Pinaceae—Pine family

Pinus L.

pine

Stanley L. Krugman and James L. Jenkinson

Dr. Krugman retired from the World Bank and the USDA Forest Service's Washington Office;
Dr. Jenkinson, plant physiologist emeritus, retired from the USDA Forest Service's
Pacific Southwest Research Station

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

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

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

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

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

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

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

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

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

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

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

Scientific name & synonym(s)	Common name(s)	Occurrence
***P. elliottii* var. *densa* Little & Dorman**	**South Florida slash pine**	Sandy plains of central to S Florida, E & W Florida coasts; lower Florida Keys
***P. elliottii* var. *elliottii* Engelm.** *P. caribaeu* Morelet	**slash pine,** pitch pine, swamp pine, yellow slash pine, Honduras pine	Coastal plains of lower South Carolina S to central Florida, W to S Mississippi, SE Louisiana
***P. engelmannii* Carr.** *P. latifolia* Sarg. *P. apacheca* Lemmon	**Apache pine,** Arizona longleaf pine	Sierra Madre Occidental; Aguascalientes, SW Zacatecas N through W Mexico into SE Arizona, SW corner of New Mexico
***P. flexilis* James**	**limber pine,** Rocky Mountain white pine	Subalpine; Sierra Nevada, Great Basin ranges, Rocky Mtns; New Mexico N to Alberta, Canada; W in Idaho, Utah, Nevada, into S California
***P. gerardiana* D. Don** *P. aucklandii* Lodd. *P. chilghoza* Ehh.	**chilgoza pine,** Gerard pine	Himalayas, dry valleys; E Afghanistan, contiguous N Pakistan, N India
***P. glabra* Walt.**	**spruce pine,** cedar pine, bottom white pine	Coastal plains of E South Carolina to N Florida, W to S Mississippi, SE Louisiana
***P. halepensis* P. Mill.** *P. alepensis* 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
***P. heldreichii* Christ** *P. heldreichii* var. *leucodermis* (Ant.) Markgr. *P. eucodermis* Ant. *P. nigra* var. *leucodermis* (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
***P. jeffreyi* Grev. & Balf.** *P. ponderosa* var. *jeffreyi* (Grev. & Balf.) E. Murr.	**Jeffrey pine**	Sierra Nevada–Cascade & Klamath Mtns, coastal & transverse–peninsular ranges of California to SW Oregon, Baja California Norte, W Nevada
***P. kesiya* Royle & Gordon** *P. khasya* Royle *P. insularis* Endl.	**Khasi pine,** Benguet pine	High elevations of E India, SE Tibet, Burma, SW Yunnan to N Thailand, Laos, S Vietnam, W Luzon, Philippines
***P. koraiensis* Sieb. & Zucc.**	**Korean pine,** cedar pine	Mtns of South Korea to North Korea through E Manchuria, S Chabarovsk, Siberia; Japan (central Honshu & Shikoku)
***P. lambertiana* Dougl.**	**sugar pine,** *piño real*	Sierra Nevada–Cascade & Klamath Mtns, coastal & transverse–peninsular ranges of California to N Oregon, Baja California Norte, W Nevada
***P. leiophylla* var. *chihuahuana* (Engelm.) Shaw** *P. chihuahuana* Engelm.	**Chihuahua pine,** yellow pine, *piño real*	Sierra Madre del Sur, trans–Mexico volcanic belt, Sierra Madre Occidental; Oaxaca, Vera Cruz W to Michoacán; N in W Mexico to SE Arizona, SW New Mexico
***P. merkusii* Junghuhn & Vriese ex Vriese**	**Merkus pine,** Tenasserim pine	Mtns, low elevations of SE Burma, N Thailand, Cambodia, Laos, Vietnam, Hainan, N Sumatra, Philippines (W Luzon & N Mindoro)
***P. monophylla* Torr. & Frém.** *P. cembroides* var. *monophylla* (Torr. & Frém.) Voss	**singleleaf piñyon,** 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
***P. monticola* 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
***P. mugo* Turra** *P. montana* Miller	**Swiss mountain pine,** mugho (or mugo) pine, dwarf mountain pine	Subalpine areas in central & S Europe: Pyrenees, Alps, Carpathian Mtns, Balkan Mtns; Austria, Switzerland, N Italy, E France; N to Germany, Czech Republic & Slovakia into S Poland, E into W Ukraine, Romania; Yugoslavia to N Albania, W Bulgaria; central Italy; S France, NE Spain
***P. muricata* D. Don** *P. remorata* 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
***P. nigra* Arnold** *P. nigra* var. *austriaca* (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

