication for management and conservation. Proceedings, International Symposium; 1995 August 20–25; Seattle. Ottawa: NRC Press.

Stout AB, Schreiner EJ. 1933.   Results of a project in hybridizing poplars. Journal of Heredity 24: 216–229.

Stromberg JC. 1993.   Fremont cottonwood–Gooding willow riparian forests: a review of their ecology, threats, and recovery potential. Journal of the Arizona–Nevada Academy of Science 3: 98–110.

Stromberg JC, Patten DT, Richter BD. 1991.   Flood flows and dynamics of Sonoran riparian forests. Rivers 2(3): 221–235.

Tauer CG. 1979.   Seed tree, vacuum, and temperature effects on eastern cottonwood seed viability during extended storage. Forest Science 25: 112–114.

P

Tauer CG. 1995.   Unpublished data.  Stillwater: Oklahoma State University, Department of Forestry.

Trappe JM. 1964.   *Populus trichocarpa* seeds endure adversities. Tree Planters' Notes 65: 31.

Valentine FA. 1975.   Genetic control of sex ratio, earliness and frequency of flowering in *Populus tremuloides*. In: Proceedings, 22nd Northeastern Forest Tree Improvement Conference : 111–129.

Viereck EG. 1987.   Alaska's wilderness medicines: healthful plants of the Far North. Edmonds, WA: Northwest Publishing. 107 p.

Viereck LA. 1970.   Forest succession and soil development adjacent to the Chena River in interior Alaska. Arctic and Alpine Research 2(1): 1–26.

Viereck LA, Foote MJ. 1970.   The status of *Populus balsamifera* and *P. trichocarpa* in Alaska. Canadian Field-Naturalist 84(2): 169–173.

Viereck LA, Little EL Jr. 1972.   Alaska trees and shrubs. Agric. Handbk. 410. Washington, DC: USDA Forest Service. 265 p.

Walker LR, Zasada JC, Chapin FS III. 1986.   The role of life history processes in primary succession on an Alaskan floodplain. Ecology 67(5): 1243–1253.

Wang BSP. 1982.   Long-term storage of *Abies, Betula, Larix, Picea, Pinus,* and *Populus* seeds. In: Proceedings, International Symposium on Forest Tree and Seed Storage; 1980 September 23–27; Chalk River, ON. Ottawa: Canadian Forestry Service: 142–160.

Wettstein WV. 1933.   Die Kreuzungsmethode und die Beschreibung von F1 bastarden bei *Populus*. Zeitschrift für Zuchtung A [Pflanzenzuchtung] 18(4): 597–626.

Weigel D, Nilsson O. 1995.   A developmental switch sufficient for flower initiation in diverse plants. Nature 377: 495–500.

Williamson AW. 1913.   Cottonwood in the Mississippi Valley. Bull. 24. Washington, DC: USDA. 62 p.

Winton LL. 1968a.   Plantlets from aspen tissue cultures. Science 160: 1234–1235.

Winton LL. 1968b.   Fertilization in forced aspen and cottonwood. Silvae Genetica 17(1): 20–21.

Wycoff HB. 1960.   Cottonwood seeding at the Mason State Tree Nursery. Tree Planters' Notes 41: 13.

Wyckoff GW. 1975.   Procedures for crossing bigtooth and quaking aspen [unpublished manuscript]. Appleton, WI: Institute of Paper Chemistry. 13 p.

Wyckoff GW. 1996.   Unpublished data. Grand Rapids, MN: University of Minnesota, Aspen & Larch Genetics Cooperative and USDA Forest Service, North Central Experiment Station.

Wyckoff GW, Li B, Enebak S. 1995.   Annual Report of the University of Minnesota/Institute of Paper Science and Technology Aspen & Larch Genetics Cooperative. Rep. 6. 75 p.

Wyckoff GW, Harder ML. 1996.   Unpublished data. Grand Rapids, MN: University of Minnesota Aspen & Larch Genetics Cooperative and USDA Forest Service, North Central Experiment Station.

Zasada JC. 1996.   Unpublished data. Grand Rapids, MN: USDA Forest Service, North Central Research Station.

Zasada JC, Densmore RA. 1977.   Changes in seed viability during storage for selected Alaskan Salicaceae. Seed Science and Technology 5: 509–518.

Zasada JC, Densmore RA. 1979.   A trap to measure *Populus* and *Salix* seedfall. Canadian Field-Naturalist 93(1): 77–79.

Zasada J[C], Densmore R[A]. 1980.   Alaskan willow and balsam poplar seed viability after 3 years storage. Tree Planters' Notes 31(2): 9–10.

Zasada JC, Viereck LA. 1975.   Effect of temperature and stratification on germination of Alaska Salicaceae. Canadian Journal of Forest Research 5: 333–337.

Zasada JC, Viereck LA, Parkerson RH, Foote MJ, Wolff JO, Lankford LA. 1981.   Natural regeneration of balsam poplar following harvesting in the Susitna Valley, Alaska. Forestry Chronicle 57(2): 57–65.

Zasada JC, Norum RA, Van Veldhuizen RM, Teutsch CE. 1983.   Artificial regeneration of trees and shrubs in experimentally burned upland black spruce/feather moss stands in Alaska. Canadian Journal of Forest Research 3: 903–913

Fabaceae—Pea family

# *Prosopis* **L.**

## mesquite

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**Growth habit, occurrence, and use.** Mesquites—the genus *Prosopis*—are deciduous, thorny shrubs or small trees native to the tropical or subtropical regions of the Western Hemisphere, Africa, the Middle East, and India (Sargent 1965). Three native and 1 naturalized species are considered here (table 1); all are small trees, rarely exceeding heights of 15 m. Mesquite wood is an excellent source of fuel and charcoal and enjoys heavy local use for fenceposts, crossties, and furniture. Mesquite legumes make high-quality forage for livestock and wildlife, and the seeds were widely used by native American peoples in the Southwest (Davis and others 1975; Martin and Alexander 1974; Vines 1960). The crude protein contents of honey and velvet mesquite seeds are 31 and 24%, respectively (Becker and Grosjean 1980), and the legumes of honey mesquite are high in carbohydrates (Harden and Zolfaghari 1988). Mesquite flowers are a source of excellent honey, especially in Hawaii (Skolmen 1990). The tree is a hardy nitrogen-fixer and has been planted for erosion control in Hawaii, as well as for highway landscaping and mine spoil reclamation in the Southwest (Day and Ludeke 1980).

**Flowering and fruiting.** Mesquite's tiny, perfect flowers are greenish white or greenish yellow in color. They are 2 to 3 mm in diameter and are borne in spike-like axillary racemes some 3 to 10 cm long. Flowering of the mesquites occurs generally from late March to September in the Southwest (Sargent 1965; Vines 1960). In Hawaii, mesquite begins to flower at ages of 3 to 4, and although flowering can occur throughout the year, it is most frequent in January to March (Skolmen 1990). The fruit is an indehiscent legume (pod) that ripens from August to September (figure 1) (Martin and Alexander 1974). Ripe legumes are typically yellowish in color, although legumes of velvet mesquite may also be a mottled red and black at maturity (Ffolliott and Thames 1983). Legumes of mesquite, honey mesquite, and velvet mesquite are flat in shape and vary from 10 to 30 cm in length. Those of screwbean mesquite are coiled and may be as long as 70 cm. The flat, tan or brown seeds range from 1.5 to 7 mm in length (Ffolliott and Thames 1983; Sargent 1965) (figure 2).

**Figure 1**—*Prosopis juliflora,* mesquite: legume.



| Table 1—*Prosopis,* mesquite: nomenclature and occurrence | | |
|---|---|---|
| **Scientific name & synonym(s)** | **Common name(s)** | **Occurrence** |
| *P. glandulosa* **Torr.**<br>*P. chilensis* var. *glandulosa* (Torr.) Standl.<br>*P. juliflora* var. *glandulosa* (Torr.) Cockerell | **honey mesquite** | E Texas & Oklahoma to Utah, S California, & N Mexico |
| *P. juliflora* **(Sw.) DC.** | **mesquite,** *kiawe* (Hawaii) | Mexico, S to Brazil & Peru |
| *P. pubescens* **Benth.** | **screwbean mesquite,** screwbean, *tornillo* | Trans-Pecos Texas to Utah & S California |
| *P. velutina* **Woot.**<br>*P. juliflora* var. *velutina* (Woot.) Sarg. | **velvet mesquite,** mesquite | SW New Mexico, central Arizona, NW Mexico |

**Figure 2**—*Prosopis juliflora*, mesquite:   longitudinal section through a seed (**left**) and seeds (**right**).
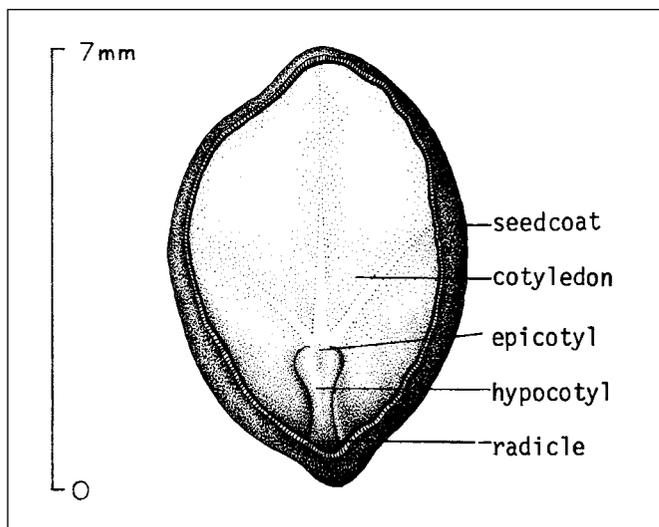


Good seed production data are lacking, but there is a record from southern California of an average of 7.2 kg (16 lb) of fruits per tree from velvet mesquite (Felker and others 1984). In the same record, other yield averages were 2.2 kg/tree (5 lb) for honey mesquite, and less than 1 kg/tree (2 $^1/_4$ lb) for screwbean mesquite. There are numerous species of insects that feed on seeds of the mesquites; seed beetles (Bruchidae) are the most important group (Johnson 1983; Solbrig and Cantino 1975).

**Collection, extraction, and storage.**   Ripe legumes may be stripped from trees by hand or picked up from the ground. Seed extraction and cleaning are not easy. One suggested method is to dry the legumes thoroughly (which may require oven-drying in humid climates) then running them through mechanical scarifiers or hammermills, and then screening out or blowing away the trash (Brown and Belcher 1979; Martin and Alexander 1974). Another method is to soak the legumes to soften them, then force the pulpy legumes and seeds through a sausage grinder with holes large enough for the seeds to pass. Hand grinders will suffice for small lots and commercial meat grinders have been successful for large lots (Skolmen 1990). Filled seeds may be separated from insect-damaged or immature seeds with aspirators or other blowers. If the seeds are dry, water flotation can also be used to separate good from damaged seeds. There are few seed yield and weight data for these 4 mesquite species: 1 kg of mesquite legumes may yield from 19,900 to 35,300 seeds (1 pound yields 9,025 to 16,000 seeds) (Goor and Barney 1968). Mesquite and honey mesquite average 8,000 to 30,000 seeds/kg (3,625 to 13,600/lb) (Glendening and Paulsen 1955; Von Carlowitz

1986), while as many as 38,300/kg (17,400/lb) have been reported for mesquite (Martin and Alexander 1974). Detailed studies of seed longevity are not available, but mesquite seeds, like those of most leguminous species, are orthodox in storage behavior. This means that seeds with low moisture contents may be stored at low temperatures for long periods without loss of viability. Air-dried seeds can be stored at ambient room temperature for at least 9 months with little loss in viability (Skolmen 1990). Martin (1948) reported that herbarium samples of velvet mesquite germinated after 44 years. Furthermore, mesquite seeds have been stored in liquid nitrogen (−196 °C) for 30 days without loss of viability (González-Benito and others 1994).

**Pregermination treatments.**   Like most Fabaceae, mesquites have very hard seedcoats (that is, hardseededness) that require scarification as a pretreatment for timely germination. Small samples, such as those used in germination tests, can be scarified effectively by nicking each seed with a knife (Martin and Alexander 1974) or rubbing it on rough sandpaper, or by treating a small seedlot with a mechanical scarifier. For seedlots of any size, water soaks are often effective. For mesquite and honey mesquite, 48 hours in cold or tepid water or 1 hour in boiling water has been recommended (Von Carlowitz 1986). Seedcoat hardness may vary by year or seed source, however, and acid scarification may be required on some seedlots. For mesquite, 10 minutes in sulfuric acid increased the germination of a seedlot from 64 to 88% (Skolmen 1990). The safest procedure to use with hot water or acid treatments is to treat a few small samples to determine the best treatment period.

**Germination.**   Some increases in germination capacity of mesquite seeds that resulted from scarification are shown in table 2. Germination of scarified seeds was complete 10 days after exposure to the test conditions. When velvet

**Table 2**—*Prosopis,* mesquite:  germination test conditions and results

| Seed age (yr) | Scarification treatment | Germination medium | Temp (°C) | | Avg % germination |
|---|---|---|---|---|---|
| | | | Day | Night | |
| 11 | Nicking | Wet paper | 27 | 27 | 98 |
| 50 | Nicking | Wet paper | 27 | 27 | 60 |
| — | None | Wet paper | 27 | 27 | 18 |
| — | $H_2SO_4$ | Wet sand | 30 | 20 | 88 |

**Source:**  Martin and Alexander (1974).

mesquite seeds were scarified with a knife, 94 to 100% of the seedlot germinated when kept at a constant 27 °C in the dark (Glendening and Paulsen 1955). Germination is epigeal (figure 3).

**Nursery practices.**  There are few published guidelines for nursery practices, but growing mesquite seedlings should not be too difficult. Cox and others (1993) recommended a sowing depth of 1 to 2 cm ($2/5$ to $4/5$ in) for velvet mesquite. Greenwood cuttings from young plants of mesquite, honey mesquite, and velvet mesquite can be rooted in mist chambers (Felker and Clark 1981).

**Figure 3**—*Prosopis juliflora*, mesquite:  seedling development at 1, 2, 5, 10, and 25 days after germination.
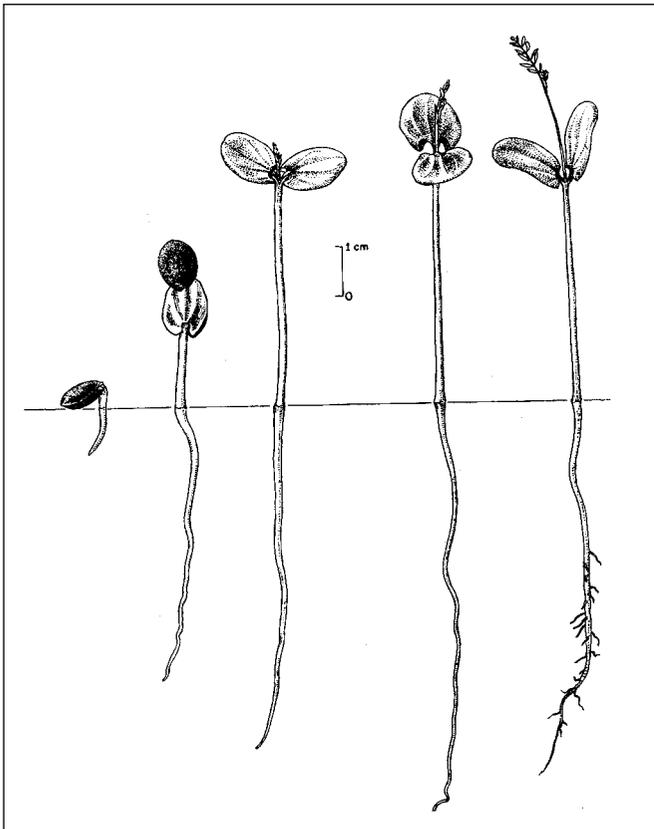
## References

Becker R, Grosjean OKK. 1980.  A compositional study of pods of two varieties of mesquite (*Prosopis glandulosa, P. velutina*). Journal of Agricultural and Food Chemistry 28: 22–25.

Brown FM, Belcher E. 1979.  Improved technique for processing *Prosopis* seed. Tree Planters' Notes 30(3): 19.

Cox JR, De Alba-Avila A, Rice RW, Cox JN. 1993.  Biological and physical factors influencing *Acacia constricta* and *Prosopis velutina* establishment in the Sonoran Desert. Journal of Range Management 46: 43–48.

Davis CA, Barkley RC, Haussamen WC. 1975.  Scaled quail foods in southeastern New Mexico. Journal of Wildlife Management 39: 496–502.

Day AD, Ludeke KL. 1980.  Direct seeding of tree species on copper mine wastes in the southwestern United States. Journal of Environmental Quality 9: 304–306.

Felker P, Clark PR. 1981.  Rooting of mesquite (*Prosopis*) cuttings. Journal of Range Management 34: 466–468.

Felker P, Clark PR, Osborn JF, Cannell GH. 1984.  *Prosopis* pod production: comparison of North American, South American, Hawaiian, and African germplasm in young plantations. Economic Botany 38: 36–51.

Ffolliott PF, Thames JL. 1983.  Handbook on taxonomy of *Prosopis* in Mexico, Peru and Chile. Rome: FAO. 31 p.

Glendening GE, Paulsen HA Jr. 1955.  Reproduction and establishment of velvet mesquite, as related to invasion of semidesert grasslands. Tech. Bull. 1127. Washington, DC: USDA Forest Service. 50 p.

González-Benito ME, Cazé-Filho J, Pérez C. 1994.  Cryopreservation of seeds of several legume species. Plant Varieties and Seeds 7:23–27 [Seed Abstracts 18(2): 499; 1995].

Goor AY, Barney CW. 1968.  Forest tree planting in arid zones. New York: Roland Press. 344 p.

Harden ML, Zolfaghari R. 1988.  Nutritive composition of green and ripe pods of honey mesquite (*Prosopis glandulosa,* Fabaceae). Economic Botany 42: 522–532.

Johnson CD. 1983.  Handbook on seed insects of *Prosopis* species. Rome: FAO. 55 p.

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

Martin SC. 1948.  Mesquite seeds remain viable after 44 years. Ecology 29: 393.

Martin SC, Alexander RR. 1974.  *Prosopis juliflora* (Sw.) DC., mesquite. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 656–657.

Sargent CS. 1965.  Manual of the trees of North America (exclusive of Mexico). 2nd ed. New York: Macmillan. 996 p.

Skolmen RG. 1990.  *Prosopis pallida* (Humb. & Bonpl. ex Willd.) H.B.K., kiawe. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 2, Hardwoods. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 583–586.

Solbrig OT, Cantino PD. 1975.  Reproductive adaptations in *Prosopis* (Leguminosae, Mimosoideae). Journal of the Arnold Arboretum 56: 185–210.

Vines RA. 1960.  Trees, shrubs and woody vines of the Southwest. Austin: University of Texas Press. 1104 p.

Von Carlowitz PG. 1986.  Multipurpose tree and shrub seed directory. Nairobi: International Council for Research in Agroforestry. 265 p.

Rosaceae—Rose family

# *Prunus* L.

## cherry, peach, and plum

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**Growth habit, occurrence, and use.**    The genus *Prunus*—often called the stone fruits—is one of the most important genera of woody plants. Its 5 well-marked subgenera include the plums and apricots *(Prunophora)*, the almonds and peaches *(Amygdalus)*, the umbellate cherries *(Cerasus)*, the deciduous racemose cherries (*Padus*), and the evergreen racemose or laurel cherries *(Laurocerasus)*. Plums can be distinguished from peaches and almonds by lack of a terminal bud, multiple flowers from a bud, and an elongated pedicel (Janick and Moore 1996). Plums can be distinguished from cherries by the lack of a terminal bud, the presence of a suture, a waxy bloom on the fruit, and a flatter pit.

Nearly 200 species—ranging from prostrate shrubs to trees over 30 m tall—are found in the Northern Temperate Zone, with a few in Central and South America (Harlow and Harrar 1958; LHBH 1978; Rehder 1940). By far the greatest number of species of cherries occur in eastern Asia (Hedrick 1915), but most of the long-cultivated food-producing species originated in Europe and western Asia (table 1). Over 100 species have been brought under cultivation, mostly as food crops or ornamentals (Rehder 1940), and 32 of the more important species for planting in the United States are described in table 1.

Many of the stone fruits have been cultivated since ancient times for their edible fruits and a few for edible seeds (almonds). Wild species have also been a source of food for Native Americans and early European settlers in this country and are still used to some extent. Many selections of wild plums have been propagated for fruit production. Several species are useful as ornamentals because of their showy flowers, variety of growth habits, relatively fast growth and ease of cultivation, and adaptability to a wide variety of soils and climates (Hedrick 1915; Olson and Nagle 1965; Rehder 1940; Strausbaugh and Core 1964).

Trees for fruit production and many ornamentals are propagated by budding or grafting, but seed production is necessary to grow the rootstocks and in breeding programs. The most important rootstock species and their scion combinations include almond rootstock for almonds and plums; apricot for apricots; mazzard cherry for sweet cherries; mahaleb cherry for sweet and sour cherries; peach for peaches, almonds, apricots, and plums; American plum for plums in cold climates; Bessey cherry for dwarf peaches; bullace plum (St. Julien types) for plums; myrobalan plum (mariana types) for almonds and plums; and myrobalan plum (myrobalan types) for plums (Cochran and others 1961; Sudworth 1908). Certain strains of peach, mahaleb cherry, and myrobalan plum are preferred for use as rootstocks because of their resistance to pests or for other qualities (Cochran and others 1961; Hedrick 1915).

Black cherry is the most important timber-producing species in the genus, but several others that attain sufficient size, such as mazzard cherry and mahaleb cherry in Europe and Japanese flowering cherry (*P. serrulata* Lindl.) in Japan, are used for wood products. Minor products include drugs, cordials, flavorings, honey, and perfume oil (Edlin 1967; Hedrick 1915). Probably all wild species are useful to wildlife as food. Birds and mammals eat the fruit, rodents eat the seeds, and deer (*Odocoileus* spp.) and beaver (*Castor canadensis*) use the leaves, twigs, and bark (Grisez 1974; Martin and others 1951; Van Dersal 1938). Several thicket-forming species of plums and cherries provide cover. Livestock feed on several species but others can be poisonous (Van Dersal 1938). Several species are used for erosion control and in shelterbelts (Engstrom and Stoeckeler 1941; Grisez 1974). In addition to those indicated in table 1, sour cherry, European bird cherry, and sloe are used for erosion control in Russia; and the same species plus mazzard cherry, apricot, myrobalan plum, garden plum, and pin cherry are used in shelterbelts (Al'benskii and Nikitin 1956; Koreisho and Morozov 1955).

**Geographic races and cultivars.**    Very few racial differences affecting seed characteristics have been recognized.

**Table 1**—*Prunus,* cherry, peach, and plum:  nomenclature, growth habit, and occurrence

| Scientific name synonym(s) | Common name(s) | Growth habit | Occurrence |
|---|---|---|---|
| *P. alleghaniensis* **Porter** | **Allegheny plum,** sloe, Allegheny sloe, Porter plum | Tree or shrub | Connecticut to Pennsylvania & S in mtns to Georgia; also in Michigan |
| *P. americana* **Marsh.** | **American plum,** wild yellow plum, red plum, goose plum, hog plum | Tree or shrub | Massachusetts to Manitoba, New Mexico, central Texas & NW Florida |
| *P. angustifolia* **Marsh.** | **Chickasaw plum,** sand plum | Tree or shrub | Missouri, S Nebraska to NW Texas & Louisiana; naturalized E to central Florida, New Jersey, & Illinois |
| *P. armeniaca* **L.** *Armeniaca vulgaris* Lam. | **apricot** | Tree | W Asia; occasional escape from cultivation |
| *P. avium* **(L.) L.** *P. cerasus avium* L. *Cerasus avium* Moench | **mazzard cherry,** sweet cherry, gean,* bird cherry* | Tree | Europe & W Asia; naturalized locally in SE Canada & E US |
| *P. caroliniana* **(P. Mill.) Ait.** | **Carolina laurel cherry,** wild orange | Tree (evergreen) | North Carolina to Texas |
| *P. cerasifera* **Ehrh.** *P. domestica* var. *myrobalan* L. *P. myrobalana* Loisel. *P. korolkowi* Vilm. | **myrobalan plum,** * cherry plum, marianna plum, flowering plum | Tree | W Asia; spread from cultivation from Washington to California, also in Michigan to Vermont, S to Ohio, New Jersey, & in Tennessee |
| *P. cerasus* **L.** *Cerasus vulgaris* Mill. | **sour cherry,** pie cherry | Tree | W Asia & SE Europe; naturalized locally from Nova Scotia & Michigan to N Florida & W-ward |
| *P. domestica* **L.** *P. damascena* Dierb. *P. communis* Huds. | **garden plum,** plum, European plum | Tree | W Asia & Europe; naturalized locally in SE Canada, NE US & Oregon |
| *P. domestica* **var.** *insititia* **(L.) Fiori & Paoletti** *P. domestica insititia* Fiori & Paoletti | **bullace plum,** damson, damson plum | Tree or shrub | W Asia & Europe; naturalized locally from Nova Scotia & Maine to New York SW-ward |
| *P. dulcis* **(P. Mill) D.A. Webber** *Prunus amygdalus* Batsch *Amygdalus dulcis* P. Mill. *P. communis* (L.) Arcang. *Amygdalus communis* L. | **almond** | Tree | W Asia & possibly North Africa; occasional escape from cultivation |
| *P. emarginata* **(Dougl. ex Hook.) D. Dietr.** *P. mollis* Walpers *Cerasus prunifolia* Greene | **bitter cherry,** wild cherry, narrowleaf cherry | Shrub or tree | British Columbia to S California, Arizona, & Montana |
| *P. fasciculata* **(Torr.) Gray** | **desert almond** | Shrub | California to Utah |
| *P. fremontii* **S. Wats** | **desert apricot** | Shrub | S California |
| *P. gracilis* **Engelm. & Gray** | **Oklahoma plum** | Shrub | Arkansas to Texas |
| *P. hortulana* **Bailey** | **hortulan plum** | Tree | S Indiana to Iowa, Oklahoma, Arkansas, Alabama & W Tennessee |
| *P. ilicifolia* **(Nutt. ex Hook & Arn.) D. Dietr.** | **hollyleaf cherry,** islay, evergreen cherry | Tree or shrub (evergreen) | Pacific Coast region, central to S California & in N Lower California, & Mexico |

Differences in seed size, germination percentages, and other characteristics have been recognized, but these are likely to be treatment differences or simply random variations. For example, the moisture content of seeds (which is seldom reported) and tree-to-tree variation can have more effect than place of origin on numbers of seeds per weight (Grisez 1974). According to Hedrick (1915), "Cherries of any variety grown on poor soils or in uncongenial climates tend to have large stones and little flesh, while the pits are smaller and there is more flesh with the opposite extremes in environment." The weights of black cherry seeds increase with latitude (Pitcher 1984), ranging from 7 g in Florida to 14 g in northern Michigan. There is a significant negative correlation (r = –0.35) between seed size and germination in that smaller seeds have better germination (Pitcher 1984).

**Table 1**—*Prunus,* cherry, peach, and plum:   nomenclature, growth habit, and occurrence (continued)

| Scientific name synonym(s) | Common name(s) | Growth habit | Occurrence |
|---|---|---|---|
| *P. laurocerasus* **L.** | **laurel cherry,** cherry-laurel | Tree (evergreen) | SE Europe, SW Asia |
| *P. mahaleb* **L.**<br>*Cerasus mahaleb* Mill. | **mahaleb cherry,** mahaleb, St. Lucie cherry, perfumed cherry | Tree | W Asia & Europe; naturalized locally in SW Canada & NE US |
| *P. maritima* **Marsh.** | **beach plum** | Shrub | Maine to Delaware |
| *P. munsoniana* **W. Wight & Hedrick** | **wildgoose plum,** Munson plum | Tree or shrub | Kansas, Kentucky, Texas & N Mississippi; naturalized E to  S Ohio & Georgia |
| *P. padus* **L.**<br>*P. racemosa* Lam.<br>*Padus racemosa* (Lam.) Schneid.<br>*Cerasus padus* (L.) DC. | **European bird cherry,** mayday tree | Tree | Europe & N Asia to Korea & Japan; spread from cultivation in Canada & NE US |
| *P. pensylvanica* **L. f.**<br>*P. persicifolia* Desf.<br>*P. montana* Marsh.<br>*P. lanceolata* Willd. | **pin cherry,** fire cherry, wild red cherry, bird cherry | Tree or shrub | Newfoundland to British Columbia S to Colorado, South Dakota, Pennsylvania, & in mtns to Georgia |
| *P. persica* **(L.) Batsch**<br>*Amygdalus persica* L.<br>*Persica vulgaris* Mill. | **peach,** common peach | Tree | China; naturalized locally, New England, S Ontario & Michigan to E Texas & Florida |
| *P. pumila* **L.**<br>*P. depressa* Pursh | **sand cherry** | Shrub | New Brunswick to Manitoba, Illinois, & New Jersey |
| *P. pumila* **var.** *besseyi* **Bailey (Gleason)**<br>*P. prunella* Daniels<br>*P. pumila besseyi* (Bailey) Waugh.<br>*P. susquehanae* Willd.<br>*Cerasus canadensis* Mill. | **Bessey cherry,** western sand cherry, Rocky Mountain cherry | Shrub | Manitoba to Wyoming S to Kansas & Colorado |
| *P. serotina* **Ehrh.**<br>*P. virginiana* L.<br>*Padus virginiana* (L.) Mill.<br>*Padus serotina* Borkh. | **black cherry,** rum cherry, wild cherry wild black cherry, | Tree | Nova Scotia, S Ontario & Minnesota to E Nebraska, E Texas, & central Florida; also in Mexico & Guatemala |
| *P. spinosa* **L.** | **sloe,** blackthorn | Shrub or tree | Europe, N Africa, & W Asia; naturalized locally in SE Canada & NE US |
| *P. subcordata* **Benth.** | **Klamath plum,** Pacific plum, Sierra plum, western plum | Tree or shrub | W & S Oregon to central California |
| *P. tomentosa* **Thunb.**<br>*P. trichocarpa* Bge.<br>*Cerasus tomentosa* Wall. | **Manchu cherry,** Nanking cherry downy cherry | Shrub | China, Japan, & Himalayas; central & N Great Plains |
| *P. umbellata* **Ell.** | **hog plum** | Tree | North Carolina to Florida, Alabama, & Mississippi |
| *P. virginiana* **L.**<br>*P. nana* DuRoi<br>*P. demissa* (Nutt.) D. Dietr.<br>*Padus nana* (DuRoi) Borkh. | **common choke cherry** | Tree or shrub | Newfoundland to British Columbia, S to S California, New Mexico, Kansas, Illinois, Maryland, & S in mtns to Georgia |

**Sources:**    Grisez (1974), Wasson (2001).

\*   Names commonly used for the wild form.

There often are great differences among cultivars or groups within each of the domesticated fruit species, particularly in the percentage of viable seeds. In mazzard and sour cherries, the late-ripening cultivars, which require 80 days from flowering to fruit ripening, produce seedcrops with nearly 100% sound seeds. On the other hand, early cultivars, which require 60 days or less to ripen, produce almost no sound seeds. Those ripening in 60 to 75 days are intermediate (Tukey 1927). The final stage of fruit development is the rapid growth of the pericarp, and in early ripening cultivars of these species and peach, this stage begins before the embryo reaches full size (Tukey 1936). Garden plum also shows wide variation in germination capacity among cultivars tested under identical conditions (Suszka 1967). Immature embryos have been brought to a germinable stage by (1) growing excised embryos in artificial

culture, (2) storing whole fruit (Hesse and Kester 1955), and (3) not picking until the fruit is over-mature (Zielinski 1958). Current technology allows the successful culture of ovules as small as 0.6 mm (Janick and Moore 1996). Only 32% of embryos <10 mm long produce plants, compared to 78% for larger embryos (Ramming 1990).

Non-viability of apparently normal seeds derived from crossbreeding cherries or plums has been a problem (Cochran and others 1961). The Duke cherries—hybrids of mazzard cherry and sour cherry—often have empty seeds (Hedrick 1911).

Flowering and fruit-ripening dates vary among cultivars of a species grown in the same location (Hedrick 1911, 1915; Kester 1969). Individual trees of black cherry vary in a similar manner (Grisez 1974), and the same variation can be expected in other wild species. The food quality of fruit varies greatly among wild plants of Bessey cherry and the plums. Selections of 15 species of plums have been grown under cultivation for their fruit (Hedrick 1911, 1915).

American plum seeds from northern Minnesota germinate much better at a temperature of 10 °C than at higher temperatures, whereas those from Nebraska germinated as well and more rapidly at 21 °C (night) to 27 °C (day) (Grisez 1974).

In apricots, the variety called Russian apricot is hardier than the typical form (Grisez 1974). Mazzard cherry cultivars require 5 to 6 days longer to begin germination in stratification than wild mazzard cherry (Suszka 1967).

In a provenance study of black cherry, Cech and Kitzmiller (1968) found that the pattern of variation for seed traits is random throughout most of its range. However, seeds from the southern and southwestern parts of the range in the United States were characteristically lighter in weight and smaller in diameter as well as having thinner endocarps than seeds from other areas. Geographic locations and mother trees contributed about equally to the variability in total germination.

**Flowering and fruiting.** The flowers of nearly all species are bisexual. They normally have 5 white or pink petals and 15 to 20 or more stamens. In general, the pistil matures 3 or 4 days before the stamens (Hedrick 1915). The flowers are solitary, in umbel-like clusters or racemes, and usually appear before or with the leaves. The flowers are insect-pollinated. Except for plums and sweet cherries, most species are self-fertile and thus a tree will set fruit without a cross-pollinator (Janick and Moore 1996).

