M

Berberidaceae—Barberry family

Mahonia Nutt.

Oregon-grape

Don Minore, Paul O. Rudolf, and Franklin T. Bonner

Dr. Minore retired from USDA Forest Service's Pacific Northwest Research Station, Corvallis, Oregon; Dr. Rudolf (deceased) retired from the USDA Forest Service's North Central Forest Experiment Station; Dr. Bonner is a scientist emeritus at the USDA Forest Service's Southern Research Station, Mississippi State, Mississippi

Growth habit, occurrence, and use. *Mahonia*—the Oregon-grape—is a genus of about 100 evergreen shrubs native to Asia, Europe, North Africa, and the Americas (Ahrendt 1961). Some authorities (Hitchcock and others 1964) place these species in the genus *Berberis*, and that nomenclature was accepted in the 1974 edition of this book (Rudolf 1974). However, most authorities (LBHB 1976; USDA NRCS 1999) now separate the genera by placing the evergreen species with compound leaves in *Mahonia*. The distinction is far from clear, however: "barberry" is a common name for some *Mahonia* species (table 1) and intergeneric hybrids have been reported (Ahrendt 1961).

Several Oregon-grape species are valued as ornamentals because of their foliage, flowers, or fruits (Bailey 1939; Dirr and Heuser 1987; Rehder 1940; Schlosser and others 1992). Like the closely related barberries, Oregon-grapes also are of value for wildlife food (Decker and others 1991), cover, and erosion-control planting. The names, heights, habits, and ripe fruit colors of some common species are listed in table 1. Six species that have potential value for conservation planting are listed in table 2. Like the barberries, some Oregon-grapes are alternate hosts for the black stem rust of grains—*Puccinia graminis* Pers: Pers). Some species, for example, hollyleaf barberry, Cascade Oregon-grape, and Oregon-grape, are resistant (Rehder 1940).

Like the seeds of the genus *Berberis*, seeds of some members of the genus *Mahonia* contain chemical substances of potential commercial value. The seeds of the Beale

Table 1—*Mahonia,* Oregon-grape: nomenclature, height, and color of ripe fruit

Scientific name & synonym	Common name(s)	Height at maturity (m)	Color of ripe fruit
M. aquifolium **(Pursh) Nutt.** *B. cerberis aquifolium* Pursh	**hollyleaf barberry,** Oregon grapeholly	0.6–3.0	Blue-black, bloomy
M. bealei **(Fortune) Carr.** *B. bealei* Fortune	**Beale Oregon–grape,** leatherleaf mahonia	1.8–3.0	Light blue, bloomy
M. fortunei **(Lindl.) Fedde** *B. fortunei* Lindl.	**Chinese mahonia**	1.5–1.8	Purple-black
M. fremontii **(Torr.) Fedde** *B. fremontii* Torr.	**Fremont mahonia**	0.9–4.6	Bluish black
M. haematocarpa **(Woot.) Fedde** *B. haematocarpa* Woot.	**red barberry**	0.9–3.7	Blood red
M. japonica **(Thunb.) DC.**	**Japanese mahonia**	1.8–3.0	Blue
M. nervosa **(Pursh) Nutt.** *B. nervosa* Pursh	**Cascades Oregon–grape,** Cascades barberry	0.3–1.8	Deep blue, bloomy
M. nevinii **(Gray) Fedde** *B. nevinii* Gray	**Nevin barberry**	0.9–1.8	Yellowish red to deep red
M. pinnata **(Lag.) Fedde** *B. pinnata* (Lag.)	**cluster mahonia**	2.4–3.0	Pruinose blue
M. repens **(Lindl.) G. Don** *B. repens* Lindl.	**Oregon–grape,** creeping barberry	0.3–2.4	Purple, bloomy

Sources: Ahrendt (1961), Dirr (1990), Dirr and Heuser (1987), Hitchcock and others (1964), McMinn (1951), Rehder (1940), Rudolf (1974), USDA NRCS (1999), Vines (1960).

Table 2—*Mahonia*, Oregon-grape: occurrence of species used for conservation planting.

Species	Occurrence
M. aquifolium	British Columbia to Alberta, S to W Montana, W Idaho, through Washington & Oregon to California
M. fremonti	Extreme W Texas, New Mexico, Arizona, California, Colorado, Utah, & Nevada at 1,220 to 2,130 m, & in Baja California & Sonora, Mexico
M. haematocarpa	Dry, sunny sites up to 1,340 m in W Texas, Colorado, New Mexico, Arizona, & adjacent Mexico
M. nervosa	British Columbia S to central California, mainly W of Cascades in Oregon & Washington, E to N Idaho
M. nevinii	California
M. repens	Montana to British Columbia, S to New Mexico & California, including W South Dakota

Source: Rudolf (1974).