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

Scientific name & synonym(s)	Common name(s)	Occurrence
***P. palustris* P. Mill.** *P. australis* Michx. f.	**longleaf pine,** southern pine, longstraw pine	Coastal plains of SE Virginia to central Florida, W to N Louisiana, E Texas
***P. parviflora* Sieb. & Zucc.** *P. pentaphylla* Mayr *P. himekomatsu* Miyabe & Kudo	**Japanese white pine**	Mtns of Japan (Kyushu, Tsushima, Shikoku, Honshu, Sado, & S Hokkaido); South Korea (Ullung Island)
***P. patula* Schiede ex Schtdl. & Cham.**	**Mexican weeping pine**	Sierra Madre Oriental, Mexico; central Oaxaca N to Querétaro, SW Tamaulipas; Guatemala, El Salvador, Honduras, Nicaragua
***P. peuce* Griseb.** *P. excelsa* var. *peuce* (Griseb.) Beissn.	**Balkan pine,** Macedonian pine, Greek stone pine	High elevations of Balkan Peninsula: SW Yugoslavia, E Albania, SW Bulgaria, extreme N Greece
***P. pinaster* Aiton** *P. maritima* Poir.	**maritime pine,** cluster pine, pinaster pine	SW Europe & Mediterranean Basin: Iberian Peninsula, SE France + Corsica; W Italy + Sardinia & Pantalleria; Morocco, coastal E Algeria
***P. pinea* 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
***P. ponderosa* var. *ponderosa* 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
***P. ponderosa* var. *scopulorum* 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
***P. pumila* Regel** *P. cembra* var. *pumila* 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
***P. pungens* 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
***P. quadrifolia* Parl. ex Sudworth**	**Parry piñyon,** nut pine, pinyon	Semiarid, low elevations of San Jacinto Mtns, SW California, S to Sierra San Pedro Mártir, Baja
***P. radiata* D. Don** *P. insignis* Dougl.	**Monterey pine,** radiata pine, insignis pine	Coastal central California, in Año Nuevo Point, Monterey, & Cambria areas; Cedros Island & N Guadalupe Island, Mexico
***P. resinosa* 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
***P. rigida* 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
***P. roxburghii* Sarg.** *P. longifolia* Roxb.	**Chir pine,** longleaf Indian pine	Himalayas, monsoon belt; N Pakistan E through N India, Nepal, Sikkim, Bhutan
***P. sabiniana* 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
***P. serotina* Michx.** *P. rigida* var. *serotina* (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
***P. sibirica* Du Tour** *P. cembra* var. *sibirica* 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
***P. strobiformis* Engelm.** *P. flexilis* var. *reflexa* Engelm. *P. reflexa* (Engelm.) Engelm. *P. ayacahuite* var. *brachyptera* 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
***P. strobus* var. *chiapensis* Martínez**	**Chiapas white pine**	Mtns of S Mexico (Chiapis) & Guatemala
***P. sylvestris* L.**	**Scots pine,** Scotch pine	Eurasia: Scotland, Scandinavia, Germany, France, & Spain E to Turkey, Caucasus Mtns; Central & E Europe through Ural Mtns, N Kazakhstan, Siberia to Sea of Okhotsk, N Mongolia, N Manchuria
***P. taeda* L.**	**loblolly pine,** Arkansas pine, North Carolina pine, oldfield pine	Coastal Plains, Piedmont; Delaware S to central Florida; W through Georgia, S Tennessee, Gulf Coast states to SE corner Oklahoma, E Texas
***P. thunbergiana* Franco** *P. thunbergii* Parl.	**Japanese black pine**	Maritime Japan (Honshu to N Ryukyu Islands), South Korea (Cheju Island)
***P. torreyana* Parry ex Carr.**	**Torrey pine,** Soledad pine, Del Mar pine	Maritime S California (NE Santa Rosa Island) & coastal bluffs of San Diego County
***P. virginiana* P. Mill**	**Virginia pine,** scrub pine, Jersey pine, spruce pine	Piedmont & Appalachian Mtns; Long Island, New York to Chesapeake Bay, S to N Georgia, central Alabama; W to Ohio, S Indiana, W Kentucky, Tennessee, NE Mississippi
***P. wallichiana* A.B. Jacks.** *P. excelsa* Wall. *P. griffithii* McClelland *P. nepalensis* de Chambr.	**blue pine,** Bhutan pine, Himalayan pine	Himalayas, mid-high elevations: NE Afghanistan, N Pakistan, N India E through Nepal, Bhutan, NE India, S Tibet to N Burma, NW Yunnan
***P. washoensis* Mason & Stockwell**	**Washoe pine**	W edge of Great Basin; E slope Mt Rose, W Nevada; Bald Mtn Range in N Sierra Nevada; S Warner Mtns, NE California

