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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.

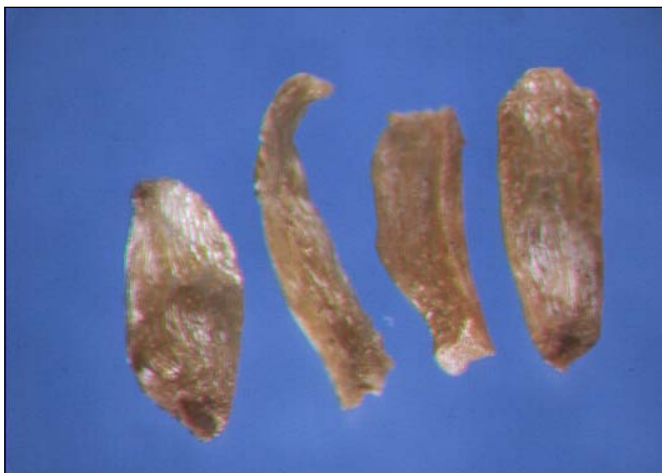
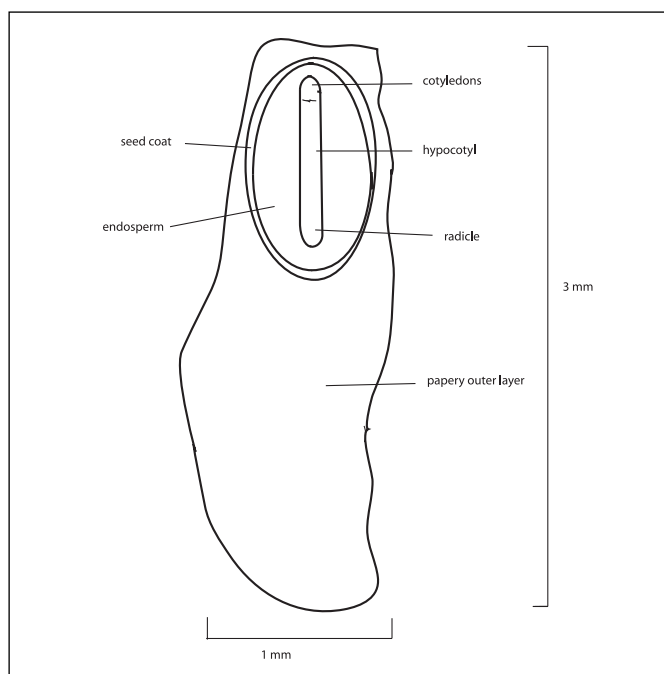


Figure 2—*Pieris floribunda*, mountain andromeda: longitudinal section of a seed.



the seeds germinate readily without pretreatment (Kruse 1987). Seeds do not require light for germination, but daily photoperiods as short as $\frac{1}{2}$ 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 $\frac{1}{2}$ 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 fluorescent lamps as the light source, which provided a photosynthetic photon flux (400 to 700 nm) of 69 $\mu\text{mol}/\text{m}^2/\text{sec}$ (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 ($\frac{1}{4}$ -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 practice is to fertilize seedlings at the first-true-leaf stage with a half-strength solution of a 15-45-5 (N:P₂O₅:K₂O) 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 vegetatively 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).

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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 piñons 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
<i>P. albicaulis</i> 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
<i>P. aristata</i> Engelm. <i>P. balfouriana</i> var. <i>aristata</i> (Engelm.) Engelm.	bristlecone pine, foxtail pine, hickory pine	Subalpine; E central California, Nevada, Utah, N Arizona; central Colorado & N New Mexico
<i>P. arizonica</i> Engelm. <i>P. ponderosa</i> var. <i>arizonica</i> (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
<i>P. armandii</i> Franch.	Armand pine	Mid-high elevations of mtns in central China to SW China, N Burma, E Tibet; Hainan, Taiwan; Japan (N Ryuku Islands)
<i>P. attenuata</i> Lemmon <i>P. tuberculata</i> Gord.	knobcone pine	Rocky slopes & ridges of Klamath Mtns, coastal ranges & Sierra Nevada in SW Oregon & California; Baja California Norte
<i>P. balfouriana</i> Grev. & Balf.	foxtail pine, Balfour pine	Subalpine California; central, S Klamath Mtns, S Sierra Nevada
<i>P. banksiana</i> Lamb. <i>P. divaricata</i> (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
<i>P. brutia</i> Tenore <i>P. halepensis</i> var. <i>brutia</i> (Ten.) Elwes & Henry	Calabrian pine	Crete, Cyprus, Lebanon, W Syria, Turkey to NE Greece, Black Sea; Caucasus Mtns; N Iraq
<i>P. canariensis</i> C. Smith	Canary Island pine, Canary pine	Dry slopes of Canary Islands (Hierro, La Palma, Tenerife, Gomera, & Gran Canaria), Spain
<i>P. caribaea</i> Morelet <i>P. bahamensis</i> Griseb. <i>P. hondurensis</i> Loock	Caribbean pine	W Bahamas; W Cuba, Isle of Pines; Caribbean Central America, Belize S to Nicaragua
<i>P. cembra</i> L. <i>P. montana</i> 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
<i>P. cembroides</i> Zucc.	Mexican piñon, 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
<i>P. clausa</i> (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
<i>P. contorta</i> var. <i>bolanderi</i> (Parl.) Vasey	Bolander pine	Coastal N California: acid podsol soils of Mendocino White Plains in Mendocino Co.
<i>P. contorta</i> var. <i>contorta</i> 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
<i>P. contorta</i> var. <i>latifolia</i> 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
<i>P. contorta</i> var. <i>murrayana</i> (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
<i>P. coulteri</i> D. Don <i>P. ponderosa</i> ssp. <i>coulteri</i> (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
<i>P. densiflora</i> 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
<i>P. echinata</i> 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
<i>P. edulis</i> Engelm. <i>P. cembroides</i> var. <i>edulis</i> (Engelm.) Voss	piñon, 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
<i>P. elliottii</i> var. <i>densa</i> Little & Dorman	South Florida slash pine	Sandy plains of central to S Florida, E & W Florida coasts; lower Florida Keys
<i>P. elliottii</i> var. <i>elliottii</i> Engelm. <i>P. caribaeu</i> 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
<i>P. engelmannii</i> Carr. <i>P. latifolia</i> Sarg. <i>P. apachea</i> Lemmon	Apache pine , Arizona longleaf pine	Sierra Madre Occidental; Aguascalientes, SW Zacatecas N through W Mexico into SE Arizona, SW corner of New Mexico
<i>P. flexilis</i> 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
<i>P. gerardiana</i> D. Don <i>P. aucklandii</i> Lodd. <i>P. chilgoza</i> Ehh.	chilgoza pine , Gerard pine	Himalayas, dry valleys; E Afghanistan, contiguous N Pakistan, N India
<i>P. glabra</i> Walt.	spruce pine , cedar pine, bottom white pine	Coastal plains of E South Carolina to N Florida, W to S Mississippi, SE Louisiana
<i>P. halepensis</i> P. Mill. <i>P. alepensis</i> Poir.	Aleppo pine , 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
<i>P. heldreichii</i> Christ <i>P. heldreichii</i> var. <i>leucodermis</i> (Ant.) Markgr. <i>P. eucodermis</i> Ant. <i>P. nigra</i> var. <i>leucodermis</i> (Ant.) Rehd.	Heldreich pine , Balkan pine, Bosnian pine, graybark pine	High elevations of Balkan Peninsula, Albania to SW Yugoslavia, extreme N Greece, SW to SW Bulgaria, & SW Italy
<i>P. jeffreyi</i> Grev. & Balf. <i>P. ponderosa</i> var. <i>jeffreyi</i> (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
<i>P. kesiya</i> Royle & Gordon <i>P. khasya</i> Royle <i>P. insularis</i> Endl.	Khasi pine , Benguet pine	High elevations of E India, SE Tibet, Burma, SW Yunnan to N Thailand, Laos, S Vietnam, W Luzon, Philippines
<i>P. koraiensis</i> Sieb. & Zucc.	Korean pine , cedar pine	Mtns of South Korea to North Korea through E Manchuria, S Chabarovsk, Siberia; Japan (central Honshu & Shikoku)
<i>P. lambertiana</i> Dougl.	sugar pine , <i>piño real</i>	Sierra Nevada–Cascade & Klamath Mtns, coastal & transverse–peninsular ranges of California to N Oregon, Baja California Norte, W Nevada
<i>P. leiophylla</i> var. <i>chihuahuana</i> (Engelm.) Shaw <i>P. chihuahuana</i> Engelm.	Chihuahua pine , yellow pine, <i>piño real</i>	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
<i>P. merkusii</i> Junghuhn & Vriese ex Vriese	Merkus pine , Tenasserim pine	Mtns, low elevations of SE Burma, N Thailand, Cambodia, Laos, Vietnam, Hainan, N Sumatra, Philippines (W Luzon & N Mindoro)
<i>P. monophylla</i> Torr. & Frém. <i>P. cembroides</i> var. <i>monophylla</i> (Torr. & Frém.) Voss	singleleaf piñon , nut pine, pinyon, piñon	Semiarid mtns of NW Arizona, W Utah to SE Idaho, W through Nevada to E California, S to Baja California Norte
<i>P. monticola</i> Dougl. ex D. Don	western white pine , Idaho white pine, 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
<i>P. mugo</i> Turra <i>P. montana</i> 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
<i>P. muricata</i> D. Don <i>P. remorata</i> Mason	bishop pine , prickle-cone pine, Santa Cruz Island pine	Coastal mtns; California Coast Ranges, Santa Rosa & Santa Cruz Islands; Baja California Norte, Cedros Island, Mexico
<i>P. nigra</i> Arnold <i>P. nigra</i> var. <i>austriaca</i> (Hoess) Aschers. & Graebn.	Austrian pine , 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
<i>P. palustris</i> P. Mill. <i>P. australis</i> Michx. f.	longleaf pine, southern pine, longstraw pine	Coastal plains of SE Virginia to central Florida, W to N Louisiana, E Texas
<i>P. parviflora</i> Sieb. & Zucc. <i>P. pentaphylla</i> Mayr <i>P. himekomatsu</i> Miyabe & Kudo	Japanese white pine	Mtns of Japan (Kyushu, Tsushima, Shikoku, Honshu, Sado, & S Hokkaido); South Korea (Ullung Island)
<i>P. patula</i> Schiede ex Schtdl. & Cham.	Mexican weeping pine	Sierra Madre Oriental, Mexico; central Oaxaca N to Querétaro, SW Tamaulipas; Guatemala, El Salvador, Honduras, Nicaragua
<i>P. peuce</i> Griseb. <i>P. excelsa</i> var. <i>peuce</i> (Griseb.) Beissn.	Balkan pine, Macedonian pine, Greek stone pine	High elevations of Balkan Peninsula: SW Yugoslavia, E Albania, SW Bulgaria, extreme N Greece
<i>P. pinaster</i> Aiton <i>P. maritima</i> Poir.	maritime pine, cluster pine, pinaster pine	SW Europe & Mediterranean Basin: Iberian Peninsula, SE France + Corsica; W Italy + Sardinia & Pantalleria; Morocco, coastal E Algeria
<i>P. pinea</i> L.	Italian stone pine, umbrella pine, stone pine	Iberian Peninsula & Mediterranean Coast of France, W Italy, Albania, Greece, Turkey; NE Turkey; Lebanon; Ibiza, Majorca; Sardinia, Sicily; Corfu, Crete, & Cyprus
<i>P. ponderosa</i> var. <i>ponderosa</i> P. & C. Lawson.	Pacific ponderosa pine, western yellow pine, bull pine, rock pine, blackjack pine	Sierra Nevada–Cascade Mtns, coastal & transverse– peninsular ranges, Klamath Mtns; California to W Nevada, N through Oregon, Washington, Idaho, W Montana, to S British Columbia
<i>P. ponderosa</i> var. <i>scopulorum</i> Engelm.	Rocky Mountain ponderosa pine, western yellow pine, blackjack pine	Rocky Mtns, Sierra Madre Oriental; Montana, SW North Dakota S in Wyoming, Colorado, New Mexico, trans–Pecos Texas to Coahuila, San Luis Potosi; E to central Nebraska; W in Utah, Arizona to Nevada
<i>P. pumila</i> Regel <i>P. cembra</i> var. <i>pumila</i> Pall.	Japanese stone pine, dwarf Siberian pine	NE Asia; E Siberia, Lake Baikal, Lena River regions E to Bering Sea & Sea of Okhotsk; N Mongolia; E Manchuria to South Korea; Sakhalin; Kamchatka, Kuril Islands to central Honshu, Japan
<i>P. pungens</i> Lamb.	Table Mountain pine, hickory pine, mountain pine, prickly pine	Appalachian Mtns of SW Pennsylvania, W Maryland through E West Virginia, W Virginia to E Tennessee, W North Carolina, extreme NE Georgia
<i>P. quadrifolia</i> Parl. ex Sudworth	Parry piñon, nut pine, pinyon	Semiarid, low elevations of San Jacinto Mtns, SW California, S to Sierra San Pedro Mártir, Baja
<i>P. radiata</i> D. Don <i>P. insignis</i> Dougl.	Monterey pine, radiata pine, insignis pine	Coastal central California, in Año Nuevo Point, Monterey, & Cambria areas; Cedros Island & N Guadalupe Island, Mexico
<i>P. resinosa</i> Soland.	red pine, Norway pine, hard pine, pitch pine	Great Lakes region, Appalachian Mtns; SE Manitoba E to Nova Scotia, N Newfoundland; S to Wisconsin, N Illinois, Pennsylvania, New Jersey; NE West Virginia
<i>P. rigida</i> P. Mill.	pitch pine, hard pine, bull pine	Appalachian Mtns in N Georgia, Kentucky, E Tennessee N through Pennsylvania, Delaware to SE Ontario, & central Maine
<i>P. roxburghii</i> Sarg. <i>P. longifolia</i> Roxb.	Chir pine, longleaf Indian pine	Himalayas, monsoon belt; N Pakistan E through N India, Nepal, Sikkim, Bhutan
<i>P. sabiniana</i> Dougl. ex Dougl.	Digger pine, bull pine, gray pine	Dry slopes, low-mid elevations; California, in S Klamath Mtns, coastal ranges, Cascade Mtns–Sierra Nevada
<i>P. serotina</i> Michx. <i>P. rigida</i> var. <i>serotina</i> (Michx.) Clausen	pond pine, marsh bay pine, pocosin pine	SE US, coastal plains of central & N Florida N to lower New Jersey, W to central & SE Alabama
<i>P. sibirica</i> Du Tour <i>P. cembra</i> var. <i>sibirica</i> Loud.	Siberian stone pine	Ural Mtns of Russia, E across central Siberia to Stanovoy Mtns, S through Sayan Mtns, Lake Baikal region to N Mongolia
<i>P. strobiformis</i> Engelm. <i>P. flexilis</i> var. <i>reflexa</i> Engelm. <i>P. reflexa</i> (Engelm.) Engelm. <i>P. ayacahuite</i> var. <i>brachyptera</i> Shaw	southwestern white pine, border limber pine, Mexican white pine	Sierra Madre Occidental & Oriental; S Rocky Mtns; Durango, central Mexico N to E Arizona, SW San Luis Potosi N to extreme W Texas, N through New Mexico to SW Colorado