Of the 2 ovules, only 1 normally develops, resulting in a 1-seeded drupe. The drupe is thick and fleshy (except in the almonds) and has a hard, bony endocarp surrounding the seed itself (figures 1–3) (Fernald 1950; LHBH 1976; Kester

1969; Knuth 1906–09; Rehder 1940). The developed endocarp and seed are commonly called the stone or pit. Dates of flowering and fruiting are listed in table 2. Seeds are distributed mainly by birds and mammals (Grisez 1974). Fruit diameters of most species are between 5 and 25 mm, but

**Figure 1**—*Prunus*, cherry, peach, plum: seeds of *P. americana*, American plum (**upper left**), *P. angustifolia*, Chickasaw plum (**upper middle**); *P. armenica*, apricot (**upper right**); and *P. persica*, peach (**bottom**).
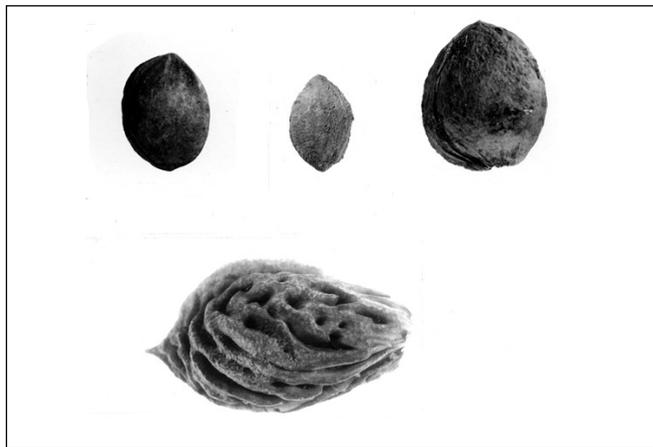


**Figure 2**—*Prunus*, cherry, peach, plum: seeds of *P. avium*, mazzard cherry (**top left**); *P. padus*, European bird cherry (**top right**); *P. pumila* var. *besseyi*, Bessey cherry (**second row left**); *P. pensylvanica*, pin cherry (**second row right**); *P. cerasus*, sour cherry (**third row left**); *P. pumila*, sand cherry (**third row right**); *P. marginata*, bitter cherry (**fourth row left**); *P. serotina*, black cherry (**fourth row right**); *P. mahaleb*, mahaleb cherry (**fifth row left**); *P. virginiana*, common choke cherry (**fifth row right**); *P. subcordata*, Klamath plum (**bottom left**); and *P. umbellata*, hog plum (**bottom right**).
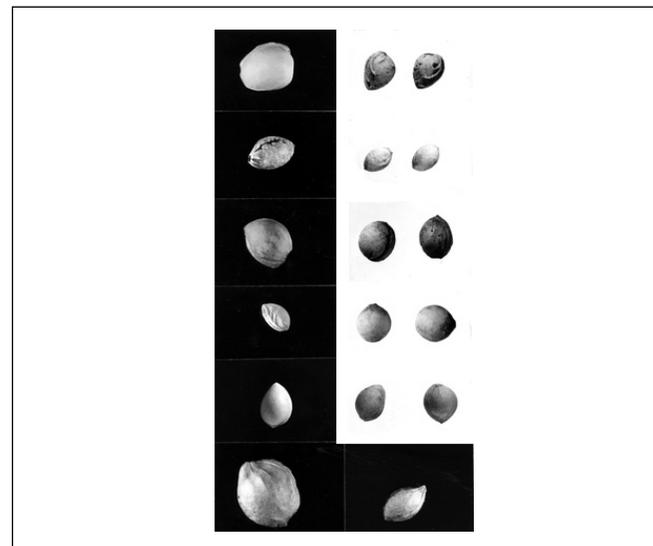
**Table 2**—*Prunus,* cherry, peach, and plum:   phenology of flowering and fruiting

| Species | Location | Flowering | Fruit ripening | Seed dispersal |
|---|---|---|---|---|
| P. alleghaniensis | Scattered | Late Apr–May | Aug–Sept | — |
| P. americana | — | Mar–May | June–Oct. | June–Oct |
| P. angustifolia | — | Mar–Apr | May–July | May–July |
| P. armeniaca | California | Feb–Mar | May–June | — |
| | USSR | Mar–Apr | July | July–Aug* |
| P. avium | NE US | Apr–May | June–July | — |
| P. caroliniana | SE US | Mar–Apr | Sept–Oct | — |
| P. cerasifera | Geneva, New York | May 12† | July 15–Aug 10 | — |
| | USSR | Apr–May | Aug | — |
| P. cerasus | — | Apr–May | June–July | — |
| | Geneva,  New York | May 8–18† | June–July | — |
| P. domestica | Geneva,  New York | May 12–21† | July 15–Oct 1 | — |
| | USSR | May | Aug | — |
| P. d. var. insititia | US & Canada | Late Apr–May | Aug–Sept | — |
| | Geneva,  New York | May 16–21† | Aug 20–Oct 1 | — |
| P. dulcis | California | Mid Feb–Mar | Late Aug–Oct* | — |
| P. emarginata | — | Apr–June | July–Sept | Aug–Sept* |
| P. hortulana | SE US | Mar–May | Aug–Oct | — |
| P. ilicifolia | — | Mar–May | Sept–Oct* | Oct–Dec |
| P. laurocerasus | SE Europe & Asia Minor | Apr–May | July–Aug | — |
| P. mahaleb | NE US & SE Canada | Apr–May | July | — |
| P. maritima | Maine to Delaware | Apr–June | Sept–Oct | — |
| P. munsoniana | — | Mar–May | July–Sept* | — |
| | Geneva, New York | May 20–24† | July 15–Sept 10 | — |
| P. padus | Philadelphia & vicinity | End Apr–early May | Late June–July | — |
| | USSR | May–early June | June–Aug | Aug* |
| P. pensylvanica | — | Late Mar–early July | July–Sept | — |
| | Warren Co., Pennsylvania | May 1–15 | Late July–early Aug | — |
| P. persica | NE US | Apr–May | July–Sept | — |
| | SE US | Feb–Apr | May–Aug | — |
| P. pumila | — | May–July | July–Sept | — |
| P. pumila. var. besseyi | Nebraska | Apr–May | July–Sept | July–Sept |
| P. serotina | Central Mississippi | Early Apr | June–July | July |
| | N Pennsylvania | Late May–early June | Late Aug–Sept | Aug 20–Sept; rarely Nov |
| | — | Late Apr–June 10 | June–Sept. | July 1–Sept |
| P. spinosa | USSR | Apr–May | Aug–Sept | Sept |
| P. subcordata | — | Mar–May | Aug–Sept | — |
| P. tomentosa | Cheyenne, Wyoming | Early May | Late July | Early Aug |
| | Bismarck, N Dakota | May 10–15 | July 10–15 | July 15–Sept 1 |
| P. umbellata | SE United States | Mar–Apr | Aug–Sept | — |
| P. virginiana | E US | Late Apr–early June | July–Oct | — |
| | Warren Co., Pennsylvania | May 10–20 | Early Aug | — |
| | California | — | Aug–Sept* | — |

**Sources:**   Altman and Dittmer (1962), Bailey (1976), Bonner (1975), Fernald (1950), Grisez (1974), Hedrick (1911), Hedrick (1915), Hitchcock and others (1961), Kester (1969), Koreisho and Morozov (1955), Long (1923), McMinn (1959), Mirov and Kraebel (1937, 1939), Munz and Keck (1959), Pane (1966), Petrides (1958), Radford and others (1964), Rehder (1940), Sudworth (1908), Van Dersal (1938).
\* Collecting dates.
† Average dates of height of bloom for one to several cultivars.

those of almonds, apricots, plums, and peaches are larger (table 3).

**Collection of fruits.**    *Prunus* fruits should be collected when fully mature (Al'benskii and Nikitin 1956; Swingle 1925; Zielinski 1958); doing so facilitates cleaning and is more likely to result in good germination (Grisez 1974; Huntzinger 1968). It is especially important in certain cultivars when the seeds are in a critical stage at the time the fruits are ripe and may not develop to a sound condition if

the fruits are picked prematurely (Tukey 1927). Height, seed-bearing age, seedcrop frequency, and fruit descriptions of 24 species are listed in table 3. Color and condition of the fruits indicate maturity. For those species in which the ripe fruit color is nearly black, the preripe color is red. In red-fruited species, the preripe color may be yellowish or partly green and red (Grisez 1974). Almonds are ready to harvest when the husks (mesocarps) of fruits in the inner parts of the tree crown have split (Kester 1969).

**Figure 3**—*Prunus persica*, peach: longitudinal section through a seed showing no endosperm. Seven species of *Prunus* have seeds without endosperm and 20 species have seeds with endosperm.
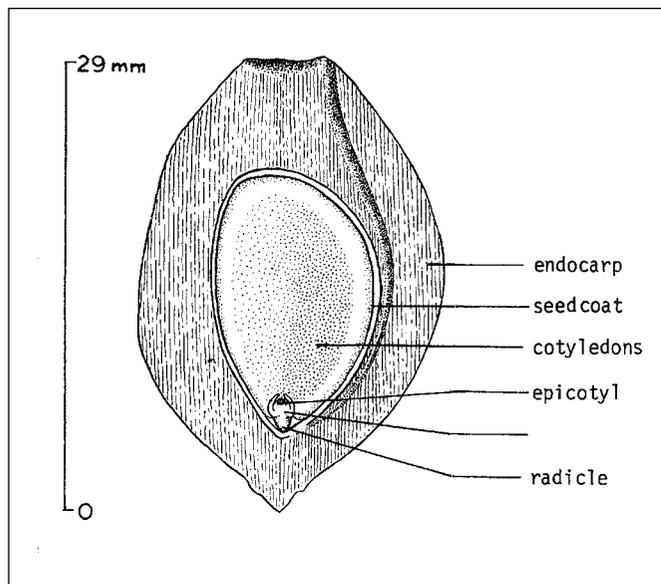


Fruits are collected by hand-stripping or by spreading sheets of suitable material under trees to catch the natural fall or fruits that are shaken or beaten off the tree (Grisez 1974; Huntzinger 1968; Stoeckeler and Jones 1957). Small quantities can be picked from the ground (Huntzinger 1971). Black cherry fruits may be collected from trees felled in logging, but when fruits have reached the dead-ripe stage, a high proportion of them will be knocked off during felling (Huntzinger 1968). Mechanical tree shakers are used in many commercial fruit orchards (Kester 1969; Miller 1960). There is even a machine to pick prunes (certain cultivars of garden plum) from the ground (Miller 1960).

Fruits may be carried in bags in small quantities—or in large quantities if they are to be processed immediately (Huntzinger 1971)—but boxes or baskets provide better protection against bruising and spoilage (Al'benskii and Nikitin 1956). Commercial cherries are often transported in water (Tennes and others 1968). Although this method was designed to protect the fruit, it could also be used to prevent spoilage and fermentation until the seeds are cleaned.

**Extraction of seeds**. Although satisfactory results have been obtained in a few cases by handling and sowing whole fruits (Engstrom and Stoeckeler 1941; Huntzinger 1968), it is generally desirable to clean the seeds of all pulp and juice (Heit 1945; Huntzinger 1968; Marcet 1951; Nyholm 1951; Robertson 1948–49; Shumilina 1949).

Cleaning is done by macerators or hammermills with water to float off or screen out the pulp (Defler 1937; Dorn and Flick 1969; Grisez 1974; Hartman and Kester 1959; Huntzinger 1968; Steavenson 1940; Stoeckeler and Jones 1957). Hammermills should have worn or rounded hammers and be run at low speed (Mugford 1969). Small quantities may be cleaned by soaking and rubbing the fruits over a screen (Haut 1938; Jones 1963; Paton 1936) or by use of a household food blender (Huntzinger 1968).

Fermentation has been used to soften fruit to facilitate cleaning (Engstrom and Stoeckeler 1941; Grisez 1974; Rudolf 1961), but it is risky because the germination capacity of seeds may be severely reduced if seeds are allowed to become too warm or ferment too long (Cochran and others 1961; Engstrom and Stoeckeler 1941; Fogle 1958; Heit 1967). Fruits that are badly infested with brown rot should be discarded because this disease can spread through the seedlot (Janick and Moore 1996).

There is little need to separate out sound seeds in most species because the percentage of sound seeds is usually 96 to 100%, but it may be desirable in certain cultivars of commercial fruits. Separation of sound seeds of sour cherry has been done with 95% ethyl alcohol, density 0.8114 (Tukey 1927). A 17% salt solution (density 1.176) has been used to separate the heavy seeds of mazzard cherry, mahaleb cherry, and pin cherry, but the method is not always reliable (Cummings and others 1933). Seeds that float in water can be removed in the cleaning process, but some seeds that sink are not viable (Swingle 1925; Tukey 1927). The same methods should not be used with dried seeds because included air spaces can cause good seeds to float.

Seed yields and weights are listed in table 4. Additional data include the following weights per volume of fruit: sour cherry nested in water, 77 kg/hl (60 lb/bu) (Tennes and others 1968); black cherry, 72 kg/hl (56 lb/bu) (Stoeckeler and Jones 1957); and Manchu cherry, 77 to 85 kg/hl (60 to 66 lb/bu) (Grisez 1974). A bushel of black cherry fruit yields 5 kg (11 lb) of seed (Stoeckeler and Jones 1957).

**Storage.** Early experiences suggested that excessive drying for storage was detrimental (Cochran and others 1961; Engstrom and Stoeckeler 1941; Fogle 1958; Grisez 1974; Huntzinger 1968; Olson and Nagle 1965; Stoeckeler and Jones 1957); however, what was excessive was not defined. Very early ripening female parents may not produce fruits with fully mature embryos and these fruits should not be allowed to dessicate (Janick and Moore 1996). Apricot seeds can be dried to 6% moisture, mazzard cherry to 9 to 11%, and mahaleb cherry to 8% for storage without impair-

**Table 3**—*Prunus,* cherry, peach, and plum:   height, seed-bearing age, seedcrop frequency, fruit color, and fruit size

| Species | Height at maturity (m) | Year first cultivated | Min seed-bearing age (yrs) | Years between large crops | Ripe fruit color | Fruit size (mm) | |
|---|---|---|---|---|---|---|---|
| | | | | | | Diameter | Length |
| *P. alleghaniensis* | 4.9 | 1889 | 4 | 1 | Dark purple | 10 | — |
| *P. americana* | 3–9 | 1768 | 4 | 1–2 | Red or yellowish | 20–30 | — |
| *P. angustifolia* | 4.3–7.6 | ~ 1874 | 2 | — | Red or yellow | 10–20 | — |
| *P. armeniaca* | 10.4 | Early | 5 | 2 | Yellowish with red | 30+ | — |
| *P. avium* | 9–30.5 | Early | 6–7* | 1 | Yellow to red or purplish black | 20–25 | — |
| *P. caroliniana* | 5.5–12 | — | — | — | Black | 10–13 | 10–13 |
| *P. cerasifera* | 8.2 | Early | 3 | 2–3 | Red | 16–25 | — |
| *P. cerasus* | 9–15 | Early | 6-7* | 1 | Light to dark red | 8–25 | — |
| *P. domestica* | 9–12 | Early | 5 | — | Often blue-purple | 30+ | — |
| *P. d. var. insititia* | 6–7.6 | Early | — | — | Yellow to bluish black | 25+ | 15–20 |
| *P. dulcis* | 3–9 | Early | 4†,6–7 | 1 | Brownish | 30+ | 30–60 |
| *P. emarginata* | 1–15 | 1918 | — | — | Bright red | 8–12 | — |
| *P. fasciculata* | 1–2.4 | — | — | — | — | 13 | |
| *P. fremontii* | 1.5–3.7 | — | — | — | Yellowish | 15–20 | 13 |
| *P. gracilis* | 4.6 | — | — | — | Red | 13 | — |
| *P. hortulana* | 9 | — | 3 | — | Red to yellow | 25 | — |
| *P. ilicifolia* | 7.6–9 | Pre-1925 | 3 | — | Purple or black | 13–17 | 25 |
| *P. laurocerasus* | 5.5 | — | — | — | Purple to black | 10 | 8–13 |
| *P. mahaleb* | 6–10 | Early | 3 | 1–2 | Black | 8–10 | 6–10 |
| *P. maritima* | 3 | — | 3 | — | Purple | 13–25 | 20 |
| *P. munsoniana* | 6–9 | Pre-1909 | 3 | — | Red or yellow | 20–30 | 15–25 |
| *P. padus* | 15 | Early | — | 2 | Black in typical variety | 6–8 | — |
| *P. pensylvanica* | 3–12 | 1773 | 2 | — | Light red | 5–7 | — |
| *P. persica* | 3–7.6 | Early | 3 | 1–2 | Yellow to red | 30–60 | 30–75 |
| *P. pumila* | 0.3–2.4 | 1756 | — | — | Purple-black | 10 | 10 |
| *P. var. besseyi* | 0.3–1.2 | 1892 | 2–3 | — | Purple to black | 15 | — |
| *P. serotina* | 15.3–33.5 | 1629 | 5 | 1–5 | Black | 7–10 | 6–10 |
| *P. spinosa* | 4 | Early | — | 1–2 | Blue-black | 10–15 | 15 |
| *P. subcordata* | 3–7.6 | ~ 1850 | — | 2 | Red or yellow | 20–30 | 15–30 |
| *P. tomentosa* | 1.8–3 | 1870 | 2–3 | 1–2 | Red | 10–31 | 15 |
| *P. umbellata* | — | — | 3 | — | Black, red, yellow | 10–15 | 10–13 |
| *P. virginiana* | 1.8–9 | 1724 | — | — | Red-purple to dark purple | 8 | — |

**Sources:**  Bailey (1976), Everett (1957), Fernald (1950), Giersbach and Crocker (1932), Grisez (1974), Gysel and Lemien (1964), Hedrick (1911, 1915), Huntzinger (1971), Kester (1969),  Koreisho and Morozov (1955),  Munz and Keck (1959), Peck (1961), Petrides (1958), Rehder (1940),  Strausbaugh and Core (1964), Van Dersal (1938).
\* Minimum commercial seed-bearing age.
† Ages are for seedling stock; grafted or budded stocks bear seeds 1 or 2 years younger (Wright 1966).

ing their germination (Suszka 1964). Seeds to be sown or stratified immediately need not be dried at all. Seeds to be used within a few weeks or months should only be surface-dried; apparently, excessive drying of seeds to be used within a year of collection is often harmful (Grisez 1974; Huntzinger 1968). For storage of 1 year or more, it is desirable to reduce the moisture content of seeds below the surface-dry condition. For mazzard cherry, the optimum moisture content is 9 to 11%, with optimum temperatures of –1 to 3 °C for storage up to 3 years and –10 °C for longer storage (Suszka and others 1996). The results of several storage studies are reported in table 5. In most cases, drying is done at room temperatures or lower. Surface drying usual-

ly requires only a few hours (Huntzinger 1968). The moisture content of black cherry seeds has been reduced from about 14% to 5% by drying at 32 °C for 3 hours (Huntzinger 1971).

Sealed containers are preferred for Prunus seeds if the moisture content is to be closely controlled. Seeds of mazzard cherry were dried to a moisture content of 11% and stored in sealed bottles at 1 °C for 4 $^1/_2$ years. During this period, viability decreased from 93% to 84% (Suszka 1970). Plastic bags have been satisfactory for storage of black cherry seeds for at least 3 years at cold temperatures (Huntzinger 1971). Cloth sacks may serve for short periods in cool temperatures (Suszka 1967). Maheleb cherry and

**Table 4**—*Prunus*, cherry, peach, and plum:  seed data

| Species | Seed weight/45 kg (100 lb) of fruit — Range kg | Range lb | Average kg | Average lb | Cleaned seeds/weight — Range /kg | Range /lb | Average /kg | Average /lb | Samples |
|---|---|---|---|---|---|---|---|---|---|
| P. alleghaniensis | — | — | — | — | — | — | 2,950 | 338 | 1 |
| P. americana | 3–15 | 7–34 | 9 | 19 | 550–1,500 | 250–680 | 870 | 395 | 27+ |
| P. angustifolia | 4–14 | 8–30 | 7 | 16 | 770–1,530 | 350–694 | 1,030 | 467 | 14+ |
| P. armeniaca | | | | | | | | | |
|   USA | 14–18 | 30–40 | — | — | 200–560 | 91–254 | 317 | 144 | 10+ |
|   USSR | 5–7 | 10–15 | — | — | 270–495 | 123–225 | 382 | 173 | — |
| P. avium | | | | | | | | | |
|   USA | 3–11 | 7–25 | 3 | 12 | 1,450–3,000 | 658–1,361 | 2,360 | 1,070 | 9+ |
|   USSR | 7–8 | 15–18 | — | — | 1,640–2,770 | 3,616–6,108 | 4,740 | 2,150 | — |
| P. cerasifera | — | 5 | 10 | | 782–1,330 | 355–603 | 994 | 451 | 7+ |
| P. cerasus | — | — | 9 | 20 | 1,510–4,000 | 685–1,815 | 2,910 | 1,320 | 6+ |
| P. domestica | — | — | 5 | 10 | 416–907 | 189–411 | 597 | 271 | 5+ |
| P. d. var. insititia | — | — | 3 | 7 | 625–1,920 | 284–871 | 1,380 | 626 | 3+ |
| P. dulcis | — | — | — | — | 126–225 | 57–102 | 181 | 82 | 3+ |
| P. emarginata | — | — | 11 | 25 | 4,120–8,790 | 1,869–3,987 | 7,020 | 3,184 | 6+ |
| P. ilicifolia | — | — | — | — | 200–240 | 91–109 | 220 | 100 | 2+ |
| P. mahaleb | 9–11 | 20–25 | — | — | 4,800–5,600 | 2,177–2,540 | 5,200 | 2,359 | — |
| P. munsoniana | — | — | — | — | 900–2,240 | 408–1,016 | 1,690 | 767 | 3+ |
| P. padus | — | — | 9 | 20 | 6,600–12,300 | 2,994–5,580 | 8,910 | 4,042 | 5+ |
| P. pensylvanica | 7–12 | 16–27 | — | — | 8,000–21,800 | 3,629–9,889 | 14,200 | 6,442 | 6+ |
| P. persica | — | — | 9 | 20 | 72–244 | 33–111 | 156 | 71 | 6+ |
| P. pumila | | | | | | | | | |
|   typical | — | — | — | — | 2,460–4,000 | 1,116–1,815 | 2,920 | 1,325 | 4+ |
|   var. besseyi | 7–13 | 15–28 | 10 | 21 | 1,500–4,000 | 681–1,815 | 2,400 | 1,090 | 10+ |
| P. serotina | | | | | | | | | |
|   fresh seeds | — | — | 9 | 20 | 2,800–6,040 | 1,270–2,740 | 4,240 | 1,923 | 68 |
|   fresh & stored seeds | 6–15 | 14–33 | 10 | 21 | 2,840–13,800 | 1,288–6,260 | 5,370 | 2,436 | 197 |
| P. spinosa | — | — | 5 | 10 | 1,970–2,670 | 894–1,211 | 2,240 | 1,016 | — |
| P. subcordata | — | — | — | — | 450–631 | 204–286 | 556 | 252 | 4+ |
| P. tomentosa | 3–5 | 7–12 | 5 | 10 | 1,730–6,400 | 785–2,903 | 4,740 | 2,150 | 9+ |
| P. virginiana | 8–11 | 18–25 | 9 | 20 | 3,010–8,400 | 1,315–3,810 | 4,790 | 2,173 | 19 |

**Sources:** Benjdl (1954), Cech and Kitzmiller (1968), Chittenden (1927), Cumming and others (1933), Defler (1937), Engstrom and Stoeckeler (1941), Everett (1957), Glazebrook (1941), Grisez (1974), Huntzinger (1971), King (1947), Koreisho and Morozov (1955), Krefting and Roe (1949), Krier (1948), Mirov and Kraebel (1937, 1939), Swingle (1939), USDA (1961), Van Dersal (1938).

myrobalan plum can be stored up to 2 winters at room temperature in jute sacks without loss of viability (Grzeskowiak and others 1983). Pin cherry seeds retained high viability after 10 years of storage at 1 to 3 °C under sealed conditions (Dirr and Heuser 1987).

Normally, storage temperatures should be within the range 0.6 to 5 °C, although American plum, mazzard cherry, and mahaleb cherry have been successfully stored at room temperatures for 2 to 5 years. American plum seeds can be stored at room temperature up to 30 months without loss of germinative capacity (Giersbach and Crocker 1932). Manchu cherry seeds stored for 21 months at room temperature did not lose viability (Dirr and Heuser 1987). Dried seeds of mazzard and mahaleb cherries and myrobalan plum can be stored up to 3 winters at –1 or –3 °C without signifi-

cant loss of viability (Grzeskowiak and others 1983). Over 80% germination was obtained on black cherry seedlots containing 5% moisture after storage for 3 years in a freezer, but seedlots with about 15% moisture were completely spoiled when frozen (Huntzinger 1971).

Warm storage at a high moisture content for only a few months is harmful to seeds of mazzard cherry (Coe and Gerber 1934; Suszka 1967), black cherry (Huntzinger 1968), common choke cherry (Engstrom and Stoeckeler 1941), and probably other species as well. Black cherry seedlots should not be stored warm and moist more than 4 or 5 weeks, although about 2 weeks of such storage immediately after cleaning may be helpful for seeds about to be stratified (Huntzinger 1971).

| Tables 5—*Prunus,* cherry, peach, and plum: germination of seeds after dry storage* | | | |
|---|---|---|---|
| **Species & storage period** | **Storage temp (°C)** | **Moisture content (%)** | **Germination (%)** |
| *P. americana* | | | |
| 18 months | 7–10 | Dry | 70 |
| 53 months | 7–10 | Dry | 45 |
| 18 months | Lab temp | Dry | 72 |
| 53 months | Lab temp | Dry | 16 |
| 18 months | 30+ | Dry | 62 |
| 53 months | 30+ | Dry | 0 |
| *P. avium* | | | |
| 7 years | –5 | ~10? | 91–97 |
| 15 years | –5 | ~10? | 98 |
| 55 months | 1 | 11 | 84 |
| 55 months | 1 | 11 | 88† |
| 8-12 months | 3 | 9–11 | 98–100 |
| 207 days | –3 | 8.6 | 100* |
| 214 days | –3 | 9.0 | 99† |
| 570 days | –3 | 8.6 | 100† |
| 571 days | –3 | 9.5 | 94† |
| 935 days | –1 | 8.3 | 99† |
| 213 days | –3 | 9.0 | 99† |
| 214 days | –3 | 8.9 | 98† |
| 568 days | –3 | 8.6 | 100† |
| *P. pensylvanica* | | | |
| 2 months | –18 | Dry | 95 |
| 6 years | 1–3 | Low | 74 |
| 10 years | 1–3 | Low | 76 |
| *P. serotina* | | | |
| 1 year | –18 to –14 | 4–6 | 52 |
| 2 years | –18 to –14 | 4–6 | 81 |
| 3 years | –18 to –14 | 4–6 | 81 |
| 5 years | –18 to –14 | 4–6 | 47 |
| 8 years | –18 to –14 | 4–6 | 66 |
| 1 year | –18 to –14 | 11–13 | 4 |
| 2 years | –18 to –14 | 11–13 | 7 |
| 3 years | –18 to –14 | 11–13 | 1 |
| 5 years | –18 to –14 | 11–13 | 4 |
| 8 years | –18 to –14 | 11–13 | 0 |
| 1 year | 0.5–5 | 4–6 | 63 |
| 2 years | 0.5–5 | 4–6 | 81 |
| 3 years | 0.5–5 | 4–6 | 90 |
| 5 years | 0.5–5 | 4–6 | 69 |
| 8 years | 0.5–5 | 4–6 | 56 |
| 1 year | 0.5–5 | 11–13 | 72 |
| 2 years | 0.5–5 | 11–13 | 88 |
| 3 years | 0.5–5 | 11–13 | 77 |
| 5 years | 0.5–5 | 11–13 | 0 |
| 8 years | 0.5–5 | 11–13 | 0 |

**Sources:** Ellis and Hong (1986), Giersbach and Crocker (1932), Grisez (1976), Heit (1967), Huntzinger (1971), Laidlaw (1983), Michalska and Suszka (1980c&d), Solovieva (1966, 1978), Suszka (1970).

† Viability determined by indigo carmine embryo-staining test (2 hours in 0.05% solution at 20 °C).

**Pregermination treatments and germination tests.**
*Prunus* seeds have embryo dormancy and require a period of after-ripening in the presence of moisture and oxygen to overcome it. Because of their stony endocarps, *Prunus* seeds are often been thought to have seedcoat dormancy. The endocarp may offer some resistance to germination, but it is permeable to water and *Prunus* is not truly hard-seeded (Hartman and Kester 1959; Heit 1967; Tukey 1924).

Several mechanical and chemical methods have been used in attempts to crack, remove, or soften the endocarp, including freezing, mechanical scarification, boiling water, sulphuric acid, citric acid, lye, or hydrogen peroxide. In most cases, no advantage could be shown, and in many cases the treatments were detrimental. Peach seeds can be removed from the endocarp by applying pressure in the dorsal–ventral axis with a vise or special hand-clippers with a 2-sided blade (Janick and Moore 1996).

Removal of the endocarp by hand hastened or increased germination in American plum (Giersbach and Crocker 1932), almond (Gaudio and Pedone 1963), mazzard cherry (Zielinski 1958), sour cherry (Havis and Gilkeson 1949), peach (Crocker 1927, 1931), and sloe (Shumilina 1949). There was no advantage for bullace plum (Grisez 1974). Soaking for 48 hours in 0.1% citric acid resulted in 89% germination of black cherry; untreated seeds in this study germinated 57% (Jones 1963). In other studies, no advantage could be shown for citric acid treatments (Huntzinger 1968). Notching the endocarp and notching plus a hydrogen peroxide soak increased germination of an early-ripening mazzard cherry cultivar but had no effect on a late-ripening cultivar (Zielinski 1958). Gibberellin treatments apparently can substitute for a portion of the stratification period in apricot (Chao and Walker 1966), mazzard cherry (Fogle and McCrory 1960; Pillay 1962), garden plum (Janick and Moore 1996), and peach (Chao and Walker 1966), but it was effective only when the endocarp had been removed. Germination of mahaleb cherry seeds that were stored dry for several months was improved by 3 days of water-soaking prior to stratification (Swingle 1925).

Because good germination has been attained on stratified seeds of nearly all species of *Prunus* (table 6), it is evident that other pregermination treatments are not necessary if a seedlot is handled properly.

Although sand has often been used as a stratification medium, peat or sand–peat mixtures are preferred (Crocker 1930; Fogle and McCrory 1960; Huntzinger 1968; Shumilina 1949). Vermiculite was as good as peat in a test with black cherry seeds (Huntzinger 1971). Peat provides a larger and more constant supply of both air and water than sand (Crocker 1930; Shumilina 1949). The seeds are thoroughly mixed with the moist stratification medium. When peat is used, it should be soaked, then squeezed to remove all free water. The seeds should be mixed with about 1 to 3 times their volume of the medium (Crocker 1930; Grisez 1974; Huntzinger 1971). Seeds that had been dried for storage or those requiring a long period of after-ripening are sometimes stratified underground, in basements, or in shade prior to cold stratification or fall-sowing (Koreisho and Morozov 1955; Shumilina 1949).

Published results of experimental comparisons among various stratification temperatures for several species show that constant temperatures from 2 to 5 °C are more favorable than those below 1.7 °C or above 8 °C (Coe and Gerber 1934; Crocker 1931; Haut 1938). Seeley and Damavandy (1985) found that the optimum chilling temperature was

between 4 and 6 °C for apricot, mazzard cherry, mahaleb cherry, and peach. The most suitable temperature for stratification of almond (cv. 'Truioto') with endocarp was 10 °C for 26 days (Therios 1982). A regularly alternating temperature range of 2 to 4 °C was better than constant 3 °C for 2 cultivars of mazzard cherry (Zielinski 1958).

Stratification periods necessary for after-ripening vary by species (table 6). In general, species and cultivars from warm climates require less chilling than those from cold climates. Satisfactory germination of the many cultivated species not included here can probably be attained by following general recommendations and the stratification requirements for closely related species of the same climatic zones.

Lockley (1980) stratified 13 open-pollinated families of common choke cherry for 10, 16, and 24 weeks at 3 °C and germinated the seeds at 3 alternating temperature regimes of 10 to 16 °C, 16 to 21 °C, and 21 to 27 °C. All germinating seeds were provided with 14 hours of light during the high-temperature portion of the cycle. Stratification for 10 weeks was inadequate. The best results, 77% germination on the average, were found with 16 weeks of stratification and germination at 21 to 27 °C. After 24 weeks of cold stratification, over 50% of the common choke cherry seeds germinated in stratification. There was a significant correlation (r = 0.67) between field emergence and laboratory germination at 16 to 21 °C and 21 to 27 °C when the seeds received 16 weeks of stratification. Common choke cherry families with low germination at 21 to 27 °C after 10 weeks of stratification were also low germinators in the nursery (r = 0.68).

In a comprehensive study on stones of 7 widely planted species of *Prunus* including several cultivars and seed sources, germination was much higher after warm plus cold stratification than after cold stratification only. The schedule was 14 days at 20 °C followed by 189 days at 3 °C (Suszka 1967). Seedlots of sloe given 2 weeks of warm stratification treatment followed by 18 weeks of chilling yielded 80% germination (Gordon and Rowe 1982). Myrobalan plum and garden plum germination was promoted by 2 weeks of warm stratification at 20 °C before chilling (Michalska and Suszka 1980b). Muller and others (1990) found that 3 cycles of warm and cold stratification at a moisture content of 30% improved the germination of mazzard cherry. Virtually full germination of Mazzard cherry seedlots was achieved with 2 weeks at 20 °C, 8 weeks at 3 °C, 2 weeks at 25 °C, then 3 °C for the remainder of the treatment (Michalska and Suszka 1980a).

**Table 6**—*Prunus,* cherry, peach, and plum:   stratification periods, germination test conditions, and results

| Species | Recommended stratification (days) | | Germ. test conditions Temp (°C) | | | Avg germination | Samples | Viability |
| | Warm* | Cold† | Day | Night | Days | (%) | | (%) |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| *P. alleghaniensis* | 0 | 150 | 10 | 10 | 60 | 25 | 7 | — |
| *P. americana* | 0 | 90–150 | 10 | 10 | 60 | 60 | 21 | 74 |
| *P. angustifolia* | 0 | 60–120 | — | — | 60 | 55 | — | 90 |
| *P. armeniaca* | | | | | | | | |
|   endocarp removed | 0 | 0 | — | 7 | 7 | 14 | 90 | 3 |
|   endocarp intact | 14 | 189 | 3 | 3 | ‡ | 95 | — | 4 |
|   endocarp intact | 0 | 80–90 | 5 | 5 | ‡ | 95 | — | — |
| *P. avium* | | | | | | | | |
|   endocarp removed | 0 | 90–125 | 21 | 21 | — | 91 | — | 69 |
|   endocarp intact | 0 | 120–180 | 21 | 21 | — | 76 | 10+ | — |
|   endocarp intact | 14 | 189 | 3 | 3 | ‡ | 88 | — | — |
| *P. caroliana* | 0 | 30–60 | — | — | — | — | — | — |
| *P. cerasifera* | — | 196 | å1 | å7 | 28 | 65 | 2 | — |
| *P. cerasus* | 0 | 90–150 | — | — | — | — | 82 | — |
| *P. domestica* | 14 | 189 | 3 | 3 | ‡ | 56 | 15 | — |
| | 0 | 120–150 | — | — | — | — | 85 | — |
| | 0 | 90 | 2 | 2 | — | — | 91 | — |
| *P. domestica* var. *insititia* | 0 | 84–112 | 18 | 18 | — | 89 | 7 | — |
| *P. dulcis* | 0 | 65 | 2 | 2 | ‡ | — | 90 | — |
| *P. emarginata* | 0 | 90–126 | 24 | 24 | 60 | 4 | 3+ | — |
| *P. ilicifolia* | | | | | | | | |
|   fresh seed | 0 | 0 | — | — | — | — | — | — |
|   stored seed | 0 | 90 | — | — | — | — | 24 | — |
| *P. laurocerasus* | 0 | 60–90 | — | — | — | — | — | — |
| *P. mahaleb* | 0 | 80–100 | — | — | — | 89 | 5 | — |
| | 14 | 189 | 3 | 3 | ‡ | 55 | 3 | — |
| *P. maritima* | 0 | 90 | — | — | — | — | 39 | — |
| *P. munsoniana* | 0 | 80–100 | — | — | — | 100 | 10 | — |
| *P. padus* | | | | | | | | |
|   fresh seeds | 0 | 100–120 | — | — | — | 85 | — | — |
|   stored seeds | 14 | 210 | 3 | 3 | ‡ | 50 | 3 | — |
| *P. pensylvanica* | 60 | 90 | 25 | 10 | 60 | 62 | 2 | 91 |
| *P. persica* | | | | | | | | |
|   endocarp intact | 0 | 98–105 | 5(§41) | 5(§41) | ‡ | 32 | 8 | — |
|   endocarp removed | 0 | 70–105 | 5(§41) | 5(§41) | ‡ | 82 | 8 | 92 |
| *P. pumila* var. *besseyi* | 0 | 120 | — | — | — | 60 | 72 | — |
| *P. serotina* | 0 | 120 | 26 | 10 | 40–60 | 86 | 32 | 80 |
| | 14 | 189 | 3 | 3 | ‡ | 90 | 3 | — |
| *P. spinosa* | 0 | 170 | — | — | — | — | 90 | — |
| *P. subcordata* | 0 | 90 | — | — | 100 | 1 | — | — |
| *P. tomentosa* | 0 | 60–90 | — | — | — | 11 | — | 86 |
| *P. virginiana* | 0 | 120–160 | 25 | 10 | 40 | 77 | 3 | 62 |

**Sources:**   Afanasiev (1940, 1942), Al'benshkii and Nikitin (1956), Chadwick (1935), Chao and Walker (1966), Coe and Gerber (934) Crocker (1927, 1931), Defler (1937), Dirr and Heuser (1987), Emery (1964), Engstrom and Stoeckeler (1941), Everett (1957), Fogle (1958), Fogle and McCrory (1960), Glazebrook (1941), Giersbach and Crocker (1932), Grisez (1974), Haut (1932, 1938), Havis and Gilkeson (1949), Hesse and Kester (1955), Heit (1938), Kester (1969), Koreisho and Morozov (1955), Krefting and Roe (1949), Morov and Kraebel (1937), Pollock (1959), Probocskal (1963), Roe (1941), Suszka (1964, 1967), Swingle (1939), Tukey (1924), USDA (1961).

\* Seeds were in a moist medium at a constant temperature of 20 °C or at a temperature alternating diurnally from 30 °C (8 hours) to 20 °C (16 hours).
† Seeds were in a moist medium at a temperature between 0.6 °C and 5 °C; 2.8 to 5 °C was better.
‡ Germination occurred during the stratification period.
§ Results were similar at 10 °C.
II Adequate germination was reported at unspecified temperatures.

To achieve germination greater than 90%, Seeley and Damavandy (1985) found that apricot seeds need 50 days of chilling; mazzard cherry seeds, 120 days; mahaleb cherry seeds, 100 days; and peach seeds, 90 days of chilling before germination. Zigas and Coombe (1977) reported that 10 weeks of stratification at 3 °C was enough time to remove any inhibitory properties of the testa of peach seeds. The best treatment reported for mazzard cherry seeds in Europe is alternating cold and warm stratification without medium, with seeds at 28 to 30% moisture: 2 weeks at 20 °C, 6 weeks at 3 °C, 2 weeks at 25 °C, 4 weeks at 3 °C, 2 weeks at 25 °C, then 11+ weeks at 3 °C, with the treatment ending when 40 to 50% of the seeds readily germinate at 3 °C (Suszka and others 1996).