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

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

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

As a general rule, seeds from pines growing in moist regions are smaller than those from sources in dry regions and seeds from moist regions normally produce seedlings that are faster growing and less deeply rooted than those from dry regions. Seeds from southern sources differ from those from northern sources. Seeds from northern sources often require longer moist chilling times than seeds from southern ones to release seed dormancy and enable germination. Trees from southern sources grow faster, are able to grow for a longer time during the growing season, and are more prone to winter freezing damage and less prone to damage from hard frosts in late spring and early autumn than are trees from northern sources (Krugman and Jenkinson 1974; Squillace and Silen 1962; Wells 1969; Wright 1962).

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

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

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

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

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

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

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

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

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

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

Pinus banksiana—Jack pine seeds from various sources differ in seed size, cone traits, seedling and tree growth, tree form, and susceptibility to insect and disease damage (King 1971; Yeatman 1974). Cone serotiny in Minnesota changes from closed cones in the north to chiefly open cones in the south (Rudolph and others 1959). Seeds tend to be larger from trees growing in warmer parts of the range (Fowells 1965), and seedlings from lower latitudes show less winter needle coloration than those from higher latitudes (Stoeckeler and Rudolf 1956). In Canada, height growth was greater for seeds from areas with longer growing seasons; height growth of selections moved north was better than that of those moved south (Holst 1962). Growth in provenance tests follows a largely clinal pattern that is linked to environmental gradients of latitude and length and temperature of the growing season at seed origin (Rudolph and Laidly 1990; Rudolph and Yeatman 1982).

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

Pinus canariensis—Canary Island pine is native only to the Canary Islands, where it is found at 640 to 2,195 m above sea level (Magini and Tulstrup 1955). Seedlings grown from seeds from the various islands and an array of elevations showed marked differences in winter cold hardiness when grown at the USDA Forest Service's Institute of Forest Genetics nursery near Placerville, California. Seedlings from a seed source at 1,220 m on Tenerife Island showed more cold damage than those from a source at 1,890 m there. Seedlings from a source from 1,890 m on Palma Island, however, were badly damaged, suggesting that sources on different islands differ in their susceptibility to cold (Krugman and Jenkinson 1974).

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

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

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

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

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

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

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

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

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

Pinus edulis—Piñyon has 2 forms (Ronco 1990). The single-needle form, var. *fallax* Little, ranges near 1,830 m in the mountains of central and eastern Arizona, in the Grand Canyon, and in parts of New Mexico. Seeds of var. *fallax* tend to be larger and have a thicker seedcoat than seeds of the 2-needle form, var. *edulis*. Moreover, the var. *fallax,* unlike the more widespread var. *edulis*, seldom produces seeds in quantity (Little 1968).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Pinus ponderosa—Ponderosa pine, one of the most widely ranging pines in North America, has 2 distinct varieties: Pacific (var. *ponderosa*) and Rocky Mountain (var. *scopulorum*) Engelm. (Oliver and Ryker 1990). The varieties differ in a host of traits, including needle length and number per fascicle, xylem resin monoterpenes, cone and seed size, seed isozymes, seed dormancy and germination rate, seasonal patterns of seedling top and root growth capacity (RGC), seedling and tree survival, growth rate, stem form, drought tolerance, cold hardiness, disease resistance, and susceptibility to hail (Callaham 1962; Conkle and Critchfield 1988; Eldridge and Dowden 1980; Fowells 1965; Hoff 1988; Jenkinson 1976, 1980; Larson 1966; Read 1980, 1983; Read and Sprackling 1981; Rehfeldt 1986a&b; Smith 1977; Squillace and Silen 1962; Van Haverbeke 1986a; Wang 1977; Weidman 1939; Wells 1964).