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

Scientific name & synonym(s)	Common name(s)	Occurrence
<i>P. strobus</i> var. <i>chiapensis</i> Martínez <i>P. sylvestris</i> L.	Chiapas white pine Scots pine, Scotch pine	Mtns of S Mexico (Chiapis) & Guatemala 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 Coastal Plains, Piedmont; Delaware S to central Florida; W through Georgia, S Tennessee, Gulf Coast states to SE corner Oklahoma, E Texas Maritime Japan (Honshu to N Ryukyu Islands), South Korea (Cheju Island)
<i>P. taeda</i> L.	loblolly pine, Arkansas pine, North Carolina pine, oldfield pine	
<i>P. thunbergiana</i> Franco <i>P. thunbergii</i> Parl.	Japanese black pine	
<i>P. torreyana</i> Parry ex Carr.	Torrey pine, Soledad pine, Del Mar pine	Maritime S California (NE Santa Rosa Island) & coastal bluffs of San Diego County
<i>P. virginiana</i> 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
<i>P. wallichiana</i> A.B. Jacks. <i>P. excelsa</i> Wall. <i>P. griffithii</i> McClelland <i>P. nepalensis</i> 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
<i>P. washoensis</i> 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 (Callahan 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
<i>P. albicaulis</i>	6–33	1852	20–30	3–5
<i>P. aristata</i>	6–15	1861	20	102
<i>P. arizonica</i>	23–27	—	15–20	2–3
<i>P. armandii</i>	18–37	1895	20	—
<i>P. attenuata</i>	5–15	1847	5–8	1
<i>P. balfouriana</i>	11–18	1852	20	5–6
<i>P. banksiana</i>	17–30	1783, earlier	3–15	3–4
<i>P. brutia</i>	20–30	—	7–10	1
<i>P. canariensis</i>	30	—	15–20	3–4
<i>P. caribaea</i>	18–30	—	—	—
<i>P. cembra</i>	10–23	1746	25–30	6–10
<i>P. cembroides</i>	5–8	1830	—	5–8
<i>P. clausa</i>	5–24	1832	5	1–2
<i>P. contorta</i>				
var. <i>contorta</i>	6–12	1855	4–8	1
var. <i>latifolia</i>	8–46	1853	5–10	1
var. <i>murrayana</i>	15–30	—	4–8	1
<i>P. coulteri</i>	9–23	1832	8–20	3–6
<i>P. densiflora</i>	21–37	1854	20–30	2
<i>P. echinata</i>	2–30	1726	5–20	3–10
<i>P. edulis</i>	3–12	1848	25–75	2–5
<i>P. eliottii</i>				
var. <i>densa</i>	8–26	—	8–12	1–5
var. <i>elliottii</i>	24–30	—	7–10	3
<i>P. engelmannii</i>	15–21	—	28–30	3–4
<i>P. flexilis</i>	6–24	1861	20–40	2–4
<i>P. gerardiana</i>	15–24	1839	—	—
<i>P. glabra</i>	24–27	—	10	—
<i>P. halepensis</i>	15–24	1683	15–20	1
<i>P. heldreichii</i>	18–30	1865	—	—
<i>P. jeffreyi</i>	18–55	1853	8	2–4
<i>P. kesiya</i>	30–46	—	5–10	1
<i>P. koraiensis</i>	27–46	1861	15–40	1–5
<i>P. lambertiana</i>	30–69	1827	40–80	3–5
<i>P. leiophylla</i> var. <i>chihuahuana</i>	9–24	—	28–30	3–4
<i>P. merkusii</i>	18–30	—	10–20	1–2
<i>P. monophylla</i>	6–15	1848	20–25	1–2
<i>P. monticola</i>	27–61	1851	7–20	3–7
<i>P. mugo</i>	2–12	1779	10	1
<i>P. muricata</i>	12–27	1846	5–6	2–3
<i>P. nigra</i>	20–50	1759	15–40	2–5
<i>P. palustris</i>	24–37	1727	20	5–7
<i>P. patula</i>	18–34	—	12–15	—
<i>P. parviflora</i>	5–30	1861	—	4–5
<i>P. peuce</i>	10–30	1863	12–30	3–4
<i>P. pinaster</i>	27–37	1660, earlier	10–15	3–5
<i>P. pinea</i>	14–23	Long history	—	—
<i>P. ponderosa</i>				
var. <i>ponderosa</i>	18–70	1826	16–20	2–5
var. <i>scopulorum</i>	15–35	—	6–20	2–5
<i>P. pumila</i>	0.3–2.5	1807	—	—
<i>P. pungens</i>	9–18	1804	5	—
<i>P. quadrifolia</i>	5–9	1885	—	1–5
<i>P. radiata</i>	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
<i>P. resinosa</i>	21–46	1756	20–25	3–7
<i>P. rigida</i>	6–30	1759, earlier	3–4	4–9
<i>P. roxburghii</i>	46–55	1807	15–40	2–4
<i>P. sabiniana</i>	12–24	1832	10–25	2–4
<i>P. serotina</i>	12–24	1713	4–10	1
<i>P. sibirica</i>	40	1837	25–35	3–8
<i>P. strobiformis</i>	8–38	1840	15	3–4
<i>P. strobus</i>	24–67	1705	5–10	3–10
<i>P. sylvestris</i>	24–40	Long history	5–15	4–6
<i>P. taeda</i>	27–34	1713	5–10	3–13
<i>P. thunbergiana</i>	30–40	1855	6–40	—
<i>P. torreyana</i>	8–18	1853	12–18	1
<i>P. virginiana</i>	15–30	1739	5	1
<i>P. wallichiana</i>	15–46	1827	15–20	1–2
<i>P. washoensis</i>	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 Tulstrup (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 (Mastrogioseppe 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 piñon 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 densiflora—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—Piñon 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 elliotii—Slash pine has 2 distinct varieties (Lohrey and Kossuth 1990). Geographic variation in the widespread var. *elliotii* 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. *elliotii*, shows a grasslike seedling stage with crowded needles, and has heavy wood with wide summer growth rings (Kraus 1963; 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. *panicci* (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*—Chihuahuan 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 piñon 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. *cebnensis* (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 north-east 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 Heimbürger 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 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 Richter 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* (Sonderregger 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; piñon; 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
<i>P. albicaulis</i>	California	July	Aug–Sept	Not shed †
<i>P. aristata</i>	Arizona	July–Aug	Sept–Oct	Sept–Oct
<i>P. arizonica</i>	Arizona	May	Sept–Oct	Oct
<i>P. armandii</i>	California	Apr–May	Aug	Aug–Sept
<i>P. attenuata</i>	California	Apr	Jan–Feb	Closed cone‡
<i>P. balfouriana</i>	California	July–Aug	Sept–Oct	Sept–Oct
<i>P. banksiana</i>	Great Lakes	May–June	Sept	Sept§
<i>P. brutia</i>	California	Mar–May	Jan–Mar	Closed cone‡
<i>P. canariensis</i>	California	Apr–May	Sept	Sept–Oct
<i>P. caribaea</i>	Cuba	Jan–Feb	July–Aug	Sept
<i>P. cembra</i>	Germany	May	Aug–Oct	Not shed†
<i>P. cembroides</i>	California	May–June	Nov–Dec	Nov–Dec
<i>P. clausa</i>	Florida	Sept–Dec	Sept	Sept§
<i>P. contorta</i>				
var. <i>contorta</i>	California	May–June	Sept–Oct	Fall§
var. <i>latifolia</i>	Rocky Mtns	June–July	Aug–Sept	Sept–Oct §
var. <i>murrayana</i>	California	May–June	Sept–Oct	Sept–Oct
<i>P. coulteri</i>	California	May–June	Aug–Sept	Octē
<i>P. densiflora</i>	California	Apr	Aug–Sept	Sept–Oct
<i>P. echinata</i>	South Carolina	Mar–Apr	Oct–Nov	Oct–Nov
<i>P. edulis</i>	Arizona	June	Sept	Sept–Oct
<i>P. elliotii</i>				
var. <i>densa</i>	Florida	Jan–Apr	Aug–Sept	Sept–Nov
var. <i>elliotii</i>	Florida	Jan–Feb	Sept–Oct	Oct
<i>P. engelmannii</i>	Arizona	May	Nov–Dec	Nov–Feb
<i>P. flexilis</i>	California, Montana	June–July	Aug–Sept	Sept–Oct
<i>P. gerardiana</i>	India, California	May–June	Sept–Oct	Nov
<i>P. glabra</i>	Mississippi	Feb–Mar	Oct	Oct–Nov
<i>P. halepensis</i>	France	May–June	Sept	Fall §
<i>P. heldreichii</i>	Italy, California	May–July	Aug–Sept	Sept–Oct
<i>P. jeffreyi</i>	California	June–July	Aug–Sept	Sept–Oct
<i>P. kesiya</i>	Philippines	Jan–Mar	Oct–Jan	Feb–Mar
<i>P. koraiensis</i>	Japan	May–June	Sept	Oct
<i>P. lambertiana</i>	California	June–July	Aug–Sept	Aug–Oct
<i>P. leiophylla</i> var. <i>chihuahuana</i>	California	May–June	Nov*	Dec–Jan
<i>P. merkusii</i>	Thailand	Jan	Apr–Jun	May–Jul
<i>P. monophylla</i>	California, Nevada	May	Aug	Sept–Oct
<i>P. monticola</i>	Idaho	June–July	Aug	Aug–Sept
<i>P. mugo</i>	Europe	May–June	Oct	Nov–Dec
<i>P. muricata</i>	California	Apr–June	Sept	Midwinter §
<i>P. nigra</i>	Ontario, Canada	May–June	Sept–Nov	Oct–Nov
<i>P. palustris</i>	SE US	Feb–Mar	Sept–Oct	Oct–Nov
<i>P. parviflora</i>	Japan	May–June	Sept	Nov
<i>P. patula</i>	Mexico, California	Feb–Apr	Dec	Midwinter §
<i>P. peuce</i>	Europe	May	Fall	Fall
<i>P. pinaster</i>	Europe, California	Apr	Nov–Dec	Dec–Jan §
<i>P. pinea</i>	Europe	May–June	Late summer*	Late summer
<i>P. ponderosa</i>				
var. <i>ponderosa</i>	California	Apr–June	Aug–Sept	Aug–Sept
var. <i>scopulorum</i>	South Dakota, Colorado	May–June	Aug–Sept	Sept–Jan
<i>P. pumila</i>	Russia	July	—	Fall or not shed †
<i>P. pungens</i>	West Virginia, California	Mar–Apr	Fall	Fall §
<i>P. quadrifolia</i>	California	June	Sept	Sept–Oct
<i>P. radiata</i>	California	Jan–Feb	Nov	Midwinter §

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

Species	Location	Flowering	Cone ripening	Seed dispersal
<i>P. resinosa</i>	Great Lakes, California	Apr–June	Aug–Oct	Oct–Nov
<i>P. rigida</i>	New Jersey	May	Sept	Fall §
<i>P. roxburghii</i>	India	Feb–Apr	Winter	Apr–May§
<i>P. sabiniana</i>	California	Mar–Apr	Oct	Oct II
<i>P. serotina</i>	SE US	Mar–Apr	Sept	Spring §
<i>P. sibirica</i>	Russia	May	Aug–Sept	Not shed †
<i>P. strobiformis</i>	Arizona	June	Sep	Sept–Oct
<i>P. strobus</i>	NE US	May–June	Aug–Sept	Aug–Sept
<i>P. sylvestris</i>	Great Britain, California	May–June	Sept–Oct	Dec–Mar
<i>P. taeda</i>	SE US	Feb–Apr	Sept–Oct	Oct–Dec
<i>P. thunbergiana</i>	Japan, Long Island	Apr–May	Oct–Nov	Nov–Dec
<i>P. torreyana</i>	California	Feb–Mar	Jun–Jul*	Sept II
<i>P. virginiana</i>	E US	Mar–May	Sept–Nov	Oct–Nov §
<i>P. wallichiana</i>	India	Apr–June	Aug–Oct	Sept–Nov
<i>P. washoensis</i>	Nevada, California	July	Aug–Sept	Sept