Seeds usually are held in cold stratification until incipient germination occurs (Giersbach and Crocker 1932; Huntzinger 1968; Suszka 1967). Visible signs of incipient germination are split endocarps or emerging radicles. When the cold period was interrupted with warmer temperatures before these stages were reached, secondary dormancy was induced (Huntzinger 1971; Suszka 1967). Michalska (1982) reported a 10-week delay in root growth of mazzard cherry when a thermal induction treatment was interjected into a 3 °C chilling period. Root growth was activated only after 12 to 16 weeks of chilling at 3 °C. In a test by Suszka (1967), seedlots of mazzard cherry were stratified for 154 days at 3 °C and then separated into 3 fractions:  intact seeds, cracked seeds, and those with emerging radicles. A sample of each fraction was sown separately at a depth of 1 cm ($^3/_8$ in) and subjected to a temperature of 20 °C. Epicotyls emerged from only 8% of the intact stones, but from 90% of the cracked seeds and from 95% of those with emerging radicles. The optimum temperature for epicotyl emergence from cracked seeds of European bird cherry, however, was between 5 and 10 °C (Suszka 1967). Seedlings have developed from up to 100% of cracked seeds of black cherry after sowing (Defler 1937; Huntzinger 1971).

Maximum germination, as judged by the presence of radicles at least 3 mm long, was obtained at 3 or  5 °C on seeds of apricot, mazzard cherry, myrobalan plum, garden plum, mahaleb cherry, European bird cherry, and black cherry (Suszka 1967). For many other species in table 6, temperatures somewhat higher than 5 °C were used for germination. Information is not available, however, on the proportion of seeds that had started to germinate during the cold stratification period before the temperature was raised. The diurnally alternating temperatures of 30 and 20 °C specified for *Prunus* in the International Rules for Seed Testing (ISTA 1996) apparently are much too high. The Association of Official Seed Analysts (AOSA 1996) specify a germination temperature of 18 to 22 °C for mazzard cherry and peach. ISTA (1996) rules specify 90 to 120 days of chilling for mazzard cherry, European bird cherry, and black cherry. Germination is hypogeal in many species as (figure 4), but epigeal in common choke cherry (figure 5).

Viability tests are usually preferred over germination tests because of the long stratification time required to break

**Figure 4**—*Prunus americanum,* American plum:    seedling development at 1, 3, 5, and 9 days after hypogeal germination.
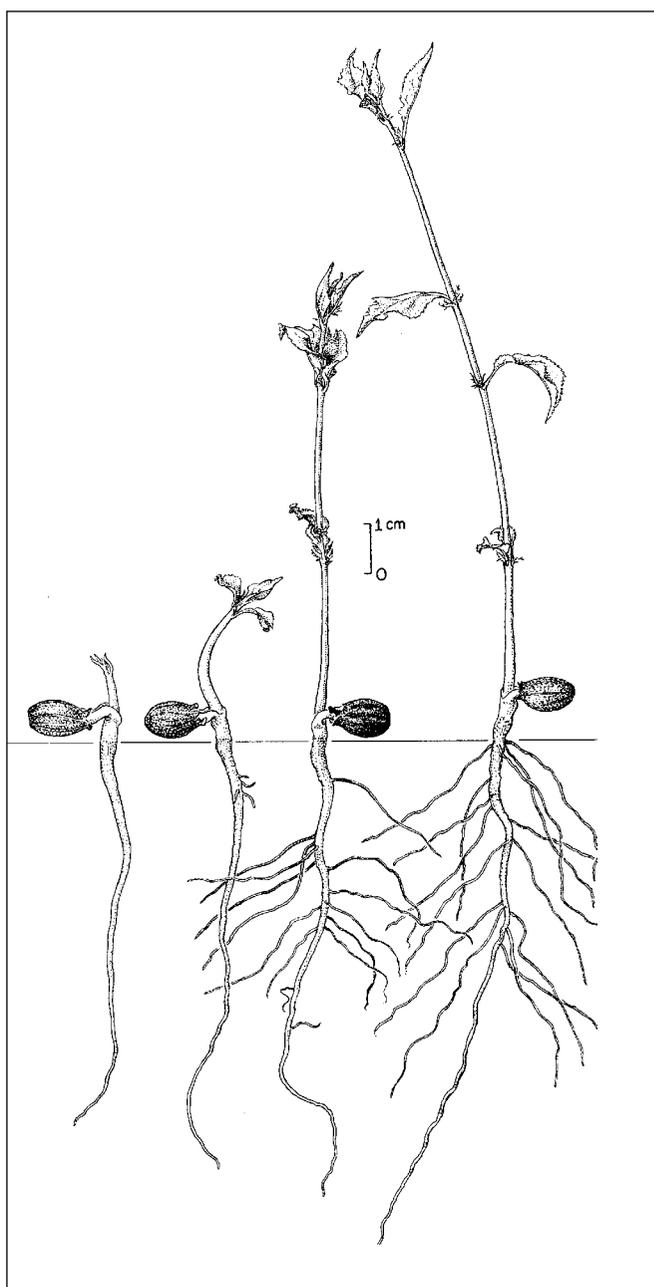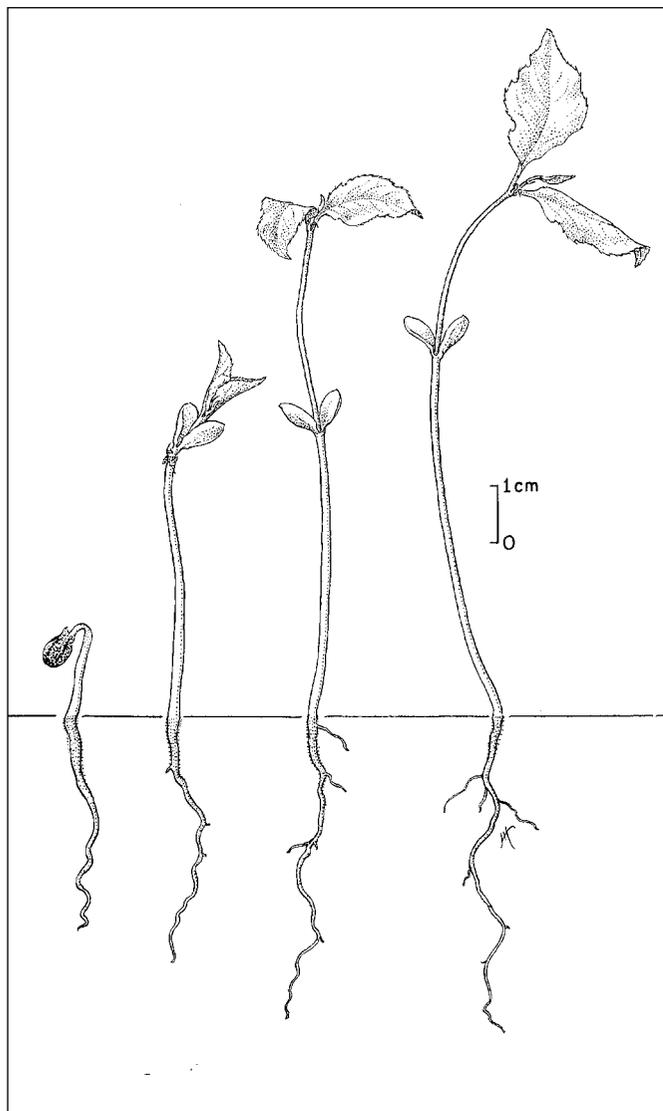
**Figure 5**—*Prunus virginianna,* common chokecherry; seedling development at 1, 3, 7, and 11 days after epigeal germination.



dormancy of most species. The excised embryo procedure is recommended by both AOSA (1996) and ISTA (1996) for all species, and it has been commonly used on American plum, almond, apricot, peach, sloe, and both wild and cultivated cherries (Chao and Walker 1966; Heit 1955; Shumilina 1949; Tukey 1944). Once the seedcoats are removed, the seeds are placed on dampened blotter paper in a 20 °C germinator for 10 days. The embryos are viable when the radicles begin to grow or the cotyledons turn green or open up.

The seeds of *Prunus* species also are easily stained with tetrazolium chloride, and they usually have high viability (table 6). The viability percentage is highly correlated with field emergence. Tetrazolium staining is recommended as an alternative method for viability tests on all *Prunus* species (AOSA 1996; ISTA 1996). The seed should be cracked and a small piece of cotyledon removed at the distal end, then soaked for 18 hours at 20 °C. The seedcoat should then be removed before incubation in a 1.0% solution for 8 to 12 hours at 30 °C (or 12 to 18 hours in 0.5%). Large-seeded species may require longer staining times. To be considered viable, the radicle tip and $1/3$ of the distal area of the cotyledons should be stained (ISTA 1996).

**Nursery practice.** Untreated *Prunus* seeds may be sown in the fall or stratified seeds may be sown in spring. Some species that require long periods for after-ripening are stratified warm and cool even before fall-sowing, or they may be planted as soon as collected (Al'benskii and Nikitin 1956; Grisez 1974; Koreisho and Morozov 1955). American and Chickasaw plums and common choke cherry seeds benefit from 30 days of warm stratification followed by 45 days of cold stratification before sowing (Huffman 1996). In fall-sowing, it is important to sow early enough to allow seeds to after-ripen before the ground freezes (Swingle 1925). Secondary dormancy can be induced in partially after-ripened seeds by high soil temperatures (Grzeskowiak and others 1983). Suszka (1978) recommends covering the nursery-bed with 10 cm (4 in) of straw mulch. Seeds should be sown in early September, or by mid-October at the latest, in the northern states (Grisez 1974; Heit 1938, 1967; Huntzinger 1971). Mulching and deeper sowing help overcome the effects of late sowing and dry climates.

Stratified seeds should be sown as early in spring as possible because high temperatures and drying can reduce germination (Haut 1932; Huntzinger 1971; Koreisho and Morozov 1955; Suszka 1967). It is best if a high proportion of the seeds in the seedlot are cracked but have not yet begun radicle elongation (Koreisho and Morozzov 1955; Suszka 1964, 1967). Long radicles are easily broken in handling and sowing. For this reason, seeds should be checked toward the end of the stratification period for emerging radicles (Huntzinger 1968, 1971). Transparent containers are ideal for this purpose. If radicle elongation starts when it is too early to sow, the temperature should be reduced to near-freezing (Afanasiev 1942).

Normal precautions may be taken against fungi during stratification and sowing, but they do not appear necessary if seedlots are properly cleaned and handled. Rodents must be kept out of the nursery, however (Grisez 1974; Huntzinger 1971).

*Prunus* seedlings reach suitable planting size in 1 or 2 years. Low seedbed densities help assure adequate size the first year and reduce the proportion of culls (Grisez 1974; Stoeckeler and Jones 1957).

Seedlings may be planted 1 m (3 ft) apart in rows 3 to 4 m (10 to 13 ft) apart to produce 3,000 seedlings/ha (7,400 seedlings/ac) (Janick and Moore 1996). Seedlings that set terminal buds may be forced by gibberellin sprays or can be cut back to stimulate growth (Janick and Moore 1996). It has been observed in the nursery that apricot trees with large leaves and unbranched shoots are more likely to produce medium or large sized fruits, but plants with much branching, very thin shoots, and small leaves are likely to have small fruit and fruit at an older age (Janick and Moore 1996). Nursery practices that have been successful are listed in table 7.

**Table 7**—*Prunus,* cherry, peach, and plum:   nursery practice

| Species | Stratification periods* (days) Fall-sowing | Spring-sowing | Seeds sown/ft² | Sowing depth (in) | Tree % | Outplanting age (yr) |
|---|---|---|---|---|---|---|
| P. americana | 0–90 | 120 | 4 | 1–2† | 33–50 | 1 |
| P. angustifolia | 0 | 15–20 | 1 | 33 | 1 | — |
| P. armeniaca | 0 | 90 | 9 | 2 | 50 | 1 |
| P. avium | 60‡ | 120 | 13 | 1–2 | — | 1 or 2 |
| P. cerasifera | 0‡ | — | 10 | 2 | 64§ | 1 |
| P. cerasus | 90‡ | 90 | 21 | — | — | 1 or 2 |
| P. domestica | 0 | — | 13 | 2 | — | 1 or 2 |
| P. mahaleb | 0–60 | 60 | — | 1–2 | 45§ | — |
| P. padus | 60‡ | 120 | 50 | 1/2–1‖ | — | 1 or 2 |
| P. persica | 0 | 85 | 0.75 | 2 | — | — |
| P. pumila var. besseyi | 0 | 120 | 6–7 | — | 77 | — |
| P. serotina | 0 | 120 | 10–20 | 1 1/2–2‖ | 7–83 | 1 |
| P. spinosa | 0‡ | 170 | 17–28 | 1–2 | 70–75§ | 1 or 2 |
| P. tomentosa | 0 | 60 | 15–30 | 1‖ | 72 | 1 |
| P. virginiana | 0 | 120–160 | 25 | _ | 3–34 | 1 or 2 |

**Sources:** Afanasijev (1962), Al'benskii and Nikitin (1956), Bailey (1969), Bejdl (1954), Engstrom and Stoeckeler (1941), Grisez (1974), Heit (1938, 1967), Huntzinger (1971), Koreisho and Morozov (1955), Nyholm (1951), Rudolf (1961), Schaaf (1938, 1940), Shoemaker and Teskey (1959), Shumilina (1940, 1949), Stoeckeler and Jones (1957), Swingle (1939), Talbert (1946).
\* Stratified in a moist medium at a temperature between 2.8 and 5 °C.
† Add a 10 to 15 cm (4- to 6-in) soil ridge to the nurserybed.
‡ Or stratify from time of collection to time of sowing when fresh seeds are used.
§ Germination percent (not tree percent).
‖ On fall-sown beds, add ~8 cm (3 in) of straw or moss for a mulch.

## References

Afanasiev M. 1940.   New seed-handling methods facilitate growing native trees. Oklahoma Agricultural Experiment Station Biennial Report 1938–40: 124–126.

Afanasiev M. 1942.   Propagation of trees and shrubs by seed. Circ. C-106. Oklahoma Agricultural Experiment Station. 43 p.

Afanasijev D. 1962.   Seed stimulation [translated from Serbo-Croatian]. Washington, DC: National Science Foundation and USDA. 15 p.

Al'benskii AV, Nikitin PD, eds. 1956.   Agrolesomeliortsiya. 3rd ed. Gos. Izd. S-kh. Lit., Moskva. [Handbook of afforestation and soil amelioration. Transl. TT 66-51098. 1967. Springfield, VA: USDC, CFSTI. 516 p.]

AOSA [Association of Official Seed Analysts]. 1996.   Rules for testing seeds. Journal of Seed Technology 16 (3): 113.

Altman PL, Dittmer DS. 1962.   Biological handbook on growth. Washington, DC: FASEB [Federation of American Societies for Experimental Biology]. 608 p.

Bejdl R. 1954.   Tresen, cilova drevina blizke budoucnosti. Lesnicka Prace 33: 354–357 [*Prunus avium*, the tree of the future. Forestry Abstracts 16: 199].

Bonner FT. 1975.   Maturation of black cherry fruits in central Mississippi. Res. Note SO-205. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 4 p.

Cech FC, Kitzmiller JH Jr. 1968.   Geographic variation in seed and seedling characteristics of black cherry (*Prunus serotina* Ehrh.). 15th North-eastern Forest Tree Improvement Conference Proceedings 1968: 53–62.

Chadwick LC. 1935.   Practices in propagation by seed. American Nurseryman 62(12): 3–9.

Chao L, Walker DR. 1966.   Effects of temperature, chemicals, and seed coat on apricot and peach seed germination and growth. Proceedings of the American Society of Horticultural Science 88: 232–238.

Chittenden AK. 1927.   Forest planting in Michigan. Michigan Agricultural Experiment Station Technical Bulletin 163. 24 p.

Cochran LC, Cooper WC, Blodgett EC. 1961.   Seeds for rootstocks of fruit and nut trees. In: Yearbook of Agriculture: Seeds. Washington, DC: USDA: 233–239.

Coe FM, Gerber RK. 1934.   Preliminary studies of the after-ripening and germination of cherry seeds. Proceedings of the Utah Academy of Science, Arts and Letters 11: 185–187.

Crocker W. 1927. Dormancy in hybrid seeds. Boyce Thompson Institute Professional Papers 6: 1–6.

Crocker W. 1930. Harvesting, storage, and stratification of seeds in relation to nursery practice. Florists Exchange 73(3): 9, 29, 34.

Crocker W. 1931. After-ripening, germination, and storage of certain rosaceous seeds. Contributions of the Boyce Thompson Institute 3: 385–404.

Cummings MB, Jenkins EW, Dunning RG. 1933. Rootstock effects with cherries: seed and phyton propagation. Vermont Agricultural Experiment Station Bulletin 352: 1–36.

Defler SE. 1937. Black cherry: characteristics, germination, growth, and yield [master's thesis]. Syracuse, NY: Syracuse University School of Forestry.

Dirr MA, Heuser CW Jr. 1987. The reference manual of woody plant propagation: from seed to tissue culture. Athens, GA: Varsity Press. 239 p.

Dorn D, Flick V. 1969. Seed cleaning equipment for removing pulp from black cherry. Tree Planters' Notes 20(3): 11–12.

Edlin HL. 1967. A modern sylva or a discourse of forest trees: 22. Rose tribe trees: Family Rosaceae. Quarterly Journal of Forestry 61: 189–197.

Emery D. 1964. Seed propagation of native California plants. Leaflets of the Santa Barbara Botanical Garden 1(10).

Engstrom HE, Stoeckeler JH. 1941. Nursery practice for trees and shrubs suitable for planting in the Prairie-Plains. Misc. Pub. 434. Washington, DC: USDA. 159 p.

Everett PC. 1957. A summary of the culture of California plants at the Rancho Santa Ana Botanic Garden, 1927–1950. Claremont, CA: Rancho Santa Ana Botanical Garden. 223 p.

Fernald ML. 1950. Gray's manual of botany. 8th ed. New York: American Book Co. 1632 p.

Fogle HW. 1958. Effects of duration of after-ripening, gibberellin and other pretreatments on sweet cherry germination and seedling growth. Proceedings of the American Society of Horticultural Science 72: 129–133.

Fogle HW, McCrory CS. 1960. Effects of cracking, after-ripening and gibberellin on germination of Lambert cherry seeds. Proceedings of the American Society of Horticultural Science 76: 134–138.

Gaudio S Del, Pedone L. 1963. Germinability of almond seeds. Annali della Sperimentazione Agraria (n.s.) 17(1/2): 91–138.

Giersbach J, Crocker W. 1932. Germination and storage of wild plum seeds. Contributions of the Boyce Thompson Institute 4: 39–51.

Glazebrook TB. 1941. Overcoming delayed germination in the seed of plants valuable for erosion control and wildlife utilization [unpublished master's thesis]. Moscow, ID: University of Idaho School of Forestry. 97 p.

Gordon AG, Rowe DCF. 1982. Seed manual for ornamental trees and shrubs. For. Comm. Bull. 59. London: Her Majesty's Stationery Office. 132 p.

Grisez TJ. 1974. Prunus, L., cherry, peach, and plum. In: Schopmeyer CS, tech coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 658–673.

Grisez TJ. 1976. Black cherry seeds stored 8 years. Tree Planters' Notes 27: 20–21.

Grzeskowiak H, Miara B, Suszka B. 1983. Long term storage of seeds of Rosaceae species, used as rootstocks for cherry, plum, apple, and pear cultivars. Arboretum Kornickie 28: 283–320.

Gysel LW, Lemmien WA. 1964. An eight-year record of fruit production. Journal of Wildlife Management 28: 175–177.

Harlow WM, Harrar ES. 1958. Textbook of dendrology. 4th ed. New York: McGraw-Hill Book Co. 561 p.

Hartman HT, Kester DE. 1959. Plant propagation: principles and practice. Englewood Cliffs, NJ: Prentice Hall. 559 p.

Haut IC. 1932. The influence of drying on the after-ripening and germination of fruit tree seeds. Proceedings of the American Society of Horticultual Science 29: 371–374.

Haut IC. 1938. Physiological studies on after-ripening and germination of fruit tree seeds. Maryland Agricultural Experiment Station Bulletin 420: 1–52.

Havis L, Gilkeson AL. 1949. Starting seedlings of Montmorency cherry. Proceedings of the American Society of Horticultural Science 53: 216–218.

Hedrick UP. 1911. The plums of New York. In: New York Department of Agriculture 18th Annual Report, Volume 3, Part 2. 616 p.

Hedrick UP. 1915. The cherries of New York. In: New York Department of Agriculture 22nd Annual Report, Volume 2, Part 2. 371 p.

Heit CE. 1938. Additional data on black cherry germination. Notes For. Invest. 16. Albany: New York Conservation Department. 1 p.

Heit CE. 1945. Fall planting of hardwood tree seed. Farm Research 11(3): 14–15.

Heit CE. 1955. The excised embryo method for testing germination quality of dormant seed. Proceedings of the Association of Official Seed Analysts 45: 108–117.

Heit CE. 1967a. Propagation from seed: 6. Hard seededness—a critical factor. American Nurseryman 125(10): 10–12, 88–96.

Heit CE. 1967b. Propagation from seed: 8. Fall planting of fruit and hardwood seeds. American Nurseryman 126(4): 12–13, 85–90.

Heit CE. 1967c. Propagation from seed: 11. Storage of deciduous tree and shrub seeds. American Nurseryman 126(10): 12–13, 86–94.

Hesse CO, Kester DE. 1955. Germination of embryos of Prunus related to degree of embryo development and method of handling. Proceedings of the American Society of Horticultural Science 65: 251–264.

Hitchcock CL, Cronquist A, Ownbey M, Thompson JW. 1961. Vascular plants of the Pacific Northwest: 3. Saxifragaceae to Ericaceae. Seattle: University of Washington Press. 614 p.

Huffman GR. 1996. Seed handling and propagation of hardwood trees and shrubs at Oklahoma Forestry Services' Forest Regeneration Center. In: Landis TD, South DB, tech. coords. National Proceedings, Forest and Conservation Nursery Associations. Gen. Tech. Rep. PNW-389. Portland, OR: USDA Forest Service, Pacific Northwest Research Station: 43–48.

Huntzinger HJ. 1968. Methods for handling black cherry seed. Res. Pap. NE-102. Upper Darby, PA: USDA Forest Service, Northeastern Forest Experiment Station. 22 p.

Huntzinger HJ. 1971. Long-term storage of black cherry seed—is it effective? Tree Planters' Notes 22(4): 3–4.

ISTA [International Seed Testing Association]. 1996. International rules for seed testing. Seed Science and Technology 24 (suppl.): 335.

Janick J, Moore JN. 1996. Fruit breeding. Volume 1, Tree and tropical fruits. New York: John Wiley & Sons. 616 pp.

Jones L. 1963. Effect of various pregermination treatments on germination of black cherry seed. Res. Note SE-8. Asheville, NC: USDA Forest Service, Southeastern Forest Experiment Station. 2 p.

Kester DE. 1969. Almonds. In: Handbook of North American nut trees. Knoxville, TN: Northern Nut Growers Association: 302–314.

King JE. 1947. The effect of various treatments to induce germination of seeds of some plants valuable for soil conservation and wildlife [master's thesis]. Moscow, ID: University of Idaho School of Forestry. 97 p.

Knuth P. 1906–1909. Handbook of flower pollination. 3 vol. Oxford: Clarendon Press.

Koreisho EG, Morozov DN, eds. 1955. Manual of afforestation and soil melioration. 2nd ed. [enl. and rev. 1966]. Israel Program for Scientific Translations 1609. 363 p.

Krefting LW, Roe EI. 1949. The role of some birds and mammals in seed germination. Ecology Monographs 19: 269–286.

Krier JP. 1948. Effects of treatments to induce germination of seeds of several species valuable for soil conservation plantings [master's thesis]. Moscow, ID: University of Idaho School of Forestry. 47 p.

Laidlaw TF. 1983. Studies on pin cherry germination: 2. The impact of temperature and temperature fluctuation in a 30 day initial treatment period preceding continuous cold stratification. Internal NOVA Rep. 1-61. Tofield, AB: Laidlaw Vegetation Consulting Ltd.

LHBH [Liberty Hyde Bailey Hortorium]. 1976. Hortus third: a concise dictionary of plants cultivated in the United States and Canada. New York: Macmillan. 1290 p.

Lockley GC. 1980. Germination of chokecherry (Prunus virginiana) seeds. Seed Science and Technology 8(3): 237–244.

Long B. 1923. Naturalized occurrence of Prunus padus in America. Rhodora 25: 169–177.

Marcet E. 1951. Beitrag zur Verbesserung des Keimprozentes bei der Vogelkirsche (Prunus avium L.). Schweizerische Zeitschrift für Forstwesen 102: 524–526 [Increased plant percent in sowings of Prunus avium. Biological Abstracts 26: 16431; 1952].

Martin AC, Zim HS, Nelson AL. 1951. American wildlife and plants. New York: McGraw-Hill. 500 p.

McMinn HE. 1959. An illustrated manual of California shrubs. Berkeley: University of California Press. 663 p.

Michalska S. 1982. Embryonal dormancy and induction of secondary dormancy in seeds of mazzard cherry (Prunus avium L.). Arboretum Kornickie 27: 311–332.

Michalska S, Suszka B. 1980a. The effect of multiple induction of dormancy in Prunus avium L. seed. In: Secondary dormancy of seeds of Prunus species. Kornik: Polish Academy of Sciences, Institute of Dendrology: 13–24.

Michalska S, Suszka B. 1980b. Effects of multiple induction of domancy on germination of seeds of various Prunus L. species. In: Secondary dormancy of seeds of Prunus species. Kornik: Polish Academy of Sciences, Institute of Dendrology: 27–40.

Michalska S, Suszka B. 1980c. Testing of the effectivness of a warm-followed-by-cold stratification of Prunus avium L. seeds, with a 3-week warm phase, when combined with an early induction of secondary dormancy. In: Secondary dormancy of seeds of Prunus species. Kornik: Polish Academy of Sciences, Institute of Dendrology: 51–56.

Michalska S, Suszka B. 1980d. Warm-followed-by-cold stratification of *Prunus avium* L. seeds as a case of the earliest possible induction of secondary dormancy. In: Secondary dormancy of seeds of Prunus species. Kornik: Polish Academy of Sciences, Institute of Dendrology: 61–67.

Miller HF Jr. 1960. Swift, untiring harvest help. In: Yearbook of Agriculture: Power to produce. Washington, DC: USDA: 164–183.

Mirov NT, Kraebel CJ. 1937. Collecting and handling of the seeds of California wild plants. Res. Note 18. Berkeley, CA: USDA Forest Service, California Forest and Range Experiment Station. 27 p.

Mirov NT, Kraebel CJ. 1939. Collecting and handling seeds of wild plants. For. Pub. 5. Washington, DC: USDA Civilian Conservation Corps. 42 p.

Mugford DG. 1969. Seed handling of fleshy-fruited species in forest nurseries. In: Proceedings, Northeastern Area Nurserymen's Conference: 19–20.

Muller C, Bonnet-Masimbert M, Laroppe E. 1990. Nouvelles voies dans le traitement des graines dormates de certains feuillus: hetre, frene, merisier. Revue Forestiere Francaise XLII: 329–345.

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

Nyholm I. 1951. Spiringsforsog med tjorn, myrobalan og seljeron [Germination experiments with hawthorn, myrobalan plum, and Swedish mountain ash]. Gartner Tidende 67: 79–81.

Olson RJ, Nagle JP. 1965. Adaptation tests of trees and shrubs for the inter-mountain area of the Pacific Northwest. Circ. 450. Pullman: Washington Agricultural Experiment Station. 43 p.

Pane MJ. 1966. Fruit setting of almonds. Cultivador Moderno 49: 343–346.

Paton RR. 1936. Preplanting treatment of black cherry seed. Journal of Forestry 34: 730.

Peck ME. 1961. A manual of the higher plants of Oregon. 2nd ed. Corvallis: Oregon State University Press. 936 p.

Petrides GA.1958. A field guide to trees and shrubs. Boston: Houghton Mifflin. 431 p.

Pillay DTN.1962. A study of the relationship of growth substances to rest period and germination of mazzard cherry seeds (*Prunus avium* L.). Dissertation Abstracts 22: 3830.

Pitcher JA. 1984. Geographic variation patterns in seed and nursery characteristics of black cherry. Res. Pap. SO-208. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 8 p.

Pollock BM, Olney HO. 1959. Studies of the rest period: 1. Growth, translocation, and respiratory changes in the embryonic organs of the after-ripening cherry seed. Plant Physiology 34: 131–142.

Probocskal E. 1963. [Stratification examinations with seeding material of bitter almonds (*Prunus amygdalus v. amara* (D.C.) Focke) and wild apricot (*Prunus armeniaca* L.)]. Kiserletugyi Kozlemenyek 56(2): 47–70.

Radford AE, Ahles HE, Bell CR. 1964. Guide to the vascular flora of the Carolinas. Chapel Hill: University of North Carolina. 383 p.

Rehder A. 1940. Manual of cultivated trees and shrubs hardy in North America. 2nd ed. New York: Macmillan. 996 p.

Ramming DW. 1990. The use of embryo culture in fruit breeding. HortScience 25(4): 393–398.

Robertson FCF. 1948–49. The pretreatment of forest seed to hasten germination. Forestry Abstracts Reprint 8: 1–12.

Roe EI. 1941. Effect of temperature on seed germination. Journal of Forestry 39: 413–414.

Rudolf PO. 1961. Collecting and handling seeds of forest trees. In: Yearbook of Agriculture: Seeds. Washington, DC: USDA: 221–226.

Schaaf M. 1938. Ninth biennial report (1937–38). Michigan Department of Conservation, Division of Forestry: 267–290.

Schaaf M. 1940. Tenth biennial report (1939-40). Michigan Department of Conservation, Division of Forestry: 279–309.

Seeley SD, Damavandy H. 1985. Response of seed of seven deciduous fruits to stratification temperatures and implication for modeling. Journal of the American Society for Horticultural Science 110(5): 726–729.

Shoemaker JS, Teskey BJE. 1959. Tree fruit production. New York: John Wiley and Sons. 456 p.

Shumilina ZK. 1940. Stratifikatsiya semyan drevesnykh i kustarnikovykh porod. Vses. Nauchnoissled Inst. Agrolesomelior. Goslestekhizdat, Moskva [Stratification of seeds of trees and shrubs. Transl. OTS-60-51012. 1961. Springfield, VA: USDC, CFSTI. 64 p.].

Shumilina ZK. 1949. Podgotovka posevu semyan drevesnykh i kustarnikovykh porod. Vses. Nauchnoissled Inst. Agrolesomelior., Goslesbumizdat, Moskva-Leningrad [Preparation of tree and shrub seed for sowing. Transl. TT 67-51300. 1967. Springfield, VA: USDC, CFSTI. 36 p.].

Solovieva MA. 1966. Long-term storage of fruit seeds. Proceedings, 17th International Horticulture Congress 1: 238.

Solovieva MA. 1978. Method of storing fruit seeds and determining their storage quality. Byulleten 'Vsesoyuznogo Instituta Rastenievodstva 77: 64–65.

Steavenson HA. 1940. The hammer mill as an important nursery implement. Journal of Forestry 38: 356–361.

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

Strausbaugh PD, Core EL. 1964. Flora of West Virginia. Bull. Ser. 65(3-1). Morgantown: West Virginia University. 1075 p.

Sudworth GB. 1908. Forest trees of the Pacific slope. Washington, DC: USDA Forest Service. 441 p.

Suszka B. 1964. Wplyw sposobu i dlugosci okresu przechowywania pestek na zdolnosc kielkowania nasion czeresni dzikiej (*Prunus avium* L.) [The influence of method and duration of stone storage on the germination capacity of mazzard cherry (*Prunus avium* L.)]. Arboretum Kornickie 9: 223–235.

Suszka B. 1967. Studia nad spoczynkiem i kielkowaniem nasion róznych gatunków z rodzaju *Prunis* L. [in Polish with English summary: Studies on dormancy and germination of seeds from various species of the genus *Prunus* L.]. Arboretum Kornickie 12: 221–282.

Suszka B. 1970. Storage of mazzard cherry (*Prunus avium* L.) seeds over many years. Arboretum Kornickie 15: 129–137.

Suszka B. 1978. Germination of tree seed stored in a partially afterripened condition. Acta Horticulturae 83: 181–187.

Suszka B, Muller C, Bonnet-Masimbert M. [Gordon A, transl.]. 1996. Seeds of forest broadleaves, from harvest to sowing. Paris: Institut National de la Recherche Agronomique. 294 p.

Swingle CF. 1925. Heavy losses follow late stratification of plum and cherry seeds. National Nurserymen 33: 197–200.

Swingle CF, comp. 1939. Seed propagation of trees, shrubs, and forbs for conservation planting. SCS-TP-27. Washington, DC: USDA Soil Conservation Service. 197 p.

Talbert TJ. 1946. General horticulture: principles and practices of orchard, small fruit, and garden culture. Philadelphia: Lea and Febiger. 452 p.

Tennes BR, Anderson RL, Levin JH. 1968. Weight to volume relationship of tart cherries. Res. Rep. 70. East Lansing: Michigan State University Agricultural Experiment Station and Cooperative Extension Service. 4 p.

Therios IN. 1982. Effects of temperature, moisture stress and pH on the germination of seeds of almond (*Prunus dulcis* 'Truoito'). Seed Science and Technology 10: 585–594.

Tukey HB. 1924. Studies of fruit seed storage and germination. New York State Agricultural Experiment Station Bulletin 509: 1–119.

Tukey HB. 1927. The viability of seed from certain cherry varieties. American Society of Horticultural Science Proceedings 24: 129–132.

Tukey HB. 1936. Development of cherry and peach fruits as affected by destruction of the embryo. Botanical Gazette 98(1): 1–24.

Tukey HB. 1944. The excised embryo method of testing the germinability of fruit seed with particular reference to peach seed. American Society of Horticultural Science Proceedings 45: 211–219.

USDA [U.S. Department of Agriculture]. 1961. Yearbook of Agriculture: Seeds. Washington, DC: USDA. 591 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.

Wasson E. 2001. Trees and shrubs: illustrated A–Z of over 8500 plants. Willoughby, NSW, Australia: Global Publishing: 568–575.

Wright JW. 1966. Unpublished data. East Lansing: Michigan State University.

Zielinski QB. 1958. Some factors affecting seed germination in sweet cherries. Proceedings of the American Society of Horticultural Science 72: 123–128.

Zigas RP, Coombe BG. 1977. Seedling development in peach, *Prunus persica* (L.) Batsch. 1. Effects of testas and temperature. 2. Effects of growth regulators. Australian Journal of Plant Physiology 4(3): 349–369.

Pinaceae—Pine family

# *Pseudotsuga* Carr.

## Douglas-fir

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**Growth habit, occurrence, and uses.** Seven species are currently included in the genus *Pseudotsuga;* they are Douglas-fir (*P. menziesii* (Mirb.) Franco) and bigcone Douglas-fir (*P. macrocarpa* (Vasey) Mayr) in North America and *P. japonica* (Shirasawa) Beissner, *P. wilsoniana* Hayata, *P. sinensis* Dode, *P. forrestii* Craib, and *P. gausseni* Flous in eastern Asia (Hermann 1982; Little 1979). The generic name—*Pseudotsuga,* meaning "false hemlock"—reflects the difficulties taxonomists had in classifying the genus (Little 1952).

Fossil records indicate that *Pseudotsuga* has been present in western North America since the Early Tertiary Epoch, and later also in Japan and perhaps in Europe (Hermann 1985). Its limited early range in North America expanded during interglacial intervals to approximately its current range.

Only 1 species, Douglas-fir, is widely distributed; the other 6 species are relatively sparse and their natural distributions are narrow and restricted. The range of Douglas-fir extends from latitude 19°N in central Mexico to 55°N in central British Columbia, and from longitude 97°W in Mexico northwesterly to the Pacific Ocean and to 128°W in British Columbia (Little 1971; Silen 1978). Two varieties are recognized—coastal Douglas-fir (var. *menziesii*) and interior Douglas-fir (var. *glauca*) (table 1). The 2 varieties adjoin and introgress in British Columbia (Li and Adams 1989; Rudloff 1972) but occur in separate territories from southern British Columbia southward. Bigcone Douglas-fir occurs only in southwestern California and is separated by 34 km from the southernmost known locality for coastal Douglas-fir (Griffin 1964). Both North American species have been propagated successfully in Europe but only Douglas-fir has gained worldwide prominence. It is the most important exotic grown in western and central Europe and is also very important in Chile, New Zealand, and Australia (Kleinschmit and Bastien 1992), becoming naturalized in several countries (Jones 1946; Ledgard 1988).