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

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

Tree growth rate increased with decrease in source elevation in early years in plantations at low, middle, and high elevations in the western Sierra Nevada, but in later years, performances of high-elevation sources at high elevation overtook those of low-elevation sources and neared those of mid-elevation sources. Wind and snow damage reduced the superiority of mid- and low-elevation sources. Wood specific gravity increased with decrease in source elevation in all plantations (Callaham and Liddicoet 1961; Conkle 1973; Echols and Conkle 1971; Namkoong and Conkle 1976). Elevational differentiation in growth also exists in Idaho populations (Rehfeldt 1986a). New Zealand provenance tests confirm and elaborate the complex combination of differences between discrete races and clinal variation, particularly for the Pacific and North Plateau races and show that the patterns of differentiation vary according to the traits assessed (Burdon and Low 1991).

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

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

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

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

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

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

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

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

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

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

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

Pinus sylvestris—Scots pine is the most widely planted introduced pine species in the United States, especially in the Northeast, Great Lakes region, central states, and the Pacific Northwest. It is now is naturalized in parts of New England and the Great Lakes region (Skilling 1990). The pine with the greatest natural range of all the pines, it grows in a host of different ecological situations, was involved in the first comparative seed source trials of pine, and is likely the most intensively studied of all pines. Its geographic varieties conservatively number from 21 to 52, and numerous forms and ecotypes have been described. Abundant variation exists within varieties, and seed sources differ in many traits, including flowering; needle, cone, and seed color; seed size, dormancy, and germination rate; root system structure, seedling and tree growth rate and form, and susceptibility to heat, cold, and drought (Brown 1969; Genys 1976; Giertych 1976; Pravdin 1964; Read 1971; Steven and Carlisle 1959; Wright 1962; Wright and others 1966). Seed size decreases from south to north, ranging from 97,240 seeds/kg (44,200/lb) in Spain to 279,400/kg (127,000/lb) in Lapland (Heit 1969). Seeds from sources in the extreme northern parts of the range and certain areas in Greece and Turkey show the highest seed dormancy (Heit 1969). Incompletely developed embryos explain part of the dormancy of northern sources (Kamra 1969). Growth rate typically decreases and cold hardiness increases from south to north. Trees from Finnish and Russian sources survived better in prairie conditions in Canada than did trees from more southern sources (Cram and Brack 1953). In Michigan, trees from certain French sources grew 3 times taller than trees from northern sources from Finland and Siberia, but northern sources were more cold hardy than southern ones (Wright 1962; Wright and others 1966). Needles of trees with origins in Asia Minor, the Balkans, southern France, and Spain remained green in winter, whereas those with Siberian and Scandinavian origins turned yellow. In Sweden, seeds from sources at north latitudes or high elevations germinated well over a wider range of temperatures than did seeds from sources at south latitudes or low elevations, and seedlings trees of southern sources grew faster and later in autumn than trees of northern sources (Kamra and Simak 1968). Trees from introduced sources produced better trees than did local sources in some European localities (Vidacovic 1991).

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

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

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

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

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

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

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

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

Natural hybrids are common, and we list but few of the many known. *P. palustris* × *taeda* (Sonderegger pine) occurs frequently in Louisiana and east Texas and is the best-known southern pine hybrid (Baker and Langdon 1990; Chapman 1922). Most natural hybrids occur infrequently in the overlaps of their parent species' ranges. Some of the better-known examples include the following:

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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Table 4—*Pinus,* pine: cone ripeness criteria (continued)

Species	Pre-ripe color	Ripe color
P. serotina	Green to yellow	Lustrous light yellow to brown
P. sibirica	Green	Violet to light gray or brown
P. strobiformis	Green	Greenish brown to dark brown
P. strobus	Green	Yellow green to light brown
P. sylvestris	Green	Dull tawny yellow, greyish or dull brown, or cinnamon brown
P. taeda	Green	Green, shiny light or dull pale reddish brown
P. thunbergiana	Deep lustrous purple	Nut brown or reddish brown
P. torreyana	Green to dark violet	Shiny deep chestnut brown to chocolate brown
P. virginiana	Green	Lustrous dark purple to reddish and dark brown
P. wallichiana	Green	Tawny yellow to light brown
P. washoensis	Purple to purplish black	Dull purple to purplish brown or light brown