Sources: Andreev (1925), Britton and Shafer (1908), Carlisle and Brown (1968), Coccozza (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), Looock (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 \times 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
<i>P. albicaulis</i>	Dark purple	Dull purple to brown
<i>P. aristata</i>	Green to brown-purple	Deep chocolate brown
<i>P. arizonica</i>	Green	Green-brown to dull yellowish buff or brown
<i>P. armandii</i>	Green	Yellowish brown
<i>P. attenuata</i>	Greenish brown	Lustrous tawny yellow to light brown
<i>P. balfouriana</i>	Deep purple	Dark brown, red-brown, or russet-brown
<i>P. banksiana</i>	Green	Lustrous tawny yellow to brown
<i>P. brutia</i>	Green	Yellow to reddish brown
<i>P. canariensis</i>	Yellow-green	Nut brown
<i>P. caribaea</i>	Green	Yellow-tan, light brown to reddish brown
<i>P. cembra</i>	Greenish violet	Purplish brown
<i>P. cembroides</i>	Green	Yellowish to reddish brown or lustrous brown
<i>P. clausa</i>	Green	Dark yellow-brown
<i>P. contorta</i>		
var. <i>contorta</i>	Purple-green	Lustrous light yellowish brown to yellow-brown
var. <i>latifolia</i>	Purple-green	Light brown
var. <i>murrayana</i>	Purple-green	Clay brown
<i>P. coulteri</i>	Green	Shiny brown to yellowish brown
<i>P. densiflora</i>	Green	Dull tawny yellow to brown
<i>P. echinata</i>	Green	Green to light brown or dull brown
<i>P. edulis</i>	Green	Light yellow-brown
<i>P. elliotii</i>		
var. <i>densa</i>	Green	Brown
var. <i>elliotii</i>	Green	Brown-yellow to brown
<i>P. engelmannii</i>	Brownish purple-green	Light brown
<i>P. flexilis</i>	Green	Lustrous yellowish brown to light brown
<i>P. gerardiana</i>	Green	Brown
<i>P. glabra</i>	Green	Green
<i>P. halepensis</i>	Green	Lustrous yellowish brown or reddish brown
<i>P. heldreichii</i>	Yellow-green	Yellowish or light brown to dull brown
<i>P. jeffreyi</i>	Dark purple to black	Dull purple to light brown
<i>P. kesiya</i>	Green	Bright brown to dark brown
<i>P. koraiensis</i>	Green	Yellowish brown
<i>P. lambertiana</i>	Green	Lustrous greenish brown to light brown
<i>P. leiophylla</i>		
var. <i>chihuahuana</i>	Green	Light brown
<i>P. merkusii</i>	Green	Light brown
<i>P. monophylla</i>	Green	Shiny deep russet brown
<i>P. monticola</i>	Green to purple-black	Yellowish beige-brown to reddish, dark brown
<i>P. mugo</i>	Violet purple	Lustrous tawny yellow to dark brown or cinnamon brown
<i>P. muricata</i>	Green to purple	Shiny light chestnut brown
<i>P. nigra</i>	Yellowish green	Shiny yellow brown to light brown
<i>P. palustris</i>	Green	Green to dull brown
<i>P. patula</i>	Green	Yellow ochre to nut brown
<i>P. parviflora</i>	Yellow-green	Leathery-woody brownish red to reddish brown
<i>P. peuce</i>	Green to yellow	Tawny yellow to light brown
<i>P. pinaster</i>	Purplish	Lustrous light brown
<i>P. pinea</i>	Green	Shiny nut brown
<i>P. ponderosa</i>		
var. <i>ponderosa</i>	Green to yellow-green, rarely purple	Lustrous brownish green or yellow-brown to russet brown
var. <i>scopulorum</i>	Green	Purplish brown
<i>P. pumila</i>	Green to violet-purple	Dull reddish or yellowish brown
<i>P. pungens</i>	Deep green to brown	Lustrous light brown
<i>P. quadrifolia</i>	Green	Yellowish or reddish brown
<i>P. radiata</i>	Green	Lustrous nut brown to light brown
<i>P. resinosa</i>	Green	Purple with reddish-brown scale tips to nut brown
<i>P. rigida</i>	Green	Lustrous brown or light yellow-brown
<i>P. roxburghii</i>	Green to brown	Light brown
<i>P. sabiniana</i>	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
<i>P. serotina</i>	Green to yellow	Lustrous light yellow to brown
<i>P. sibirica</i>	Green	Violet to light gray or brown
<i>P. strobiformis</i>	Green	Greenish brown to dark brown
<i>P. strobus</i>	Green	Yellow green to light brown
<i>P. sylvestris</i>	Green	Dull tawny yellow, greyish or dull brown, or cinnamon brown
<i>P. taeda</i>	Green	Green, shiny light or dull pale reddish brown
<i>P. thunbergiana</i>	Deep lustrous purple	Nut brown or reddish brown
<i>P. torreyana</i>	Green to dark violet	Shiny deep chestnut brown to chocolate brown
<i>P. virginiana</i>	Green	Lustrous dark purple to reddish and dark brown
<i>P. wallichiana</i>	Green	Tawny yellow to light brown
<i>P. washoensis</i>	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), Looock (1950), Luckhoff (1964), McIntyre (1929), McLemore (1961a&b), Pravdin (1963), Rehder (1940), Sargent (1965), Sudworth (1908), Troup (1921), Vahlenberg (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 piñon (**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 piñon (**upper left**); *P. arizonica*, Arizona pine (**upper center**); *P. ponderosa* var. *scopulorum*, 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. strobiformis*, southwestern white pine (**bottom left**); *P. sylvestris*, Scots pine (**bottom center**); *P. virginiana*, Virginia pine (**bottom right**).



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 piñon; *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*, piñon; *P. elliotii* 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 piñon.



pinus, 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 piñon. **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. × sandergergeri*, Sandergerger 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.

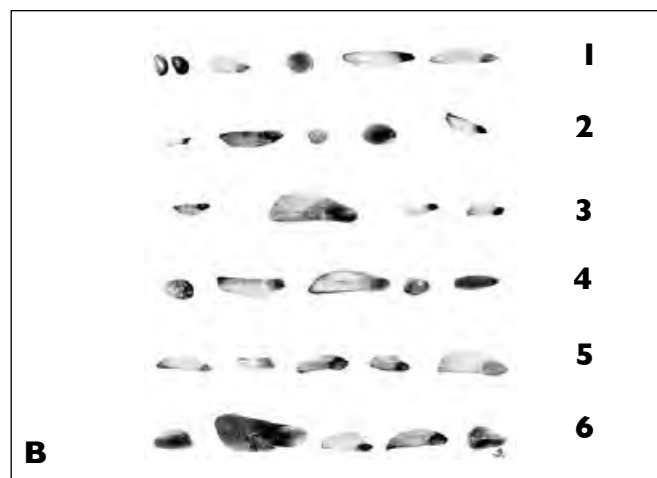
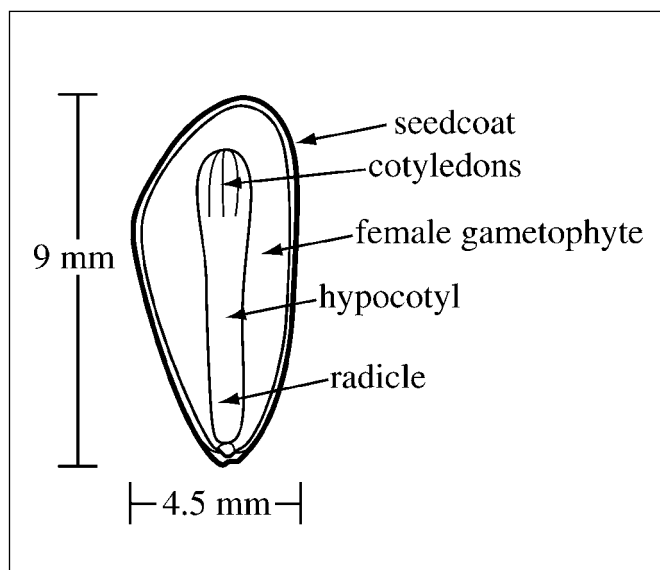


Figure 3—*Pinus ponderosa*, ponderosa pine: longitudinal section through a mature seed.



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, singleleaf, and Parry piñons 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 †
<i>P. aristata</i>	0.59–.80	Kerosene
<i>P. arizonica</i>	.88–.97	—
<i>P. contorta</i> var. <i>latifolia</i>	.43–.89	—
<i>P. densiflora</i>	1.10	—
<i>P. echinata</i>	.88	SAE 20 oil ‡
<i>P. edulis</i>	.80–.86	Kerosene
<i>P. elliotii</i>		
var. <i>densa</i>	<.89	SAE 20 oil
var. <i>elliottii</i>	<.95	SAE 20 oil
<i>P. glabra</i>	.88	SAE 20 oil
<i>P. jeffreyi</i>	.81–.86	SAE 30 oil
<i>P. lambertiana</i>	.70–.80	Kerosene
<i>P. merkusii</i>	1.00	—
<i>P. palustris</i>	.80–.89	SAE 20 oil
<i>P. ponderosa</i>		
var. <i>ponderosa</i>	.80–.89	Kerosene
	.84–.86	SAE 30 oil
var. <i>scopulorum</i>	<.85–.86	Kerosene
<i>P. radiata</i>	<1.00	Water
<i>P. resinosa</i>	.80–.94	Kerosene §
<i>P. serotina</i>	.88	—
<i>P. strobiformis</i>	.85–.95	95% ethanol
<i>P. strobus</i>	.90–.97	Linseed oil
<i>P. sylvestris</i>	.88–1.00	—
<i>P. taeda</i>	.88–.90	SAE 20 oil‡
<i>P. virginiana</i>	<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

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-

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).

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

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

Species	Cone processing schedule*				Seed storage (yr) [†]
	Boiling water dip (sec)	Air-drying (day)	Kiln-drying (hr)	Kiln temp (°C)	
<i>P. pinea</i>	—	—	—	—	18
<i>P. ponderosa</i>					
var. <i>ponderosa</i>	0	—	3	49	18
	0	4–12	0	—	—
var. <i>scopulorum</i>	0	—	2	74	>15
	0	4–12	0	—	—
<i>P. pumila</i> ‡	—	—	—	—	—
<i>P. pungens</i>	0	—	72	49	9
	0	30	0	—	—
<i>P. quadrifolia</i> §	0	2–8	0	—	—
<i>P. radiata</i>	60–120	0	48–72	49	21
	60–120	3–7	0	—	—
<i>P. resinosa</i>	0	—	13–20	54	30
<i>P. rigida</i> ¶	—	—	—	—	11
<i>P. roxburghii</i>	0	—	—	—	>4
<i>P. sabiniana</i>	0	—	48	49	5
<i>P. serotina</i>	0	—	48	41	—
<i>P. sibirica</i> ‡	—	—	—	—	>2
<i>P. strobiformis</i>	0	14	0	—	—
<i>P. strobus</i>	0	—	15–20	54	10
<i>P. sylvestris</i>	0	—	10–16	49	15
	0	3–7	0	—	—
<i>P. taeda</i>	0	—	48	41	>9
<i>P. thunbergiana</i>	0–30	5–20	0	—	11
<i>P. torreyana</i>	0	5–20	0	—	6
<i>P. virginiana</i>	0	—	2	77	>5
<i>P. washoensis</i>	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 piñon and singleleaf and Parry piñons, 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
<i>P. brutia</i>	Water
<i>P. coulteri</i>	Water
<i>P. echinata</i>	95% ethanol
<i>P. echinata</i>	Water
<i>P. elliotii</i> var. <i>elliottii</i>	Water
<i>P. glabra</i>	95% ethanol
<i>P. halepensis</i>	95% ethanol
<i>P. nigra</i>	95% ethanol
<i>P. palustris</i>	Pentane
<i>P. pinaster</i>	95% ethanol
<i>P. pinea</i>	Water
<i>P. sabiniana</i>	Water
<i>P. strobus</i>	100% ethanol
<i>P. sylvestris</i>	Petroleum ether
<i>P. taeda</i>	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	
<i>P. albicaulis</i>	Idaho	—	—	—	—	4.8–6.6	2.2–3.0	5.7	2.6	3
<i>P. aristata</i>	Arizona	40	0.6	1.42	1.1	39–42	17–19	40	18	4
<i>P. arizonica</i>	Arizona	9–23	.14–.35	.90–1.3	.7–1.0	24–26	11–19	25	11	10
<i>P. armandii</i>	France	—	—	—	—	2.6–4.1	1.2–1.9	3.5	1.6	2
<i>P. attenuata</i>	California & Oregon	—	—	0.13	.1	33–71	15–32	56	25.4	6
<i>P. balfouriana</i>	California	—	—	—	—	31–49	14–22	37	17	3
<i>P. banksiana</i>	Great Lakes	10	.15	.26–.9	.2–.7	156–551	71–250	289	131	423
<i>P. brutia</i>	Europe	—	—	—	—	17–26	7.6–11.6	20.1	9.1	5
<i>P. canariensis</i>	South Africa	—	—	—	8.8–9.9	4.0–4.5	9.3	4.2	10	
<i>P. caribaea</i>	—	—	—	—	—	52–81	24–37	68.3	31	>10
<i>P. cembra</i>	Germany	—	—	—	—	3.5–5.1	1.6–2.3	4.4	2.0	>10
<i>P. cembroides</i>	—	—	—	—	—	1.4–4.6	0.6–2.1	2.4	1.1	5
<i>P. clausa</i>	Florida	35	.52	.77–1.2	.6–.9	143–187	65–85	165	75	>10
<i>P. contorta</i>										
var. <i>contorta</i>	California	—	—	.64–1.5	.5–1.2	245–364	111–165	298	135	28
var. <i>latifolia</i>	Montana to Colorado	8–10	.1–.15	.26–1.0	.2–.8	174–251	79–114	207	94	39
var. <i>murrayana</i>	California	5.5	.1	.26	.2	256–262	116–119	258	117	4
<i>P. coulteri</i>	California	22	.33	1.03	.8	2.6–3.5	1.2–1.6	3.1	1.4	8
<i>P. densiflora</i>	Japan	20	.3	.64–1.0	.5–.8	79–141	36–64	115	52	26
<i>P. echinata</i>	—	20–30	.3–.45	.52–1.4	.4–1.1	71–161	32–73	102	46	144
<i>P. edulis</i>	Arizona	28	.4	3.3	4.25	3.3–5.5	1.5–2.5	4.2	1.9	9
<i>P. elliotii</i>										
var. <i>densa</i>	S Florida	—	—	.64–1.3	.5–1.0	31–37	14–17	34	15	30
var. <i>elliotii</i>	—	10–20	.15–.3	.77–1.0	.6–.8	21–43	10–19	30	13	404
<i>P. engelmanni</i>	Arizona	11	.16	.52	.4	—	—	22	10	1
<i>P. flexilis</i>	—	—	—	—	—	7.1–15.0	3.2–6.8	10.8	10.0	44
<i>P. gerardiana</i>	India	—	—	—	—	2.4–2.9	1.1–1.3	2.4	4.9	10
<i>P. glabra</i>	Louisiana	—	—	.13–1.3	.1–1.3	88–115	40–52	101	1.1	8
<i>P. halepensis</i>	Italy	—	—	—	—	48–88	22–40	62	46	>10
<i>P. heldreichii</i>	—	—	—	—	—	35–71	16–32	46	28	18
<i>P. jeffreyi</i>	California	35	.52	1.2–2.6	.9–2.0	5.8–11.7	2.6–5.3	8.2	3.7	26
<i>P. keisya</i>	SE Asia	—	—	—	—	44–76	20–34	59.5	27	>5
<i>P. koraiensis</i>	Korea	—	—	—	—	1.6–2.0	0.7–0.9	1.8	3.7	3
<i>P. lambertiana</i>	California	37	.56	1.9–2.6	1.5–2.0	3.3–6.0	1.5–2.7	4.6	2.1	27
<i>P. leiophylla</i> var. <i>chihuahuana</i>	—	—	—	.90–1.2	.7–.9	—	—	88	40	>1
<i>P. merkussi</i>	—	—	—	—	—	28–59	13–27	40	18.2	11
<i>P. monophylla</i>	Nevada	—	—	2.2–6.0	1.7–4.7	2.3–2.6	1.0–1.2	2.4	1.1	2
<i>P. monticola</i>	Utah	10	.15	.4–1.03	.3–.8	31–71	14–32	59	27	>99
<i>P. mugo</i>	Germany	—	—	1.03	.8	126–201	57–91	152	69	10
<i>P. muricata</i>	California	4	—	.26	.2	86–112	40–50	103	46.8	3
<i>P. nigra</i>	—	20–40	.3–.6	.52–1.5	.4–1.2	31–86	14–39	57	26	>159
<i>P. palustris</i>	Louisiana	21	.32	1.03	.8	6.6–15.4	3–7	10.8	4.9	220
<i>P. parviflora</i>	—	—	—	—	—	6.8–10.1	3.1–4.6	8.6	3.9	>3
<i>P. patula</i>	South Africa & Mexico	—	—	—	—	88–132	40–60	116	53	>3
<i>P. peuce</i>	—	—	—	—	—	22–31	10–14	24	11	6
<i>P. pinaster</i>	—	35–55	.53–.82	—	—	15–29	7–13	22	10	16
<i>P. pinea</i>	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				Clean seeds (x1,000)/wt				Lot
		/cone wt		/cone vol		Range		Avg		
		g/kg	oz/lb	kg/hl	lb/bu	/kg	/lb	/kg	/lb	
<i>P. ponderosa</i>	—	20–70	.3–1.0	.8–2.6	.6–2.0	15–51	7–23	26	12	185
var. <i>ponderosa</i>	Black Hills	39	.6	1.93	1.5	22–34	10–15	29	13	74
var. <i>scopulorum</i>	—	—	—	—	—	—	—	24	11	11
<i>P. pumila</i>	West Virginia	30	.45	.52	.4	68–84	31–38	75	34	3
<i>P. pungens</i>	California	—	—	—	—	1.8–2.6	0.8–1.2	2.1	1.0	3
<i>P. quadrifolia</i>	California	9	.14	.39	.3	23–35	10–16	29	13	7
<i>P. radiata</i>	Lake States	10–20	1.5–3	.64–1.0	.5–.8	66–166	30–76	115	52	529
<i>P. resinosa</i>	Pennsylvania/ New York	20–30	.3–.45	1.03	.8	94–181	42–82	136	62	10
<i>P. rigida</i>	India	—	—	—	—	6.8–25	3–11	12	25	36
<i>P. roxburghii</i>	California	—	—	—	—	1.2–1.4	0.5–0.6	1.3	0.6	3
<i>P. sabiniana</i>	SE US	—	—	.52	.4	104–139	47–63	119	54	4
<i>P. serotina</i>	Siberia	—	—	—	—	3.5–4.6	1.6–2.1	4.0	1.8	>10
<i>P. sibirica</i>	Arizona	80	11.2	3.5	2.7	5.5–6.4	2.5–2.9	6.0	2.7	10
<i>P. strobiformis</i>	—	20–30	.3–.45	.4–2.2	.3–1.7	39–117	17.5–53	58	26	300
<i>P. strobus</i>	Europe, E US	20	.3	.5–0.8	.4–.6	74–245	33.8–111	165	75	>346
<i>P. sylvestris</i>	—	20–30	.3–.45	.8–1.7	.6–.63	27–58	12–26	40	18	652
<i>P. taeda</i>	Japan, Korea, NE US	—	—	.26–1.0	.2–.8	57–110	26–50	75.0	34	50
<i>P. thunbergiana</i>	California	—	—	—	—	8.8–17.6	.4–.8	11.0	0.5	7
<i>P. torreyana</i>	—	30	.45	.64–1.2	.5–.9	101–201	46–91	122	55	30
<i>P. virginiana</i>	India	—	—	—	—	16–23	7–10	20	9	163
<i>P. wallichiana</i>										