In North America, Douglas-fir naturally occupies a wide span of elevations and climatic conditions. Coastal Douglas-fir is found on soils derived from marine, glacial, and vol-

**Table 1**—*Pseudotsuga,* Douglas-fir: nomenclature and occurrence

| Scientific name & synonyms | Common name(s) | Occurrence |
|---|---|---|
| ***P. macrocarpa* (Vasey) Mayr**<br>*Abies douglasii* var. *macrocarpa* Torr.<br>*A. macrocapa* Vasey | **bigcone Douglas-fir**,<br>bigcone-spruce, desert-fir | Mtns of SW California |
| ***P. menziesii* var. *glauca* (Beissn.) Franco**<br>*P. douglasii* var. *glauca* Mayr<br>*P. menziesii* var. *caesia* (Schwerin) Franco<br>*P. taxifolia* var. *glauca* (Beissn.) Sudworth | **interior Douglas-fir,**<br>blue Douglas-fir, Rocky<br>Mountain Douglas-fir,<br>Colorado Douglas-fir,<br>inland Douglas-fir | Central British Columbia & SW Alberta,<br>S in mtns to N & central Mexico, from<br>E Washington, Oregon, Nevada, & W Arizona<br>to E Montana, Wyoming, Colorado,<br>New Mexico, & NW Texas |
| ***P. menziesii* var. *menziesii* (Mirb.)<br>Franco**<br>*P. douglasii* var. *viridis* Schwerin<br>*P. menziesii* var. *viridis* (Schwerin) Franco<br>*P. mucronata* (Raf.) Sudworth<br>*P. taxifolia* (Lamb.) Britton | **coastal Douglas-fir,**<br>green Douglas-fir,<br>Oregon Douglas-fir,<br>Douglas-fir,<br>Douglas-spruce | SW British Columbia through Washington &<br>Oregon to central California, E into Cascade<br>& Sierra Nevada ranges to W Nevada |

**Sources:** Griffin and Critchfield (1976), Hermann (1982), Hermann and Lavender (1990), Little (1952, 1971, 1979), McDonald (1990), Minnich (1982).

canic origins at elevations from sea level to 1,250 m in the north to 2,300 m near its southern limits in the Sierra Nevada (Hermann and Lavender 1990). Interior Douglas-fir is found on soils derived from many parent materials at elevations from 550 to 2,440 m in the north and from 1,550 to 3,260 m in southern Arizona. Bigcone Douglas-fir is also found on a wide variety of soils at elevations from 275 to 2,400 m on gentle to steep slopes (McDonald 1990). The altitudinal distribution of these species shifts from southerly slopes at high elevations or in northern parts of their ranges to northerly slopes in the southern parts in response to the interacting limitations of temperature and moisture. The presence of large canyon live oaks—*Quercus chrysolepis* Liebm.—apparently modifies fire intensity and appears to be a third crucial influence on distribution of bigcone Douglas-fir (Minnich 1977, 1980).

Both species are found in pure and mixed stands, generally as dominants or codominants, and grow to large sizes that vary by elevation and site. On favorable sites, mature bigcone Douglas-fir trees average 24 to 30 m tall and 61 cm or more in dbh; the largest living individual is 44.2 m tall and 213 cm dbh (AFA 2000). Interior Douglas-fir trees average 30 to 37 m tall and 38 to 102 cm dbh; the largest individual now on record is 42.4 m tall and 255 cm dbh (AFA 2000). Coastal Douglas-fir grows much larger; heights of 76 m and diameters of 150 to 180 cm are common on favorable sites. The largest living tree is 85.6 m tall and 408 cm in diameter (AFA 2000). The lifespan of bigcone and interior Douglas-firs is up to 400 years and that for coastal Douglas-fir about 500 years (Hermann and Lavender 1990; McDonald 1990). The recorded maximums are 622 years for bigcone Douglas-fir and 1,400 years for coastal Douglas-fir (McArdle and others 1961; McDonald 1990).

Because of its wide distribution and many desirable characteristics, Douglas-fir is a major factor in timber production, watershed protection, wildlife habitat, and aesthetics whereas bigcone Douglas-fir's contribution is primarily local and limited. Douglas-fir is the premier species used where strength is needed in construction—laminated beams and arches, timbers, poles, piling, and structural plywood—and also for general construction, fiberboard, millwork, furniture, and specialty products. It is also the leading species used in the West for sulfate pulp (Panshin and Zeeuw 1970) and for Christmas trees.

To further its propagation within and beyond its native range, Douglas-fir's genetic and regeneration traits have been studied intensively. Clinal genetic variation has been demonstrated in both the coastal and interior varieties for many traits, including survival, growth, form, phenology,

insect and disease resistance, cold hardiness, wood characteristics, and chemical composition (Campbell 1986; Campbell and Sorensen 1978; Campbell and Sugano 1993; Ching and Bever 1960; Griffin and Ching 1977; Joly and others 1989; Li and Adams 1989; Read and Sprackling 1976; Rehfeldt 1979, 1989; Schowalter 1988; Silen 1978; Sorensen 1983; St. Clair and Adams 1991; Strauss and Tsai 1988). Because the survival and growth of Douglas-fir at a given location varies by the genetic source used, much effort has been expended in defining guidelines and zones for informed use of seeds and stock beyond the local geographic and climatic area of origin (Campbell 1991; Kleinschmit and Bastien 1992; Randall 1996; Rehfeldt 1981, 1983a&b.) Inspection systems have been developed to ensure that Douglas-fir seedlots and stock are correctly labeled and their origins certified (Portlock 1992; Schrumpf and Pfeifer 1993.)

Efforts to genetically improve Douglas-fir began over 50 years ago (Isaac 1949) and have developed into large long-term cooperative programs in western North America and abroad. In the Pacific Northwest, most of the seeds used in reforestation of coastal Douglas-fir now come from seed orchards (Daniels 1995). The species' use in the breeding zone of origin and other breeding zones is guided by results of outplanting tests and general rules for seed transfer (Randall 1996). A 10% gain in juvenile height growth is predicted for selections representing 6 low-elevation breeding zones in western Oregon and Washington (Stonecypher and others 1996). An international program for genetic improvement of Douglas-fir was started in 1967 and is continuing under IUFRO agencies involving 59 institutions in 36 countries (Kleinschmit and Bastien 1992). Other genetic improvement efforts involve selection for Christmas trees (Douglass and TerBush 1975; Silen 1978) hybridization (Rehfeldt 1977), and clonal propagation (Silen 1978). Many cultivars of Douglas-fir have been propagated by horticulturists (Hermann 1982).

**Flowering and fruiting.** Male and female strobili burst bud during late winter and spring (table 2), about a year after their initiation as axillary bud primordia (Allen and Owens 1972). Male strobili are generally borne abundantly over much of the crown on the proximal half of year-old shoots; these strobili become somewhat pendant when mature and are about 2 cm long. Female strobili develop more distally on year-old shoots that are located primarily in the upper half of the crown. The female strobili are erect at the time of pollen shedding and measure about 3 cm long; their appearance is dominated by large trident bracts (Allen and Owens 1972). The color of female strobili (seed cones) ranges from deep green to deep red, and that of male strobili

**Table 2**—*Pseudotsuga,* Douglas-fir:   phenology of flowering and fruiting

| Species | Location | Flowering | Cone ripening | Seed dispersal |
|---|---|---|---|---|
| *P. macrocarpa* | S California | February–mid-Apr | Early Aug–early Oct | Late Aug–late Oct |
| *P. menziesii* var. *glauca* | Central Colorado (elev. 2,060–2,880 m) | Mid-Apr–early May | — | — |
| | Montana (elev. 700–1,700 m) | Late May–early June | Late July–early Aug | Late Aug–mid-Sept* |
| | Northern Idaho (elev. 820–1,000 m) | Early May–late June | Mid-Aug | Early Sept* |
| | Central Oregon | Mid-May–mid-June | — | Mid-Aug–mid-Sept* |
| *P. menziesii* var. *menziesii* | Coastal British Columbia | Late Mar–mid-May | Aug | Sept–late Mar |
| | W-central Oregon & W Washington | Mid-Mar–early June† | Aug | Late Aug–late Mar‡ |
| | S Oregon | Early Apr–early  May | — | Mid-Aug* |
| | N California | — | August | Sept–early  winter§ |

**Sources:**  Allen (1942), Allen and Owens (1972), Ching and Ching (1962), Gashwiler (1969), Gause (1966), Griffith (1968), Isaac (1943), McDonald (1990, 1992), Morris (1952), Owston and Stein (1974), Roeser (1942), Silen (1963), Sorensen and Campbell (1971), Sudworth (1908).

\* Beginning dates only.

† Upslope  progression in pollen shedding and female receptivity averaged 23.5 m of elevation per day on 4 transects in western Oregon and Washington (Silen 1963).

‡ About 70 to 90% of the seeds usually disperse in September and October; most of the remainder disperse between November and March (Allen 1942; Isaac 1943).

§ Seedfall usually greatest in October (McDonald 1992).

from yellow to deep red. Strobili of the same sex tend to be of uniform color on individual trees, but the color of the males and females may differ (Griffith 1968).

Seed cones become receptive to pollination when they have emerged by half to two-thirds from the bud scales, and they remain so for at least 6 to 10 days (Ho 1980; Owens and others 1991; Silen 1978). Pollen dispersal occurs for 20 to 30 days in a given locality (Silen 1963). Seed cones soon become pendant, and fertilization takes place about 10 weeks after pollination (Allen and Owens 1972). Seeds develop through late spring and summer, reaching maturity in August or early September. Cones generally begin to dry and turn brown in August or September, and most seeds are released in September and October (table 2).

Calendar dates for phenological events vary with latitude and elevation (Silen 1963), between individual trees in a locality (Orr-Ewing 1956), and by position within the crown (Orr-Ewing 1956; Roeser 1942). Timing also varies from year to year, depending on weather conditions. Because cones open by drying, time of seed dispersal is particularly influenced by low humidity and drying winds in late summer and fall.

The mature cones of Douglas-fir are readily identified by their 3-lobed bracts, which protrude beyond the cone scales (figure 1). On each scale are 2 seeds that have relatively large wings (figure 2). One side of the seed is variegated light brown; the other is more glossy and dark brown. Embryos are linear (figure 3). The number of filled seeds per cone varies widely and tends to be greater for large

**Figure 1**—*Pseudotsuga menziesii* var. *menziessii,* coast Douglas-fir:   mature, closed cones have characteristic 3-lobed protruding bracts.



cones (Willis 1917). In interior Douglas-fir, filled-seed numbers ranged from 20 to 30 per cone in some collections (Owston and Stein 1974). For coastal Douglas-fir, filled-seed numbers ranged from 4 to 54 per cone in 309 collections from individual 35-year-old trees in northwestern Oregon (Olson and Silen 1975). Numbers averaged 16 per cone in collections from 127 individual trees in 10 westside areas located from north-central Washington to south-central Oregon (Willis and Hofmann 1915) and 19.4 per cone (range 2 to 35) in collections made between 1966 and 1978

**Figure 2**—*Pseudotsuga*, Douglas-fir: seeds of *P. macrocarpa*, bigcone Douglas-fir (**top**) and *P. menziesii*, Douglas-fir (**bottom**); the 2 varieties of the latter bear seeds similar in appearance and anatomy.
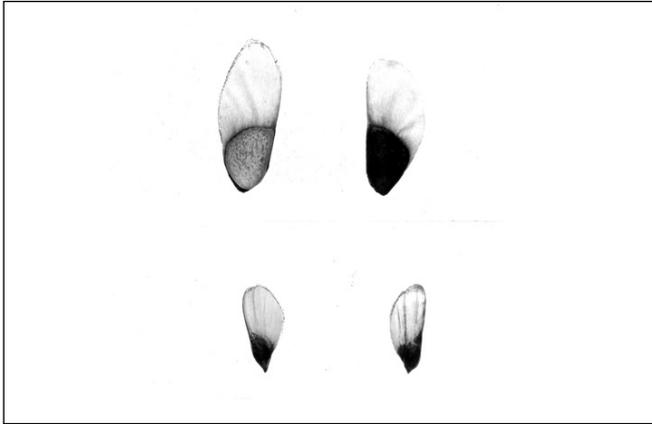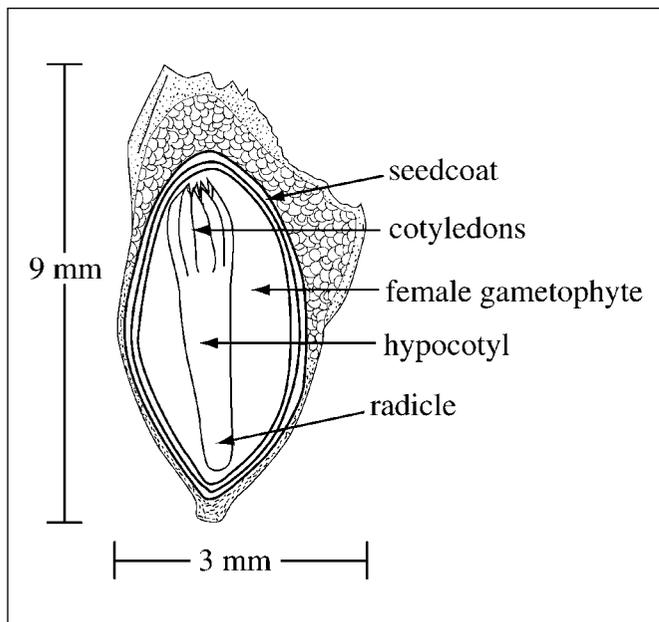


**Figure 3**—*Pseudotsuga menziesii*, Douglas-fir: longitudinal section through a seed showing fully developed embryo.

from 923 individual trees with sparse to good crops in 95 coastal and Cascade stands in Oregon and Washington (Sorensen 1997).

The seeds of Douglas-fir are disseminated by gravity and wind; their distribution varies widely—it is influenced by crop abundance, tree height and position, wind velocity, and other factors (Isaac 1930). Most seeds of bigcone Douglas-fir fall beneath the tree of origin; wider dissemination occurs primarily during high winds (McDonald 1990). Some Douglas-fir cones remain attached to the tree for a year or more after seed dispersal.

Seed production in Douglas-fir is highly variable from tree to tree. In a good seed year, an average mature, forest-grown coastal Douglas-fir produces about 0.45 kg (1 lb) of cleaned seeds (Isaac 1943), whereas widely spaced trees may produce 0.91 kg (2 lb) or more (Allen 1942; Isaac 1943). Because not all trees produce seeds, stand production averages considerably less than 0.45 kg (1 lb) of seeds per tree (Isaac 1943). Trees 100 to 200 years old are most prolific, but cones on younger trees are larger and contain more viable seeds (Willis 1917; Willis and Hofmann 1915). In young stands, seed production of coastal Douglas-fir begins at 7 to 10 years of age and somewhat later for interior Douglas-fir (table 3). When cultural and chemical techniques are used to stimulate precocious flowering, seeds have been produced on 2- to 5-year-old Douglas-firs, but pollen production is sparse (Silen 1978). Bigcone Douglas-firs may bear cones beginning about age 20, but they are rare on trees less than 40 years old (McDonald 1990).

Generally, some seeds are produced annually by coastal Douglas-fir except for about 1 year in any 4- to 5-year period (Isaac 1943; Reukema 1982); however, higher crop failure rates have been reported (McDonald 1992). Stand conditions as well as environmental and internal factors make the crop cycle erratic (Baron 1969; Eis 1973; Lowry 1966; Owens and others 1991). Abundant crops have occurred from 2 to 11 years apart (table 3). The seed production cycle for interior Douglas-fir is quite similar. Bigcone Douglas-fir usually has small cone crops; abundant crops occur infrequently and usually only in localized areas (USDA FS & CDF 1955–1971).

The existence of a cone crop cannot be confirmed until about 2 months before seedfall; poor pollination, frost, cone abortion, insects, and other factors may cause widespread failure after cones are visible (Owens and others 1991). Forecasts of crop potential are possible 12 months in advance of seedfall by counts of female buds (Allen 1941) or 17 months in advance by counts of male buds (Silen 1967). Bud counts are more accurate in predicting crop failures than in forecasting successful crops.

The high economic value of Douglas-fir seeds, especially genetically improved seeds, has prompted many studies, including those on the following topics: (1) factors affecting seed set (Owens and others 1991); (2) effects of inbreeding level on filled seed production (Woods and Heaman 1989); (3) influence of reproductive phenology on genetic diversity of seed crops (Copes and Sniezko 1991; El-Kassaby and Askew 1991); and (4) differences in fruitfulness between clonal and seedling orchards (El-Kassaby and others 1989). Cultural practices to stimulate seed production in natural

**Table 3**—*Pseudotsuga,* Douglas-fir:   height, seed-bearing age, crop frequency, and cone length

| Species | Mature height (m) | Minimum seed-bearing age (yr) | Years between large seedcrops | Cone length (cm) |
|---|---|---|---|---|
| *P. macrocarpa* | 9–30 | 20* | — | 11–17 |
| *P. menziesii* | | | | |
|   var. *glauca* | 23–49 | 20 | 3–10 | 4–7 |
|   var. *menziesii* | 27–91 | 7–10† | 2–11 | 6–10 |

**Sources:**   Allen (1942), Boe (1954), Gause (1966), Hermann and Lavender (1990), Lowry (1966), McArdle and others (1961), McDonald (1990), Roeser (1942), Sudworth (1908).

\* Occasionally earlier on good, open sites (Gause 1966).

† The  minimum age for commercial collections has been considered 20 to 25 years (Allen 1942).

stands or seed orchards include thinning and spacing (Reukema 1982, Williamson 1983); fertilization (Edwards 1986); girdling (Wheeler and others 1985; Woods 1989); top pruning (Copes 1973); and use of growth regulators alone (Ross and others 1980) or in combination with girdling, root-pruning, top-pruning, and branch-thinning (Ross and Bower 1991; Ross and Currell 1989; Ross and others 1985). In 1990, Cress and Daniels reported that existing coastal Douglas-fir seed orchards had the production potential to reforest 11 million acres with genetically improved stock by the year 2000.

Hedlin and others (1980) have developed a key for the many insects that damage cones and seeds of Douglas-fir. The Douglas-fir cone moth (*Barbara colfaxiana Kearfott*) causes major damage throughout the range of Douglas-fir but is most persistent in dry areas (Miller and Ruth 1989). As few as 3 larvae can destroy all of the seeds in a cone. The Douglas-fir cone gall midge (*Contarinia oregonensis* Foote) is another major destroyer of seeds, particularly in wet areas; severe infestations can destroy an entire crop. The Douglas-fir seed chalcid (*Megastigmus spermotrophus* Wachtl.) is found on both Douglas-fir and bigcone Douglas-fir and frequently destroys 2 to 15% of the crop. Other insect pests include the western flower thrips (*Frankliniella occidentalis* Pergande), which feeds on Douglas-fir pollen in California; Douglas-fir cone scale midge (*Contarinia washingtonensis* Johnson); coneworms (*Dioryctria abietivorella* Groté, *D. pseudotsugella* Munroe, and *D. reniculelloides* Mutuura and Munroe); western conifer seed bug (*Leptoglossus occidentalis* Heidemann); and the fir cone looper (*Eupithecia spermaphaga* Dyar). The western spruce budworm (*Choristoneura occidentalis* Freeman) has also caused heavy damage to flower buds, flowers, and developing cones (Dewey 1970; Frank and Jenkins 1987).

A variety of efforts have been made to assess and curb insect damage to cones and seeds of Douglas-fir. The effects of cone and seed insects were evaluated in natural stands (Shearer 1984) and in Douglas-fir seed orchards (Schowalter and Haverty 1989; Schowalter and others 1985). Dombrosky and Schowalter (1988) suggested an inventory monitoring system to better identify causes of seed loss, and Miller (1986) described damage prediction systems to judge the need for protection from the Douglas-fir cone gall midge and other insects. Rappaport and Volney (1989) found that control of one pest resulted in increased damage from another. Insecticide treatments have been tested for protecting against all cone and seed insects (Stein and Koerber 1989; Stein and Tilden 1987; Summers and Miller 1986), and specifically from the cone gall midge and seed chalcid (Stein and Markin 1986) and the western spruce budworm (Stipe and Green 1981). The role of 2 recently identified pests, the Douglas-fir twig mining beetle (*Pityophthorus orarius* Bright) and a flightless weevil (*Lepesoma lecontei* (Casey), have also been investigated (Rappaport and Wood 1989; Sexton and Schowalter 1991).

Douglas-fir flowers, cones, and seeds are also affected by frost, small mammals, and birds. Buds, flowers, and conelets are periodically damaged by spring frosts (Roeser 1942; Silen and Keene 1969; Timmis 1977). Squirrels start clipping cones early, but they cut cones in large quantities mainly after seeds mature (Lavender and Engstrom 1956; Moore 1940; White and White 1985).

**Collection of cones.**   Douglas-fir cones are collected from untended natural stands; from natural stands tended for seed production; from seed orchards; and even from trees growing in yards, playgrounds, and parks. The scope of collection ranges from a few cones for scientific or personal purposes to region-wide collections to achieve technical or commercial objectives. Thus, collection techniques range from simple hand methods to highly mechanized efforts with commensurate preharvest planning and organization

(Brown 1983; Maxwell and Aldhous 1967). Whatever the size of the collection, the same key considerations are involved—where, when, and how to collect and how to care for the cones afterward.

With 2 varieties to choose from and demonstrated genetic, geographic, and ecologic adaptation within each, choosing the right source from which to collect Douglas-fir cones is complex. Fortunately, the general axiom to collect seeds from sources ecologically similar to where they are to be used has been implemented by designation of seed zones (Rudolf 1974; Stein and others 1986) and development of seed transfer guidelines (Campbell 1986, 1991; Campbell and Sugano 1993; Randall 1996; Rehfeldt 1981, 1983a&b). Though much less is known about genetic variation in bigcone Douglas-fir, the same attention should be given to ecologically matching the seed source to the planting location.

Seeds are sufficiently ripe and ready for collection from 3 to 4 weeks before cones begin to open and shed seeds (Allen 1958a; Finnis 1950; Rediske 1969). This short collection period may start as early as August at low elevations and latitudes and as late as October at high elevations and latitudes (table 2), and it also varies with yearly weather conditions and from tree to tree (Allen 1958a; Brown 1983).

In general, cone color is not a good indicator of seed ripeness; browning of the external bracts is more diagnostic (Ching and Ching 1962). Ripeness is best determined by cutting cones open to reveal the seeds' color and appearance. The seedcoat should be golden brown to dark brown and the seed-wing light brown to tan; the endosperm should be full and firm; and the embryo should be yellowish green and fill most of its cavity (Brown 1983; Ching and Ching 1962; Finnis 1950; Willis 1917). Sample cones are cut longitudinally to check on seed ripeness and estimate seed yield. The count of filled seeds visible on one cut surface multiplied by 4.5 approximates the number of filled seeds per cone (Olson and Silen 1975). An average of 5 filled seeds per cut surface is generally needed for an economic large-scale harvest; lesser yields may be sufficient when supplies are scarce or only minor quantities are needed (Douglass and TerBush 1975; Portlock 1996; Schaefer and Miller 1985).

Douglas-fir cones are collected from standing trees, from felled trees or tops, and from squirrel caches. A whole array of spurs, ladders, cable methods, lifts, and axillary devices are used to assist climbers in getting into the crowns of tall trees and safely collecting cones (Matusz 1964; Portlock 1996). Vehicle-mounted lifts are often used in seed orchards. Shaking the cones from trees has been accomplished without serious crown damage (Copes 1985; Copes and Randall 1983; USDA FS 1972). Cost-effective methods

have been devised to aerially rake crowns or clip tops by helicopter (Camenzind 1990; Wallinger 1985). Gathering squirrel-cut cones from the ground or from caches is still a key method of obtaining cones from tall trees in natural stands (Brown 1983; Maxwell and Aldhous 1967; White and White 1985). Squirrel caches provide a means of extending the harvest season, as the cones are usually cached in moist areas and remain closed. However, damage from molds may be greater than in cones harvested from trees. Silvicultural and practical advantages and disadvantages of each collecting method have been summarized by Edwards (1985).

Picked cones are bagged, then transported either first to a collection station or directly to a processing plant where they may be held before seeds are extracted, cleaned, and stored. Two concerns are paramount: keeping the collected cones adequately identified and ensuring good ventilation to prevent killing seeds from overheating or molding. A label on the inside and outside of each bag or container should at least indicate the species, geographic location, elevation, date, and signature of the collector (Stein and others 1986). Plastic mesh bags are preferred over burlap sacks because of better aeration and thus decreased likelihood of contamination by molds. To facilitate air circulation and cone expansion, bags are usually filled only half full, loosely tied, and kept in shade on racks at field sites, collection stations, and even during transport (Brown 1983).

Cones may be stored for 2 to 4 months under dry, well-ventilated conditions without impairing seed viability (Bloomberg 1969; Lavender 1958; Rediske 1961; Rediske and Shea 1965). In fact, under good cone storage conditions, seeds may benefit from after-ripening (Bloomberg 1969; Rediske 1961), whereas lengthy storage of green cones under warm moist conditions can result in severe seed losses from increased molding (Rediske and Shea 1965). Because of tree-to-tree variation in time of seed ripening, any broad-scale collection contains cones with immature seeds that need after-ripening (Allen 1958a; Olson and Silen 1975; Rediske 1961; Silen 1958). Currently, some processors after-ripen cones in well-ventilated, refrigerated vans at temperatures of 7 to 10 °C (Lippitt 1996). Air-drying cones in protected, well-ventilated storage for several weeks or longer is more common, however (Brown 1983; Schaefer and Miller 1985).

**Extraction, cleaning, and storage of seeds.** At most extractories, Douglas-fir cones are at least partially air-dried during storage, then kiln-dried to fully open them. Where warm, low-humidity conditions prevail, air-drying may be sufficient, but in much of the West, some supplemental heat is necessary. Slow drying at moderate temperature is recom-

mended (table 4), as high heat applied to green cones and seeds of high moisture content can be very damaging (Allen 1958b; Hall 1984; Morris 1936; Willis 1917). Cones may be moistened just before kiln-drying to overcome any case-hardening and to facilitate a uniform rate of drying (Brown 1983). Cones of coastal Douglas-fir open fully with loss of 35 to 51% of their wet weight (Willis 1917).

Seeds are extracted from fully open cones in a variety of tumbling devices, ranging from a hand-turned, screen-covered wooden frames to large rotary combination dryer-tumblers (Stein and others 1974). Because both heat and sharp impacts can damage Douglas-fir seeds (Allen 1958b), loose seeds are often removed at several stages of process-ing—before kiln-drying, during drying, and during tum-bling. A seed moisture content of 7.5% (wet weight basis) or less is sought during kiln-drying or by later supplemental conditioning (Brown 1983).

Post-extraction processing of seeds usually includes (1) screening to separate seeds from cone scales, dirt, and debris, (2) de-winging, and (3) fanning or blowing to remove hollow seeds, wings, and dust. Vibrating, air, or gravity separators; soaking and drying; and other methods may be used to get seedlots extra clean (Hergert and others 1971; Lowman 1975; Sweeney and others 1991). Elimination of small seeds by sizing is not recommended, however, as this reduces genetic diversity (Silen and Osterhaus 1979). In every stage of cleaning, sharp impacts need to be minimized to produce Douglas-fir seedlots of highest quality (Allen 1958b). An attainable processing stan-dard for Douglas-fir is 98% for purity and 80% or higher for viability (Brown 1983; Lippitt 1996; Stein and others 1986).

Cone sizes and seed weights of Douglas-fir vary by vari-ety, year, geographic location, elevation, aspect, stand age and density, tree and family, and time of collection (Hermann and Lavender 1968; Kozak and others 1963; Olson and Silen 1975; Silen and Osterhaus 1979; Sorensen 1967, 1980, 1983; St. Clair and Adams 1991; Willis and

Hofmann 1915). Bigcone Douglas-fir has much larger cones and yields more seeds per weight of cones (table 4). Its smallest seeds average 5 times the weight of the largest seeds of interior and coastal Douglas-firs (table 5).

For coastal Douglas-fir, the number of cones per volume ranged from 977 to 5,067/hl (344 to 1,784/bu) in collections from 309 individual 35-year-old trees (Olson and Silen 1975); in collections from 127 individual 15- to 600-year-old trees, cones per volume ranged from 1,988 to 5,441/hl (700 to 1,916/bu) (Willis and Hofmann 1915). For both coastal and interior Douglas-fir, size of seeds tends to decrease from southern to northern latitudes, that is, to increase in number per weight (table 5). Douglas-fir seeds near the coast tend to be smaller than those from further inland, and seeds from lower elevations are sometimes smaller than those from higher elevations (Griffin and Ching 1977; Hermann and Lavender 1968; Lippitt 1996; Sorensen 1967, 1983; Sorensen and Miles 1978; Sweet 1965). Seeds produced in a seed orchard from trees of coastal Oregon ori-gins were similar in weight to those produced by trees in untended stands (table 5).

Seeds of Douglas-fir are usually stored at or near –18 °C at moisture contents of 5 to 9% (wet weight basis) in sacks or plastic-lined fiberboard drums (Brown 1983; Stein and others 1986). Viability of good seedlots can be maintained for many years under these storage conditions; 85 to 87% germination of several coastal Douglas-fir seedlots has been maintained for 27 years (Lippitt 1996). Moderate to good seed viability has been maintained for varying lengths of storage around 0 to 5 °C, but viability declines rapidly in storage at room temperature and at high moisture content (Allen 1957, 1962a; Barton 1954; Schubert 1954).

**Pregermination treatments and germination tests.** Pregermination treatment of Douglas-fir seeds strongly influences their subsequent response to various germination conditions. Most seedlots benefit from stratification, but some do not require stratification, some are harmed by it,

**Table 4— *Pseudotsuga,* Douglas-fir:   cone drying schedules and seed yield data**

| Species | Cone drying schedule | | | Cone wt/cone vol | | Seed yield | | |
| | Air-drying (days) | Kiln-drying | | | | Seed wt/cone vol | | Ratio seed wt/ 100 cone wt |
| | | Time (hr) | Temp (°C) | kg/hl | lb/bu | kg/hl | lb/bu | |
|---|---|---|---|---|---|---|---|---|
| P. marocarpa | 8–10 | — | — | 32–39 | 25–30 | 1.03 | 0.8 | 2.8 |
| P. menziesii | | | | | | | | |
|   var. *glauca* | 4–60 | 2–10 | 38–43 | 32–77 | 25–60 | 0.65–1.03 | 0.5–0.8 | 1.0–1.3 |
|   var. *menziesii* | 8–60 | 16–48 | 32–43 | 39–64 | 30–50 | 0.26–1.03 | 0.2–0.8 | 0.5–2.0 |

**Sources:**   Brown (1983), Owston and Stein (1974), Radcliffe (1952), Swingle (1939).

| **Table 5**—*Pseudotsuga,* Douglas-fir: cleaned seeds per weight | | | | | |
|---|---|---|---|---|---|
| | **Average** | | **Range** | | |
| **Species & location** | **/kg** | **/lb** | **/kg** | **/lb** | **Samples[a]** |
| *P. macrocarpa* | | | | | |
|   S California | 7,145 | 3,241 | 6,137–8,115 | 2,800–3,681 | 2 |
|   S California | 7,716 | 3,500 | 6,614–9,921 | 3,000–4,500 | 2 |
|   S California | 11,001 | 4,990 | 9,259–13,927 | 3,460–6,317 | 3 |
|   S California | 6,748 | 3,061 | — | — | 1 |
| *P. menziesii* var. *glauca* | | | | | |
|   Arizona | 70,768 | 32,100 | 52,911–75,619 | 24,000–34,300 | 8 |
|   New Mexico | 83,555 | 37,900 | 72,312–90,830 | 32,800–41,200 | 8 |
|   Colorado | 85,539 | 38,800 | 73,414–96,122 | 33,300–43,600 | 33 |
|   Montana | 88,405 | 40,100 | 79,807–99,869 | 36,200–45,300 | 14 |
|   E Washington | 102,354 | 46,427 | 101,834–103,093 | 46,191–46,762 | 3 |
|   British Columbia | 97,665 | 44,300 | 62,832–117,506 | 28,500–53,300 | 19 |
|   British Columbia | 119,905 | 54,388 | 104,166–163,398 | 47,249–74,116 | 23 |
| *P. menziesii* var. *menziesii* | | | | | |
|   Coastal California | | | | | |
|     Fog-belt | 86,882 | 39,409 | 80,257–104,058 | 36,404–47,200 | 4[b] |
|     Inland | 70,028 | 31,764 | 55,618–78,493 | 25,228–35,604 | 5[c] |
|   California | 71,752 | 32,546 | 33,951–116,845 | 15,400–53,000 | 41 |
|   N California | 67,250 | 30,504 | 40,858–109,171 | 18,409–49,519 | 20[d] |
|   California | | | | | |
|     Zones 090 | 72,305 | 32,797 | 63,268–93,268 | 28,698–42,605 | 62 |
|     Zones 300 | 65,538 | 30,181 | 54,780–81,359 | 24,848–36,904 | 29 |
|     Zones 500 | 56,906 | 25,812 | 48,028–69,867 | 21,785–31,691 | 37 |
|   W Oregon | 76,278 | 34,599 | 58,343–99,109 | 26,464–44,955 | 8[d] |
|   W Oregon | 110,498 | 50,121 | 84,104–126,263 | 38,149–57,272 | 10 |
|   NW Oregon | 99,503 | 45,134 | 69,589–182,150 | 31,565–82,622 | 309[e] |
|   W-central Oregon | 83,333 | 37,799 | 62,501–109,409 | 28,350–49,627 | 39 |
|   W Oregon | 78,626 | 35,664 | 59,000–98,000 | 26,762–44,452 | 8[f] |
|   Oregon & Washington | 84,336 | 38,254 | 77,162–125,664 | 35,000–57,000 | 127[g] |
|   Oregon & Washington | 86,589 | 39,276 | 73,634–102,458 | 33,400–46,474 | 97 |
|   Coastal Oregon (seed orchard) | 87,268 | 39,584 | 76,128–110,972 | 34,531–50,336 | 23 |
|   Washington Cascades | 81,183 | 36,824 | 75,074–87,336 | 34,053–39,615 | 2[d] |
|   W Washington | 77,499 | 35,153 | 74,999–79,999 | 34,019–36,287 | 2[f] |
|   W Washington | 116,822 | 52,990 | 82,576–153,845 | 37,456–69,783 | 46 |
|   British Columbia | 86,999 | 39,462 | 65,001–99,999 | 29,484–45,359 | 4[f] |
|   British Columbia | 130,891 | 59,371 | 107,411–173,012 | 48,721–78,749 | 21 |
|   British Columbia | 93,584 | 42,449 | 79,807–120,593 | 36,200–54,700 | 16 |

**Sources:** Allen (1942), Bialobok and Mejnartowicz (1970), Ching and Bever (1960), Griffin and Ching (1977), Heit (1968), Lippitt (1996), Olson and Silen (1975), Owston and Stein (1974), Rafn (1915), Randall (1997), St. Clair and Adams (1991), Sweet (1965), Willis and Hofmann (1915).
a Data represent seedlots of unknown size and number of trees unless otherwise noted.
b Four locations representing 41 elevation points (stands) totaling 87 trees.
c Five locations representing 44 elevations points (stands) totaling 94 trees.
d Each provenance (sample) represented by 10 trees under 50 years of age.
e Collected over the entire season (August 12 to September 15) from individual 35-year-old trees growing at 122 to 518 m of elevation.
f Each sample collected from 14 to 89 trees within a 40-km radius.
g From individual open-pollinated parent trees.

and some that need it are harmed by too lengthy stratification (Allen 1960; Allen and Bientjes 1954; Gosling 1988; Jensen and Noll 1959; Taylor and others 1993). Based on accumulated experience, seeds of coastal Douglas-fir generally require or benefit from stratification, those of interior Douglas-fir from northern sources may benefit, those from southern sources may not benefit, and the response to stratification by bigcone Douglas-fir is unknown (Allen 1960, 1962c; Heit 1968).