Sources: Bailey (1939), Barnett and McLemore (1967b), Britton and Shafer (1908), Cerepnin (1964), Cooling (1968), Dallimore and Jackson (1967), den Ouden and Boom (1965), Fowells (1965), Jacaline and Lizardo (1958), Krugman and Jenkinson (1974), Little EL (1940, 1950), Lizardo (1950), Loock (1950), Luckhoff (1964), McIntyre (1929), McLemore (1961a&b), Pravdin (1963), Rehder (1940), Sargent (1965), Sudworth (1908), Troup (1921), Wahlenberg (1946), Wakeley (1954).
Note: See table 2 for intervals between large cone crops and table 3 for cone ripening and seed dispersal dates.

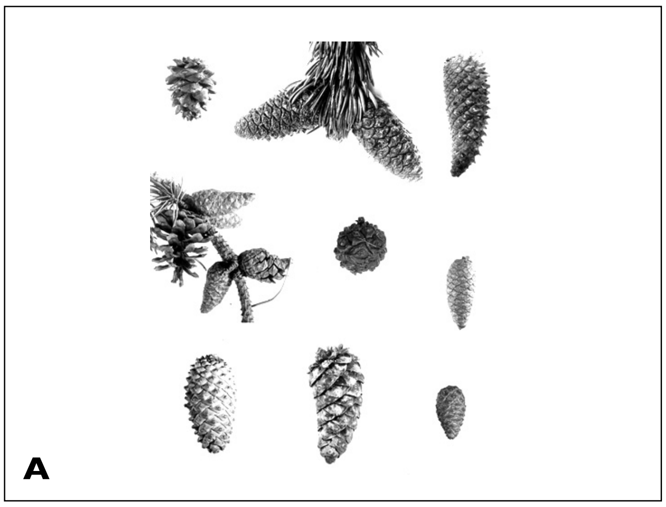


Figure 1A —*Pinus,* pine: mature cones, collected before seed dispersal, of *P. albicaulis*, whitebark pine (**upper left**); *P. aristata*, bristlecone pine (**upper center**); *P. attenuata*, knobcone pine (**upper right**); *P. banksiana*, jack pine (**center left**); *P. cembroides*, Mexican piñyon (**center middle**); *P. clausa*, sand pine (**center right**); *P. engelmannii*, Apache pine (**bottom left**); *P. flexilis*, limber pine (**bottom center**); *P. leiophylla* var. *chihuahuana*, Chihuahua pine (**bottom right**).

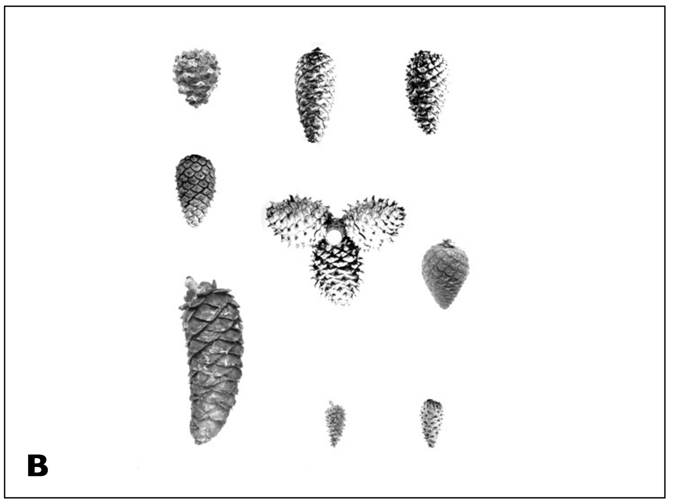


Figure 1B —*Pinus*, pine: mature cones, collected before seed dispersal, of *P. monophylla*, singleleaf piñyon (**upper left**); *P. arizonica*, Arizona pine (**upper center**); *P. ponderosa* var. *scopoulorum*, Rocky Mountain ponderosa pine (**upper right**); *P. rigida*, pitch pine (**center left**); *P. pungens*, Table Mountain pine (**center middle**), *P. serotina*, pond pine (**center right**); *P. strobiformus*, southwestern white pine (**bottom left**); *P. sylvestris*, Scots pine (**bottom center**); *P. virginiana*, Virginia pine (**bottom right**).