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
<i>P. muricata</i>	0	20–30
<i>P. nigra</i>	0	0–60
<i>P. palustris</i>	0	0–30
<i>P. parviflora</i> †	90	90
<i>P. patula</i>	60	60
<i>P. peuce</i> §	0–60	60–180
<i>P. pinaster</i> ‡	0	60
<i>P. pinea</i> ‡	0	0
<i>P. ponderosa</i>		
var. <i>ponderosa</i>	0	30–60
var. <i>scopulorum</i>	0	0–60
<i>P. pumila</i>	120–150	120–150
<i>P. pungens</i>	0	0
<i>P. quadrifolia</i>	0	0–30
<i>P. radiata</i>	0–7	7–20
<i>P. resinosa</i>	0	60
<i>P. rigida</i>	0	0–30
<i>P. roxburghii</i>	0	0
<i>P. sabiniana</i> II	60–120	60–120
<i>P. serotina</i>	0	0–30
<i>P. sibirica</i> †	60–90	60–90
<i>P. strobiformis</i>	60–120	60–120
<i>P. strobus</i>	30–60	60
<i>P. sylvestris</i>	0	15–90
<i>P. taeda</i>	30–60	30–60
<i>P. thunbergiana</i>	0	30–60
<i>P. torreyana</i>	30–90	30–90
<i>P. virginiana</i>	0–30	30
<i>P. wallichiana</i>	0–15	15–90
<i>P. washoensis</i>	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.

II 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	Germination test condition					Germinative energy			
		Daily light (hr)	Seed medium	Temp (°C)*		Days	Rate amt (%)	Time (days)	Total (mean %)	Samples
				Light	Dark					
<i>P. albicaulis</i>	+	8	A, P	30	20	28	—	—	—	—
	+	0	pe, s	21	10	365	—	—	30	2
<i>P. aristata</i>		0	A, P	30	20	14	—	—	—	—
		24	P	32	21	22	75	7	91	74
		0	pe, s	35	20	30	—	—	86	>7
<i>P. arizonica</i>		0	P, pl	—	24	20	52	10	75	8
<i>P. attenuata</i>	+	24	A, P	22	26	30	79	5	92	1
		8	s	30	20	120	69	10	85	4
<i>P. banksiana</i>		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
<i>P. canariensis</i>	+	0	A	—	20	28	58	20	74	9
		8	A	20	20	21	63	7	76	4
<i>P. caribaea</i>		>8	P	30	20	21	—	—	72	3
<i>P. cembra</i>	+	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
<i>P. cembroides</i>		0	B, P	—	20	28	—	—	—	—
<i>P. clausa</i>		8	K	20	20	21	86	14	90	19
		8	s + v	21	16–18	30	85	20	90	—
<i>P. contorta</i>										
var. <i>contorta</i>	+	>8	A, P, v	30	20	28	—	—	60	3
		0	pe, s	30	20	50	—	—	80	29
var. <i>latifolia</i>	+	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. <i>murrayana</i>		10	s	26	26	30	—	—	75	3
<i>P. coulteri</i>	+	0	P, s	30	20	28	—	—	—	—
	+	8	s, v	30	20	28	—	—	37	7
<i>P. densiflora</i>		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
<i>P. echinata</i>		>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
<i>P. edulis</i>	+	0	A	30	20	28	—	—	—	—
	+	0	P	32	21	16	80	7	96	4
<i>P. elliotii</i>										
var. <i>densa</i>		>8	s + v	22	22	32	30–79	7–11	32–82	30
		16	K	22	22	28	86	7	87	28
var. <i>elliotti</i>		>8	A, P	30	20	28	—	—	—	—
		16	K	22	22	26	80	10	89	392
	+	16	K	22	22	26	75	9	84	83
<i>P. engelmannii</i>		0	P	32	21	16	70	4	88	4
<i>P. flexilis</i>	+	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
<i>P. gerardiana</i>		0	A	—	21	30–60	—	—	47	2
<i>P. glabra</i>	+	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
<i>P. halepensis</i>		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	Germination test condition					Germinative energy			
		Daily light (hr)	Seed medium	Temp (°C)*		Days	Rate amt (%)	Time (days)	Total (mean %)	Samples
				Light	Dark					
<i>P. heldreichii</i>	+	8	A, P	30	20	28	—	—	—	—
	+	8	A	30	20	40	—	—	72	14
		—	A	—	21	40	—	—	69	1
<i>P. jeffreyi</i>	+	8	A, P, s	30	20	28	—	—	—	—
	+	24	P	22	26	30	95	5	99	1
		0	v	30	20	21	—	—	79	5
<i>P. kesiya</i>		8	A	30	20	28	82	14	86	1
<i>P. koraiensis</i>	+	0	s	30	20	60	14	25	18	1
	+	>8	P	30	20	28	—	—	85–95	4
<i>P. lambertiana</i>	+	0	P, s	30	20	28	—	—	—	—
	+	—	v	30	20	28	—	—	59	5
	+	24	P, s	22	26	30	49	21	55	1
<i>P. leiophylla</i> var. <i>chihuahuana</i>		0	pl	—	24	22	60	6	70	3
<i>P. merkusii</i>		8	A	30	20	21	—	—	59	1
		8	A	20	20	21	—	—	67	1
<i>P. monophylla</i>		24	pl	75	21	35	39–50	7	86–90	2
<i>P. monticola</i>	+	0	P, s	30	20	28	—	—	—	—
	+	8	pl + s	22	22	71	39	11	44	11
<i>P. mugo</i>		8	A, P	30	20	14–21	—	—	—	—
		0	A	—	20	30	25	10	45	30
		8	A	30	20	20	76	10	80	30
<i>P. muricata</i>		0	A	30	20	35	—	—	—	—
	+	0	v	30	20	21	—	—	38	5
	+	24	P	22–26	—	30	70	7	85	1
<i>P. nigra</i>		8	A, P	30	20	14	91	10	92	49
		0	A	30	20	30	54	10	86	49
<i>P. palustris</i>		16	P	20	20	21	—	—	—	—
		16	s + v	22	22	30	90	10	95	100
<i>P. parviflora</i>		0	P	22	18	10–14	—	—	—	—
	+	8	s	30	20	28	71	35	—	—
	+	>8	A	25	25	28	—	—	80	1
<i>P. peuce</i>	+	0	s	30	20	28	—	—	—	—
		0	A	20	22	30	—	—	69	4
<i>P. pinaster</i>		8	A	20	20	35	—	—	—	—
	+	8	A, P	20	20	28	41	7	79	8
	+	0	A	—	20	30	70	20	83	5
<i>P. pinea</i>	+	0	s	—	20	21	—	—	—	—
	+	8	A	20	20	21	30	7	81	4
		0	A	—	18	22	88	14	98	3
<i>P. ponderosa</i>										
var. <i>ponderosa</i>	+	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. <i>scopulorum</i>		16	K	22	22	30	84	11	86	4
		0	s	20	30	30–60	50	19	64	40
<i>P. pumila</i>	+	>8	A	30	20	21	—	—	77	9
<i>P. pungens</i>		0	pe + s	—	21–29	45–60	—	—	55	3
		0	pe, s	—	24	40	—	—	65	9
<i>P. quadrifolia</i>	+	24	A	22–26	—	30	46	9	69	1
<i>P. radiata</i>	+	8	A	30	20	28	—	—	—	—
		>8	P	20	20	25	16	7	81	9
		>8	v	30	20	28	—	—	67	15
<i>P. resinosa</i>		0	A, P	30	20	14	69	10	83	23
		0	s	30	20	30	25–75	7–25	75	551
<i>P. rigida</i>		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	Germination test condition					Germinative energy			
		Daily light (hr)	Seed medium	Temp (°C)*		Days	Rate amt (%)	Time (days)	Total (mean %)	Samples
				Light	Dark					
<i>P. roxburghii</i>		0	A	—	20–22	30	—	—	83	5
		0	s	—	—	30	79	10	81	135
<i>P. sabiniana</i>	+	0	s	—	22	30	—	—	76	3
	+	24	A	22–26	—	30	—	—	13	1
<i>P. serotina</i>		8	pl + s	22	22	21	90	10	73	1
<i>P. sibirica</i>	+	0	s	20	30	60	—	—	7	1
		0	A	20	22	>60	—	—	40	4
<i>P. strobiformis</i>		0	A	30	20	35	—	—	94	8
		0	pl	—	24	46	—	—	39	31
<i>P. strobus</i>	+	>8	A, P	30	20	21	—	—	—	—
	+	>8	K	30	20	40	33	8	100	20
	+	>8	K	22	22	40	—	—	93	28
<i>P. sylvestris</i>		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
<i>P. taeda</i>		>8	A, P	30	20	28	—	—	—	—
		16	pl + s	22	22	30	90	17	90	481
<i>P. thunbergiana</i>		>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
<i>P. torreyana</i>	+	0	pe, s	27	18	60	—	—	81	21
<i>P. virginiana</i>		>8	A	30	20	21	—	—	—	—
		>8	K	22	22	28	87	10	90	29
		0	pe, s	30	20	30	—	—	65	5
<i>P. wallichiana</i>		>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.

pinus, 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).

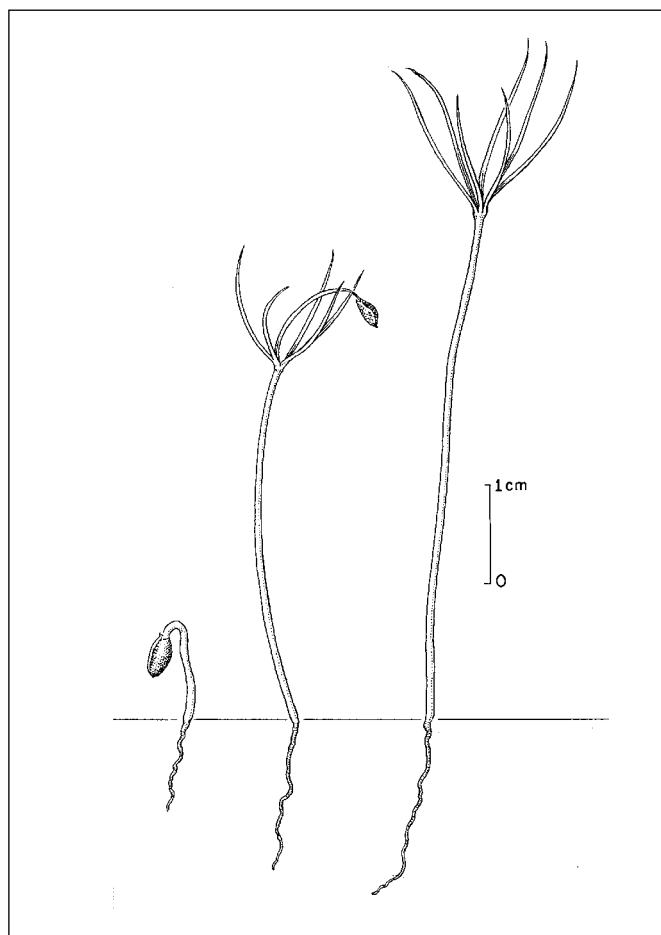
Seeds of some pines, including Swiss stone pine, Korean, Japanese white, and Siberian pine, may have immature embryos at the time of cone collection. Seed germination has been increased by placing seeds first in moist, warm stratification for several months and then in cold stratification for several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

Table 11—*Pinus*, pine: nursery practices

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

II 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/m² (15 to 75/ft²). 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 m² (2 to 20 oz/100 ft²) 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/m² (120/ft²), whereas another drill-sows 60 seeds/m (18/ft) in rows spaced 15 cm (6 in) apart to get 375 seedlings/m² (35/ft²). 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 piñon, 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 piñon, 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).

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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 panicle 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).

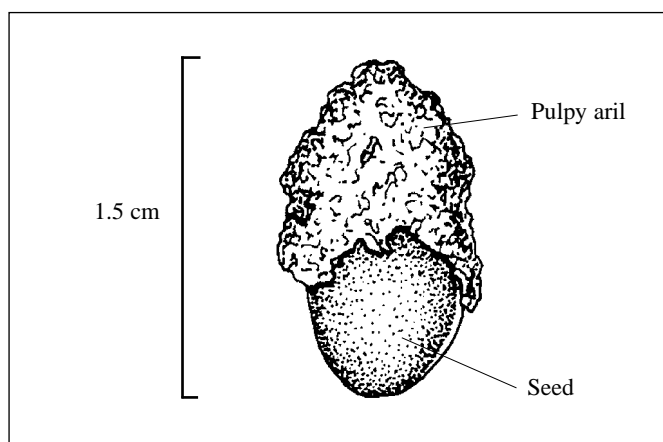
Collection, extraction, and storage. Legumes may be picked from the trees or from the ground, and air-dried in the sun. Seeds can be removed by hand-flailing or by use of a macerator, and pod fragments can be removed with screens. There are no long-term seed storage data for *guamúchil*, but these are 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).