Stratification overcomes different degrees of seed dormancy that may be related to seed source and family, year of collection, cone and seed drying conditions, length and kind of storage, and other causes (Allen 1960; Allen and Bientjes 1954; El-Kassaby and others 1992; Jensen and Noll 1959; Sorensen 1991). Several pretreatments used with or in lieu of stratification also stimulate germination or reduce pathogen damage. These include a light rinse with cold or hot water, fungicide, bleach, hydrogen peroxide, ethanol, polyethylene glycol, or ethylene (Borno and Taylor 1975;

Ching 1959; Dumroese and others 1988; James and others 1988; Li and others 1994; Paci 1987; Shearer and Tackle 1960; Trappe 1961; Wenny and Dumroese 1987).

For seedlots that benefit, stratification speeds the rate of germination; for many, it also increases total germination (table 6). Although the increase in total germination was often not large, it occurred in 76.1% of samples submitted for standard service testing (Jensen and Noll 1959). The increase in germination may be substantial after lengthy stratification when seeds are tested at low temperatures or have been produced in seed orchards (Allen 1960, 1962c; Campbell and Sorensen 1984; Jones and Gosling 1994; Muller and others 1999; Sorensen 1991). Even small gains are important when using valuable improved seeds.

Douglas-fir seeds are usually stratified "naked," that is, without medium. For testing, dry seeds are often placed directly on the moistened substratum in a closed dish, or soaked in tap water for 24 hours, drained, and then placed in a closed container or bag to prechill at 2 to 5 °C for 3 weeks (AOSA 2001).

The official germination test procedures for both coastal and interior Douglas-firs require paired samples—one prechilled for 21 days at 2 to 5 °C and one not—then subjected to alternating day and night temperatures of 30 °C for 8 hours and 20 °C for 16 hours, with light at least during the high temperature period (AOSA 2001; ISTA 1996). Test duration is 21 days. A variety of absorbent blotters and other materials may be used as substratum—Sponge Rok®, ver-

miculite, Terralite®, and mixtures with sand. Alternating temperatures are prescribed because these yielded the highest and most consistent germination in comparison tests (Jensen and Noll 1959). But given appropriate prechilling and germinating periods, Douglas-fir will germinate with or without light in constant temperatures from 10 to 30 °C but higher temperatures cause damage (Allen 1960, 1962c; Gosling 1988; Jones and Gosling 1994; Sorensen 1991; Wright 1931). Seed position influences rate of germination; when the side of the seed that developed against the cone scale is on top, 50% germination on a moist surface is obtained in 4.6 days versus 6.3 days for those of opposite orientation, and response varies among seeds of different geographic origin (Sorensen and Campbell 1981). Rate of germination also varies among seedlots and is not directly linked with total viability (Thomson and El-Kassaby 1993). Average germination and germinative energy data from source-paired comparisons and other test experiences are listed in table 6.

Germination conditions for bigcone Douglas-fir are relatively untested (table 6). Techniques that work well for the other Douglas-fir species may prove satisfactory.

Several methods are used to quickly appraise the quality and vitality of Douglas-fir seeds when approximations are adequate or time is too short for germination tests. Determining viability by a tetrazolium (TZ) test is officially recognized and standard procedures have been designated (AOSA 2000). Seeds are soaked in water at room temperature (20 to 25 °C) overnight, then sliced longitudinally,

**Table 6**—*Pseudotsuga,* Douglas-fir: stratification periods, germination conditions, and results

| Species | Stratifi-cation* (days) | Moist medium | Temp (°C) Day | Night† | Days | Germinative energy Amt (%) | Time (days) | Germ. capacity (%) Avg | Range | Samples |
|---|---|---|---|---|---|---|---|---|---|---|
| *P. macrocarpa* | 28 | Vermiculite | 30 | 20 | 28 | — | — | 31 | — | 3 |
| | — | — | — | — | 100 | 14 | 60 | 28 | 14–36 | 3 |
| | — | Sand | 27 | 21 | 20–90 | — | — | 30 | 15–57 | 5 |
| *P. menziesii* var. *glauca* | 21 | Sponge Rok® | 30 | 20 | 14–21 | 60 | 9 | 68 | 24–83 | 8 |
| | 0 | Sponge Rok | 30 | 20 | 21–35 | 40 | 12 | 60 | 27–75 | 8 |
| | 30 | Paper | 30 | 20 | 17 | 70 | 10 | 78 | — | 3‡ |
| | 0 | Paper | 30 | 20 | 29 | 76 | 9 | 84 | — | 3‡ |
| | 20–40 | Vermiculite | 25 | 25 | 30 | — | — | 95 | 86–100 | 6 |
| | 0 | Vermiculite | 25 | 25 | 50 | — | — | 93 | 88–98 | 6 |
| *P. menziesii* var. *menziesii* | 21 | Sponge Rok | 30 | 20 | 14–35 | 55 | 10 | 81 | 38–95 | 194 |
| | 0 | Sponge Rok | 30 | 20 | 28–35 | 54 | 17 | 75 | 29–93 | 194 |
| | 20–40 | Vermiculite | 25 | 25 | 30 | — | — | 87 | 34–100 | 20 |
| | 0 | Vermiculite | 25 | 25 | 50 | — | — | 84 | 42–100 | 20 |
| | 28 | — | 30 | 20 | 28 | — | — | 84 | 66–98 | 129 |

**Sources:** Allen (1962c), Lippitt (1996), Owston and Stein (1974), Rafn (1915).

* Seeds stratified "naked" (Allen and Bientjes 1954) or on moist Sponge Rok, vermiculite, or paper at 0 to 5 °C.

† Alternating temperatures included 8 hours of light during the high temperature period; light apparently was provided with constant temperature.

‡ Var. *glauca* from north-central Colorado seed sources.

soaked in a 1% TZ solution at 30 to 35 °C for 4 to 6 hours (or longer at lower temperatures), and evaluated. Healthy endosperm and embryo tissue stains uniformly pink to red. Vitality can also be determined by 2 other tests. In the one test, embryos are excised and placed in conditions favorable for growth for several days (Heit 1955); in the other test, radicle tips are cut and the seeds soaked in weak hydrogen peroxide solution under conditions that promote radicle elongation (Ching and Parker 1958). In a visual test, the oldest and simplest, seeds are cut open to determine if they are full or empty, insect damaged, or shriveled and their quality judged by the appearance and color of the endosperm and embryo; this test is still useful for a quick evaluation, particularly in the field. Seeds can be evaluated non-destructively from x-ray views, which can reveal full, empty, shriveled, and insect-filled contents, as well as any damage to the seedcoat and interior (Belcher and Vozzo 1979). Estimates of Douglas-fir seed viability are now similar if measured by x-radiography and by germination, TZ, or hydrogen peroxide testing (Hardin 1981).

**Nursery practices.** Millions of Douglas-fir seedlings are grown in both bareroot and container nurseries. Bareroot production predominates in the United States; container production predominates in Canada. Many sizes of seedlings are produced, ranging from small 1+0 to 3+0 bareroot stock; 1-year-old container (plug) stock; and 1+1, 1+2, 2+1, 2+2, or plug+1 transplants. Use of 1+1 transplants is now very common and plug+1s are gaining attention. Extra large stock is often used to combat animal damage or competing vegetation and for restoration plantings in riparian areas.

Technology for the production of Douglas-fir seedlings is detailed and varies by nursery and the type and size of stock to be produced. Careful management of growing-medium fertility and drainage in both bareroot and container nurseries is critical for growth and hardiness of Douglas-fir. The factors and specific techniques involved in producing bareroot Douglas-fir seedlings are presented in the Forest Nursery Manual (Duryea and Landis 1984); those for containers in the multiple-volume Container Tree Nursery Manual (Landis and others 1989, 1990a&b, 1992, 1995). The concept and practices for producing seedlings with morphological and physiological characteristics targeted for specific field conditions were brought together in a symposium (Rose and others 1990).

Production and grading practices have the potential of influencing the genetic composition as well as the physical characteristics of the seedling populations produced (Campbell and Sorensen 1984; El-Kassaby and Thomson

1996; Sorensen and Campbell 1993; St. Clair and Adams 1993). Thus, every nursery practice needs scrutiny to avoid severely altering the intrinsic characteristics for which each seedlot is valued.

Both bareroot and container nurseries usually sow stratified seeds as early in late winter or spring as possible to maximize growth and vigor of first-year seedlings (Sorensen 1996). Fall-sowings can produce even larger seedlings, but the risk of seed losses over winter from natural causes is usually too great (Duryea 1984). Before sowing outdoors or in containers, seeds are commonly soaked in tap water at 10 to 22 °C for 24 to 48 hours, drained of excess water, perhaps surface-dried, and then prechilled in 2-kg (5-lb) quantities per plastic bag in a cooler at 1 to 5 °C (Allen 1962b; Allen and Bienjes 1954; Johnson 1983; Tanaka 1984). A breather tube may be inserted in the neck of the bag and such intermediate tending as rinsing, addition of water, and turning may be done during 28 to 60 or even 90 days of stratification. Results from germination tests help guide the choice and length of pretreatments applied to individual seedlots. Germination is epigeal (figure 4).

When necessary, stratified Douglas-fir seeds can be stored for later use. Stratified seeds that were air-dried and stored at relatively high moisture content at 2 °C for 3 months or oven-dried to 7 to 15% moisture content and

**Figure 4**—*Pseudotsuga menziesii* var. *menziesii, coast* Douglas-fir: epigeal seedling development at 2, 5, 8, and 22 days after emergence from a peat moss–vermiculite potting mixture.
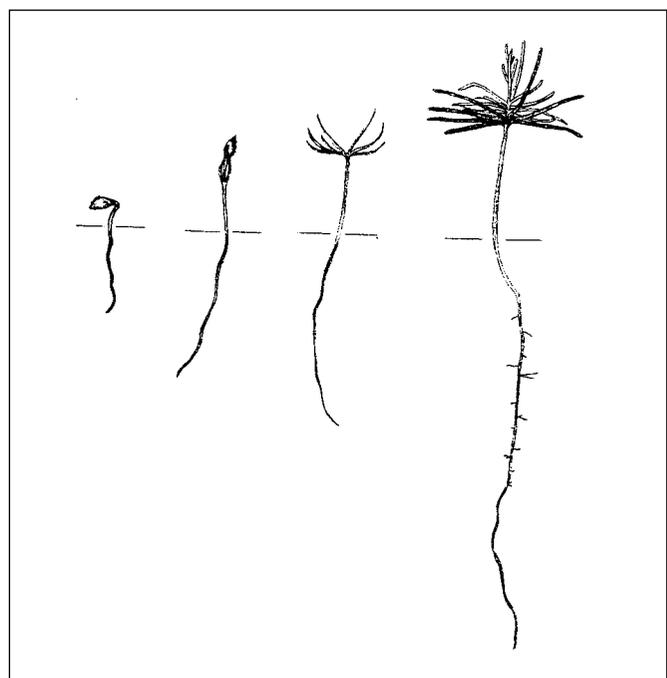
stored at –7 to 3 °C for 9 months or more retained the viability and stratification effect (Allen 1962b; Belcher 1982; Danielson and Tanaka 1978; Jones and Gosling 1994; Muller and others 1999). In other trials, viability was retained by partial drying of stratified seeds followed by low temperature storage, but the stratification effect was lost (Hedderwick 1970; Malavasi and others 1985). Seeds cannot be held in stratification indefinitely; seeds of some lots will deteriorate and those of others will germinate (Allen 1960; Danielson and Tanaka 1978; Sorensen 1980, 1991).

For bareroot production, most Douglas-fir seeds are drill-sown at a depth of 3 to 6 mm (0.1 to 0.2 in). The larger seeds of bigcone Douglas-fir are usually sown at a depth of 13 mm (0.5 in). Seedbed density varies depending on the stock size desired. For 2+0 Douglas-fir stock, seedling densities vary from 161 to 323/m$^2$ (15 to 30/ft$^2$); for 1+1s, bed densities of first-year seedlings range from 538 to 753/m$^2$ (50 to 70/ft$^2$) (Thompson 1984). Seedbed density has more effect on size of seedlings produced, and on their subsequent field survival and growth, than does irrigation frequency or undercutting and wrenching (Stein 1988).

Irrigation is used in bareroot nurseries to supply moisture to seeds and seedlings, prevent overheating or frost damage, promote growth, and augment other practices such as fertilizing and root wrenching (Duryea 1984). Carefully planned irrigation regimes are also used to control moisture stress, harden seedlings, and initiate dormancy. Specific irrigation regimes should be developed for each nursery and kind of stock—seedlings can be harmed by either too much or too little water.

The fertilizer mix and the timing and number of applications must also be developed for each bareroot nursery. Physical and chemical characteristics of the soil and irrigation water and the density of the seedling crop are critical influencing factors. A pH of 5.0 to 6.0 has been suggested for nurseries in the Pacific Northwest and 5.5 to 6.5 for nurseries in Intermountain region, as well as concomitant target levels for key mineral elements (Youngberg 1984). Most nurseries stop fertilizing in July or early August to promote seedling hardening (Duryea 1984).

Almost all bareroot nurseries undercut Douglas-fir seedlings to stimulate root growth in the upper soil layers (Duryea 1984). Timing, frequency, and depth vary by nursery and stock type. Eighty percent of nurseries in the Pacific Northwest also wrench the roots of Douglas-fir seedlings to promote fibrous root systems, stress and harden seedlings, control shoot height, and aerate the soil.

Many other cultural techniques including transplanting, weed and pest control, top pruning, and mycorrizhal inoculation are used to condition bareroot Douglas-fir seedlings for specific field conditions. Emphasis continues on fine tuning and evaluating seedling quality. Thus, an array of morphological and physiological tests have been developed to assess the quality of Douglas-fir seedlings (Duryea 1985; Jenkinson and others 1993; Rose and others 1993, 1997). Grading criteria and target sizes have been recognized for different types of stock (Iverson 1984), but more importantly, the trend is to specify seedlings by height and stem caliper as well as by stock type.

In containers, plantable stock can be produced in one season in greenhouses, outdoors under shade, or in the open. Douglas-fir grows well in the containers commonly used in forestry. High-quality, well-stratified seeds are particularly important in producing container-grown Douglas-fir. Other important considerations include keeping the pH of the potting mixture between 4.5 and 6.0; using growing practices that produce seedlings with tops and roots in balance; and hardening the seedlings to withstand direct sunlight and cold.

Fast growth of Douglas-fir is achieved in containers by providing greater control of the growth environment than possible in a bareroot nursery (Landis and others 1995). A precise growing regime must be developed suited to the capabilities at the individual container facility and the requirements of the stock to be produced. For example, Wenny and Dumroese (1992) describe a regime for producing interior Douglas-fir container stock at a facility in Idaho. Producing this variety in a single season requires use of artificial light to lengthen the photoperiod early in the growing season.

To produce extra hardy, compact stock, seedlings are grown in containers for the first year and in outdoor beds for a second year. The resulting plug+1 stock has a very fibrous root system and is usually larger and sturdier than 1+1 stock (Iverson 1984).

Douglas-fir is also propagated commercially by adventitious rooting of cuttings (Myers and Howe 1990; Ritchie 1991). Cuttings are rooted in 1 season, transplanted to a bareroot nursery in the fall to overwinter, and then grown for 1 year as bareroot stock. Over 5 years, stock from cuttings has performed similarly to 1+1 transplants. Cuttings from juvenile wood root better than those from older wood and have less plagiotropic tendencies (Copes 1992). Juvenile meristems are produced in quantity by accelerating first-year growth of stock plants (Ritchie 1994) or by maintaining juvenility on older trees by pruning (Copes 1992). Limited numbers of Douglas-fir emblings are produced by micropropagation techniques (Gupta and Grob 1995; Hutzell and

Durzan 1993; Tabor and others 1998). Rapid multiplication of superior genetic strains is made possible by practical vegetative propagation.

**Seedling care.** Whether bareroot or container-grown, Douglas-fir stock is best able to withstand the shock of lifting, storage, and outplanting when dormant, that is, after adapting to winter conditions. Midseason reductions in applying water and fertilizer, root wrenching, and other techniques are used to slow growth and enhance the normal climatic progression toward dormancy.

Because Douglas-fir seedlings are quite vulnerable, great care should be taken to minimize mechanical damage, desiccation, and molding during lifting, processing, storage, transportation, and planting. Protective practices include hydrating seedlings before lifting; minimizing exposure of lifted seedlings to direct sunlight, temperature extremes, and wind; preventing metabolic over-heating; misting during processing; storing and transporting them at low temperatures in bags or cartons with vapor barriers; and minimizing handling and exposure during field planting (Burdett and Simpson 1984).

Properly hardened Douglas-fir nursery stock can be stored for lengthy periods at temperatures just above or below freezing (Burdett and Simpson 1984; Hee 1986). Freezer storage prevents molding and some dormancy developments that would occur if seedlings were exposed outdoors (Ritchie 1987). Frozen bareroot and container seedlings should be thawed before they are planted (Hee 1986; Rose and Haase 1997).

Douglas-fir is usually outplanted any time from late fall through spring, depending on local climate. Winter and early spring plantings are usually best in areas with mild winters west of the Cascade Mountains. The planting season may extend into early summer in interior regions and at high elevations where snow lingers. Seedlings are extracted from most types of containers either before storage or before shipment to the field. Bigcone Douglas-fir was planted periodically from 1905 to 1975 in Los Angeles County, California, but results are unknown (McDonald 1990); in contrast, there is overwhelming evidence on successful plantings of coastal and interior Douglas-fir.

Nursery managers are dedicated to producing the size and vigor of Douglas-fir stock needed for an extremely wide range of field conditions. In many instances, the kind of stock required and the nursery practices needed to produce it are well defined; in some instances, however, either the stock or the field practices need improvement. Specific trials testing variations in a nursery's practices for producing stock of different sources may be needed, for example, "lifting windows" as investigated by Jenkinson and others (1993).

## References

Allen GS. 1941. A basis for forecasting seed crops of some coniferous trees. Journal of Forestry 39: 1014–1016.

Allen GS. 1942. Douglas fir (*Pseudotsuga taxifolia* (Lamb.) Britt.): a summary of its life history. Res. Note 9. Victoria: British Columbia Forest Service. 27 p.

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. 1958a. Factors affecting the viability and germination behavior of coniferous seed: 2. Cone and seed maturity, *Pseudotsuga menziesii* (Mirb.) Franco. Forestry Chronicle 34: 275–282.

Allen GS. 1958b. 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 behavior of coniferous seed: 4. Stratification period and incubation temperature, *Pseudotsuga menziesii* (Mirb.) Franco. Forestry Chronicle 36: 18–29.

Allen GS. 1962a. The deterioration of Douglas-fir seed under various storage conditions. Forestry Chronicle 38: 145–147.

Allen GS. 1962b. Factors affecting the viability and germination behavior of coniferous seed: 5. Seed moisture content during stratification and secondary storage, *Pseudotsuga menziesii* (Mirb.) Franco. Forestry Chronicle 38: 303–308.

Allen GS. 1962c. Factors affecting the viability and germination behavior of coniferous seed: 6. Stratification and subsequent treatment, *Pseudotsuga menziesii* (Mirb.) Franco. Forestry Chronicle 38: 485–496.

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

Allen GS, Owens JN. 1972. The life history of Douglas-fir. Ottawa: Environment Canada, Forestry Service. 139 p.

AFA [American Forestry Association]. 2000. The national register of big trees, 2000–01. American Forests 106(1): 22–64.

AOSA [Association of Official Seed Analysts]. 2000. Tetrazolium testing handbook. Lincoln, NE: Association of Official Seed Analysts. 21+ p.

AOSA [Association of Official Seed Analysts]. 2001. Rules for testing seeds. Lincoln, NE: Association of Official Seed Analysts. 126 p.

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

Barton LV. 1954. Storage and packeting of seeds of Douglas fir and western hemlock. Contributions from Boyce Thompson Institute 18: 25–37.

Belcher EW. 1982. Storing stratified seeds for extended periods. Tree Planters' Notes 33(4): 23–25.

Belcher E, Vozzo JA. 1979. Radiographic analysis of agricultural and forest tree seeds. Contrib. 31. In: Handbook on seed testing. Association of Official Seed Analysts. 117 p.

Bialobok S, Mejnartowicz L. 1970. Provenance differentiation among Douglas fir seedlings. Arboretum Kornickie 15: 197–220.

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

Boe KN. 1954. Periodicity of cone crops for 5 Montana conifers. Proceedings of the Montana Academy of Sciences 14: 5–9.

Borno C, Taylor IEP. 1975. The effect of high concentrations of ethylene on seed germination of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco). Canadian Journal of Forest Research 5: 419–423.

Brown GG. 1983. Seed cone collection procedures, seed extraction, and seed storage. International Plant Propagators' Society Combined Proceedings 33: 56–64.

Burdett AN, Simpson DG. 1984. Lifting, grading, packaging, and storing. In: Duryea ML, Landis TD, eds. Forest nursery manual: production of bare-root seedlings. The Hague: Martinus Nijhoff/Dr. W. Junk Publishers: 227–234.

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

Campbell RK. 1986. Mapped genetic variation of Douglas-fir to guide seed transfer in southwest Oregon. Silvae Genetica 35: 85–96.

Campbell RK. 1991. Soils, seed-zone maps, and physiography: guidelines for seed transfer of Douglas-fir in southwestern Oregon. Forest Science 37: 973–986.

Campbell RK, Sorensen FC. 1978. Effect of test environment on expression of clines and on delimitation of seed zones in Douglas-fir. Theoretical and Applied Genetics 51: 233–246.

Campbell RK, Sorensen FC. 1984. Genetic implications of nursery practices. In: Duryea ML, Landis TD, eds. Forest nursery manual: production of bareroot seedlings. The Hague: Martinus Nijhoff/Dr. W. Junk Publishers: 183–191.

Campbell RK, Sugano AI. 1993. Genetic variation and seed zones of Douglas-fir in the Siskiyou National Forest. Res. Pap. PNW-RP-461. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 23 p.

Ching KK, Bever D. 1960. Provenance study of Douglas-fir in the Pacific Northwest region. Silvae Genetica 9: 11–17.

Ching TM. 1959. Activation of germination in Douglas fir seed by hydrogen peroxide. Plant Physiology 34: 557–563.

Ching TM, Ching KK. 1962. Physical and physiological changes in maturing Douglas-fir cones and seeds. Forest Science 8: 21–31.

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

Copes DL. 1973. Effects of annual leader pruning on cone production and crown development of grafted Douglas-fir. Silvae Genetica 22: 167–173.

Copes DL. 1985. Effects of leader topping and branch pruning on efficiency of Douglas-fir cone harvesting with a tree shaker. Res. Note PNW-431. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 8 p.

Copes DL. 1992. Effects of long-term pruning, meristem origin, and branch order on the rooting of Douglas-fir stem cuttings. Canadian Journal of Forest Research 22: 1888–1894.

Copes DL, Randall WK. 1983. Tree shaking machine aids cone collection in a Douglas-fir seed orchard. Res. Note PNW-406. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 8 p.

Copes DL, Sniezko RA. 1991. The influence of floral bud phenology on the potential mating system of a wind-pollinated Douglas-fir orchard. Canadian Journal of Forest Research 21: 813–820.

Cress DW, Daniels JD, comps. & eds. 1990. Forest seed orchards of western Oregon, western Washington, and northern California. Centralia, WA: Daniels and Associates. 322 p.

Daniels J. 1995. Managing genetic resources of Pacific Northwest forests. Western Forester 40(7): 1, 6–7.

Danielson HR, Tanaka Y. 1978. Drying and storing stratified ponderosa pine and Douglas-fir seeds. Forest Science 24: 11–16.

Dewey JE. 1970. Damage to Douglas-fir cones by *Choristoneura occidentalis*. Journal of Economic Entomology 63: 1804–1806.

Dombrosky SA, Schowalter TD. 1988. Inventory monitoring for estimating impact of insects on seed production in a Douglas-fir seed orchard in western Oregon. Journal of Economic Entomology 81: 281–285.

Douglass BS, TerBush FA. 1975. Collecting forest tree seeds and growing your own seedlings. Portland, OR: USDA Forest Service, Pacific Northwest Region, State and Private Forestry. 32 p.

Dumroese RK, James RC, Wenny DL, Gilligan CJ. 1988. Douglas-fir seed treatments: effects on seed germination and seedborne organisms. In: Landis TD , tech coord. Proceedings, Combined Meeting of the Western Forest Nursery Associations. 1988 August 8–11; Vernon, BC. Gen. Tech. Rep. RM-167. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: 155–160.

Duryea ML. 1984. Nursery cultural practices: impacts on seedling quality. In: Duryea ML, Landis TD, eds. Forest nursery manual: production of bareroot seedlings. The Hague: Martinus Nijhoff/Dr W. Junk Publishers: 143–164.

Duryea ML, ed. 1985. Evaluating seedling quality: principles, procedures, and predictive abilities of major tests. Proceedings of a workshop; 1984 October 16–18; Corvallis, OR. Corvallis: Oregon State University, Forest Research Laboratory. 143 p.

Duryea ML, Landis TD, eds. 1984. Forest nursery manual: production of bareroot seedlings. The Hague: Martinus Nijhoff/Dr W. Junk Publishers. 385 p.

Edwards DGW. 1985. Cone prediction, collection, and processing. In: Shearer RC, comp. Proceedings, Conifer Tree Seed in the Inland Mountain West Symposium; 1985 August 5–6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: USDA Forest Service, Intermountain Research Station: 78–102.

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

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

El-Kassaby YA, Askew GR. 1991. The relation between reproductive phenology and reproductive output in determining the gametic pool profile in a Douglas-fir seed orchard. Forest Science 37: 827–835.

El-Kassaby YA, Edwards DGW, Taylor DW. 1992. Genetic control of germination parameters in Douglas-fir and its importance for domestication. Silvae Genetica 41: 48–54.

El-Kassaby YA, Fashler AMK, Crown M. 1989. Variation in fruitfulness in a Douglas-fir seed orchard and its effect on crop-management decisions. Silvae Genetica 38: 113–121.

El-Kassaby YA, Thomson AJ. 1996. Parental rank changes associated with seed biology and nursery practices in Douglas-fir. Forest Science 42: 228–235.

Finnis JM. 1950. Seed maturity in Douglas fir. Res. Note 18. Victoria: British Columbia Forest Service. 8 p.

Frank CJ, Jenkins MJ. 1987. Impact of the western spruce budworm (Lepidoptera: Tortricidae) on buds, developing cones, and seeds of Douglas-fir in west central Idaho. Environmental Entomology 16: 304–308.

Gashwiler JS. 1969. Seed fall of three conifers in west-central Oregon. Forest Science 15: 290–295.

Gause GW. 1966. Silvical characteristics of bigcone Douglas-fir (*Pseudotsuga macrocarpa* (Vasey) Mayr). Res. Pap. PSW-39. Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. 10 p.

Gosling PG. 1988. The effect of moist chilling on the subsequent germination of some temperate conifer seeds over a range of temperatures. Journal of Seed Technology 12(1): 90–98.

Griffin AR, Ching KK. 1977. Geographic variation in Douglas-fir from the coastal ranges of California. Silvae Genetica 26: 149–157.

Griffin JR. 1964. A new Douglas-fir locality in southern California. Forest Science 10: 317–319.

Griffin JR, Critchfield WB. 1976. The distribution of forest trees in California. Res. Pap. PSW-82 (reprinted). Washington, DC: USDA Forest Service. 118 p.

Griffith BG. 1968. Phenology, growth, and flower and cone production of 154 Douglas fir trees on the University Research Forest as influenced by climate and fertilizer, 1957–1967. For. Bull. 6. Vancouver: University of British Columbia, Faculty of Forestry. 70 p.

Gupta PK, Grob JA. 1995. Somatic embryogenesis in conifers. In: Jain S, Gupta P, Newton R, eds. Somatic embryogenesis in woody plants. Volume 1. Dordrecht, The Netherlands: Kluwer Academic Publishers: 81–98.

Hall O. 1984. The effects of dry heat on tree seed germination: lodgepole pine, slash pine and Douglas fir. Newsletter of the Association of Official Seed Analysts 58(3): 117–121.

Hardin E. 1981. Quick test vs. standard germination test. In: Proceedings, Intermountain Nurseryman's Association and Western Forest Nursery Association Combined Meeting; 1980 August 12–14; Boise, ID. Gen. Tech. Rep. INT-109. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 71–73.

Hedderwick GW. 1970. Prolonged drying of stratified Douglas fir seed affects laboratory germination. Commonwealth Forestry Review 49(2): 130–131.

Hedlin AF, Yates HO III, Tovar DC, Ebel BH, Koerber TW, Merkel EP. 1980. Cone and seed insects of North American conifers. Ottawa: Environment Canada, Canadian Forestry Service. 122 p.

Hee SM. 1986. Freezer storage practices of Weyerhaeuser nurseries. In: Landis TM, tech. coord. Proceedings, Combined Western Forest Nursery Council and Intermountain Nursery Association Meeting. 1986 August 12–15; Tumwater, WA. Gen. Tech. Rep. RM-137. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: 62–66.

Heit CE. 1955. The excised embryo method for testing germination quality of dormant seed. Proceedings of the Association of Official Seed Analysts 45: 108–117.

Heit CE. 1968. Propagation from seed: 17. Testing and growing Douglas fir seeds from different sources. American Nurseryman 128(10): 12–16, 40, 42, 44, 46–49, 52, 54–60.

Hergert GB, Wang BSP, Yeatman CW. 1971. A belt cleaner for small samples of tree seed. Forestry Chronicle 47: 40–41.

Hermann RK. 1982. The genus *Pseudotsuga*: historical records and nomenclature. Spec. Pub. 2a. Corvallis, OR: Oregon State University, School of Forestry, Forest Research Laboratory. 29 p.

Hermann RK. 1985. The genus *Pseudotsuga*: ancestral history and past distribution. Spec. Pub. 2b. Corvallis, OR: Oregon State University, School of Forestry, Forest Research Laboratory. 32 p.

Hermann RK, Lavender DP. 1968. Early growth of Douglas-fir from various altitudes and aspects in southern Oregon. Silvae Genetica 17: 143–151.

Hermann RK, Lavender DP. 1990. *Pseudotsuga menziesii* (Mirb.) Franco, Douglas-fir. In: Burns RM, Honkala BH, tech coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 527–540.

Ho RH. 1980. Pollination mechanism and seed production potential in Douglas-fir. Forest Science 26: 522–528.

Hutzell MJ, Durzan DJ. 1993. Improved aseptic germination and controlled growth for micropropagation of Douglas fir. In: Ahuja MR, ed. Micropropagation of woody plants. Dordrecht, The Netherlands: Kluwer Academic Publishers: 367–372.

ISTA [International Seed Testing Association]. 1996. International rules for seed testing: rules 1996. Seed Science and Technology 24 (Suppl.): 1–335.

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

Isaac LA. 1943. Reproductive habits of Douglas-fir. Washington, DC: Charles Lathrop Pack Forestry Foundation. 107 p.

Isaac LA. 1949. Better Douglas fir forests from better seed. Seattle: University of Washington Press. 65 p.

Iverson RD. 1984. Planting stock selection: meeting biological needs and operational realities. In: Duryea ML, Landis TD, eds. Forest nursery manual: production of bare-root seedlings. The Hague: Martinus Nijhoff/Dr W. Junk Publishers: 261–266.

James RL, Gilligan CJ, Dumroese RK, Wenny DL. 1988. Microwave treatments to eradicate seedborne fungi on Douglas-fir seed. Rep. 88-7. Missoula, MT: USDA Forest Service, Northern Region, State and Private Forestry. 8 p.

Jenkinson JL, Nelson JA, Huddleston ME. 1993. Improving planting stock quality: the Humboldt experience. Gen. Tech. Rep. PSW-143. Albany, CA: USDA Forest Service, Pacific Southwest Research Station. 219 p.

Jensen LA, Noll E. 1959. Experience in germination testing of Pacific Northwest Douglas fir seed. Proceedings of the Association of Official Seed Analysts 49(1): 107–113.

Johnson CJS. 1983. Conifer seed sources, testing, stratification, and sowing for the Industrial Forestry Association. International Plant Propagators' Society Combined Proceedings 1983 33: 64–66.

Joly RJ, Adams WT, Stafford SG. 1989. Phenological and morphological responses of mesic and dry site sources of coastal Douglas-fir to water deficit. Forest Science 35: 987–1005.

Jones EW. 1946. The regeneration of Douglas fir, *Pseudotsuga taxifolia* Britt., in the new forest. Journal of Ecology 33: 44–54.

Jones SK, Gosling PG. 1994. "Target moisture content" prechill overcomes the dormancy of temperate conifer seeds. New Forests 8: 309–321.

Kleinschmit J, Bastien JC. 1992. IUFRO's role in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) tree improvement. Silvae Genetica 41(3): 161–173.

Kozak A, Sziklai O, Griffith BG, Smith JHG. 1963. Variation in cone and seed yield from young, open-grown Douglas firs on the U.B.C. Research Forest. Res. Pap. 57. Vancouver: University of British Columbia, Faculty of Forestry. 8 p.

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 Forest Service. 119 p.

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

Landis TD, Tinus RW, McDonald SE, Barnett JP. 1990b. The container tree nursery manual. Volume 2, Containers and growing media. Agric. Handbk. 674. Washington, DC: USDA Forest Service. 87 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 Forest Service. 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 Forest Service. 188 p.

Lavender DP. 1958. Viability of Douglas fir seed after storage in the cones. Res. Note 31. Corvallis, OR: Oregon Lands Research Center. 8 p.

Lavender DP, Engstrom WH. 1956. Viability of seeds from squirrel-cut Douglas fir cones. Res. Note 27. Salem: Oregon State Board of Forestry. 19 p.

Ledgard NJ. 1988. The spread of introduced trees in New Zealand's rangelands: South Island high country experience. Journal of the Tussock Grasslands and Mountainlands Institute [March 1988]: 1–8.

Li P, Adams WT. 1989. Range-wide patterns of allozyme variation in Douglas-fir (*Pseudotsuga menziesii*). Canadian Journal of Forest Research 19: 149–161.

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.

Lippitt L. 1996. Personal communication. Davis: California Department of Forestry and Fire Protection, Lewis A. Moran Reforestation Center.

Little EL Jr. 1952. The genus *Pseudotsuga* (Douglas-fir) in North America. Leaflets of Western Botany 6(10): 181–198.

Little EL Jr. 1971. Atlas of United States trees. Volume 1, Conifers and important hardwoods. Misc. Pub. 1146. Washington, DC: USDA Forest Service: maps 80-W & 80-N.

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

Lowman BJ. 1975. Catalog: equipment for processing small seed lots. No. 7524-2505. Missoula, MT: USDA Forest Service, Equipment Development Center. 57 p.

Lowry WP. 1966. Apparent meteorological requirements for abundant cone crop in Douglas-fir. Forest Science 12: 185–192.

Malavasi MDM, Stafford SG, Lavender DF. 1985. Stratifying, partially redrying and storing Douglas-fir seeds: effects on growth and physiology during germination. Annales des Sciences Forestieres 42(4): 371–384.

Matusz S. 1964. Collection of seeds from standing trees. Geneva: FAO Joint Committee on Forest Working Techniques and Training of Forest Workers. 72 p.

Maxwell HA, Aldhous JR. 1967. Seed collection in North-west America. Commonwealth Forestry Review 46(1): 51–62.

McArdle RE, Meyer WH, Bruce D. 1961. The yield of Douglas fir in the Pacific Northwest. Tech. Bull. 201, rev. Washington, DC: USDA Forest Service. 74 p.

McDonald PM. 1990. *Pseudotsuga macrocarpa* (Vasey) Mayr, bigcone Douglas-fir. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 520–526.

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

Miller GE. 1986. Sampling major Douglas-fir cone and seed insects in British Columbia. In: Rouques A, ed. Proceedings, 2nd Conference of the Cone and Seed Insects Working Party S2.07-01, IUFRO; 1986 Sept. 3–5; Briancon, France. Victoria, BC: Canadian Forestry Service, Pacific Forestry Centre: 103–112.

Miller GE, Ruth DS. 1989. The relative importance of cone and seed insect species on commercially important conifers in British Columbia. In: Proceedings, 3rd Cone and Seed Insects Working Party Conference. 1988 June 26–30; Victoria, BC. Victoria, BC: Canadian Forestry Service: 25–34.

Minnich RA. 1977. The geography of fire and big-cone Douglas-fir, Coulter pine, and western conifer forests in the east Transverse Ranges, Southern California. In: Proceedings, Symposium on the Environmental Consequences of Fire and Fuel Management in Mediterranean Ecosystems; 1977 August 1–5; Palo Alto, CA. Gen. Tech. Rep. WO-3. Washington, DC: USDA Forest Service: 443–450.

Minnich RA. 1980. Wildfire and the geographic relationships between canyon live oak, Coulter pine, and bigcone Douglas-fir forests. In: Plumb TR, tech. coord. Proceedings, Symposium on the Ecology, Management, and Utilization of California Oaks; 1979 June 26–28; Claremont, CA. Gen. Tech. Rep. PSW-44. Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station: 55–61.