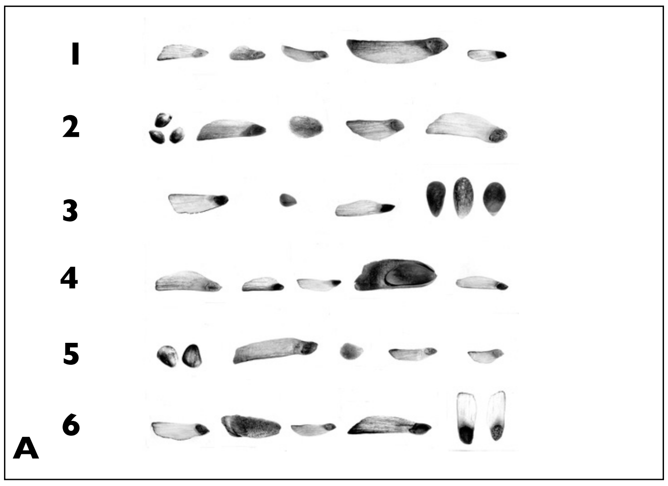
1970; Krugman and Jenkinson 1974). Seeds and cones of Italian stone and Chihuahua pines require 3 years to ripen (Dallimore and Jackson 1967; Little 1950). Seeds of Torrey pine are said to take 3 years to mature, but evidence suggests that the seeds of this pine mature in 2 years, whereas the cones require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

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

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

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

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



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

In pines with serotinous cones—including knobcone, jack, Calabrian, sand, Rocky Mountain lodgepole, Aleppo, bishop, maritime, Table Mountain, and Monterey pines—some or all of the mature cones remain closed for several to many years, or they open on the tree only at irregular intervals (Dallimore and Jackson 1967; Fowells 1965; Sudworth 1908). Besides their closed-cone habit, jack, sand, lodgepole/shore, and pitch pines have forms whose cones open promptly at maturity (Fowells 1965;, Krugman and Jenkinson 1974; Rudolph and others 1959). The closed-cone habit results from 3 factors: an extremely strong adhesion between adjacent, overlapping cone scales beyond the ends of the winged seeds (LeBarron and Roe 1945, Little and Dorman 1952a); cone structure; and the nature of the scale tissue systems described. The scales appear to be bonded by a resinous substance. The melting point of this resin seal is between 45 and 50 °C for Rocky Mountain lodgepole pine (Critchfield 1957). Heat, especially that of fire, melts the resin so that the cones open. Still other pines, such as whitebark, Japanese stone, Swiss stone, and Siberian pines, shed partly opened or unopened cones, and their seeds are dispersed only when the cones disintegrate on the ground (Dallimore and Jackson 1967; Mirov 1967; Pravdin 1963; Sudworth 1908).

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

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

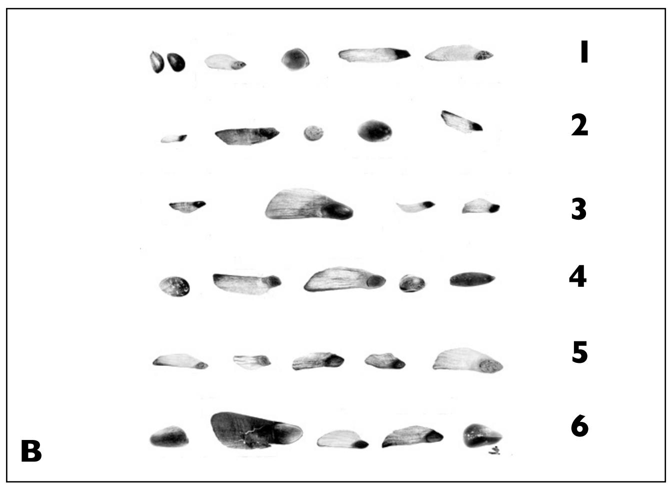
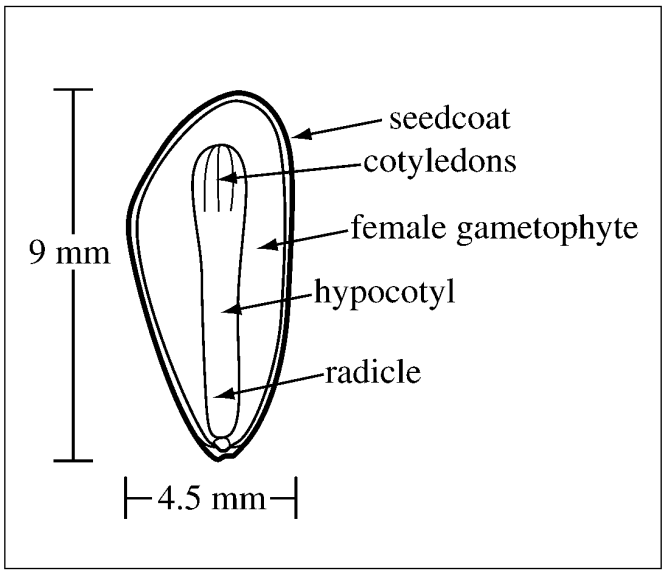