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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 Schmidting 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 Schmidting 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
<i>P. occidentalis</i> L. <i>P. occidentalis</i> var. <i>Sarg. glabrata</i> (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
<i>P. orientalis</i> L.	oriental planetree	SE Europe, W Asia to India; planted in US as an ornamental
<i>P. racemosa</i> Nutt.	California sycamore , California planetree, western sycamore, <i>aliso</i>	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
<i>P. occidentalis</i>	E US	Mar–May	Sept–Nov	Jan–Apr
<i>P. orientalis</i>	NE US	May	Sept–Oct	—
<i>P. racemosa</i>	—	—	June–Aug	June–Dec

Sources: Bonner (1974), Wells and Schmidting (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 Schmidting 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 Schmidting 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**).

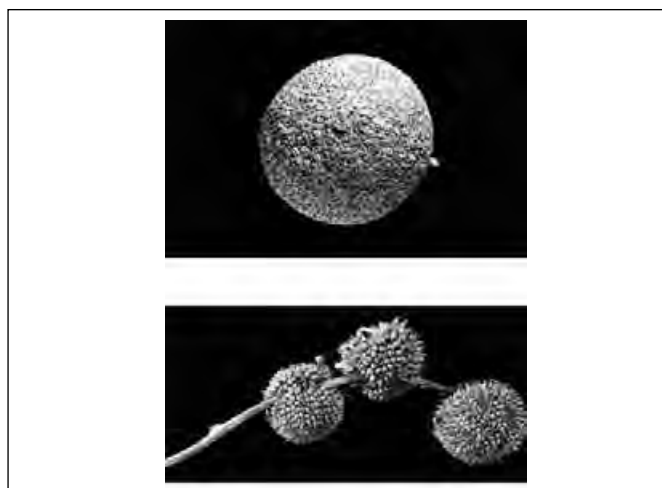


Figure 2—*Platanus*, sycamore: single achenes of *P. occidentalis*, American sycamore (**top**) and *P. racemosa*, California sycamore (**bottom**).

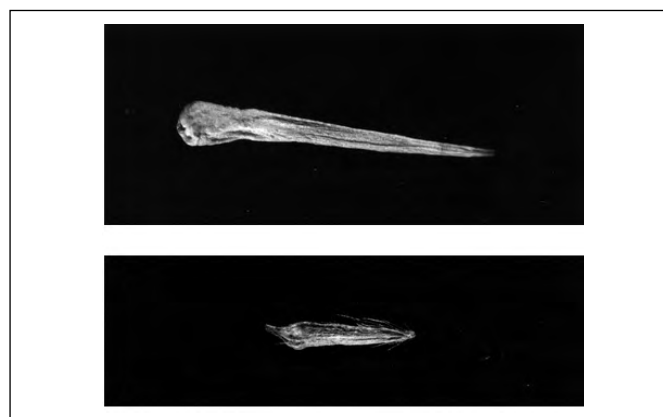
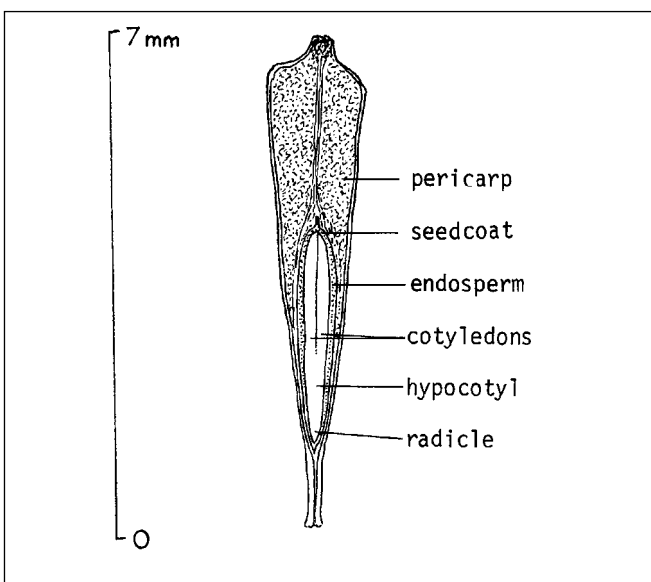


Figure 3—*Platanus occidentalis*, American sycamore: longitudinal section through a seed.



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 ($7/64 \times 3/4$ 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 example, 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 (GA₃) 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	Cleaned seeds/weight				Samples
		Range		Average		
		/kg	/lb	/kg	/lb	
<i>P. occidentalis</i>	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
<i>P. orientalis</i>	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).

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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.

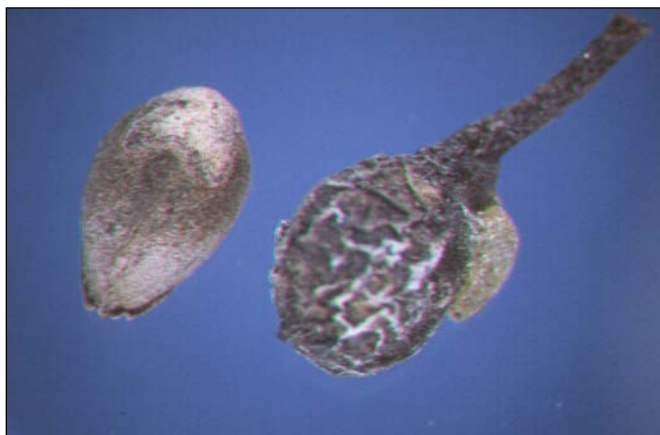
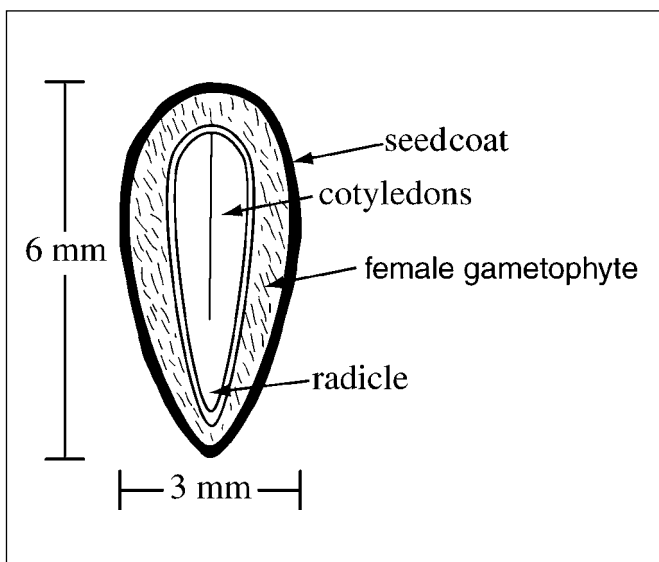


Figure 2—*Platycladus orientalis*, oriental arborvitae: longitudinal section through a seed.



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 $1\frac{1}{2}$ 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 ($\frac{1}{4}$ to $\frac{3}{8}$ 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).

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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
<i>P. x acuminata</i> Rydb. (pro sp.) <i>P. acuminata</i> var. <i>rehderi</i> (Sarg.)	lanceleaf cottonwood , lanceleaf poplar, smooth-bark cottonwood, & Andrews poplar	S Alberta, Montana, W North Dakota, Wyoming, W Nebraska, E Colorado, & New Mexico
<i>P. alba</i> L.	white poplar , abele	Central & S Europe to W Siberia & Central Asia
<i>P. angustifolia</i> James	narrowleaf cottonwood , narrowleaf poplar, black cottonwood, mountain cottonwood, <i>álamo</i>	S Saskatchewan & Alberta S to Arizona, W Nebraska, & trans-Pecos Texas; also in N Mexico (Chihuahua)
<i>P. balsamifera</i> L.	balsam poplar , tacamahac poplar, cottonwood, hackmatack, tacamahac	Alaska to Labrador, S to New York & Oregon
<i>P. balsamifera</i> L. spp. <i>trichocarpa</i> (Torr. & Gray ex Hook.) Brayshaw <i>P. trichocarpa</i> 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
<i>P. x canescens</i> (Ait.) Sm. (pro sp.) <i>P. deltoides</i> Bartr. ex Marsh.	gray poplar eastern cottonwood , eastern poplar	Europe & W Asia Quebec to North Dakota, S to Texas & Florida
<i>P. deltoides</i> Bartr. ex Marsh. ssp. <i>monilifera</i> (Ait.) <i>P. deltoides</i> var. <i>occidentalis</i> Ryb.	plains cottonwood , plains poplar, cottonwood, Texas cottonwood	SW Utah, Nevada, to N California, S to Arizona & New Mexico, NW Mexico
<i>P. deltoides</i> Bartr. ex Marsh. ssp. <i>wislizeni</i> S. Wats. <i>P. fremontii</i> var. <i>wislizeni</i> S. Wats.	Rio Grande cottonwood , Rio Grande poplar, cottonwood, valley cottonwood, Wislizenus cottonwood, <i>álamo</i>	S Colorado, S Utah, New Mexico, W Texas, & N Mexico
<i>P. euphratica</i> Olivier	Euphrates poplar , bahan, Gharab-Palk-Saf-Saf	Spain & W Morocco to Kenya, E to Central Asia
<i>P. fremontii</i> S. Wats.	Fremont cottonwood , Fremont poplar, cottonwood, Arizona cottonwood, Macdougal cottonwood, <i>álamo</i>	SW Utah, Nevada, to N California, S to Arizona & New Mexico, NW Mexico
<i>P. grandidentata</i> Michx.	bigtooth aspen , largetooth aspen, aspen, poplar, popple	Nova Scotia to NE North Dakota, S to Iowa & Pennsylvania, & along Appalachian Mtns to North Carolina
<i>P. heterophylla</i> 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
<i>P. laurifolia</i> Lebed.	laurel poplar	Siberia
<i>P. maximowiczii</i> A. Henry	Japanese poplar	NE Asia & Japan
<i>P. nigra</i> L.	black poplar , European black poplar	Europe & W Asia
<i>P. x petrowskiana</i> R.I. Schrod. ex Regel	Petrowsky poplar , Russian poplar	Europe
<i>P. sieboldii</i> Miq.	Siebold aspen , Japanese aspen	Japan
<i>P. simonii</i> Carriere	Simon poplar	NW China to Korea
<i>P. tremula</i> L.	European aspen , tremble, Zitterpappel	Europe, North Africa, & NE Asia
<i>P. tremuloides</i> Michx.	quaking aspen , quaking asp, aspen, golden aspen, mountain aspen, trembling aspen, Vancouver aspen poplar, popple, <i>álamo blanco</i>	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 (CO₂) 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
<i>P. x acuminata</i>	10.7–15.4 (18.5)	1898	5–10	1
<i>P. alba</i>	15.4–42.1	LC	10–15	—
<i>P. angustifolia</i>	10.7–15.4 (18.5)	1893	—	1
<i>P. balsamifera</i>	18.5–36.3	Before 1689	8–10	—
<i>P. balsamifera</i> spp. <i>trichocarpa</i>	15.4–61.5	1892	10	1
<i>P. x canescens</i>	29.2–30.8 (40)	LC	8–15	—
<i>P. deltoides</i>	24.6–58.5	Before 1750	10	1
spp. <i>monilifera</i>	12.3–30.8	1908	10	1
spp. <i>wislizeni</i>	2.3–30.8 (40)	1894	5	1
<i>P. fremontii</i>	15.4–30.8	1904	5–10	1
<i>P. grandidentata</i>	9.2–27.7 (30.8)	1772	10–20	4–5
<i>P. heterophylla</i>	24.6–27.3 (30.8)	1656	10	1
<i>P. laurifolia</i>	to 15.4	1830	8–10	—
<i>P. maximowiczii</i>	to 30.2	Before 1890	10	1
<i>P. nigra</i>	18.5–30.8	LC	8–12	1
<i>P. simonii</i>	to 12.3+	1862	10	—
<i>P. tremula</i>	21.5–38.5	LC	8–10	4.5
<i>P. tremuloides</i>	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
<i>P. x acuminata</i>	Nebraska	May	July
<i>P. alba</i>	Nebraska	Apr–May	Early June
	NE US	Apr–May	May–June
	S Michigan	Mar–Apr	May–June
<i>P. balsamifera</i>	Alberta	Late Apr	Early June–early July
	Lake States	Apr–May	May–June
	Interior Alaska	May–June	July
<i>P. balsamifera</i> spp. <i>trichocarpa</i>	Vancouver Island, British Columbia	Apr–June	Late May–mid-July
<i>P. x canescens</i>	Great Lakes region	Late Apr	Late May
<i>P. deltoides</i>	Lower Mississippi Valley	Early Mar–early Apr	Mid-May–late Aug
	NE US	Apr–early May	May–mid-June
spp. <i>monilifera</i>	Alberta	—	late June–early Aug
	Lincoln, Nebraska	Apr–May	June
spp. <i>wislizeni</i>	Albuquerque, New Mexico	Apr–May	June–July
<i>P. fremontii</i>	Central Arizona	mid-Feb–mid-Mar	Mar–Apr
<i>P. grandidentata</i>	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
<i>P. heterophylla</i>	Mississippi	Mar–May	Apr–July
<i>P. maximowiczii</i>	Rochester, New York	Late Apr	Aug
<i>P. nigra</i>	Rochester, New York	Apr	Late May
<i>P. tremula</i>	N Great Lakes region	Mid-Apr	Mid-May
<i>P. tremuloides</i>	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
<i>P. tremula</i>	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-existent.

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 bigtooth 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 bigtooth 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. × roulei* Boivin.