Minnich RA. 1982. *Pseudotsuga macrocarpa* in Baja California. Madroño 29(1): 22–31.

Moore AW. 1940. Wild animal damage to seed and seedlings on cut-over Douglas fir lands of Oregon and Washington. Tech. Bull. 706. Washington, DC: USDA. 28 p.

Morris WG. 1936. Viability of conifer seed as affected by seed- moisture content and kiln temperature. Journal of Agricultural Research 52: 855–864.

Morris WG. 1952. Phenological data filed Dec. 9, 1952. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 7 p.

Muller C, Falleri E, Laroppe E, Bonnet-Masimbert M. 1999. Drying and storage of prechilled Douglas fir, *Pseudotsuga menziesii*, seeds. Canadian Journal of Forest Research 29: 172–177.

Myers JF, Howe GE. 1990. Vegetative propagation of Rocky Mountain Douglas-fir by stem cuttings. Tree Planters' Notes 41(3): 3–6.

Olson DL, Silen RR. 1975. Influence of date of cone collection on Douglas-fir seed processing and germination: a case history. Res. Pap. PNW-190. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 10 p.

Orr-Ewing AL. 1956. Controlled pollination techniques for Douglas fir. Forest Science 2: 251–257.

Owens JN, Colangeli AM, Morris SJ. 1991. Factors affecting seed set in Douglas-fir (*Pseudotsuga menziesii*). Canadian Journal of Botany 69: 229–238.

Owston PW, Stein WI. 1974. *Pseudotsuga* Carr., Douglas-fir. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 674–683.

Paci M. 1987. Effetti del trattamento con PEG sulla germinazione del seme di *Pinus nigra* Arn., *Larix decidua* Mill. e *Pseudotsuga menziesii* Franco. Italia Forestale-e-Montana 42(2): 73–82.

Panshin AJ, Zeeuw C de. 1970. Textbook of wood technology. 3rd ed. Volume 1. New York: McGraw-Hill. 705 p.

Portlock FT. 1992. Forest tree seed certification in Canada under the OECD Scheme and ISTA rules: summary report for 1986–1990. Inf. Rep. BC-X-332. Victoria, BC: Canadian Forestry Service, Pacific Forestry Centre. 10 p.

Portlock FT, comp. 1996. A field guide to collecting cones of British Columbia conifers. Victoria: British Columbia Ministry of Forests. 91 p.

Radcliffe DN. 1952. An appraisal of seed damage by the Douglas fir cone moth, in British Columbia. Forestry Chronicle 28: 19–24.

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

Randall WK. 1996. Forest tree seed zones for western Oregon (1996). Portland: Oregon Department of Forestry. 82 p. plus 20 maps.

Randall WK. 1997. Personal communication. Corvallis, OR: USDA Forest Service, Siuslaw National Forest.

Rappaport NG, Volney WJA. 1989. Effect of pest species exclusions on Douglas-fir *(Pseudotsuga menziesii* [Mirb.] Franco) cone and seed insects: implications for pest management. In: Proceedings, 3rd Cone and Seed Insects Working Party Conference; 1988 June 26–30; Victoria, BC. Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station: 142–150.

Rappaport NG, Wood DL. 1989. Host relationships in the Douglas-fir twig mining beetle, *Pityophthorus orarius* Bright (Coleoptera: Scolytidae), in a northern California seed orchard. In: Proceedings, 3rd Cone and Seed Insects Working Party Conference; 1988 June 26–30; Victoria, BC. Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station: 133–140.

Read RA, Sprackling JA. 1976. Douglas-fir in eastern Nebraska: a provenance study. Res. Pap. RM-178. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 10 p.

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

Rediske JH. 1969. Effects of cone-picking date on Douglas-fir seed quality. Forest Science 15: 404–410.

Rediske JH, Shea KR. 1965. Loss of Douglas-fir seed viability during cone storage. Forest Science 11: 463–472.

Rehfeldt GE. 1977. Growth and cold hardiness of intervarietal hybrids of Douglas-fir. Theoretical and Applied Genetics 50: 3–15.

Rehfeldt GE. 1979. Variation in cold hardiness among populations of *Pseudotsuga menziesii* var. *glauca*. Res. Pap. INT-233. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 11 p.

Rehfeldt GE. 1981. Seed transfer guidelines for Douglas-fir in North Idaho. Res. Note INT-300. Ogden, UT: USDA Forest Service, Intermoutain Forest and Range Experiment Station. 4 p.

Rehfeldt GE. 1983a. Seed transfer guidelines for Douglas-fir in Central Idaho. Res. Note INT-337. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 3 p.

Rehfeldt GE. 1983b. Seed transfer guidelines for Douglas-fir in Western Montana. Res. Note INT-329. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 3 p.

Rehfeldt GE. 1989. Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*): a synthesis. Forest Ecology and Management 28: 203–215.

Reukema DL. 1982. Seedfall in a young-growth Douglas-fir stand: 1950–1978. Canadian Journal of Forest Research 12: 249–254.

Ritchie GA. 1987. Some effects of cold storage on seedling physiology. Tree Planters' Notes 38(2): 11–15.

Ritchie GA. 1991. The commercial use of conifer rooted cuttings in forestry: a world overview. New Forests 5: 247–275.

Ritchie GA. 1994. Commercial application of adventitious rooting to forestry. In: Davis TD, Haissig BE, eds. Biology of adventitious root formation. New York: Plenum Press: 37–52.

Roeser J Jr. 1942. The influence of climate on seed production in Douglas fir. Journal of Forestry 40: 304–307.

Rose R, Haase DL. 1997. Thawing regimes for freezer-stored container stock. Tree Planters' Notes 48(1&2): 12–17.

Rose R, Campbell SJ, Landis TD, eds. 1990. Target seedling symposium. Proceedings, Combined Meeting of the Western Nursery Associations; 1990 August 13–17; Roseburg, OR. Gen. Tech. Rep. RM-200. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 286 p.

Rose R, Gleason JF, Atkinson M. 1993. Morphological and water-stress characteristics of three Douglas-fir stocktypes in relation to seedling performance under different soil moisture conditions. New Forests 7: 1–17.

Rose R, Haase DL, Kroiher F, Sabin T. 1997. Root volume and growth of ponderosa pine and Douglas-fir seedlings: a summary of eight growing seasons. Western Journal of Applied Forestry 12(3): 69–73.

Ross SD, Bower RC. 1991. Promotion of seed production in Douglas-fir grafts by girdling + gibberellin $A_{4/7}$ stem injection, and effect of retreatment. New Forests 5: 23–34.

Ross SD, Currell RC. 1989. Effect of top pruning, branch thinning and gibberellin $A_{4/7}$ treatment on the production and distribution of conebuds in Douglas-fir. Silvae Genetica 38: 177–185.

Ross SD, Pharis RP, Heaman JC. 1980. Promotion of cone and seed production in grafted and seedling Douglas-fir seed orchards by application of gibberellin $A_{4/7}$ mixture. Canadian Journal of Forest Research 10: 464–469.

Ross SD, Webber JE, Pharis RP, Owens JN. 1985. Interaction between gibberellin $A_{4/7}$ and root pruning on the reproductive and vegetative process in Douglas-fir: I. Effects on flowering. Canadian Journal of Forest Research 15: 341–347.

Rudloff E von. 1972. Chemosystematic studies in the genus *Pseudotsuga*: 1. Leaf oil analysis of the coastal and Rocky Mountain varieties of the Douglas-fir. Canadian Journal of Botany 50: 1025–1040.

Rudolf PO. 1974. Tree-seed marketing controls. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 153–166.

Schaefer RM III, Miller DL. 1985. Douglas-fir seed collection and handling. In: Shearer RC, comp. Proceedings, Conifer Tree Seed in the Inland Mountain West Symposium: 1985 August 5–6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: USDA Forest Service, Intermountain Research Station: 129–132.

Schowalter TD. 1988. Tree breeding and insects: effect of insects on the genetic diversity of Douglas-fir. Northwest Environmental Journal 4(2): 346–347.

Schowalter TD, Haverty MI. 1989. Influence of host genotype on Douglas-fir seed losses to *Contarinia oregonensis* (Diptera: Cecidomyiidae) and *Megastigmus spermotrophus* (Hymenoptera: Torymidae) in western Oregon. Enviromental Entomology 18: 94–97.

Schowalter TD, Haverty MI, Koerber TW. 1985. Cone and seed insects in Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, seed orchards in the western United States: distribution and relative impact. Canadian Entomologist 117: 1223–1230.

Schrumpf BJ, Pfeifer KM. 1993. Certification of forest reproductive materials. In: 1992/1993 Winter Workshop Proceedings, Northwest Seed Orchard Managers Association; 1993 January 27–28; Wilsonville, OR. Portland, OR: Daniels and Associates. 5 p.

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

Sexton JM, Schowalter TD. 1991. Physical barriers to reduce damage by *Lepesoma lecontei* (Coleoptera: curculionidae) to conelets in a Douglas-fir seed orchard in western Oregon. Journal of Economic Entomology 84: 212–214.

Shearer RC. 1984. Influence of insects on Douglas-fir, *Pseudotsuga menziessii* (Mirb.) Franco, and western larch, *Larix occidentalis* Nutt., cone and seed production in western Montana. In: Yates Ho III, ed. Proceedings, IUFRO Cone and Seed Insects Working Party Conference, Working Party S2.07.01; 1984; Asheville NC. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 112–121.

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.

Silen RR. 1958. Artificial ripening of Douglas-fir cones. Journal of Forestry 56: 410–413.

Silen RR. 1963. Effect of altitude on factors of pollen contamination of Douglas-fir seed orchards. Journal of Forestry 61: 281–283.

Silen RR. 1967. Earlier forecasting of Douglas-fir cone crop using male buds. Journal of Forestry 65: 888–892.

Silen RR. 1978. Genetics of Douglas-fir. Res. Pap. WO-35. Washington, DC: USDA Forest Service. 34 p.

Silen RR, Keane G. 1969. Cooling a Douglas-fir seed orchard to avoid pollen contamination. Res. Note PNW-101. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 10 p.

Silen R, Osterhaus C. 1979. Reduction of genetic base by sizing of bulked Douglas-fir seed lots. Tree Planters' Notes 30(1): 24–30.

Sorensen F. 1967. Two-year results of a west-east transect-provenance test of Douglas-fir in Oregon. Res. Note PNW-72. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 8 p.

Sorensen FC. 1980. Effect of date of cone collection and stratification period on germination and growth of Douglas-fir seeds and seedlings. Res. Note PNW-346. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 11 p.

Sorensen FC. 1983. Geographic variation in seedling Douglas-fir (*Pseudotsuga menziesii*) from the western Siskiyou Mountains of Oregon. Ecology 64: 696–702.

Sorensen FC. 1991. Stratification period and germination of Douglas-fir seed from Oregon seed orchards: two case studies. Res. Note PNW-499. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 22 p.

Sorensen FC. 1996. Effects of length of seed chilling period and sowing date on family performance and genetic variance of Douglas-fir seedlings in the nursery. New Forests 12: 187–202.

Sorensen FC. 1997. Personal communication. Corvallis, OR: USDA Forest Service, Pacific Northwest Research Station.

Sorensen FC, Campbell RK. 1971. Correlation between dates of floral and vegetative bud flush in Douglas-fir. Res. Note PNW-143. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 4 p.

Sorensen FC, Campbell RK. 1981. Germination rate of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seeds affected by their orientation. Annals of Botany 47: 467–471.

Sorensen FC, Campbell RK. 1993. Seed weight–seedling size correlation in coastal Douglas-fir: genetic and enviromental components. Canadian Journal of Forest Research 23: 275–285.

Sorensen FC, Miles RS. 1978. Cone and seed weight relationship in Douglas-fir from western and central Oregon. Ecology 59: 641–644.

St. Clair JB, Adams WT. 1991. Effects of seed weight and rate of emergence on early growth of open-pollinated Douglas-fir families. Forest Science 37: 987–997.

St. Clair JB, Adams WT. 1993. Family composition of Douglas-fir nursery stock as influenced by seed characters, mortality, and culling practices. New Forests 7: 319–329.

Stein JD, Koerber TW. 1989. Timing of acephate implants for control of the coastal seed insect complex of Douglas-fir in northern California. In: Proceedings, 3rd Cone and Seed Insects Working Party Conference; 1988 June 26–30; Victoria, BC. Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station: 203–209.

Stein JD, Markin GP. 1986. Evaluation of four chemical insecticides registered for control of the Douglas-fir cone gall midge, *Contarinia oregonensis* (Diptera: Cecidomyiidae), and the Douglas-fir seed chalcid, *Megastigmus spermotrophus* (Hymenoptera: Torymidae), in Douglas-fir seed orchards. Canadian Entomologist 118: 1185–1191.

Stein JD, Tilden PE. 1987. Single and double application of fenvalerate and dimethoate for control of Douglas-fir seed and cone insects. Journal of Economic Entomology 80: 1076–1078.

Stein WI. 1988. Nursery practices, seedling sizes, and field performance. In: Landis TD, tech. coord. Proceedings, Combined Meeting of the Western Forest Nursery Associations; 1988 August 8–11; Vernon, BC. Gen. Tech. Rep. RM-167. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: 15–18.

Stein WI, Danielson R, Shaw N, Wolff S, Gerdes D. 1986. Users guide for seeds of western trees and shrubs. Gen. Tech. Rep. PNW-193. Portland, OR: USDA, Forest Service, Pacific Northwest Research Station. 45 p.

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.

Stipe LE, Green AK. 1981. A multiple ground application of acephate and carbaryl for protection of Douglas-fir cones from western spruce budworm. Rep. 81-22. Missoula, MT: USDA Forest Service, State & Private Forestry, Forest Pest Management. 17 p.

Stonecypher RW, Piesch RF, Helland GG, Chapman JG, Reno HJ. 1996. Results from genetic tests of selected parents of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) in an applied tree improvement program. Forest Science 42 (Monogr. 32): 1–35.

Strauss SH, Tsai CH. 1988. Ribosomal gene number variability in Douglas-fir. Journal of Heredity 79: 453–458.

Sudworth GB. 1908. Forest trees of the Pacific slope. Washington, DC: USDA Forest Service. 441 p.

Summers D, Miller GE. 1986. Experience with systemic insecticides for control of cone and seed insects in Douglas-fir seed orchards in coastal British Columbia, Canada. In: Rouques A, ed. Proceedings, 2nd Conference of the Cone and Seed Insects Working Party S2.07-01,

IUFRO; 1986 September 3–5; Briancon, France. Victoria: British Columbia Ministry of Forests and Lands: 267–283.

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

Sweet GB. 1965. Provenance differences in Pacific Coast Douglas fir. Silvae Genetica 14: 46–56.

Swingle CF, comp. 1939. Seed propagation of trees, shrubs, and forbs for conservation planting. SCS-TP-27. Washington, DC: USDA Soil Conservation Service. 198 p.

Taber RP, Chun Z, Hu W. 1998. Kinetics of Douglas-fir (*Pseudotsuga menziesii*) somatic embryo development. Canadian Journal of Botany 76: 863–871.

Tanaka Y. 1984. Assuring seed quality for seedling production: cone collection and seed processing, testing, storage, and stratification. In: Duryea ML, Landis TD, eds. Forest nursery manual: production of bareroot seedlings. The Hague: Martinus Nijhoff/Dr W. Junk Publishers: 27–39.

Taylor MA, Davies HV, Smith SB, Abruzzese A, Gosling PG. 1993. Cold-induced changes in gene expression during dormancy breakage in seeds of Douglas fir (*Pseudotsuga menziesii*). Journal of Plant Physiology 142: 120–123.

Thompson BE. 1984. Establishing a vigorous nursery crop: bed preparation, seed sowing, and early seedling growth. In: Duryea ML, Landis TD, eds. Forest nursery manual: production of bareroot seedlings. The Hague: Martinus Nijhoff/Dr W. Junk Publishers: 41–49.

Thomson AJ, El-Kassaby YA. 1993. Interpretation of seed-germination parameters. New Forests 7: 123–132.

Timmis R. 1977. Critical frost temperatures for Douglas-fir cone buds. Canadian Journal of Forest Research 7: 19–22.

Trappe JM. 1961. Strong hydrogen peroxide for sterilizing coats of tree seed and stimulating germination. Journal of Forestry 59: 828–829.

USDA FS [Forest Service]. 1972. An evaluation of two tree shakers for harvesting cones. Equip. Dev. Test Rep. 2400-4. Missoula, MT: USDA Forest Service, Equipment Development Center. 27 p.

USDA FS & CDF [Forest Service and California Division of Forestry]. 1955–1971. California cone crop reports 1955–1971. Berkeley, CA: USDA Forest Service Pacific Southwest Forest and Range Experiment Station [Res. Notes 97, 110, 126, 142, 155, 164, 188, 203, & PSW-N25] and Sacramento: California Division of Forestry [Notes 21, 25, 30, 33, 36, 40, 41, 45, & 50].

Wallinger DP. 1985. Aerial cone harvesting in British Columbia. In: Shearer RC, comp. Proceedings, Conifer Tree Seed in the Inland Mountain West Symposium; 1985 August 5–6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: USDA Forest Service, Intermountain Research Station: 133–139.

Wenny DL, Dumroese RK. 1987. Germination of conifer seeds surface-sterilized with bleach. Tree Planters' Notes 38(3): 18–21.

Wenny DL, Dumroese RK. 1992. A growing regime for container-grown Douglas-fir seedlings. Bull. 49. Moscow, ID: University of Idaho, Idaho Forest, Wildlife and Range Experiment Station. 8 p.

Wheeler NC, Masters CJ, Cade SC, Ross SD, Keeley JW, Hsin LY. 1985. Girdling: an effective and practical treatment for enhancing seed yields in Douglas-fir seed orchards. Canadian Journal of Forest Research 15: 505–510.

White JLP, White MD. 1985. Squirrel behavior influences quality of cones and seeds collected from squirrel caches: field observations. In: Shearer RC, comp. Proceedings, Conifer Tree Seed in the Inland Mountain West Symposium; 1985 August 5–6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: USDA Forest Service, Intermountain Research Station: 223–224.

Williamson RL. 1983. Seedfall under coastal Douglas-fir shelterwood stands. Northwest Science 57: 205–211.

Willis CP. 1917. Incidental results of a study of Douglas-fir seed in the Pacific Northwest. Journal of Forestry 15: 991–1002.

Willis CP, Hofmann JV. 1915. A study of Douglas fir seed. Proceedings of the Society of American Foresters 10: 141–164.

Woods JH. 1989. Stem girdling to increase seed and pollen production of coast Douglas-fir. Res. Note 103. Victoria: British Columbia Ministry of Forests. 13 p.

Woods JH, Heaman JC. 1989. Effect of different inbreeding levels on filled seed production in Douglas-fir. Canadian Journal of Forest Research 19: 54–59.

Wright E. 1931. The effects of high temperatures on seed germination. Journal of Forestry 29: 679–687.

Youngberg CT. 1984. Soil and tissue analysis: tools for maintaining soil fertility. In: Duryea ML, Landis TD, eds. Forest nursery manual: production of bareroot seedlings. The Hague: Martinus Nijhoff/Dr. W. Junk Publishers: 75–80.

Fabaceae—Pea family

# *Psorothamnus* Rydb.

## indigobush

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**Other common names.** dalea.

**Growth habit, occurrence, and use**. The indigobush genus—*Psorothamnus*—includes 9 species that are spread throughout the southwestern United States into Mexico (table 1). The majority of these shrubs are ornamental and many of them also contribute to the forage value of stock ranges. Branches of dyeweed have been used by Native Americans in southwestern Arizona and southern California for dye, medicine, and basket construction (Bean and Saubel 1972; Kearney and Peebles 1951).

**Flowering and fruiting.** Flowering occurs during the summer months (Benson and Darrow 1954). Calyx lobes are usually unequal, with the upper pair often largest. Petals emerge from the receptacle in violet, blue, or purple and white together (Jepson 1993). Fruits are indehiscent, included in or protruding from the calyx. The fruits are usually glandular and produce just 1 seed (figures 1 and 2) (Jepson 1993).

Seed collection can begin in July and continue through September for Schott dalea and smoketree as seeds get plump and change color (CALR 1993). Insect-infested seeds on the ground should be avoided. Seeds of this genus are orthodox in storage behavior and have been stored successfully under a variety of conditions (table 2).

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**Table 1**—*Psorothamnus,* indigobush: nomenclature and occurrence

| Scientific name & synonyms(s) | Common name(s) | Occurrence |
|---|---|---|
| **P. arborescens (Torr. ex Gray) Barneby**<br>*Dalea arborescens* Torr. ex. Gray.<br>*Parosela arborescens* Heller<br>*Parosela neglecta* Parish | **indigobush,***<br>Mojave dalea | San Bernadino Mtns, Mojave Desert,<br>S Nevada, Mexico |
| **P. arborescens var. arborescens<br>(Torr. ex Gray) Barneby** | **Mojave indigobush,**<br>Saunder dalea | SW Mojave Desert, Mexico |
| **P. arborescens var. minutifolius<br>(Parish) Barneby** | **Johnson dalea** | Mojave Desert, S Nevada |
| **P. arborescens var. simplifolius<br>(Parish) Barneby**<br>*P. californica*<br>*Dalea californica* S. Wats. | **California dalea** | Mojave Desert & San Bernadino Mtns. |
| **P. emoryi (Gray) Rydb.**<br>*Dalea emoryi* Gray | **dyeweed,*** dyebush | Mojave & Sonoran Deserts |
| **P. fremontii (Torr. Ex Gray) Barneby**<br>*Dalea fremontii* Torr. | **Fremont dalea** | Desert mtns to S Utah, Arizona |
| **P. polydenius (Torr. ex S. Wats.) Rydb.** | **Nevada dalea,**<br>Nevada smokebush | Mojave Desert |
| **P. schottii (Torr.) Barneby**<br>*Dalea schottii* Torr.; *Parosela schottii* Heller | **indigobush**, Schott dalea | Sonoran Desert of Arizona & Mexico |
| **P. spinosus (Gray) Barneby**<br>*Dalea spinosa* Gray; *Parosela spinosa* Heller | **smoketree,** smokebush | California deserts to Arizona & NW Mexico |

**Sources:** Jepson (1993), Munz (1962, 1974).
* Despite the name, not a source of true indigo dye.

**Figure 1**—*Psorothamnus*, indigobush:   seeds of *P. arborescens* var. *simplifolius,* California dalea (**top**); *P. schottii,* indigobush (**center**); *P. spinosa*, smoketree (**bottom**).







**Figure 2**—*Psorothamnus arborescens* var. *simplifolius,* California dalea:   longitudinal section through a seed.
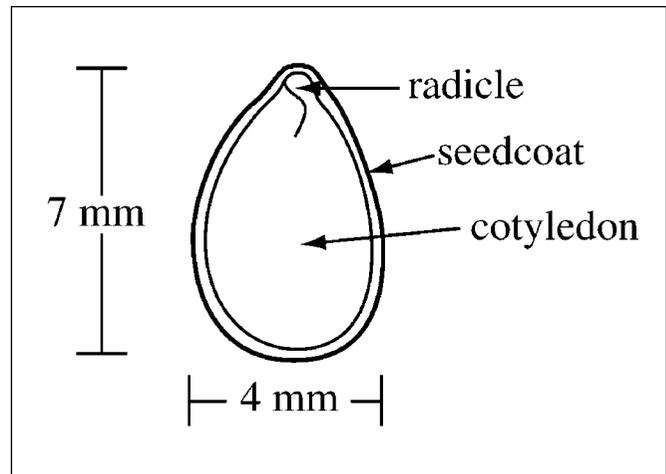


**Pregermination treatments and germination tests.** Various seed treatments have been used at the Native Plants Nursery of the U.S. Department of the Interior National Park Service's Joshua Tree National Park (JTNP); however, Emery (1988) does not suggest any pre-treatments. At JTNP, Schott dalea has been germinated by clipping and leaching seeds for 12 to 24 hours, with an average germination rate of 50%. Success with smoketree using a soak in 1:1 bleach–water solution for 30 minutes, followed by leaching for 3 to 4 hours, has resulted in an average germination rate of 40% (CALR 1993).

Other trials by Kay and others (1988) (table 2) refer to initial germination of seeds using 4 replications of 100 seeds each wrapped in damp paper toweling and stored in a growth chamber at 15 °C. Test conditions were maintained for 28 days, with germination percentages recorded every 7 days. Germination tests, conducted annually to test the effects of storage, were then averaged to a "best germination." These annual tests consisted of 4 replications of 50 seeds using the same initial testing methods.

**Nursery practice.**   Seedlings can be successfully grown in a variety of containers.  At JTNP, Schott dalea and smoketree have been successfully grown in tubes that are 76 in (30 in) long and 15 cm (6 in) in diameter and 36 cm (14 in) high and in 3.8-liter (1-gal) containers. Outplanting survival has been moderate, depending on rainfall and planting conditions (CALR 1993).

**Seedling care.**   Seedlings can be very susceptible to damping-off.  Keeping seedlings where air circulates freely and avoiding over-watering will help boost survival (CALR 1993).

**Table 2**—*Psorothamnus,* indigobush:   seed weight, initial and best germination, and storability of seeds

| Species | Seeds/weight | | Percentage germination | | Storability |
|---|---|---|---|---|---|
| | **/kg** | **/lb** | **Initial** | **Best** | |
| P. emoryi | 600 | 275 | 58 | 75 | Stores well |
| P. fremontii | 35 | 16 | 41 | 97 | 50% hard seed, stores well |
| P. polydenius | 460 | 210 | 2 | 99 | 90% hard seed, stores well |
| P. schottii | 22 | 10 | 90 | 88 | Good storage |
| P. spinosus | 50 | 23 | 22 | 58 | 17–47% hard seed, stores well |

**Source:**   Kay and others (1988).

## References

Bean LJ, Saubel KS. 1972.   Temalpakh (from the earth): Cahuilla Indian knowledge and usage of plants. Morongo Indian Reservation, CA: Malki Museum Press. 225 p.

Benson L, Darrow RA. 1954.   The trees and shrubs of the southwestern deserts. Tucson: University of Arizona Press. 437 p.

CALR [Center for Arid Lands Restoration]. 1993.   Seed test data filed 1989–1993. Twentynine Palms, CA: USDI National Park Service, Joshua Tree National Park.

Emery DE. 1988.   Seed propagation of native California plants. Santa Barbara, CA: Santa Barbara Botanical Garden. 115 p.

Jepson WL. 1993.   The Jepson manual: higher plants of California. In: Hickman JC, ed. Berkeley: University of California Press . 1400 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.

Kearny TH, Peebles RH. 1951.   Arizona flora. Berkeley: University of California Press. 1032 p.

Munz PA. 1962.   California desert wildflowers. Berkeley: University of California Press. 122 p.

Munz PA. 1974.   A flora of southern California. Berkeley: University of California Press. 1086 p.

Rutaceae—Rue family

# *Ptelea trifoliata* L.

## common hoptree

Kenneth A. Brinkman, R. C. Schlesinger, and Jill R. Barbour

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**Synonym.**   *P. trifoliata* var. *mollis* Torr. & Gray.

**Other common names.**   wafer-ash, hoptree, woolly common hoptree.

**Growth habit, occurrence, and use.**   Hoptree— *Ptelea trifolia* L.—is a shrub or small tree up to 7.5 m tall with some value for wildlife, shelterbelt, and environmental plantings. It occurs from Connecticut and New York to southern Ontario, central Michigan, and eastern Kansas; south to Texas; and east to northern Florida (Little 1953). The shrub is distributed primarily along waterways in moist forests and successfully colonized sand dunes along Lake Michigan (McLeod and Murphy 1977a). In Canada, common hoptree occurs primarily in sand on the windward side of beaches along Lake Erie (Ambrose and others 1985). Hoptree propagates sexually through seed germination on adverse beach sites because 93% of annual precipitation occurs during the growing season. The species has been cultivated since 1724 (Rehder 1940).

**Flowering and fruiting.**   Common hoptree is an obligate entomophilous, polygamo-dioecious plant. Sex ratios are skewed toward maleness, with a 60 to 40 ratio in a population (Ambrose and others 1985).

The white flowers bloom from April in the Carolinas (Fernald 1950; Radford and others 1964) to July in the North (Fernald 1950). Flowers are formed on terminal cymes with 2 ovaries, 2 stigmas, and 3 to 5 stamens (McLeod and Murphy 1977a; Radford and others 1964). Male flowers produce copious amounts of pollen grains; whereas underdeveloped staminodes of females flowers produce no pollen (Ambrose and others 1985).

Male plants have 3.7 times the amount of floral tissue for reproduction as do female plants, as determined by floral area (Ambrose and others 1985).  Despite that, there is a slight (but not significant) skewness toward female flower preference by insects (Ambrose and others 1985).

In southern Ontario, over 102 insects from nearly 40 families visited hoptree plants. Hoptree was found to be the primary host for the rare giant swallowtail— *Paptho creshontes* Cramer (Ambrose and others 1985). Insect pollinators show little preference between female and male plants.

Fruits are reddish brown, orbicular, 2-seeded samaras (figures 1 and 2) that ripen from June to November (Rehder 1940) and may persist until spring (Van Dersal 1938). The seedcoat is composed of a black, crisp outer layer with a thin, brown membranous inner layer (Ambrose and others 1985). The samara is 1.5 to 2.5 cm broad and weighs from 0.026 to 0.067 g (Radford and others 1964). Most fruits only contain 1 seed, but 10% of them may contain 2 seeds. Hoptree is an abundant seeder and the samaras are dispersed by wind.  Annual fruit production is about 300,000 samaras per hectare. The reniform seeds are 6.4 mm long, 2.3 wide, and weigh from 0.007 to 0.012 g (McLeod and Murphy 1977a). The embryo is completely embedded in endosperm tissue.

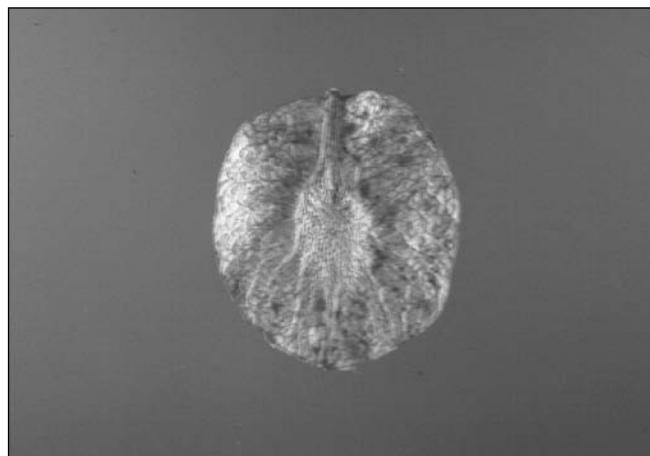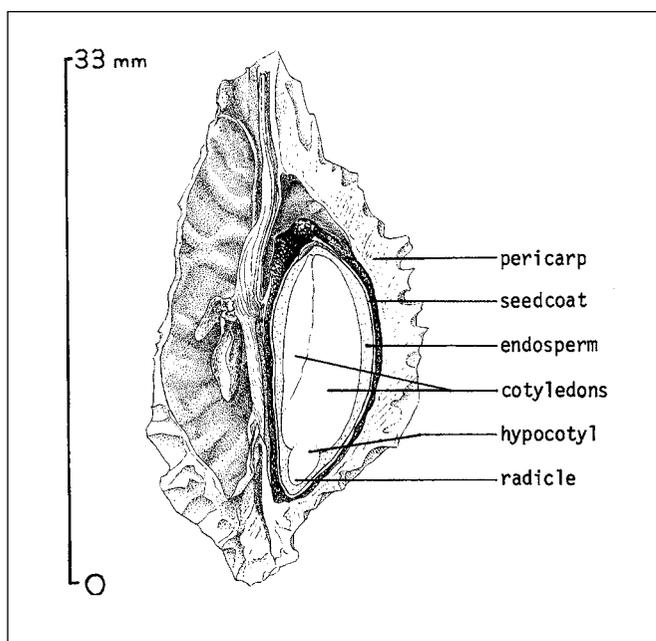**Figure 1**— *Ptelea trifoliata,* common hoptree:   fruit (samara).

**Figure 2**— *Ptelea trifoliata*, common hoptree:    longitudinal section through a samara.



**Collection and storage of seeds.**    The ripe samaras may be picked from September to November. They may require a few days of drying if they are to be stored. Because samara tissue inhibits germination, removal is recommended (McLeod and Murphy 1977b). In 5 samples, the number of samaras ranged from 19,850 to 39,700/kg (9,000 to 18,000/lb) and averaged 26,500/kg (12,000/lb). About 97% of the fruits contain sound seeds.

The seeds are apparently orthodox in storage behavior— if stored in sealed containers at 5 °C, common hoptree seeds will retain most of their viability for at least 16 months. Seedlot viability determined by the 2,3,5-triphyenyl tetrazolium chloride test was over 90% after 220 days of storage at room temperature and remained over 95% during monthly checks while the seeds were being stratified (McLeod and Murphy 1977b). Viability remained at 90% when seeds were subjected to lower temperatures during germination; higher than optimum temperatures reduced viability to 45% (McLeod and Murphy 1977b).

**Germination tests.**    Hoptree seeds have numerous barriers to germination. No germination resulted from whole fruits, punctured fruits, or whole seeds that were left unstratified (McLeod and Murphy 1977b). Unstratified embryos develop into physiological dwarfs with very short internodes and a low-vigor radicle, suggesting embryo dormancy. Excising the embryo yielded 39.5% germination; removing the seedcoat, 17%; and removing the endosperm covering

the radicle, 25% (McLeod and Murphy 1977b). Endosperm tissue is a barrier to radicle elongation, not a dormancy mechanism.

Leachates of fruit parts, diluted 50, 20, 10, and 4%, applied to embryos inhibited development. Of embryos exposed to 5 ml of leachate, only 9% of those exposed to seedcoat leachate germinated; 33% to samara leachate; 45% to endosperm leachate; and 58% to no leachate (McLeod and Murphy 1977b). Stratification negated the effect of the samara leachate on embryo germination (92%) versus the control values (100%).

Seeds must be stratified to germinate. Artificial stratification (3 °C) is only successful when the samara is removed. Seed germination of intact fruit was 6% after 211 days of cold stratification; without the samara the germination jumped to 81% after 181 days of stratification (McLeod and Murphy 1977b). During natural stratification, decomposition of the samara is 3 times that resulting from cold-room stratification. Under natural stratification, the samaras were 71% half-decomposed in 150 days compared to the negligible degradation resulting from artificial stratification (McLeod and Murphy 1977b).

Maximum laboratory germination (72%) occurred when temperature fluctuated between 16 and 22 °C; germination of 60% was the best constant temperature (17 °C) value (McLeod and Murphy 1977b). Germination of imbibed seeds exposed to 4 hours daily of 40 °C temperatures was reduced from 45% after 1 week down to 0% after 4 weeks of exposure (McLeod and Murphy 1977b). Germination tests can be made in sand flats at temperatures alternated diurnally from 25 to 10 °C. Germinative capacity in 6 tests ranged from 10 to 91% but averaged only 28% (Brinkman and Schlesinger 1974).

Germination is epigeal (figure 3). In imbibed seeds, it takes 5 to 20 days for the hypocotyl to emerge in the field. Root extension occurred over the 10 weeks following radicle emergence, with 65% completed in 4 weeks and growth about 11 cm long (McLleod and Murphy 1977b).

**Nursery practice.**    Seed should be either fall-sown or stratified over most of the winter and sown in the spring. Seedlots of cultivar 'Aurea' sown immediately after collection germinated 47%; those seeds subjected to 2 to 3 months of cold stratification and then sown germinated 100% (Dirr and Heuser 1987). If seeds are sown in the fall, the seedbeds should be mulched to reduce effects of freezing and thawing. When seeds were buried 4 cm (1 $1/_2$ in) deep, over two-thirds never emerged from the ground after germination (McLeod and Murphy 1977b). Some of the seedlings have yellow foliage color (Dirr and Heuser 1987). Propagation also is possible by layering, grafting, or budding.