Figure 3—*Pinus ponderosa,* ponderosa pine: longitudinal section through a mature seed.



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

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

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

Seeds of most pines have a membranous seedwing (figure 2). Seedwings detach readily in the hard pines (except for Canary Island, Italian stone, and Chir pines) but adhere firmly in the soft pines (except bristlecone and certain sources of foxtail pine). In nut pines such as Mexican, singleleaf, and Parry piñyons and chilgoza pine, the wings or modified wings may stay attached to the cone scale when the seeds are shed. In pines such as whitebark, Armand, Swiss stone, limber, chilgoza, Korean, Japanese stone, Siberian, and southwestern white pines, seedwings are rudimentary or nonexistent (Mirov 1967; Shaw 1914; Sudworth 1908; Troup 1921; Uyeki 1927).

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

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

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

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

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

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

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

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

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, samples 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).

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

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

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

Species	Cone processing schedule* Boiling water dip (sec)	Air-drying (day)	Kiln-drying (hr)	Kiln temp (°C)	Seed storage (yr)†
P. pinea	—	—	—	—	18
P. ponderosa					
var. ponderosa	0	—	3	49	18
	0	4–12	0	—	—
var. scopulorum	0	—	2	74	>15
	0	4–12	0	—	—
P. pumila‡	—	—	—	—	—
P. pungens	0	—	72	49	9
	0	30	0	—	—
P. quadrifolia§	0	2–8	0	—	—
P. radiata	60–120	0	48–72	49	21
	60–120	3–7	0	—	—
P. resinosa	0	—	13–20	54	30
P. rigida¶	—	—	—	—	11
P. roxburghii	0	—	—	—	>4
P. sabiniana	0	—	48	49	5
P. serotina	0	—	48	41	—
P. sibirica‡	—	—	—	—	>2
P. strobiformis	0	14	0	—	—
P. strobus	0	—	15–20	54	10
P. sylvestris	0	—	10–16	49	15
	0	3–7	0	—	—
P. taeda	0	—	48	41	>9
P. thunbergiana	0–30	5–20	0	—	11
P. torreyana	0	5–20	0	—	6
P. virginiana	0	—	2	77	>5
P. washoensis	0	4–12	0	—	8

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

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

Large numbers of seeds of certain other pines, such as piñyon and singleleaf and Parry piñyons, are harvested by shaking or beating the tree crowns and gathering extracted seeds from the ground (Krugman and Jenkinson 1974). This technique has been expanded with the net retrieval system that is used in many seed orchards of loblolly, Virginia, and eastern white pines (Bonner 1991). The system, originated in the early 1970s by the Georgia Forestry Commission (Wynens and Brooks 1979), employs large rolls of polypropylene netting (carpet backing) spread out beneath the trees. As the cones open naturally on the trees, seeds fall onto the netting, usually aided by light mechanical shaking. When most of the crop is on the netting, it is rolled up and the seeds recovered. The recovered seeds are usually very moist and trashy, so they must be carefully dried and cleaned. If this is properly done, the seed quality is not damaged (Bonner and Vozzo 1986a). The net retrieval system can be used only where an orchard mix of families is desired for seedling production. If families are to be kept separate for site-specific planting, as is becoming increasingly common for loblolly pine, cones must be collected by hand from each tree.