Figure 2—*Populus*, poplar: catkins consisting of mature but unopened capsules.—*P. deltoides* ssp. *monilifera*, plains cottonwood (**top**); *P. fremontii*, fremont cottonwood (**middle**); *P. fremontii* 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 ($1\frac{1}{2}$ 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	Seeds (millions)/weight							
	20-mesh		28-mesh		40-mesh		50-mesh	
	/g	/oz	/g	/oz	/g	/oz	/g	/oz
<i>P. alba</i>	5.09	2.31	8.89	4.03	19.71	8.94	—	—
<i>P. balsamifera</i>	—	—	7.90	3.58	8.69	3.94	—	—
spp. <i>trichocarpa</i>	2.71	1.23	4.54	2.06	—	—	—	—
<i>P. x canescens</i>	—	—	7.50	3.40	13.87	6.29	—	—
<i>P. deltoides</i>	2.93	1.33	4.92	2.23	—	—	—	—
<i>P. grandidentata</i>	—	—	—	—	21.52	9.76	39.58	17.95
<i>P. tremula</i>	—	—	—	—	17.46	7.92	—	—
<i>P. tremuloides</i>	—	—	13.19	5.98	18.46	8.37	23.62	10.70
Some hybrid crosses†								
<i>P. tremuloides</i> x <i>P. tremula</i>	—	—	10.61	4.81	17.68	8.02	38.68	17.54
<i>P. tremula</i> x <i>P. tremuloides</i>	—	—	18.43	8.36	44.10	20.00	—	—
<i>P. tremuloides</i> x <i>P. canescens</i>	—	—	—	—	16.27	7.38	—	—
<i>P. canescens</i> x <i>P. tremuloides</i>	—	—	7.74	3.51	13.38	6.07	35.57	16.13
<i>P. grandidentata</i> x <i>P. alba</i>	—	—	—	—	23.09	10.47	47.83	21.69
<i>P. alba</i> x <i>P. grandidentata</i>	4.81	2.18	10.52	4.77	15.79	7.16	35.10	15.92
<i>P. grandidentata</i> x <i>P. canescens</i>	—	—	—	—	19.45	8.82	30.96	14.04
<i>P. canescens</i> x <i>P. grandidentata</i>	—	—	7.08	3.21	10.36	4.70	31.00	14.06
<i>P. deltoides</i> x <i>P. balsamifera</i>	4.34	1.97	5.18	2.35	—	—	—	—
<i>P. deltoides</i> x <i>P. nigra</i>	4.43	2.01	6.90	3.13	60.86	27.60	—	—
<i>P. deltoides</i> x <i>P. trichocarpa</i>	3.00	1.36	4.54	2.06	—	—	—	—
<i>P. trichocarpa</i> x <i>P. balsamifera</i>	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

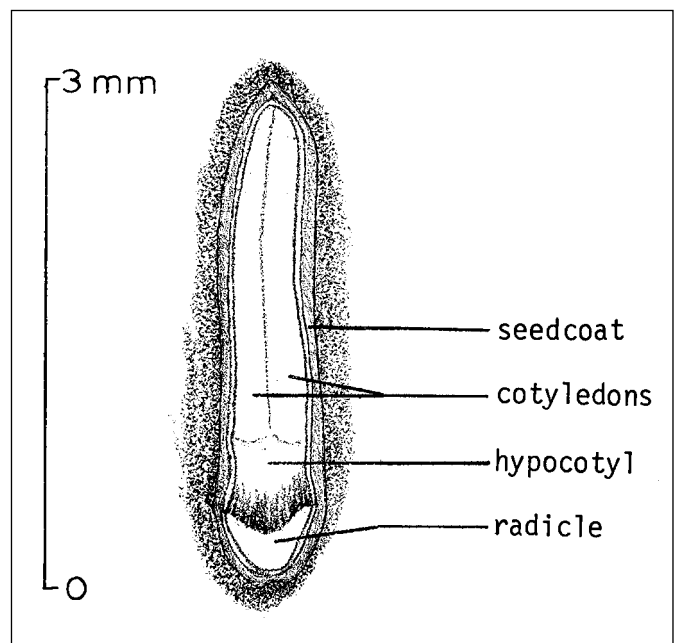
Figure 5—*Populus*, poplar: longitudinal section through the embryo of a seed.

Table 5—*Populus*, poplar, cottonwood, aspen: seed weights of non-screened samples

Species	Seeds (x million)/weight				Samples
	Range		Average		
	/kg	/lb	kg	/lb	
<i>P. deltoides</i>	0.44–3.31	0.20–1.50	0.77	0.425	6+
<i>P. deltoides</i> spp. <i>monilifera</i>	0.55–1.06	0.25–0.48	—	—	4+
<i>P. grandidentata</i>	—	—	6.62	3.00	1
<i>P. heterophylla</i>	0.31–0.36	0.14–0.16	0.34	0.15	4
<i>P. tremula</i>	5.89–16.65	2.66–7.55	8.09	3.67	30
<i>P. tremuloides</i>	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)).

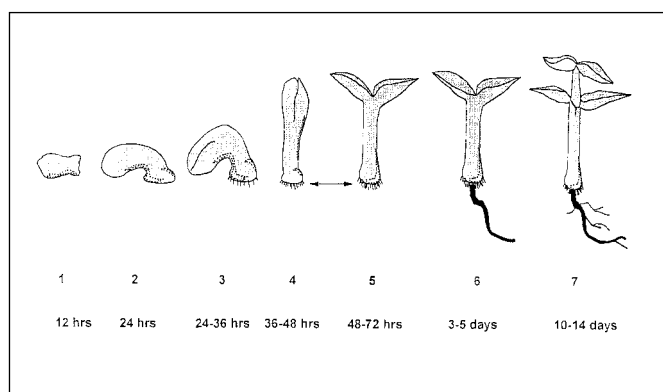
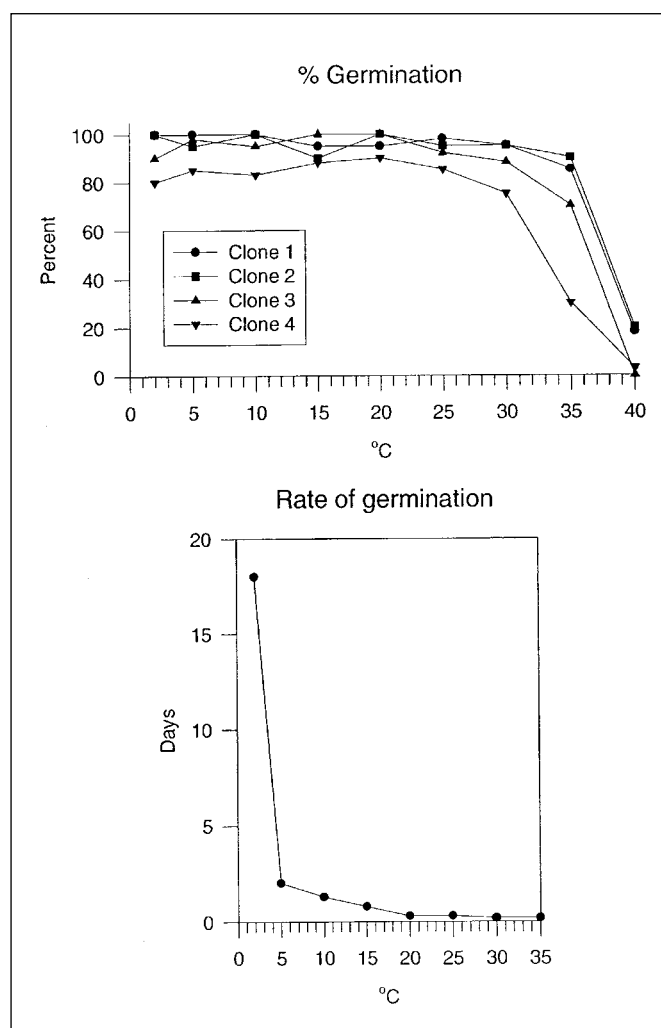


Figure 7—*Populus tremuloides*, quaking aspen: effects of temperature on percentage germination and germination rate in seeds (from McDonough 1979); rate is expressed as time for 10% of seeds to germinate.



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/m² (25/ft²) to produce 42 to 63 plantable seedlings/m² (4 to 6/ft²) at lifting. The beds are lightly watering again after sowing, then covered with 1.3-cm (1/2-in) mesh hardware cloth and 50% shade cloth (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 shade cloth 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 cm³ (21 to 27 in³) 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 cm³ (0.9 to 1.5 in³) and 1,280 cavities/m² (119/ft²). 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/m² (4 to 5 seedlings/ft²) 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).

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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).

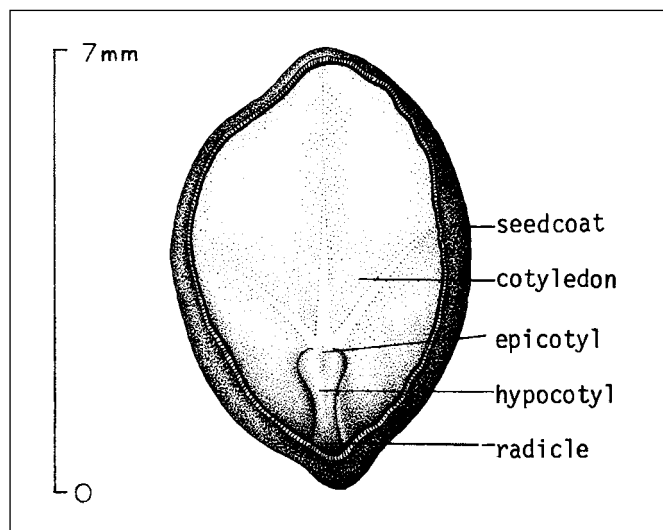
Figure 1—*Prosopis juliflora*, mesquite: legume.



Table 1—*Prosopis*, mesquite: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
<i>P. glandulosa</i> Torr. <i>P. chilensis</i> var. <i>glandulosa</i> (Torr.) Standl. <i>P. juliflora</i> var. <i>glandulosa</i> (Torr.) Cockerell	honey mesquite	E Texas & Oklahoma to Utah, S California, & N Mexico
<i>P. juliflora</i> (Sw.) DC. <i>P. pubescens</i> Benth.	mesquite, kiawe (Hawaii) screwbean mesquite, screwbean, tornillo	Mexico, S to Brazil & Peru Trans-Pecos Texas to Utah & S California
<i>P. velutina</i> Woot. <i>P. juliflora</i> var. <i>velutina</i> (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

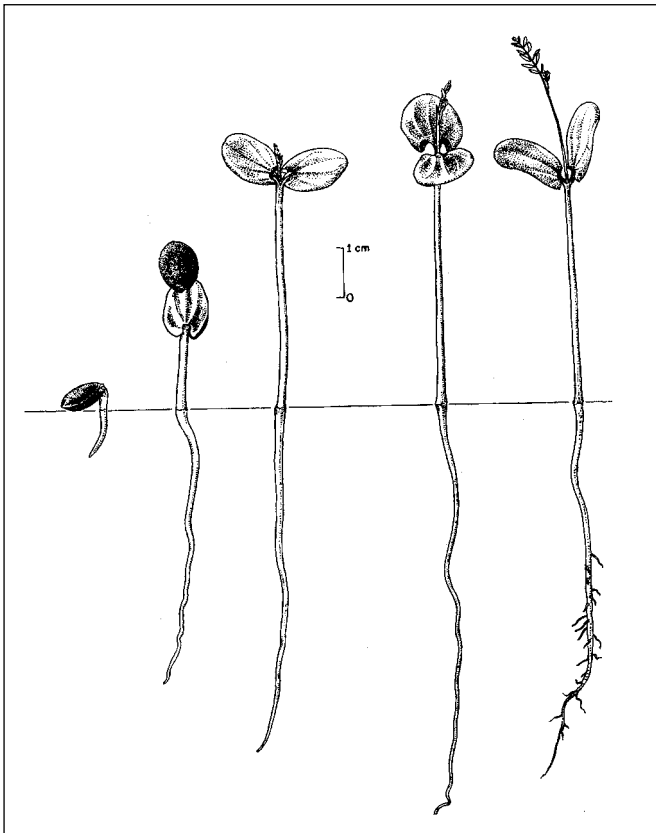
Table 2—*Prosopis*, mesquite: germination test conditions and results

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 ₂ SO 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 ($\frac{2}{5}$ to $\frac{4}{5}$ 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.

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Rosaceae—Rose family

Prunus L.

cherry, peach, and plum

Ted J. Grisez, Jill R. Barbour, and Robert P. Karrfalt

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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
<i>P. alleghaniensis</i> Porter	Allegheny plum, sloe, Allegheny sloe, Porter plum	Tree or shrub	Connecticut to Pennsylvania & S in mntns to Georgia; also in Michigan
<i>P. americana</i> Marsh.	American plum, wild yellow plum, red plum, goose plum, hog plum	Tree or shrub	Massachusetts to Manitoba, New Mexico, central Texas & NW Florida
<i>P. angustifolia</i> Marsh.	Chickasaw plum, sand plum	Tree or shrub	Missouri, S Nebraska to NW Texas & Louisiana; naturalized E to central Florida, New Jersey, & Illinois
<i>P. armeniaca</i> L. <i>Armeniaca vulgaris</i> Lam.	apricot	Tree	W Asia; occasional escape from cultivation
<i>P. avium</i> (L.) L. <i>P. cerasus avium</i> L. <i>Cerasus avium</i> Moench	mazzard cherry, sweet cherry, gean,* bird cherry*	Tree	Europe & W Asia; naturalized locally in SE Canada & E US
<i>P. caroliniana</i> (P. Mill.) Ait.	Carolina laurel cherry, wild orange	Tree (evergreen)	North Carolina to Texas
<i>P. cerasifera</i> Ehrh. <i>P. domestica</i> var. <i>myrobalan</i> L. <i>P. myrobalana</i> Loisel. <i>P. korolkowi</i> 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
<i>P. cerasus</i> L. <i>Cerasus vulgaris</i> Mill.	sour cherry, pie cherry	Tree	W Asia & SE Europe; naturalized locally from Nova Scotia & Michigan to N Florida & W-ward
<i>P. domestica</i> L. <i>P. damascena</i> Dierb. <i>P. communis</i> Huds.	garden plum, plum, European plum	Tree	W Asia & Europe; naturalized locally in SE Canada, NE US & Oregon
<i>P. domestica</i> var. <i>insititia</i> (L.) Fiori & Paoletti <i>P. domestica insititia</i> Fiori & Paoletti	bullace plum, damson, damson plum	Tree or shrub	W Asia & Europe; naturalized locally from Nova Scotia & Maine to New York SW-ward
<i>P. dulcis</i> (P. Mill.) D.A. Webber <i>Prunus amygdalus</i> Batsch <i>Amygdalus dulcis</i> P. Mill. <i>P. communis</i> (L.) Arcang. <i>Amygdalus communis</i> L.	almond	Tree	W Asia & possibly North Africa; occasional escape from cultivation
<i>P. emarginata</i> (Dougl. ex Hook.) D. Dietr. <i>P. mollis</i> Walpers <i>Cerasus prunifolia</i> Greene	bitter cherry, wild cherry, narrowleaf cherry	Shrub or tree	British Columbia to S California, Arizona, & Montana
<i>P. fasciculata</i> (Torr.) Gray	desert almond	Shrub	California to Utah
<i>P. fremontii</i> S. Wats	desert apricot	Shrub	S California
<i>P. gracilis</i> Engelm. & Gray	Oklahoma plum	Shrub	Arkansas to Texas
<i>P. hortulana</i> Bailey	hortulan plum	Tree	S Indiana to Iowa, Oklahoma, Arkansas, Alabama & W Tennessee
<i>P. ilicifolia</i> (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
<i>P. laurocerasus</i> L.	laurel cherry, cherry-laurel	Tree (evergreen)	SE Europe, SW Asia
<i>P. mahaleb</i> L. <i>Cerasus mahaleb</i> Mill.	mahaleb cherry, mahaleb, St. Lucie cherry, perfumed cherry	Tree	W Asia & Europe; naturalized locally in SW Canada & NE US
<i>P. maritima</i> Marsh.	beach plum	Shrub	Maine to Delaware
<i>P. munsoniana</i> W. Wight & Hedrick	wildgoose plum, Munson plum	Tree or shrub	Kansas, Kentucky, Texas & N Mississippi; naturalized E to S Ohio & Georgia
<i>P. padus</i> L. <i>P. racemosa</i> Lam. <i>Padus racemosa</i> (Lam.) Schneid. <i>Cerasus padus</i> (L.) DC.	European bird cherry, mayday tree	Tree	Europe & N Asia to Korea & Japan; spread from cultivation in Canada & NE US
<i>P. pensylvanica</i> L. f. <i>P. persicifolia</i> Desf. <i>P. montana</i> Marsh. <i>P. lanceolata</i> 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
<i>P. persica</i> (L.) Batsch <i>Amygdalus persica</i> L. <i>Persica vulgaris</i> Mill.	peach, common peach	Tree	China; naturalized locally, New England, S Ontario & Michigan to E Texas & Florida
<i>P. pumila</i> L. <i>P. depressa</i> Pursh	sand cherry	Shrub	New Brunswick to Manitoba, Illinois, & New Jersey
<i>P. pumila</i> var. <i>besseyi</i> Bailey (Gleason) <i>P. prunella</i> Daniels <i>P. pumila besseyi</i> (Bailey) Waugh. <i>P. susquehanae</i> Willd. <i>Cerasus canadensis</i> Mill.	Bessey cherry, western sand cherry, Rocky Mountain cherry	Shrub	Manitoba to Wyoming S to Kansas & Colorado
<i>P. serotina</i> Ehrh. <i>P. virginiana</i> L. <i>Padus virginiana</i> (L.) Mill. <i>Padus serotina</i> 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
<i>P. spinosa</i> L.	sloe, blackthorn	Shrub or tree	Europe, N Africa, & W Asia; naturalized locally in SE Canada & NE US
<i>P. subcordata</i> Benth.	Klamath plum, Pacific plum, Sierra plum, western plum	Tree or shrub	W & S Oregon to central California
<i>P. tomentosa</i> Thunb. <i>P. trichocarpa</i> Bge. <i>Cerasus tomentosa</i> Wall.	Manchu cherry, Nanking cherry downy cherry	Shrub	China, Japan, & Himalayas; central & N Great Plains
<i>P. umbellata</i> Ell.	hog plum	Tree	North Carolina to Florida, Alabama, & Mississippi
<i>P. virginiana</i> L. <i>P. nana</i> DuRoi <i>P. demissa</i> (Nutt.) D. Dietr. <i>Padus nana</i> (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**).