**Figure 3**—*Ptelea trifoliata*, common hoptree:   seedling development at 1, 2, and 10 days after germination.
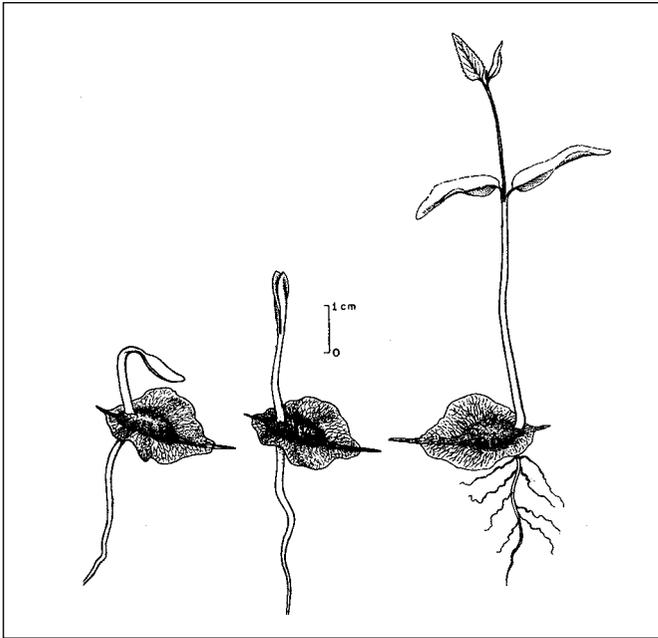
**References**

Ambrose JD, Kevan PG, Gadawski RM. 1985.   Hoptree (*Ptelea trifoliata*) in Canada: population and reproductive biology of a rare species. Canadian Journal of Botany 63: 1928–1935.

Brinkman KA, Schlesinger RC. 1974.   *Ptelea trifoliata*, common hoptree. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 684–685.

Dirr MA, Heuser Jr CW. 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. 8th ed. New York: American Book Co. 1632 p.

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.

McLeod KW, Murphy PG. 1977a.   Establishment of *Ptelea trifoliata* on Lake Michigan sand dunes. American Midland Naturalist 97(2): 350–362.

McLeod KW, Murphy PG. 1977b.   Germination ecology of Ptelea trifoliata. American Midland Naturalist 97(2): 363–372.

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.

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

# *Pterocarpus* Linn.

## *padauk, narra*

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**Growth habit, occurrence, and use.** Although there are several *Pterocarpus* species scattered throughout the tropics, only Burma *padauk* (*P. macrocarpus* Kurz) and India *padauk* (*P. indicus* Willd.), also called *narra* or Burmese rosewood, are commonly planted. Both are large trees that produce reasonably long and straight boles in closed stands but develop short boles and spreading crowns when open-grown. Older trees have moderate buttresses and large roots that run along the surface of wet or clayey soil. Both have lush, green foliage and cast a moderately dense shade. Both have naturalized in Puerto Rico but spread very slowly.

Burma padauk is native to upland areas in Myanmar, Thailand, Kampuchea, and Vietnam (Francis 1989). Because of its annual yellow floral display and pleasing foliage and form, this species has become a very popular ornamental and shade tree in Puerto Rico, Florida, and the U.S. Virgin Islands (Francis 1989). It has naturalized in (at least) Puerto Rico (Francis and Liogier 1991). Burma padauk is quite at home in frost-free areas that receive from 1,000 to 2,000 mm of mean annual precipitation.

India padauk is native to the Andaman Islands (India), Malaysia, Indonesia, and the Philippines (Little and Wadsworth 1964). Although it has virtually the same form, foliage, and floral display as the Burma padauk, India padauk requires somewhat higher rainfall (above 1,500 mm/year) (Troup 1921). It has been planted for reforestation in Hawaii (Neal 1965) and in forestry trials in Puerto Rico.

Both species have good forestry potential. They tolerate a wide range of soil types and can be planted in cleared sites or small forest openings. The wood of both species varies from yellow to dark red; the rich colors and figures are highly prized for furniture and decorative uses (Chudnoff 1984). Even the lower grades of wood are useful for posts, ship timbers, and construction because of their resistance to termites and rot (Hundley 1956; Rendle 1970).

**Flowering and fruiting.** The sweet-scented flowers are produced copiously in panicles and racemes. Individual flowers are about 1.6 cm across. They are pollinated by honey bees (*Apis mellifera* L.) and other insects. Fruits mature about 6 months after flowering and fall off the tree gradually over several months. Padauk fruits are lenticular-shaped legumes with a flat wing that circles its edge (figure 1). The straw-colored to light brown legumes of India padauk are generally 3 to 4 cm across and the light brown legumes of Burma padauk measure 4.5 to 7.5 cm across (Little and Wadsworth 1964; Little and others 1974). However, considerable variation in size occurs between the legumes of individual trees and tress from various sources within both species. Legume production usually begins in open-grown trees between 5 and 10 years of age. Large trees produce about 35 liters (1 bu) or more of legumes annually.

**Collection, cleaning, and storage.** At maturity, the legumes dry and turn from greenish yellow to straw colored or light brown. Seed-bearing branches can be clipped with pruning poles if the need for legumes is urgent. Because the legumes and their seeds do not deteriorate for several months after falling, it is more efficient to wait until most of the crop has fallen and pick up the legumes from the ground. A sample of air-dried legumes of Burma padauk grown in Puerto Rico yielded 1,067 legumes/kg (485/lb) (Francis 1989). The legumes of India padauk (source unknown) were reported to yield 1,200 to 1,300 legumes/kg (545 to 590/lb) (MacDicken and Brewbaker 1984). The seeds of padauk are fragile (figure 2) and the legumes are tough, making extraction impossible mechanically and difficult by hand. A sample of legumes of Burma padauk from Puerto Rico yielded an average of 2.6 seeds/legume (Francis 1989); shelled seeds averaged 11,500/kg (5,200/lb) (Francis and Rodríguez 1993). Padauk seeds are normally stored and planted in the legumes. Air-dried seeds in their legumes will still germinate after 1 year of storage in plastic bags at room temperature. The effect of refrigeration is unknown but probably beneficial.

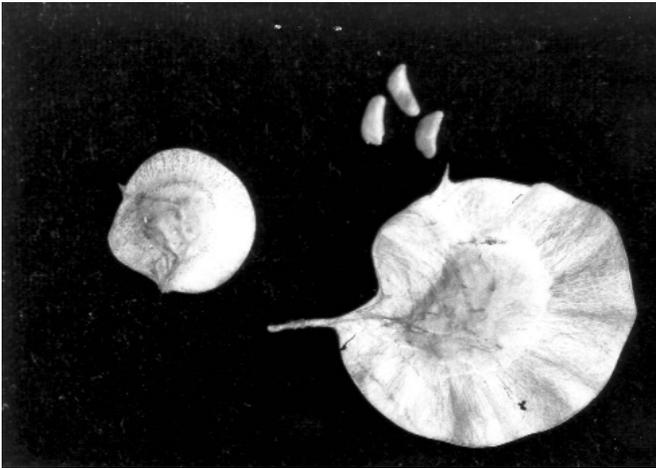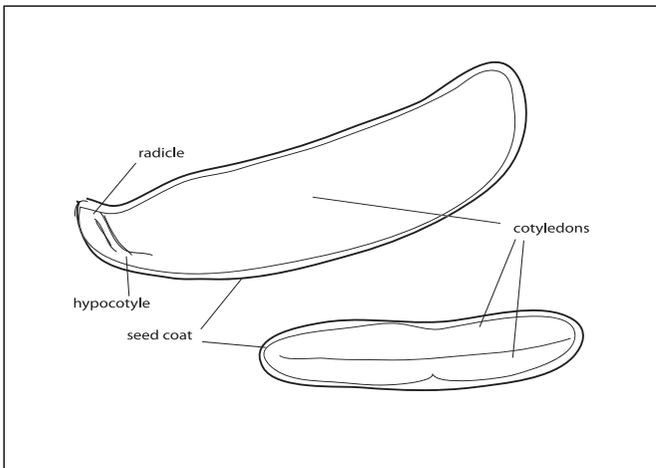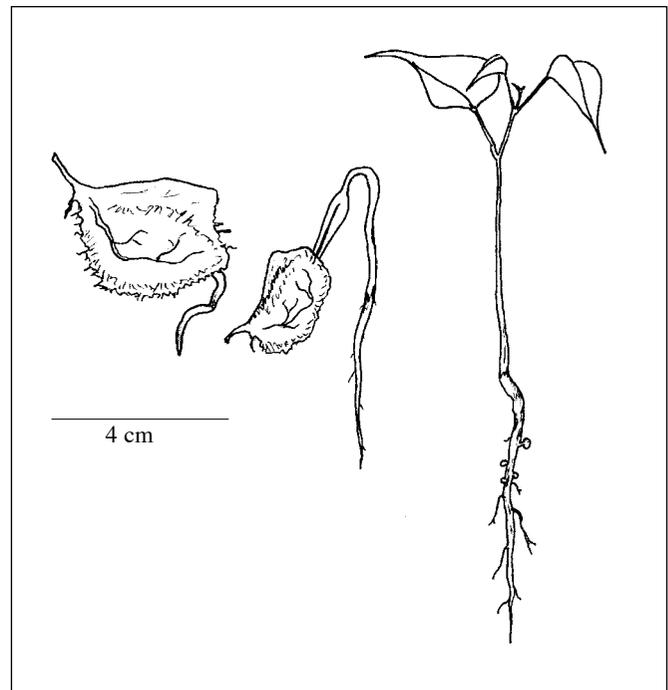**Figure 1**—*Pterocarpus macrocarpus*, Burma padauk: legumes and seeds (**top right**).

**Figure 3**—*Pterocarpus macrocarpus*, Burma padauk: germinating seed showing seedling development.

**Figure 2**—*Pterocarpus macrocarpus*, Burma padauk: longitudinal sections of seeds.

4 cm

**Germination.**    The first seeds germinate within and begin to grow through the legumes about 1 to 2 weeks after planting. The remaining seeds continue germinating for several weeks thereafter. Often 2 or 3 seedlings emerge from each legume. Germination is epigeal (figure 3). In a comparison of the germination of shelled seeds to seeds within legumes in Puerto Rico, shelled seeds germinated in 5 days and gave 70% germination within 2 weeks. Unshelled legumes did not begin germination for 11 days and only 64 seedlings/100 legumes emerged within 2 months. However, effective yield was only about two-thirds this amount because about half the seedlings occurred in multiples and only 1 germinant/legume can produce a plantable seedling. In Burma, shelled seeds gave 80 to 90% germination. Moreover, seeds from 1-year-old legumes collected from the

ground germinated better than new seeds collected from the tree (Hundley 1956). Seeds from Burma padauk germinated well (around 80% over a wide temperature range; the best temperature regime seemed to be about 30 °C day and 25 °C night (Liengsiri and Hellum 1988).

**Nursery practice.**    The use of shelled seeds would be recommended, except that they are so difficult to extract. The use of seeds in the legumes requires thinning the plants soon after germination to remove multiples. When true leaves have developed, seedlings are transplanted from the germination bed to bags filled with a potting mixture. After growing under light shade for a few months, the seedlings reach about 0.5 m (1.6 ft) in height and are ready for outplanting (Francis 1989). In Burma, seedlings in plantations grow to 0.6 to 1.2 m (2 to 4 ft) the first year and 1.2 to 2.1 m (4 to 7 ft) the second (Hundley 1956). Thirty planted trees in a small forest plantation in Puerto Rico (situated on clay soil over porous limestone) averaged 1.3 m tall at 14 months after outplanting (Francis 1989). Seedlings intended for ornamental use are often grown in 12- to 20-liter (3- to 5-gal-size) plastic pots until they reach 2 to 3 m (6.5 to 7.5 ft) in height before outplanting. In the Philippines, branch cuttings of India padauk about 8 cm (3 in) in diameter are rooted after hormone treatment to produce "instant trees" (Dalmacio and others 1978).

## References

Chudnoff M. 1984.  Tropical timbers of the world. Agric. Handbk. 607. Washington, DC: USDA Forest Service. 464 p.

Dalmacio MV, Crizaldo EN, Narra I. 1978.  Production of "instant trees." Silvitrop Philippine Forestry Journal 3(1): 55–62.

Francis JK. 1989.  *Pterocarpus macrocarpus* Kurz, Burma padauk, pradu. Res. Note SO-ITF-SM-19. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 4 p.

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.

Hundley HG. 1956.  Padauk, *Pterocarpus macrocarpus* Kurz. Burma Forester 7(1): 6–38.

Liengsiri C, Hellum AK. 1988.  Effects of temperature on seed germination in *Pterocarpus macrocarpus*. Journal of Seed Technology 12(1): 66–75.

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.

Little EL Jr, Woodbury RO, Wadsworth FH. 1974.  Trees of Puerto Rico and the Virgin Islands. Agric. Handbk. 449. Washington, DC: USDA Forest Service. 1024 p.

MacDicken KG, Brewbaker JL. 1984.  Descriptive summaries of economically important nitrogen fixing trees. Nitrogen Fixing Tree Research Reports 2: 46–54.

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

Rendle BJ. 1970.  World timber. Volume 3, Asia, Australia, and New Zealand. London: Ernest Benn Ltd. 175 p.

Troup RS. 1921.  The silviculture of Indian trees. Volume 1. Oxford: Clarendon Press. 336 p.

Rosaceae—Rose family

# *Purshia* DC. ex Poir.

## bitterbrush, cliffrose

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**Growth habit, occurrence, and use.** The bitterbrush genus—*Purshia*—as presently circumscribed comprises 8 species of decumbent to arborescent shrubs of interior western North America. Three are common in the United States (table 1). The type species—antelope bitterbrush—has an essentially northern distribution, whereas cliffrose has an essentially southern distribution, and desert bitterbrush occurs in parts of the geographic area where the other 2 species have overlapping distributions. Cliffrose, along with the 5 Mexican species of the genus, has been traditionally referred to the genus *Cowania* D. Don. Cliffrose regularly forms hybrids with antelope bitterbrush, and desert bitterbrush could be interpreted as a stabilized hybrid between these species (Stutz and Thomas 1964). In fact, molecular genetics work by Jabbes (2000) indicates that *Purshia* was derived from *Cowania*. We follow Welsh and others (1987) in treating the group as congeneric under the name *Purshia*.

Members of the genus are erect, spreading or decumbent, freely branched shrubs up to 6 m in height. They have small, alternate, simple, apically lobed leaves that may be evergreen (cliffrose) to winter deciduous (antelope bitterbrush). Layering forms of bitterbrush (principally antelope bitterbrush) may resprout after fire, but erect forms are usually not fire tolerant. Because of their interesting habits, attractive foliage, and showy flowers, bitterbrush species have potential as ornamentals in low-maintenance landscapes.

Bitterbrush species are hardy and drought tolerant. Antelope bitterbrush occurs mainly on well-drained soils over a wide elevational range and is often a principal component of mixed shrub, pinyon–juniper, ponderosa pine, and sometimes lodgepole pine communities, where it is notable as a nurse plant for conifer seedlings (Geier-Hayes 1987; McArthur and others 1983; Nord 1965; Tew 1983). It is valued as a high-protein browse for domestic and wild ungulates, being especially important on winter ranges (Bishop and others 2001; Scholten 1983). It also supplies high-quality forage during spring and summer months (Austin and Urness 1983; Ngugi and others 1992). Cliffrose grows primarily on rocky sites in blackbrush–joshua tree woodland, sagebrush–grassland, piñyon–juniper woodland, mountain brush, and ponderosa pine communities, sometimes forming extensive stands on south-facing ridge slopes (McArthur and others 1983). It is also an important browse species, especially for mule deer (*Odocoileus hemionus*) (Plummer and others 1968). Desert bitterbrush is a component of blackbrush, chaparral, and piñyon–juniper communities.

The bitterbrush species form actinorhizal root nodules that fix nitrogen when soil water is adequate (Bond 1976;

**Table 1**—*Purshia,* bitterbrush, cliffrose: common names and geographic distributions

| Scientific name & synonym(s) | Common name | Geographic distribution |
|---|---|---|
| *P. glandulosa* **Curran**<br>*P. tridentata* var. *glandulosa* (Curran) M.E. Jones | **desert bitterbrush** | SW Utah, S Nevada, & S California |
| *P. mexicana* **(D. Don) Henrickson**<br>*Cowania mexicana* D. Don | **cliffrose** | S Colorado W through Utah to S California<br>& S to New Mexico, Arizona, Sonora, & Chihuahua |
| *P. tridentata* **(Pursh) DC.** | **antelope bitterbrush** | British Columbia to W Montana, S to New Mexico, California, & N Arizona |

**Sources:** Little (1979), Sargent (1965), Vines (1960).

Kyle and Righetti 1996; Nelson 1983; Righetti and others 1983). They readily function as pioneer species that colonize harsh, steep disturbances and have been used extensively in revegetation and disturbed-land reclamation. An ethanol extract of antelope bitterbrush aerial stems was found to inhibit reverse transcriptase of HIV-1 and to contain the cyanoglucosides pushianin and menisdaurin (Nakanishi and others 1994). Unfortunately, the cyanoglucosides lacked the inhibitory activity of the original extract. Cliffrose has also been examined for beneficial secondary products (Hideyuki and others 1995; Ito and others 1999). Specific populations of antelope bitterbrush with distinctive attributes are recognized and are commercially harvested and sold, although to date only two ('Lassen' and 'Maybell') have been formally named (Davis and others 2002; Shaw and Monsen 1995).

**Flowering and fruiting.** Most of the medium to large, perfect, cream to sulfur yellow flowers of this genus appear during the first flush of flowering in April, May, or June, depending on elevation. In areas where they co-occur, antelope bitterbrush usually flowers 2 to 3 weeks before cliffrose. The flowers are borne on lateral spurs of the previous year's wood (Shaw and Monsen 1983). In cliffrose, summer rains may induce later flowering on current-year leaders, but these flowers rarely set good seeds (Alexander and others 1974). The flowers have a sweet fragrance and are primarily insect-pollinated. Each has 5 sepals, 5 separate petals, numerous stamens, and 1 to 10 pistils borne within a hypanthium. Flowers of antelope and desert bitterbrushes usually contain a single pistil with a relatively short, non-plumose style, whereas those of cliffrose contain multiple pistils. The pistils develop into single-seeded achenes with papery pericarps. In cliffrose the achenes are tipped with persistent) plumose styles, 22 to 50 mm (1 to 2 in) in length, that give the plants a feathery appearance in fruit.

The main fruit crop ripens from June through August, depending on species and elevation. Plants begin to bear seeds as early as 5 years of age. At least some fruits are produced in most years, and abundant seedcrops are produced on average every 2 to 3 years (Alexander and others 1974; Deitschman and others 1974). Cliffrose seeds (figure 1) are apparently dispersed principally by wind (Alexander and others 1974). Scatter-hoarding rodents such as chipmunks (*Tamias* spp.), disperse bitterbrush seeds (figure 2) and seedlings from rodent caches appear to account for nearly all (99%) natural recruitment as survivors from seedling clumps containing 2 to >100 individuals (Evans and others 1983; Vander Wall 1994).

**Seed collection, cleaning, and storage.** Bitterbrush plants produce more leader growth in favorable water years,



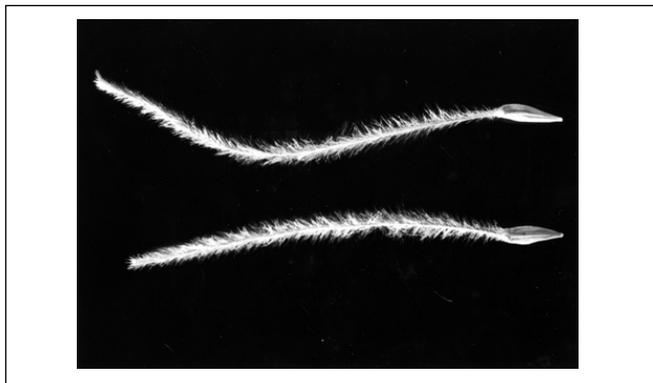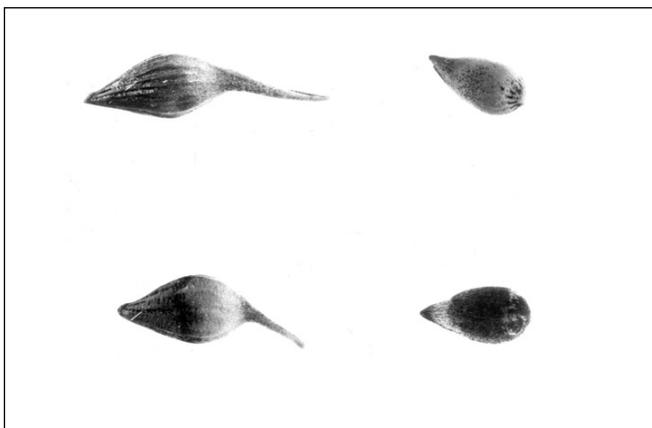**Figure 1**—*Purshia*, mexicana, cliffrose:  achenes:



**Figure 2**—*Purshia*, bitterbrush:  achenes (**left**) and cleaned seeds (**right**) of *P. glandulosa*, desert bitterbrush (**top**) and

and leader length is an indicator of the potential for seed production the following year (McCarty and Price 1942; Young and Young 1986). Fruits may be hand-stripped or beaten into hoppers or other containers when fully ripe; harvesters should take care to protect themselves from the fiberglass-like style hairs in the case of cliffrose. The window of opportunity is quite narrow, as ripe fruits are easily detached by wind and do not persist long on the plant, making close monitoring during ripening advisable. Plants in draws and other areas protected from wind may retain their seeds longer. Maturation dates for antelope bitterbrush have been predicted with reasonable accuracy using elevational and latitudinal predictors (Nord 1965). Well-timed harvests of antelope bitterbrush average 168 to 224 kg/ha (150 to 200 lb/acre) but may range up to 560 kg/ha (500 lb/acre) (Nord 1965). Fill percentages are usually high, although insects or drought stress during filling can damage the crop (Shaw and Monsen 1983). Krannitz (1997a) reported the variation in seed weight from 240 bitterbrush plants representing 10 sites in the southern Okanagan Valley of Canada varied from

5 to 46 mg/seed with the population being skewed toward the small seeds. The representative weights given in table 2 are of cleaned seeds (the smaller fraction is removed in cleaning). Krannitz also found that larger seeds had greater concentrations of nitrogen than smaller seeds and that shrubs that had been browsed most intensively the winter before seed-set had seeds with greater concentrations of magnesium (Krannitz 1997b).

A seed cleaner or barley de-bearder may be used to break the styles from cliffrose achenes and to remove the papery pericarps of bitterbrush species. The achenes (cliffrose) or seeds (bitterbrush species) may be separated from the inert material—which usually comprises from one-third (antelope bitterbrush) to two-thirds (cliffrose) of the total weight—using a fanning mill (Alexander and others 1974; Giunta and others 1978). In cliffrose, the achene is considered the seed unit, as the seed is held tightly within the pericarp and cannot be threshed out without damage. In bitterbrush species, the seeds are easily threshed free of their papery pericarps, and the seed unit is the seed itself. If properly dried (<10% moisture content), seeds of bitterbrush species can be warehouse-stored for 5 to 7 years (Belcher 1985) or even up to 15 years without losing viability (Stevens and others 1981).

**Germination and seed testing.** Bitterbrush and cliffrose seeds are mostly dormant but the inhibiting mechanism(s) is not understood (Booth 1999; Booth and Sowa 2001; Dreyer and Trousdale 1978; Meyer 1989; Meyer and Monsen 1989; Young and Evans 1976, 1981). Moist chilling is preferred for breaking dormancy (table 3). Although some collections are less dormant than others are—as indicated by germination percentages for untreated or partially treated seeds (table 3) (Booth 1999; Meyer and Monsen 1989)—there is no obvious relationship between collection site and chilling requirement (Meyer and Monsen 1989). Dormancy might be affected by high seed temperature (30 °C) while in the dry state (Meyer 1989) and is certainly affected by imbibition temperature (Booth 1999; Meyer 1989).

Young and Evans (1981) reported the required chilling period was shorter at 5 °C, than at 2 °C for all 3 species, and that adequately chilled seeds could germinate over a wide range of temperatures. A 28- to 30-day chill at 1 to 3 °C is highly recommended (AOSA 1993; Belcher 1985; Booth 1999; Meyer 1989) followed by post-chill incubation at 15 °C (10/20 °C for cliffrose). Desert bitterbrush needs only 14 days of chilling (Belcher 1985). Germination of antelope bitterbrush seeds can be facilitated by 24 hours of soaking in cold (2 °C) water prior to moist chilling, but soaking in

| Table 2—*Purshia,* bitterbrush and cliffrose:   seed yield data (seeds/weight) for mechanically cleaned seeds* | | | | |
|---|---|---|---|---|
| | **Mean** | | **Range** | |
| **Species** | **/kg** | **/lb** | **/kg** | **/lb** |
| *P. glandulosa* | 50,850 | 26,540 | 45,000–90,000 | 20,300–40,900 |
| *P. mexicana* | 129,000 | 58,600 | 108,000–210,000 | 49,000–95,000 |
| *P. tridentata* | 35,000 | 15,750 | 29,000–51,000 | 13,400–23,200 |

**Sources:** Alexander and others (1974), Belcher (1985), Deitschman and others (1974), Meyer (2002), Meyer and others (1988).

| Table 3—*Purshia,* bitterbrush and cliffrose:   germination data | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | **Mean percentage of initially viable seeds** | | | | | | | |
| **Species** | **0** | **2 wk** | **4 wk** | **6 wk** | **8 wk** | **10 wk** | **12 wk** | **Samples** |
| *P. glandulosa* | — | — | — | 93 | — | — | 100 | 1* |
| | 10 | 56 | 81 | 100 | 65 | — | 32 | 1† |
| *P. mexicana* | 6 | 33 | 83 | 94 | 100 | — | — | 6 |
| | 6 | 64 | 91 | 100 | 32 | — | 19 | 1† |
| *P. tridentata* | 2 | 43 | 88 | 98 | 100 | — | — | 13 |
| | 13 | 60 | 100 | 100 | 36 | — | 37 | 1† |

**Sources:** Deitschman and others (1974), Meyer (2002), Meyer and Monsen (1989), Young and Evans (1981).
**Note:** Values are expressed as percentage of initially viable seeds after moist chilling at to 2 °C  for 0 to 12 weeks followed by incubation at 15 °C or 10/20 °C for 4 weeks.
* These seeds were chilled at 3 to 5 °C and germination was scored during chilling.
† Decrease in germination percentage after 6 weeks was due to seed mortality during the test.

warm water (>10 °C), or holding imbibed seeds at warm temperatures, decreases seedling vigor and increases pre-germination seed-weight loss (Booth 1999; Booth and Sowa 2001). Longer, colder chilling periods (28 days, 2 °C vs 14 days, 5 °C) increases seedling vigor (Booth 1999; Booth and Morgan 1993). Recommended germination test periods are 28 days for antelope bitterbrush and cliffrose (AOSA 1993).

Soaking seeds in hydrogen peroxide (Everett and Meeuwig 1975) or a 1 to 3% solution of thiourea (Pearson 1957; Young and Evans 1981) will induce germination but these methods have not proven useful for field plantings. Booth (1999) found thiourea-treated seeds to have the lowest seedling vigor among 8 dormancy-breaking treatments and attributed the lower vigor to residual dormancy and to weight loss resulting from accelerated respiration (Booth 1999; Booth and Sowa 2001).

Tetrazolium (TZ) staining is acceptable for evaluating seed quality of bitterbrush (AOSA 1993; Weber and Weisner 1980). Meyer (2002) found no significant difference between TZ viability estimates and germination perentages after 8 weeks of chilling for either cliffrose or antelope bitterbrush. For TZ viability testing, seeds should be clipped at the cotyledon end (figure 3) and soaked in water for 6 to 24 hours. Then, the embryos can be popped-out of the cut end by gentle finger pressure and immersed in 1% TZ solution for 4 to 12 hours at room temperature before evaluation. Cliffrose must be soaked longer than bitterbrush before the embryos can be popped out.

**Field seeding and nursery practice.** Bitterbrush species are generally sown in fall or early winter in a mixture with other shrubs and forbs. They are used in upper sagebrush, piñyon-juniper woodlands, and mountain brush vegetation types to improve degraded wildlife habitat or re-vegetate bare roadcuts, gullies, south slopes, and other difficult sites (Alexander and others 1974). Because of the chilling requirement, spring-seeding should be avoided. Seeds may be drilled at a depth of 6 to 12 mm ($^1/_4$ to $^1/_2$ in) or deeper. Deeper seeding may provide some protection from rodent depredation, which can be a serious problem (Alexander and others 1974; Evans and others 1983; Vander Wall 1994). Seeding in late fall or early winter, when rodents are less active, may also alleviate this problem.

Broadcast-seeding is generally unsuccessful unless provision is made for covering the seeds. Aerial seeding is not recommended. The seedlings do not compete well with weedy annual grasses such as red brome (*Bromus rubens* L.) and cheatgrass (*B. tectorum* L.), or with heavy stands of perennial grasses. They are sensitive to frost and drought during establishment (Plummer and others 1968). Recommended (drill) seeding rates for cliffrose are 5 to 10% of the shrub mix at 8 to 10 kg/ha (7 to 9 lb/ac) (Alexander

**Figure 3**—*Purshia*: longitudinal section of *P. mexicana*, cliffrose (**top**) and *P. tridentata*, antelope bitterbrush (**bottom**).
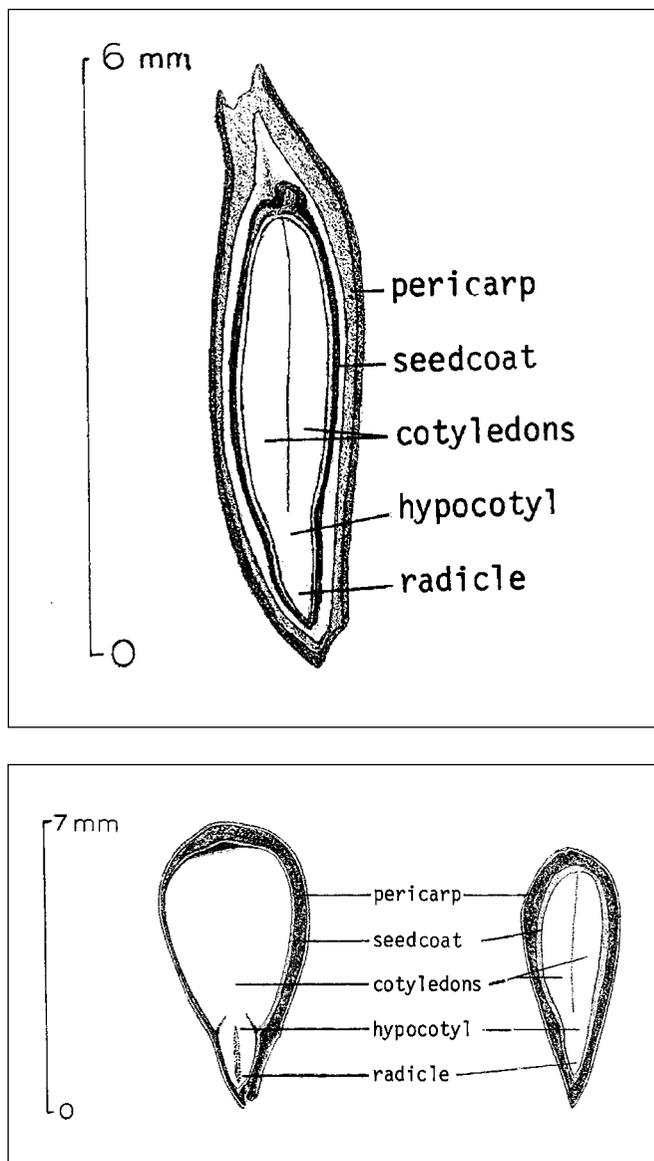




and others 1974; Plummer and others 1968) and 16 to 65 seeds/m (5 to 20 seeds/ft) for bitterbrush. The higher rates are advisable for both species when seeding in crust-forming soils. The most effective method of seeding large areas in conjunction with chaining is with a seed dribbler that drops seeds in front of the bulldozers pulling the chain.

Hand-planting into scalped sites with a tool such as a cased-hole punch planter can be very effective on a small scale (Booth 1995). The purpose of scalping is to control herbaceous competition within a half-meter (1 $^1/_2$-ft) radius of the planting spots. Treating seeds with fungicide, planting seeds in groups, and planting with vermiculite to aid in moisture retention have all improved emergence and estab-lishment of antelope bitterbrush (Booth 1980; Evans and

others 1983; Ferguson and Basile 1967). Good emergence depends on adequate snowcover (Young and others 1993).

 Bitterbrush species are readily grown as bareroot or container stock, and outplanting may succeed where direct seeding has failed (Alexander and others 1974). Care must be taken to lift or transplant stock only when the plants are hardened or dormant, as survival of actively growing plants is generally low (Landis and Simonich 1984; Shaw 1984). Plants are easier to handle and have higher survival rates if allowed to reach sufficient size before field transplanting. One-year-old bareroot stock or container seedlings 16 to 20

weeks of age are usually large enough (Alexander and others 1974; Shaw 1984). On more level terrain, a conventional tree-planter may be used (Alexander and others 1974). Transplanting should be carried out at a time and in such a way as to assure that the transplants will have adequate moisture for root development for 4 to 6 weeks after planting. This may be accomplished by planting in very early spring or by watering at the time of planting. Fall-planted seedlings may require supplemental watering. Controlling competition from weedy annual or perennial grasses before planting will enhance survival and first-season growth.

## References

Alexander RR, Jorgensen K, Plummer AP. 1974.   *Cowania mexicana* var. *stansburiana* (Torr.) Jeps., cliffrose. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 353–355.

AOSA [Association of Official Seed Analysts]. 1993.   Rules for testing seeds. Journal of Seed Technology 16(3): 1–113.

Austin DD, Urness PJ. 1983.   Summer use of bitterbrush rangelands by mule deer. In: Tiedemann AR, Johnson KL, comps. Proceedings, Research and Management of Bitterbrush and Cliffrose in Western North America; 1982 May 13–15; Salt Lake City. Gen. Tech. Rep. INT-152. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 203–212.

Belcher E. 1985.   Handbook on seeds of browse-shrubs and forbs. Tech. Pub. R8-8. Atlanta: USDA Forest Service, Southern Region. 246 p.

Bishop CJ, Garton EO, Unsworth JW. 2001.   Bitterbrush and cheatgrass quality on 3 southwest Idaho winter ranges. Journal of Range Management 54:595-602.

Bond G. 1976.   Observations on the root nodules of *Purshia tridentata*. Proceedings of the Royal Society of London (Series B) 192: 127–135.

Booth DT. 1980.   Emergence of bitterbrush seedlings on land disturbed by phosphate mining. Journal of Range Management 33: 439–441.

Booth DT. 1995.   Cased-hole punch seeder: a tool for increasing plant diversity. In: Abstracts, 48th Annual Meeting. Denver: Society for Range Management: 8.

Booth DT. 1999.   Imbibition temperatures affect bitterbrush seed dormancy and seedling vigor. Journal of Arid Environments 48: 35–39.

Booth DT, Morgan DR. 1993.   Post-germination growth related to time-to-germination for four woody plants. Journal of Seed Technology 16: 30–38.

Booth DT, Sowa S. 2001.   Respiration in dormant and non-dormant bitterbrush seeds. Journal of Arid Environments 43: 91–101.

Davis KM, Englert JM, Kujawski JL. 2002.   Improved conservation plant materials released by NRCD and cooperators through September 2002. Beltsville, MD: USDA Agricultural Research Service. 57 p.

Deitschman GH, Jorgensen KR, Plummer AP. 1974.   *Purshia*, bitterbrush. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington DC: USDA Forest Service: 686–688.

Dreyer DL and Trousdale EK. 1978.   Cucurbitacins in *Purshia tridentata*. Phytochemistry 17:325-326.

Evans RA, Young JA, Cluff GJ, McAdoo JK. 1983.   Dynamics of antelope bitterbrush seed caches. In: Tiedemann AR, Johnson KL, comps. Proceedings, Research and Management of Bitterbrush and Cliffrose in Western North America. 1982 May 13–15; Salt Lake City. Gen. Tech. Rep. INT-152. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 195–202.

Everett RL, Meeuwig RO. 1975.   Hydrogen peroxide and thiourea treatment of bitterbrush seed. Res. Note 196. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 6 p.

Ferguson RB, Basile JV. 1967.   Effect of seedling numbers on bitterbrush survival. Journal of Range Management 20: 380–382.

Geier-Hayes K. 1987.   Occurrence of conifer seedlings and their microenvironments on disturbed sites in central Idaho. Res. Pap. INT-383. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 12 p.

Giunta B, Stevens R, Jorgensen K, Plummer AP. 1978.   Antelope bitterbrush: an important wildland shrub. Pub. 78-12. Salt Lake City: Utah State Division of Wildlife Resources. 48 p.