Oregon-grape contain alkaloids that are used in folk medicine in Asia (Zhao and others 1991), and seeds of hollyleaf barberry contain tertiary alkaloids of note (Kostalova and others 1986).

Flowering and fruiting. Perfect yellow flowers are borne in the spring in racemes, panicles, umbels, fascicles, or individually, depending on the species (Ahrendt 1961). Stamens are contact-sensitive, and they respond to a tactile stimulus by snapping toward the stigma (Millet 1976, 1977). The fruit (figure 1) is a berry with one to several seeds (figures 2 and 3). A single sample of 100 fruits indicated that most Cascade Oregon-grape berries have about 3 seeds (Minore 1994). Good fruit crops are borne almost annually; the fruits ripen in the summer and autumn (table 3). Seed dispersal by both birds and mammals is widespread (Rudolf 1974; Vines 1960).

Collection of fruit; extraction and storage of seeds. Ripe fruits may be picked by hand (with gloves) or flailed onto cloths or receptacles spread beneath the bushes. The fruits may be run through a macerator or blender with water and the pulp then screened out or floated off. The seeds should then be dried superficially and either sown immediately or stored in sealed containers at temperatures slightly above freezing (Heit 1967; NBV 1946; Rudolf 1974). Seed purity and soundness can be in the 90% range (Rafn and Son nd; Rudolf 1974). Seeds of Fremont mahonia and Oregon-grape did not loose viability for 5 years when stored in unsealed containers in an unheated shed in a temperate climate (Plummer and others 1968). Fruit yields, seed yields, and numbers of seeds per weight are listed in table 4.

Figure 1—*Mahonia nervosa*, Cascade Oregon-grape: a spike of berries.

Pregermination treatments. Seeds of Fremont mahonia and red barberry usually germinate without pretreatment (Dirr and Heuser 1987; Rudolf 1974; Swingle 1939). The seeds of Fremont mahonia have some intermediate embryo dormancy, however, and germination is improved by 6 to 10 weeks of cold stratification at day/night thermoperiods of 5/1 °C (Baskin and others 1993). Beale Oregon-grape and Japanese mahonia should germinate well with only 1 to 2 months of cold stratification (Dirr and Heuser 1987). Seeds of other species also have embryo dormancy that requires cold stratification to overcome (table 5), but simple cold stratification is not always successful. Seeds of cascade Oregon-grape did not germinate after 90 days of cold stratification (Rudolf 1974); up to 5 months of treatment may be required for this species (Dirr and Heuser 1987). Immature or improperly developed embryos are probably present in some species, as maximum germination of hollyleaf barberry was obtained with 4 months of warm stratification followed by 4 months of cold stratification (Dirr and Heuser 1987). A third stratification period (cold + warm + cold) is best for seeds of Oregon-grape (McLean 1967). Under natural conditions, Oregon-grape seeds germinate in the spring after seeds are dispersed (Kern 1921).

Germination tests. Germination of seeds from 4 species of Oregon-grape has been tested in sand-filled flats, in petri dishes, on paper or blotters, or in standard germinators. Day temperatures of 16 to 30 °C, night temperatures of 13 to 21 °C, and germination periods of 20 to 95 days have been used (table 5). Actual germination tests are not prescribed for species of Oregon-grape by the International Seed Testing Association, but germination estimates with tetrazolium chloride (TZ) staining procedures are recommended (ISTA 1993). Seeds should be pre-moistened for 18 hours at 20 °C, cut open by removing a third of the seed at

Figure 2—*Mahonia*, Oregon-grape: seeds of *M. aquifolium*, hollyleaf barberry (**top left**); *M. nervosa*, Cascades mahonia (**top right**); *M. nevins*, Nevin barberry (**bottom left**); and *M. repens*, Oregon-grape (**bottom right**).