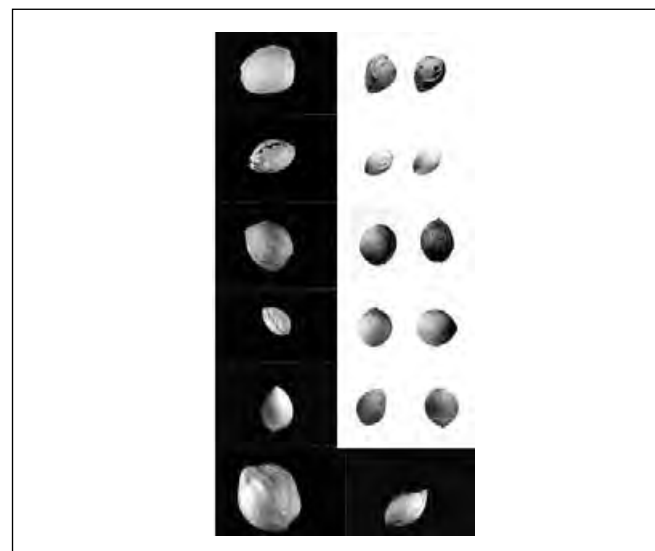


Table 2—*Prunus*, cherry, peach, and plum: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal
<i>P. alleghaniensis</i>	Scattered	Late Apr–May	Aug–Sept	—
<i>P. americana</i>	—	Mar–May	June–Oct.	June–Oct
<i>P. angustifolia</i>	—	Mar–Apr	May–July	May–July
<i>P. armeniaca</i>	California	Feb–Mar	May–June	—
	USSR	Mar–Apr	July	July–Aug*
<i>P. avium</i>	NE US	Apr–May	June–July	—
<i>P. caroliniana</i>	SE US	Mar–Apr	Sept–Oct	—
<i>P. cerasifera</i>	Geneva, New York	May 12†	July 15–Aug 10	—
	USSR	Apr–May	Aug	—
<i>P. cerasus</i>	—	Apr–May	June–July	—
	Geneva, New York	May 8–18†	June–July	—
<i>P. domestica</i>	Geneva, New York	May 12–21†	July 15–Oct 1	—
	USSR	May	Aug	—
<i>P. d. var. insititia</i>	US & Canada	Late Apr–May	Aug–Sept	—
	Geneva, New York	May 16–21†	Aug 20–Oct 1	—
<i>P. dulcis</i>	California	Mid Feb–Mar	Late Aug–Oct*	—
<i>P. emarginata</i>	—	Apr–June	July–Sept	Aug–Sept*
<i>P. hortulana</i>	SE US	Mar–May	Aug–Oct	—
<i>P. ilicifolia</i>	—	Mar–May	Sept–Oct*	Oct–Dec
<i>P. laurocerasus</i>	SE Europe & Asia Minor	Apr–May	July–Aug	—
<i>P. mahaleb</i>	NE US & SE Canada	Apr–May	July	—
<i>P. maritima</i>	Maine to Delaware	Apr–June	Sept–Oct	—
<i>P. munsoniana</i>	—	Mar–May	July–Sept*	—
	Geneva, New York	May 20–24†	July 15–Sept 10	—
<i>P. padus</i>	Philadelphia & vicinity	End Apr–early May	Late June–July	—
	USSR	May–early June	June–Aug	Aug*
<i>P. pensylvanica</i>	—	Late Mar–early July	July–Sept	—
	Warren Co., Pennsylvania	May 1–15	Late July–early Aug	—
<i>P. persica</i>	NE US	Apr–May	July–Sept	—
	SE US	Feb–Apr	May–Aug	—
<i>P. pumila</i>	—	May–July	July–Sept	—
<i>P. pumila. var. besseyi</i>	Nebraska	Apr–May	July–Sept	July–Sept
<i>P. serotina</i>	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
<i>P. spinosa</i>	USSR	Apr–May	Aug–Sept	Sept
<i>P. subcordata</i>	—	Mar–May	Aug–Sept	—
<i>P. tomentosa</i>	Cheyenne, Wyoming	Early May	Late July	Early Aug
	Bismarck, N Dakota	May 10–15	July 10–15	July 15–Sept 1
<i>P. umbellata</i>	SE United States	Mar–Apr	Aug–Sept	—
<i>P. virginiana</i>	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.

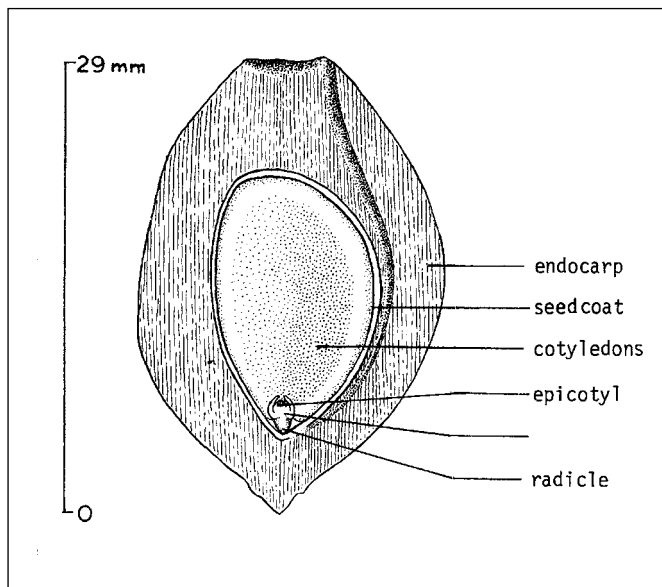
† Average dates of height of bloom for one to several cultivars.

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
<i>P. alleghaniensis</i>	4.9	1889	4	1	Dark purple	10	—
<i>P. americana</i>	3–9	1768	4	1–2	Red or yellowish	20–30	—
<i>P. angustifolia</i>	4.3–7.6	~ 1874	2	—	Red or yellow	10–20	—
<i>P. armeniaca</i>	10.4	Early	5	2	Yellowish with red	30+	—
<i>P. avium</i>	9–30.5	Early	6–7*	1	Yellow to red or purplish black	20–25	—
<i>P. caroliniana</i>	5.5–12	—	—	—	Black	10–13	10–13
<i>P. cerasifera</i>	8.2	Early	3	2–3	Red	16–25	—
<i>P. cerasus</i>	9–15	Early	6–7*	1	Light to dark red	8–25	—
<i>P. domestica</i>	9–12	Early	5	—	Often blue-purple	30+	—
<i>P. d. var. insititia</i>	6–7.6	Early	—	—	Yellow to bluish black	25+	15–20
<i>P. dulcis</i>	3–9	Early	4†, 6–7	1	Brownish	30+	30–60
<i>P. emarginata</i>	1–15	1918	—	—	Bright red	8–12	—
<i>P. fasciculata</i>	1–2.4	—	—	—	—	13	—
<i>P. fremontii</i>	1.5–3.7	—	—	—	Yellowish	15–20	13
<i>P. gracilis</i>	4.6	—	—	—	Red	13	—
<i>P. hortulana</i>	9	—	3	—	Red to yellow	25	—
<i>P. ilicifolia</i>	7.6–9	Pre-1925	3	—	Purple or black	13–17	25
<i>P. laurocerasus</i>	5.5	—	—	—	Purple to black	10	8–13
<i>P. mahaleb</i>	6–10	Early	3	1–2	Black	8–10	6–10
<i>P. maritima</i>	3	—	3	—	Purple	13–25	20
<i>P. munsoniana</i>	6–9	Pre-1909	3	—	Red or yellow	20–30	15–25
<i>P. padus</i>	15	Early	—	2	Black in typical variety	6–8	—
<i>P. pennsylvanica</i>	3–12	1773	2	—	Light red	5–7	—
<i>P. persica</i>	3–7.6	Early	3	1–2	Yellow to red	30–60	30–75
<i>P. pumila</i>	0.3–2.4	1756	—	—	Purple-black	10	10
<i>P. var. besseyi</i>	0.3–1.2	1892	2–3	—	Purple to black	15	—
<i>P. serotina</i>	15.3–33.5	1629	5	1–5	Black	7–10	6–10
<i>P. spinosa</i>	4	Early	—	1–2	Blue-black	10–15	15
<i>P. subcordata</i>	3–7.6	~ 1850	—	2	Red or yellow	20–30	15–30
<i>P. tomentosa</i>	1.8–3	1870	2–3	1–2	Red	10–31	15
<i>P. umbellata</i>	—	—	3	—	Black, red, yellow	10–15	10–13
<i>P. virginiana</i>	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				Cleaned seeds/weight				Samples
	Range		Average		Range		Average		
	kg	lb	kg	lb	/kg	/lb	/kg	/lb	
<i>P. alleghaniensis</i>	—	—	—	—	—	—	2,950	338	1
<i>P. americana</i>	3–15	7–34	9	19	550–1,500	250–680	870	395	27+
<i>P. angustifolia</i>	4–14	8–30	7	16	770–1,530	350–694	1,030	467	14+
<i>P. armeniaca</i>									
USA	14–18	30–40	—	—	200–560	91–254	317	144	10+
USSR	5–7	10–15	—	—	270–495	123–225	382	173	—
<i>P. avium</i>									
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	—
<i>P. cerasifera</i>	—	5	10	—	782–1,330	355–603	994	451	7+
<i>P. cerasus</i>	—	—	9	20	1,510–4,000	685–1,815	2,910	1,320	6+
<i>P. domestica</i>	—	—	5	10	416–907	189–411	597	271	5+
<i>P. d. var. insititia</i>	—	—	3	7	625–1,920	284–871	1,380	626	3+
<i>P. dulcis</i>	—	—	—	—	126–225	57–102	181	82	3+
<i>P. emarginata</i>	—	—	11	25	4,120–8,790	1,869–3,987	7,020	3,184	6+
<i>P. ilicifolia</i>	—	—	—	—	200–240	91–109	220	100	2+
<i>P. mahaleb</i>	9–11	20–25	—	—	4,800–5,600	2,177–2,540	5,200	2,359	—
<i>P. munsoniana</i>	—	—	—	—	900–2,240	408–1,016	1,690	767	3+
<i>P. padus</i>	—	—	9	20	6,600–12,300	2,994–5,580	8,910	4,042	5+
<i>P. pensylvanica</i>	7–12	16–27	—	—	8,000–21,800	3,629–9,889	14,200	6,442	6+
<i>P. persica</i>	—	—	9	20	72–244	33–111	156	71	6+
<i>P. pumila</i>									
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+
<i>P. serotina</i>									
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
<i>P. spinosa</i>	—	—	5	10	1,970–2,670	894–1,211	2,240	1,016	—
<i>P. subcordata</i>	—	—	—	—	450–631	204–286	556	252	4+
<i>P. tomentosa</i>	3–5	7–12	5	10	1,730–6,400	785–2,903	4,740	2,150	9+
<i>P. virginiana</i>	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 (%)
<i>P. americana</i>			
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
<i>P. avium</i>			
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†
<i>P. pensylvanica</i>			
2 months	–18	Dry	95
6 years	1–3	Low	74
10 years	1–3	Low	76
<i>P. serotina</i>			
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			Avg germination (%)	Samples	Viability (%)
	Warm*	Cold†	Temp (°C)		Days			
			Day	Night				
<i>P. alleghaniensis</i>	0	150	10	10	60	25	7	—
<i>P. americana</i>	0	90–150	10	10	60	60	21	74
<i>P. angustifolia</i>	0	60–120	—	—	60	55	—	90
<i>P. armeniaca</i>								
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	—	—
<i>P. avium</i>								
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	—	—
<i>P. caroliniana</i>	0	30–60	—	—	—	—	—	—
<i>P. cerasifera</i>	—	196	‡1	‡7	28	65	2	—
<i>P. cerasus</i>	0	90–150	—	—	—	—	82	—
<i>P. domestica</i>	14	189	3	3	‡	56	15	—
	0	120–150	—	—	—	—	85	—
	0	90	2	2	—	—	91	—
<i>P. domestica</i> var. <i>insititia</i>	0	84–112	18	18	—	89	7	—
<i>P. dulcis</i>	0	65	2	2	‡	—	90	—
<i>P. emarginata</i>	0	90–126	24	24	60	4	3+	—
<i>P. ilicifolia</i>								
fresh seed	0	0	—	—	—	—	—	—
stored seed	0	90	—	—	—	—	24	—
<i>P. laurocerasus</i>	0	60–90	—	—	—	—	—	—
<i>P. mahaleb</i>	0	80–100	—	—	—	89	5	—
	14	189	3	3	‡	55	3	—
<i>P. maritima</i>	0	90	—	—	—	—	39	—
<i>P. munsoniana</i>	0	80–100	—	—	—	100	10	—
<i>P. padus</i>								
fresh seeds	0	100–120	—	—	—	85	—	—
stored seeds	14	210	3	3	‡	50	3	—
<i>P. pensylvanica</i>	60	90	25	10	60	62	2	91
<i>P. persica</i>								
endocarp intact	0	98–105	5(§1)	5(§1)	‡	32	8	—
endocarp removed	0	70–105	5(§1)	5(§1)	‡	82	8	92
<i>P. pumila</i> var. <i>besseyi</i>	0	120	—	—	—	60	72	—
<i>P. serotina</i>	0	120	26	10	40–60	86	32	80
	14	189	3	3	‡	90	3	—
<i>P. spinosa</i>	0	170	—	—	—	—	90	—
<i>P. subcordata</i>	0	90	—	—	100	1	—	—
<i>P. tomentosa</i>	0	60–90	—	—	—	11	—	86
<i>P. virginiana</i>	0	120–160	25	10	40	77	3	62

Sources: Afanasiev (1940, 1942), Al'benschkii 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.

|| 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 ($\frac{3}{8}$ 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.