Hideyuki I, Tsutomu H, Masateru M, Takashi Y, Mutsuo K, Harukuni T, Takuo O. 1995.   Tannins from *Cowania mexicana*, and their inhibitory effects on TPA-induced EBV activation. In: Brouillard R, Jay M, Scalbert A, eds. Polyphenols 94, Paris: Institut National de la Recherche Agronomique (INRA): 419–420.

Ito H, Miyake M, Nishitani E, Mori K, Hatano T, Okuda T, Konoshima T, Takasaki M, Kozuka M, Mukainaka T, Tokuda H, Nishino H, Yoshida T. 1999. Anti-tumor promoting activity of polyphenols from *Cowania mexicana* and *Coleogyne ramosissima*. Cancer Letters 143: 5–13.

Jabbes M. 2000.   Hybridization and its evolutionary consequences in *Purshia* and *Cowania* [dissertation]. Moscow, ID: University of Idaho. 185 p.

Krannitz PG. 1997a.   Variation in magnesium and nitrogen content in seeds of antelope bitterbrush (*Purshia tridentata* (Rosaceae)). American Midland Naturalist 138: 306–321.

Krannitz PG. 1997b.   Seed weight variability of antelope bitterbrush (*Purshia tridentata:* Rosaceae). American Journal of Botany 84: 1738–1742.

Kyle NE, Righetti TL. 1996.   Observations of shoots and roots from interspecific grafted rosaceous shrubs. Journal of Range Management 49: 350–354.

Landis TD, Simonich EJ. 1984.   Producing native plants as container seedlings. In: Murphy PM, ed. The challenge of producing native plants for the Intermountain area. Gen. Tech. Rep. INT-168. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 16–25.

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

McArthur ED, Stutz HC, Sanderson SC. 1983.   Taxonomy, distribution, and cytogenetics of *Purshia, Cowania*, and *Fallugia* (Rosoideae, Rosaceae). In: Tiedemann AR, Johnson KL, comps. Proceedings, Research and Management of Bitterbrush and Cliffrose in Western North America; 1982 April 13–15; Salt Lake City. Gen. Tech. Rep. INT-152. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 4–24.

McCarty EC, Price R. 1942. Growth and carbohydrate content of important mountain forage plants in central Utah as affected by clipping and grazing. Tech. Bull. 818. Washington, DC: USDA. 51 p.

Meyer SE. 1989. Warm pretreatment effects on antelope bitterbrush (*Purshia tridentata*) germination response to chilling. Northwest Science 63: 146–153.

Meyer SE. 2002. Unpublished data. Provo, UT: USDA Forest Service, Intermountain Research Station.

Meyer SE, Monsen SB. 1989. Seed germination biology of antelope bitterbrush (*Purshia tridentata*). In: Wallace A, McArthur ED, Haferkamp MR, comps. Proceedings, Symposium on Shrub Ecophysiology and Biotechnology; 1987 June 30–July 2; Logan, UT. Gen. Tech. Rep. INT-256. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 147–157.

Meyer SE, Kitchen SG, Wilson GR, Stevens R. 1988. Proposed rule for *Cowania mexicana*—cliffrose. Association of Official Seed Analysts Newsletter 63: 24–25.

Nakanishi T, Nishi M, Somekawa M, Murata H, Mizuno M, Iinuma M, Tanaka T, Murata J. 1994. Structures of new and known cyanoglucosides from a North American plant, *Purshia tridentata* DC. Chemical Pharmaceutical Bulletin 42:2251–2255.

Nelson DL. 1983. The occurrence and nature of *Actinorhizae* on *Cowania stansburiana* and other Rosaceae. In: Tiedemann AR, Johnson KL, comps. Proceedings, Research and Management of Bitterbrush and Cliffrose in Western North America; 1982 April 13–15; Salt Lake City. Gen. Tech. Rep. INT-152. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 225–239.

Ngugi KR, Powell J, Hinds FC, Olsen RA. 1992. Range animal diet composition in southcentral Wyoming. Journal of Range Management 45: 542–545.

Nord EC. 1965. Autecology of bitterbrush in California. Ecological Monographs 35: 307–334.

Pearson BO.1957. Bitterbrush seed dormancy broken with thiourea. Journal of Range Management 10: 41–42.

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.

Righetti TL, Chard CH, Munns DN. 1983. Opportunities and approaches for enhancing nitrogen fixation in *Purshia, Cowania* and *Fallugia*. In: Tiedemann AR, Johnson KL, comps. Proceedings, Research and Management of Bitterbrush and Cliffrose in Western North America; 1982 April 13–15; Salt Lake City. Gen. Tech. Rep. INT-152. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 214–224 .

Sargent CS. 1965. Manual of the trees of North America (exclusive of Mexico). 2 volumes; 2nd corr. ed. New York: Dover. 934 p.

Scholten GC. 1983. Bitterbrush management on the Boise wildllife management area. In: Tiedemann AR, Johnson KL, comps. Proceedings, Research and Management of Bitterbrush and Cliffrose in Western North America; 1982 April 13–15; Salt Lake City. Gen. Tech. Rep. INT-152. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 153–162.

Shaw N. 1984. Producing bareroot seedlings of native shrubs. In: Murphy PM, ed. The challenge of producing native plants for the intermountain area. Gen. Tech. Rep. INT-168. Ogden, UT: Forest Service, Intermountain Forest and Range Experiment Station: 6–15.

Shaw NL, Monsen SB. 1983. Phenology and growth habits of nine antelope bitterbrush, desert bitterbrush, stansbury cliffrose, and apache plume accessions. In: Tiedemann AR ,Johnson KL, comps. Proceedings, Research and Management of Bitterbrush and Cliffrose in Western North America; 1982 April 13–15; Salt Lake City. Gen. Tech. Rep. INT-152. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 55–69.

Shaw NL, Monsen SB. 1995. "Lassen" antelope bitterbrush. In: Roundy BA, comp. Proceedings, Wildland Shrub and Arid Land Restoration Symposium; 1993 October 19–21; Las Vegas, NV. Gen. Tech. Rep. INT-GTR-315. Ogden, UT: USDA Forest Service, Intermountain Research Station: 364–371.

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.

Stutz HC, Thomas KL. 1964. Hybridization and introgression in *Cowania* and *Purshia*. Evolution 18: 183–185.

Tew RK. 1983. Bitterbrush distribution and habitat classification on the Boise National Forest. In: Tiedemann AR, Johnson KL, comps. Proceedings, Research and Management of Bitterbrush and Cliffrose in Western North America; 1982 April 13–15; Salt Lake City. Gen. Tech. Rep. INT-152. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 32–36.

Vander Wall SB. 1994. Seed fate pathways of antelope bitterbrush: dispersal by seed-caching yellow pine chipmunks. Ecology 75: 1911–1926.

Vines RA. 1960. Trees, shrubs, and woody vines of the Southwest. Austin: University of Texas Press. 1104 p.

Weber GP, Weisner LE. 1980. Tetrazolium testing procedures for native shrubs and forbs. Journal of Seed Technology 5: 23–34.

Welsh SL, Atwood ND, Higgins LC, Goodrich S. 1987. A Utah flora. Great Basin Naturalist Mem. 9. Provo, Utah: Brigham Young University Press. 894 p.

Young JA, Evans RA. 1976. Stratification of bitterbrush seeds. Journal of Range Management 29: 421–425.

Young JA, Evans RA. 1981. Germination of seeds of antelope bitterbrush, desert bitterbrush, and cliffrose. Washington, DC: USDA Science and Education Administration. Agric. Res. Results W-17/January 1981. 39 p.

Young JA, Young CG. 1986. Collecting, processing, and germinating seeds of wildland plants. Portland, OR: Timber Press. 236 p.

Young JA, Wight JR, Mowbray JE. 1993. Field stratification of antelope bitterbrush seeds. Journal of Range Management 46: 325–330.

Rosaceae—Rose family

# *Pyrus* L.
## pear

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**Growth habit, occurrence, and use.** The pear genus—*Pyrus*—probably originated in the mountain regions of what is now western and southwestern China and evolved and spread eastward and westward. Throughout the world, 24 primary species are presently recognized (table 1). Pear species are not native to North or South America (Rehder 1986), although some species have naturalized here.

The common pear (*P. communis*), which is cultivated for its fruit, probably originated from complex hybridization of wild progenitors, the wild European pear, *P. korschinskyi* (synonym = *P. pyraster*), and *P. communis* var. *caucasica* in the region of the Caucasus Mountains (Westwood 2002). Fruits of the common pear are pyriform, although the fruits of its progenitors tend to be round. The astringent fruits of the snow pear and hybrids between the common pear and the snow pear have been used in Western Europe to produce the fermented cider-like beverage called "perry."

Pears have been cultivated in Asia for at least 3,000 years (Kikuchi 1946). The fruits of many pears cultivated in Asia tend to be round. Lombard and Westwood (1987) consider that the (Japanese or Chinese) sand pear was the first pear species domesticated for its edible fruit. The Ussuri pear, the other predominant Asian species, has small, round astringent fruits. Natural hybridization between these 2 wild species occurred in central China and selection for large fruited, edible types has been occurring for several thousand years.

Most modern Japanese and Korean pear cultivars are derived from the sand pear. The principle commercial pears in China are derived from 3 species—sand and Ussuri pears and the hybrid species *P.* × *bretschneideri,* which is also known as the "Chinese white pear" (Lombard and Westwood 1987; Teng and others 2002). Recent analysis of pear species using DNA markers such as simple sequence repeats (SSR) suggest that the Chinese white pear is closely related to both sand and Ussuri pears (Yamamoto and others 2002) and might be considered as a subspecies of sand pear (Teng and others 2002).

Several Asian species have fruits with the size and shape of a pea. The Japanese and Korean pea pears and the evergreen pear are considered by some to be varieties or subspecies of Callery pear (Rehder 1986; Yu 1979). The birchleaf pear has the smallest sized fruit of the pea pears.

The common pear has naturalized in the United States (Gill and Pogge 1974). The Ussuri pear, introduced from Asia about 1855, has been grown on the northern Great Plains in shelterbelt and environmental plantings and in New England. It has contributed genes for cold-hardiness and resistance to fire blight in pear breeding programs (Stushnoff and Garley 1982). Other traits inherent in this species include vigor, dense growth, attractive glossy foliage, and scarlet autumn leaf color. Pear cultivars adapted to warm winter areas have been derived from the Pashia pear of central Asia. The pendulous form of the willow-leaf pear makes it a unique ornamental landscape plant. Flowering ornamental selections of the Callery pear and the evergreen pear are widely planted as street trees in the United States. The use of the evergreen pear is limited to warm-winter areas such as California and the more southerly states. These species are often referred to as "flowering pears" in the urban landscape. The Callery pear has become naturalized in the eastern United States and is now considered a weed in some areas such as the Maryland suburbs of Washington, DC.

Pears are deciduous, rarely evergreen, sometimes thorny trees or shrubs. Their leaves are serrate, crenate, or entire; rarely lobed. The petioles are stipulate and the buds are involute, with imbricate scales.

**Flowering and fruiting.** Pear species are cross-compatible sexual diploids (x = 17). Individual genotypes are generally self-incompatible. The perfect flowers bloom on 2-year or older spurs, between March and April in the Northern Hemisphere and appear before or with the new leaves (table 2). The inflorescence consists of 6 to 8 flowers occurring in umbel-like racemes. Petals are white, or rarely pinkish with reflexed or spreading sepals, 20 to 30 pink, red,

**Table 1—** *Pyrus,* pear:   nomenclature, growth habit, and occurrence

| Scientific name & synonym(s) | Common name(s) | Growth habit | Range & extensions |
|---|---|---|---|
| **P. amygdaliformis Vill.**<br>*P. sinaica* Dom.-Cours. | **almond-leaf pear** | Shrub to small tree, 1–2 m | Mediterranean Europe & Asia Minor |
| **P. betulifolia Bunge** | **birch-leaf pear** | Large tree, 5–6 m | Central & N China |
| **P. calleryana Decne.** | **Callery pear,** pea pear, Chinese pea pear | Medium tree, 3–5 m | Central & S China |
| **P. communis L.**<br>*P. asiae-mediae* Popov;   *P. balansae* Decne<br>*P. boissieriana* Buhse;   *P. elata* Rubtzov<br>*P. medvendevii* Rubtzov | **common pear,** European pear, cultivated pear | Large broad pyramidal tree, 5–6 m | W to SE Europe, Turkey; in world-wide cultivation |
| **P. communis ssp. caucasica (Fed.) Browicz**<br>*P. caucasica* Fed. | **Caucasus pear** | Large tree, 5–6 m | SE Europe, Greece |
| **P. cordata Desv.** | **heart-leaf pear,** Plymouth pear | Shrub to small tree, 2–3 m | SW England, W France, Spain, & Portugal |
| **P. cossonii Rehder**<br>*P. longipes* Coss, S. Dur. | **Algerian pear** | Medium tree, 3–4 m | Algeria |
| **P. dimorphophylla Makino**<br>*P. calleryana* var.  *dimorphophylla* (Makino) Koidz | **Japanese pea pear** | Medium tree, 3–4 m | Japan |
| **P. elaeagrifolia Pall.**<br>*P. kotschyana* Boiss ex Deone | **elaeagnus-leaf pear** | Medium tree, 3–4 m | SE Europe, Russia, & Turkey |
| **P. fauriei C.K. Schneid.**<br>*P. calleryana* var. *fauriei* (Schneid.) Rehd. | **Korean pea pear** | Shrub to small tree, 1–2 m | Korea |
| **P. gharbiana Trab.** | — | Small tree, 1–2 m | Morocco & W Algeria |
| **P. glabra Boiss.** | — | Medium tree, 3–4 m | Iran |
| **P. koehnii C.K. Schneid** | **evergreen pear** | Small to medium tree, 1–3 m | Taiwan & SE China |
| **P. korshinskyi Litv.**<br>*P. pyraster* Burgsd.<br>*P. communis* var. pyraster | **wild European pear** | Tree to 15 m | Afghanistan; W Russia; Central Asia |
| **P. mamorensis Trab.** | **Mamor Mountain pear** | Small tree | Morocco |
| **P. nivalis Jacq.** | **snow pear,** perry pear | Thornless medium tree, 3–4 m | W Central & S Europe |
| **P. pashia Buch.-Ham. ex D.Don**<br>*P. kumaoni* Decne<br>*P. varoilosa* Wall ex G. Don.<br>*P. wilhelmii* C. Schneid. | **Pashia pear,** India wild pear | Medium tree, 3–4 m | Pakistan, India, & Nepal |
| **P. pseudopashia T.T. Yu** | **Kansu pear** | Tree | NW China (Yunnan & Guizhou) |
| **P. pyrifolia (Burm.f.) Nakai**<br>*P. serotina* Rehd. | **sand pear,** Japanese pear, Chinese pear | Medium to large tree, 3–5 m | China, Japan, Korea, & Taiwan |
| **P. regelii Rehder**<br>*P. heterophylla* Regel G.Schmalh | **Regel pear** | Shrub or tree to 1–2 m | S central Asia & Afghanistan |
| **P. salicifolia Poll.** | **willow-leaf pear** | Small tree, 1–2 m | NW Iran, Armenia, Turkey, & S Russia |
| **P. syriaca Boiss.** | **Syrian pear** | Small tree, 1–2 m | Middle East, SW Russia |
| **P. ussuriensis Maxim.;**   *P. lindleyi Rehd.*<br>*P. ovoidea* Rehd.<br>*P. sinensis* Lindley | **Ussuri[an] pear,** Harbin pear, Manchurian pear | Small to medium tree, 1–3 m | Siberia, N China, Korea, Mongolia |
| **P. xerophylla T.T. Yu** | — | Tree | N China |

**Sources:**    LHBH (1976), Bell (1991), Hedrick (1921), Lombard and Westwood (1987), Rehder (1986).

## Table 2—*Pyrus*, pear: flowering and fruiting dates*

| Species | Bloom season† | Ripening season‡ |
|---|---|---|
| *P. amygdaliformis* | M–ML | L |
| *P. betulifolia* | M–ML–L | L |
| *P. calleryana* | E–EM–M | L |
| *P. communis* (wild types) | EM–M–ML | EM–M–ML–L |
| *P. communis* (cultivars) | E–EM–M–ML–L | E–EM–M–ML–L |
| *P. cordata* | M–ML–L | ML–L |
| *P. cossonii* | M–ML–L | M–ML–L |
| *P. dimorphophylla* | E–M–ML | L |
| *P. elaeagrifolia* | EM–M–ML | ML |
| *P. fauriei* | EM–M–ML | ML–L |
| *P. gharbiana* | ML | ML |
| *P. glabra* | EM | M–ML |
| *P. hondoensis* | EM–M–ML | M–ML–L |
| *P. koehnei* | E–EM–M–ML | L |
| *P. korshinskyi* | EM–M–ML | EM–M–ML–L |
| *P. mamorensis* | ML | L |
| *P. nivalis* | ML | ML–L |
| *P. pashia* | E–EM–M–ML–L | L |
| *P. pyrifolia* (wild types) | EM–M | M–ML–L |
| *P. pyrifolia* (cultivars) | EM–M–ML | EM–M–ML–L |
| *P. regelii* | M–ML | ML |
| *P. salicifolia* | EM–M–ML | ML–L |
| *P. syriaca* | EM–M | ML–L |
| *P. ussuriensis* (wild types) | E–EM | EM–M–M– L |
| *P. ussuriensis* (cultivars) | E–EM–M | M–ML–L |

* Observations made at the USDA ARS National Clonal Germplasm Repository in Corvallis, OR, 1988 through 1994.
† Average full bloom: E = March 13–March 23, EM = March 24–April 2, M = April 3–April 7, ML = April 8–April 17, L = April 18–April 26.
‡ Average fruit ripening: E = before July 6, EM = July 6–August 8, M = August 9–August 25, ML = August 26–September 28, L = after September 28.

or purple anthers, 2 to 5 free styles that are closely constricted at the base, and 2 ovules per locule.

The fruit is a globose or pyriform pome with persistent or deciduous calyx. Most Asian species, with the exception of the Ussuri pear, have deciduous calyxes. The fruit of different species ranges from about 0.5 to 20 cm in length and are quite diverse (figure 1). The extracarpellary tissue, which comprises the bulk of the fruit flesh, may contain sclerenchyma, that is, stone cells. The ground-color of the fruit skin may change from green to yellow or red during maturation, and russeted lenticels may be prominent on some species. Environmental conditions, such as humidity, may cause russeting or browning of the maturing skin. The ripening season for cultivated pears in the Northern Hemisphere ranges from June through December (table 2). Fruit from some species can be eaten directly from the tree, whereas others may require a period of cold storage to ripen or soften the fruit before it can be eaten. Common pears growing wild in Russia are reported to be biennial producers (Al'benskii and Nikitin 1956).

**Collection of fruits; extraction and storage of seeds.**
The mature fruits can be picked from trees or some can be shaken to the ground. Seeds (figure 2) can be recovered by macerating the fruit, drying the pulp, and using a screen to extract the seeds. Small quantities of seeds can also be effectively removed by carefully transversely cutting fruit to expose the locules. Water can also be used to float immature seeds, flesh, and skin away from viable seeds, which sink. Each ripe fruit contains up to 10 smooth black (or nearly black) seeds, each with a thin layer of endosperm (Gill and Pogge 1974). The seeds can then be air-dried. Pear seed characteristics differ greatly by species (figure 3). The small-seeded species—*P. gharbiana,* from N. Africa, and the birch-leaf pear—contain more than 88,000 seeds/kg (40,000/lb). The largest seeded species—Regel, Syrian, and Mamor Mountain pears—contain 11,000 or fewer seeds/kg (5,000 or fewer/lb). The domesticated species contain about 22,000 to 26,000 seeds/kg (10,000 to 12,000/lb) (table 3). Pears are outcrossing species, so seedlings will not be identical to parental genotypes.

**Figure I**—*Pyrus,* pear:　fruit and seed of *P. ussuriensis,* Ussuri pear (**left**); seeds of *P. calleryana,* Callery pear (**right**).
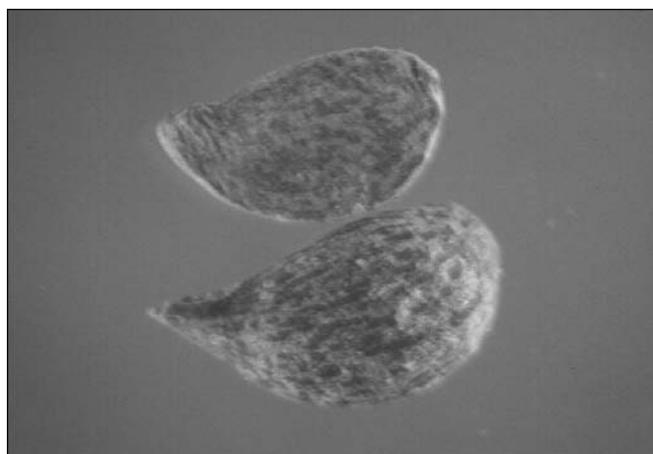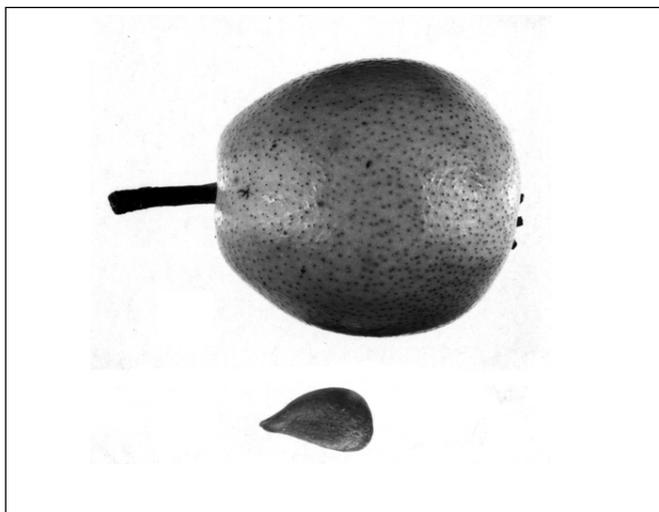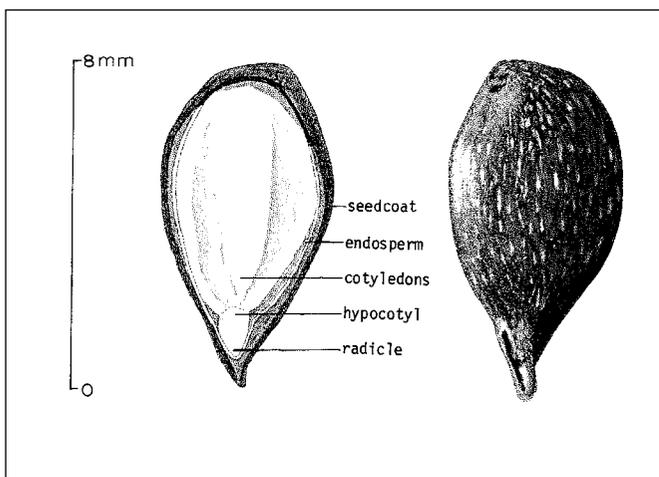




**Figure 3**—*Pyrus,* pear:　seeds of *P. cossonii,* Algerian pear (X); *P. amygdaliformis,* almond-leaf pear (X); *P. betulifolia,* birch-leaf pear (X); *P. calleryana,* Callery pear (X); *P. communis,* common pear (X); *P. cordata,* heart-leaf pear (X); *P. dimorphophylla,* Japanese pea pear (X); *P. elaeagrifolia,* elaeagnus-leaf pear (X); *P. fauriei,* Korean pea pear (X); *P. gharbiana* (X); *P. koehnii,* evergreen pear (X); *P. korshinskyi* wild European pear (X); *P. mamorensis,* Mamor Mountain pear (X); *P. nivalis,* snow pear (X); *P. pashia,* Pashia pear (X); *P. pseudopashia,* Kansu pear (X); *P. pyrifolia,* sand pear (X); *P. regelii,* Regel pear (X); *P. salicifolia,* willow-leaf pear (X); *P. syriaca,* Syrian pear (X); *P. ussuriensis,* Ussuri pear (X); *P. xerophylla* (X).

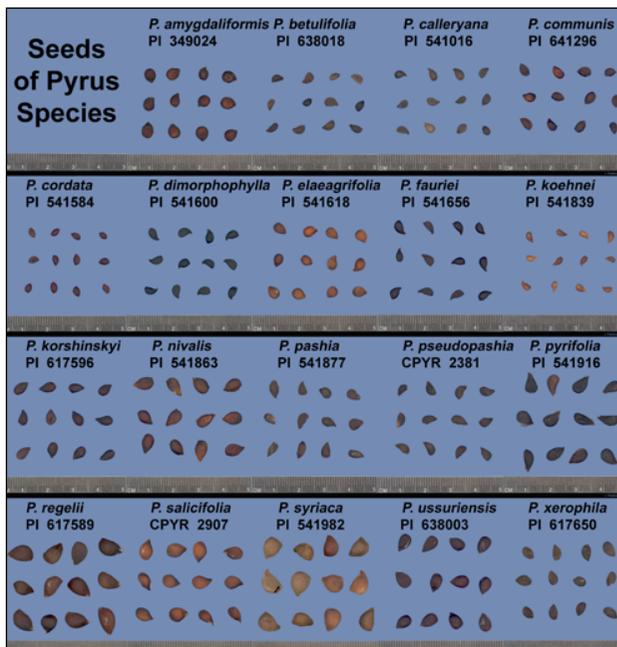**Figure 2**—*Pyrus communis* L., common pear:　longitudinal section through a seed.





**Germination.**　Seeds of pears extracted from fresh mature fruit in the fall or winter have dormant embryos that require stratification. Species differ in their stratification requirements (table 3). Seed preparation for germination includes a thorough washing and 1 day of water soaking prior to stratification. Seeds must be stratified for 60 to 100 days at about 4 °C. Germination is epigeal (figure 4) and may require from 5 to 30 days at 20 °C (Ellis and others 1985; Macdonald 1986). Because of the long stratification periods required for germination, official seed testing rules (AOSA 1993; ISTA 1993) recommend tetrazolium staining or the excised embryo test. For the excised embryo test,

### Table 3—*Pyrus*, pear:   seed properties

| Species | Chilling requirement (days) | Best chilling temp (°C) | Seed size Length (mm) | Seed size Width (mm) | L/W ratio | Seeds/wt /kg | Seeds/wt /lb |
|---|---|---|---|---|---|---|---|
| P. amygdaliforms | 25–27 | 7 | 6.7 | 4.2 | 1.60 | 24,000 | 11,000 |
| P. betulifolia | 55–86 | 4 | 4.0 | 2.3 | 1.74 | 90,000 | 41,000 |
| P. calleryana | 30–87 | 7 | 5.2 | 2.6 | 2.00 | 55,000 | 25,000 |
| P. communis ssp. caucasica | 130 | 4 | 7.7 | 4.2 | 1.83 | 40,000 | 18,000 |
| P. communis (domestic) | 90 | 4 | 8.4 | 4.8 | 1.77 | 22,000 | 10,000 |
| P. cordata | — | 4 | 4.6 | 2.6 | 1.77 | 86,000 | 39,000 |
| P. dimorphophylla | 65–88 | 7 | 5.2 | 2.8 | 1.86 | 77,000 | 35,000 |
| P. elaeagrifolia | 90–127 | 4 | 6.7 | 4.2 | 1.6 | 22,000 | 10,000 |
| P. fauriei | 38–88 | 7 | 4.7 | 2.9 | 1.62 | 57,000 | 26,000 |
| P. gharbiana | 60–78 | 7 | 4.6 | 2.4 | 1.92 | 99,000 | 45,000 |
| P. koehnii | — | 7 | 4.4 | 2.4 | 1.83 | 79,000 | 36,000 |
| P. mamorensis | 50–58 | 7 | 8.9 | 5.9 | 1.51 | 11,000 | 5,000 |
| P. nivalis | 110 | 4 | 10.0 | 4.3 | 2.32 | 18,000 | 8,000 |
| P. pashia | 15–43 | 10 | 6.5 | 3.1 | 2.10 | 55,000 | 25,000 |
| P. pyrifolia | 120–170 | 4 | 8.7 | 4.4 | 1.98 | 26,000 | 12,000 |
| P. regelii | — | — | 11.3 | 7.6 | 1.49 | 7,000 | 3,000 |
| P. salicifolia | — | 4 | 7.2 | 4.6 | 1.59 | 24,000 | 11,000 |
| P. syriaca | — | 7 | 9.3 | 6.2 | 1.50 | 9,000 | 4,000 |
| P. ussuriensis | 100 | 7 | 7.4 | 4.5 | 1.64 | 20,000 | 9,000 |

**Sources:**   Gill and Pogge (1974), Lombard and Westwood (1987), Rudolph (1949), Swingle (1939), Westwood and Bjornstad (1968), Yerkes (1930), Young and Young (1992)

**Figure 4**—*Pyrus communis*, common pear:   seedling development at 1, 2, 3, 6, and 12 days after germination.
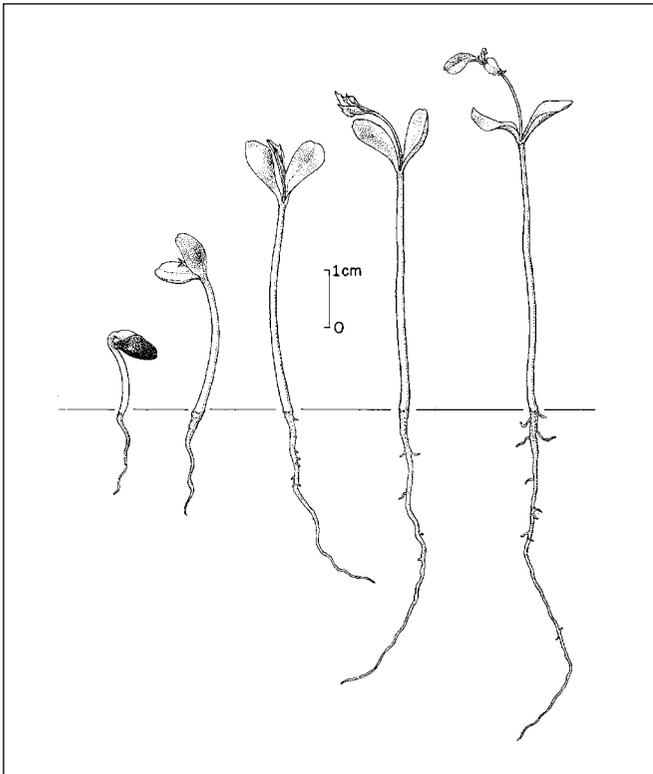


embryos should be germinated for 10 to 14 days at alternating temperatures of 18/22 °C (AOSA 1993).

**Nursery practice.**   Seeds are planted thickly, about 13 mm ($^1/_2$ in) deep in a seedbed, and allowed to grow for 1 season. The following spring, plants are dug, their roots and top are cut back, and they are transplanted to nursery rows. After a second season, the rootstock are of correct size for budding in the fall (Hartmann and others 1990). Seedlings of 1+0 nursery stock can be either field-planted or root-pruned at a depth of 15 to 20 cm (6 to 8 in) and transplanted for 1 year (Gill and Pogge 1974). Common pear seedlings may be subject to powdery mildew, which is caused by *Podosphaera leucotricha* (Ellis & Everh.) E.S. Salmon, and by root rots.

Cultivars are propagated by budding or grafting onto rootstocks. Bench-grafting dormant scions onto bareroot rootstocks is no longer common in large-scale nursery production. Nursery trees can be produced more efficiently by T-budding onto field-grown rootstocks in late summer when the bark is "slipping." Chip-budding is an alternative technique for seasons when the rootstock bark is not slipping (Frecon 1982). A whip-and-tongue graft or cleft-graft is commonly used when top-working growing trees in early spring. Scions can be grafted a few centimeters off the ground on a young rootstock, as in side-grafting, or multiple grafts can be placed higher up onto scaffold branches to convert an older tree over to a different cultivar, that is, top-working.

Seedlings of wild native species are used as rootstocks throughout the world (Lombard and Westwood 1987). In North America, seedlings of commercial cultivars of common pear such as 'Bartlett' or 'Winter Nelis' are grown for rootstocks. Seedlings of the Callery pear and birch-leaf pear are often used as rootstocks for Asian cultivars. Seedlings of the Ussuri pear may be used as rootstocks where extreme cold hardiness is needed. Pears are potentially graft-compatible with a number of other genera in the Maloideae subfamily, including serviceberry (*Amelanchier*), cotoneaster (*Cotoneaster*), hawthorn (*Crataegus*), apple (*Malus*), medlar (*Mespilus*), squaw-apple (*Peraphyllum*), mountain-ash (*Sorbus*), and others (Lombard and Westwood 1987; Postman 1992). The common quince (*Cydonia oblonga* Mill.) has traditionally been used as a dwarfing rootstock for edible European pears.

## References

Al'benskii AV, Nikitin PD, eds. 1956. Agrolesomeliortsiya. Ed. 3 Gos. izd. S-kh. Lit., Moskva. [Handbook of afforestation and soil amelioration. Transl. TT 66-51098, 1967. Springfield, VA: USDC CFSTI, 516 p.].

AOSA [Association of Official Seed Analysts]. 1993. Rules for testing seeds. Journal of Seed Technology 16(3): 1–113.

LHBH [Liberty Hyde Bailey Hortorium]. 1976. Hortus third: a concise dictionary of plants cultivated in the United States and Canada. New York: Macmillan. 1290 p.

Bell RL. 1991. Pears (*Pyrus*). In: Moore JN, Ballington JR Jr, eds. Genetic resources of temperate fruit and nut crops. Wageningen, The Netherlands: International Society for Horticultural Science: 657–697

Ellis RH, Hong TD, Roberts EH. 1985. Handbook of seed technology for genebanks. Volume 2, Compendium of specific germination and test recommendations. Rome: FAO International Board of Plant Genetic Resources.

Gill JD, Pogge FL. 1974. *Pyrus*, pear. In: Seeds of woody plants in the United States. Agriculture Handbook 450. Washington, DC: USDA Forest Service: 584–586.

Hartmann HT, Kester DE, Davies F. 1990. Plant propagation: principles and practices. 5th ed. Englewood Cliffs, NJ: Prentice Hall. 662 p.

Hedrick UP. 1921. The pears of New York. Geneva, NY: New York Agricultural Experiment Station. 636 p.

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

Kikuchi A. 1946. Speciation and taxonomy of Chinese pears [in Japanese]. Collected Records of Horticultural Research, Faculty of Agriculture, Kyoto University 3: 1–11.

Lombard PB, Westwood MN. 1987. Pear rootstocks. In: Rom RC, Carlson RF, eds. Rootstocks for fruit trees. New York: Wiley: 145–183.

Macdonald B. 1986. Practical woody plant propagation for nursery growers. Portland, OR: Timber Press. 660 p.

Postman JD. 1992. Graft compatibility of different pome fruit genera. Pomona 25(3):15–17.

Rehder A. 1986. Manual of cultivated trees and shrubs. 2nd ed, Portland, OR: Dioscorides Press: 401–406.

Rudolf PO. 1949. First the seed, then the tree. In: USDA Yearbook of Agriculture (1949): Trees: 127–135.

Stushnoff C, Garley B. 1982. Breeding for cold hardiness. In: van der Zwet T, Childers NF, eds. The pear. Gainesville, FL: Horticultural Publications: 189–205.

Swingle CF, comp. 1939. Seed propagation of trees, shrubs, and forbs for conservation planting. SCS-TP-27. Washington, DC: USDA Soil Conservation Service. 187p.

Teng Y, Tanabe K, Tamura F, Itai A. 2002. Genetic relationships of *Pyrus* species and cultivars native to east Asia revealed by randomly amplified polymorphic DNA markers. Journal of the American Society for Horticultural Science 127(2): 262-270.

Westwood MN. 2002. Personal communication. Corvallis, OR: Oregon State University.

Westwood MN, Bjornstad HO. 1968. Chilling requirements of dormant seeds of 14 pear species as related to their climatic adaptation. Proceedings of the American Society of Horticultural Science 92: 141–149.

Yamamoto T, Kimura T, Sawamura Y, Manabe T, Kotobuki K, Hayashi T, Ban Y, Matsuta N. 2002. Simple sequence repeats for genetic analysis in pear. Euphytica 124:129-137.

Yeo DY, Reed BM. 1995. Micropropagation of three *Pyrus* rootstocks. HortScience 30(3): 620–623.

Yerkes GE. 1930. Raising root stocks from seed in the United States. International Horticulture Congress Proceedings 9: 83–91.

Young JA, Young CG. 1992. Seeds of woody plants in North America. Rev. ed. Portland, OR: Dioscorides Press. 407 p.

Yu T. 1979. Taxonomy of the fruit tree in China [in Chinese]. Beijing: China Agriculture Press.