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

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

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

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

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

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

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

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

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

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

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

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

Southern species, except for longleaf pine, are de-winged in mechanical de-wingers that spray a fine mist of water on the seeds as they slowly tumble; capacities are about 90 kg/hr. The seeds and wing fragments must be dried for separation, and if seed moisture goes above 10% during the process, additional drying may be necessary (Bonner 1991). Longleaf pine must be de-winged dry. In a few pines, de-winging can be simplified by first wetting the seeds and then drying them. Proper redrying precludes loss in seed quality (Wang 1973). The loose seedwings can be fanned out (Stoeckeler and Slabaugh 1965; Wakeley 1954). Mechanical

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

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

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

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

After de-winging and cleaning are completed, empty seeds of many pines can be separated from the filled ones with gravity tables or aspirators (see chapter 3). This separation can also be done by simple flotation in water for many species, such as loblolly, Coulter, and Italian stone pines. It is also possible to use organic liquids of suitable specific gravity on small lots of other species (table 7), but immersing seeds in an organic liquid like ethanol, pentane, or petroleum ether may reduce seed viability. Such reduction can be minimized by using a short immersion time and evaporating all traces of the organic liquid from the seeds retained before use (Barnett 1970). Seeds sorted in organic solvents should be used right away and not stored, as the potential for damage increases in storage (Bonner 1997). If plain water is used to float off empty seeds, the retained seeds should be dried to moisture contents between 5 and 10% before they are stored. Seedlots of some pines, notably lodgepole pine, can be upgraded with the IDS (incubation-drying-separation) method developed in Sweden (Simak 1984) (see chapter 3). Cleaned seeds per weight are known for 65 species and varieties, and cone and seed yields are available for many of them (table 8).

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

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

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

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

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

P

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

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

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

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

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

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

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

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

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

† Seeds were extracted from old cones.

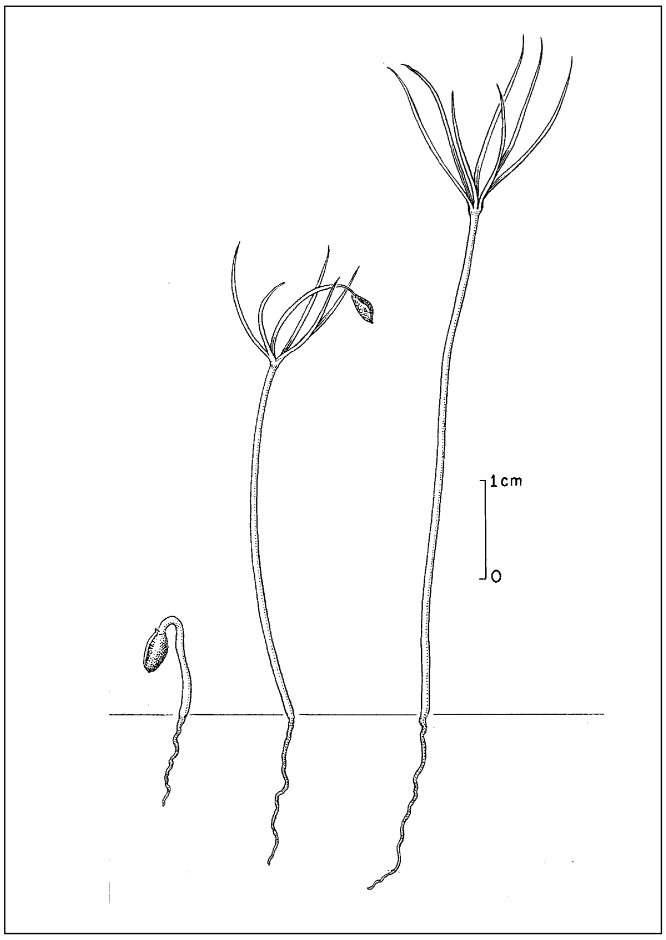
pines, but extended cold stratification, 6 to 9 months of moist chilling, is much more effective (Heit 1968b; Krugman 1966). In any case, acid scarification is not recommended for pine seeds (Krugman and Jenkinson 1974).

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

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

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

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



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

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

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

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

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

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

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Table 11—*Pinus,* pine: nursery practices

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

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

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

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

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

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

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

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

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

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

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

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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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