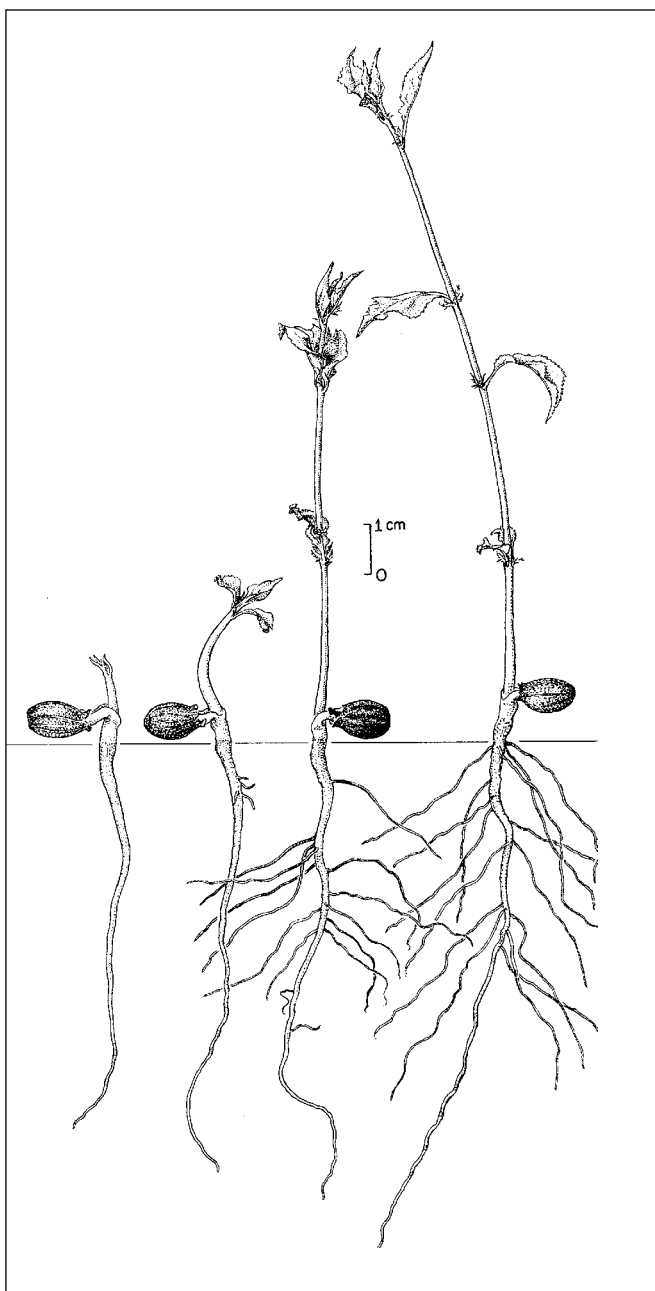
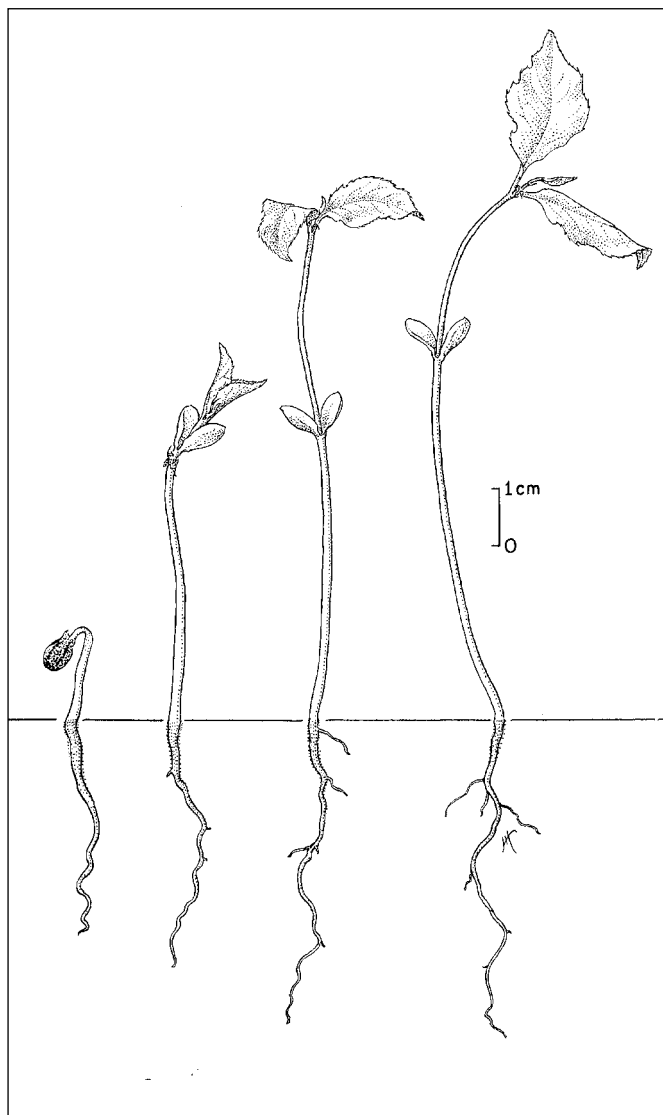


Figure 5—*Prunus virginiana*, common chokecherry; seedling development at 1, 3, 7, and 11 days after epigeal germination.



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 $\frac{1}{3}$ 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 nurserybed 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 Morozov 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)		Seeds sown/ft ²	Sowing depth (in)	Tree %	Outplanting age (yr)
	Fall-sowing	Spring-sowing				
<i>P. americana</i>	0–90	120	4	1–2†	33–50	1
<i>P. angustifolia</i>	0	15–20	1	33	1	—
<i>P. armeniaca</i>	0	90	9	2	50	1
<i>P. avium</i>	60‡	120	13	1–2	—	1 or 2
<i>P. cerasifera</i>	0‡	—	10	2	64§	1
<i>P. cerasus</i>	90‡	90	21	—	—	1 or 2
<i>P. domestica</i>	0	—	13	2	—	1 or 2
<i>P. mahaleb</i>	0–60	60	—	1–2	45§	—
<i>P. padus</i>	60‡	120	50	1/2–1	—	1 or 2
<i>P. persica</i>	0	85	0.75	2	—	—
<i>P. pumila</i> var. <i>besseyi</i>	0	120	6–7	—	77	—
<i>P. serotina</i>	0	120	10–20	1 1/2–2	7–83	1
<i>P. spinosa</i>	0‡	170	17–28	1–2	70–75§	1 or 2
<i>P. tomentosa</i>	0	60	15–30	1	72	1
<i>P. virginiana</i>	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.

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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. gaussenii* 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
<i>P. macrocarpa</i> (Vasey) Mayr <i>Abies douglasii</i> var. <i>macrocarpa</i> Torr. <i>A. macrocarpa</i> Vasey	bigcone Douglas-fir, bigcone-spruce, desert-fir	Mtns of SW California
<i>P. menziesii</i> var. <i>glauca</i> (Beissn.) Franco <i>P. douglasii</i> var. <i>glauca</i> Mayr <i>P. menziesii</i> var. <i>caesia</i> (Schwerin) Franco <i>P. taxifolia</i> var. <i>glauca</i> (Beissn.) Sudworth	interior Douglas-fir, blue Douglas-fir, Rocky Mountain Douglas-fir, Colorado Douglas-fir, inland Douglas-fir	Central British Columbia & SW Alberta, S in mtns to N & central Mexico, from E Washington, Oregon, Nevada, & W Arizona to E Montana, Wyoming, Colorado, New Mexico, & NW Texas
<i>P. menziesii</i> var. <i>menziesii</i> (Mirb.) Franco <i>P. douglasii</i> var. <i>viridis</i> Schwerin <i>P. menziesii</i> var. <i>viridis</i> (Schwerin) Franco <i>P. mucronata</i> (Raf.) Sudworth <i>P. taxifolia</i> (Lamb.) Britton	coastal Douglas-fir, green Douglas-fir, Oregon Douglas-fir, Douglas-fir, Douglas-spruce	SW British Columbia through Washington & Oregon to central California, E into Cascade & 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; Schrumph 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
<i>P. macrocarpa</i>	S California	February–mid-Apr	Early Aug–early Oct	Late Aug–late Oct
<i>P. menziesii</i> var. <i>glauca</i>	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*
<i>P. menziesii</i> var. <i>menziesii</i>	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. *menziesii*, coast Douglas-fir: mature, closed cones have characteristic 3-lobed protruding bracts.

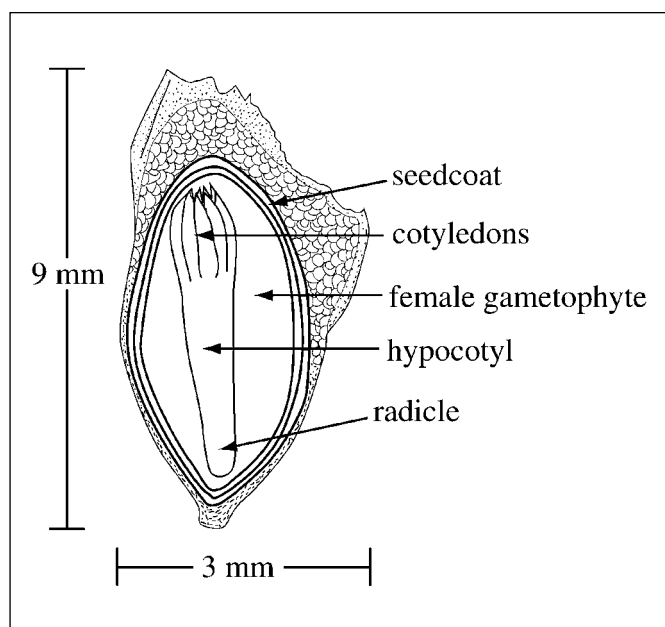


cones (Willis 1917). In interior Douglas-fir, filled-seed numbers ranged from 20 to 30 per cone in some collections (Owston and Stein 1974). For coastal Douglas-fir, filled-seed numbers ranged from 4 to 54 per cone in 309 collections from individual 35-year-old trees in northwestern Oregon (Olson and 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 Snieszko 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)
<i>P. macrocarpa</i>	9–30	20*	—	11–17
<i>P. menziesii</i>				
var. <i>glauca</i>	23–49	20	3–10	4–7
var. <i>menziesii</i>	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 big-cone 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 processing—before kiln-drying, during drying, and during tumbling. 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 standard 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 variety, 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 origins 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			Seed yield				
	Air-drying (days)	Kiln-drying		Cone wt/cone vol kg/hl lb/bu		Seed wt/cone vol kg/hl lb/bu		Ratio seed wt/ 100 cone wt
		Time (hr)	Temp ($^{\circ}\text{C}$)					
<i>P. marocarpa</i>	8–10	—	—	32–39	25–30	1.03	0.8	2.8
<i>P. menziesii</i>								
var. <i>glauca</i>	4–60	2–10	38–43	32–77	25–60	0.65–1.03	0.5–0.8	1.0–1.3
var. <i>menziesii</i>	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

Species & location	Average		Range		Samples ^a
	kg	lb	kg	lb	
<i>P. macrocarpa</i>					
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
<i>P. menziesii</i> var. <i>glauca</i>					
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
<i>P. menziesii</i> var. <i>menziesii</i>					
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	Stratification* (days)	Germination conditions				Germinative energy		Germ. capacity (%)		
		Moist medium	Temp (°C)		Days	Amt (%)	Time (days)	Avg	Range	Samples
			Day	Night†						
<i>P. macrocarpa</i>	28	Vermiculite	30	20	28	—	—	31	—	3
	—	—	—	—	100	14	60	28	14–36	3
	—	Sand	27	21	20–90	—	—	30	15–57	5
<i>P. menziesii</i> var. <i>glauca</i>	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
<i>P. menziesii</i> var. <i>menziesii</i>	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).

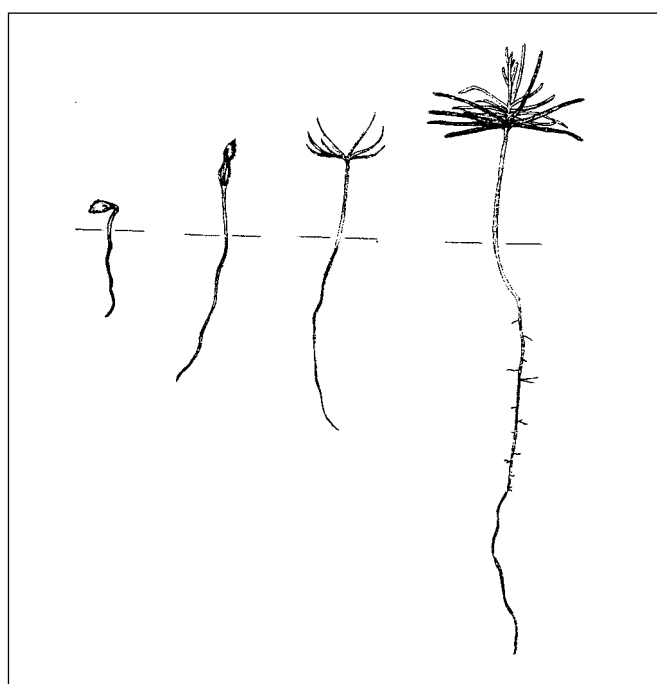
Production and grading practices have the potential of influencing the genetic composition as well as the physical characteristics of the seedling populations produced (Campbell and Sorensen 1984; El-Kassaby and Thomson

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/m² (15 to 30/ft²); for 1+1s, bed densities of first-year seedlings range from 538 to 753/m² (50 to 70/ft²) (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 mycorrhizal inocu-

lation 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 out-

doors (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).

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