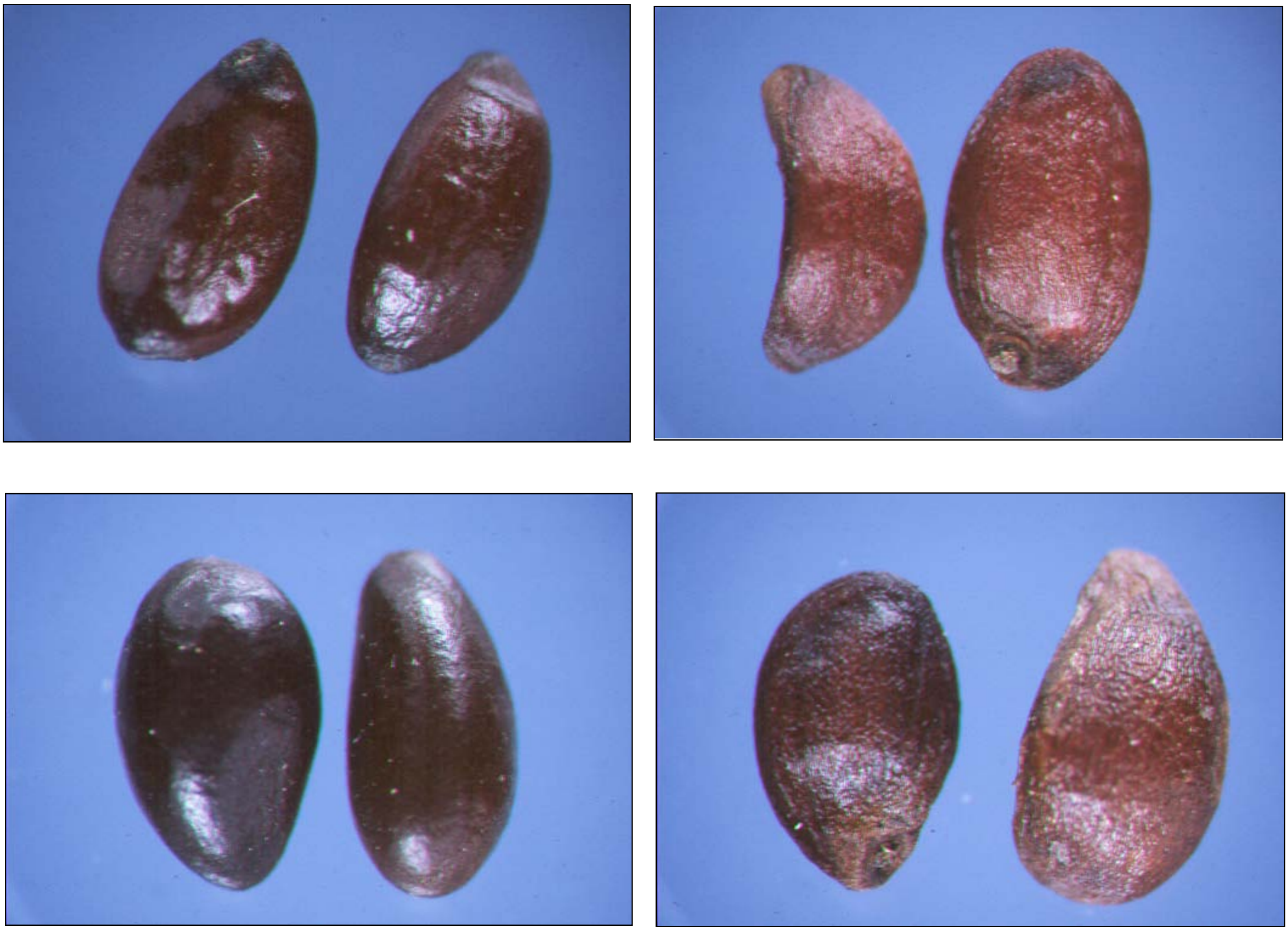


Table 3—*Mahonia*, Oregon-grape: phenology of flowering and fruiting

Species	Location (& altitude)	Flowering	Fruit ripening
M. aquifolium	Mineral Co., Montana (975 m)	Late Apr–early May	Late July–early Aug
	Jackson Co., Oregon (685 m)	Mar–May	Sept–Oct
M. fremontii	Texas, NE US	May–June	Aug–Sept
	Utah & California	May–June	July –Aug
M. haematocarpa	Texas & SW US	Spring	June–Aug
M. nervosa	Clackamas Co., Oregon (90 m)	Early Apr	Mid–Aug
	Jackson Co., Oregon (990 m)	Mid-May	Late Aug
	—	Apr–June	July–Aug
M. nevinii	California	Mar–May	June
M. repens	Black Hills, South Dakota (1,830 m)	May –June	June–July
	—	Apr– May	Aug–Sept

Sources: Bailey (1939), Loiseau (1945), McMinn (1951), Mirov and Kraebel (1939), NBV (1946), Ohwi (1965), Plummer and others (1965), Radford and others (1964), Rudolf (1974), Van Dersal (1938), Vines (1960), Wappes (1982), Wyman (1947).

Table 4—*Mahonia,* Oregon-grape: seed yield data

Species	Place collected	Fruit weight/vol kg/hl	Fruit weight/vol lb/bu	Seed weight/fruit vol kg/hl	Seed weight/fruit vol lb/bu	Cleaned seeds x1,000 /weight Range /kg	Range /lb	Average /kg	Average /lb	Samples
M. aquifolium	Jackson Co., Oregon	44	34	4	3	—	—	73	33	1
	Pacific Northwest	—	—	—	—	84–95	38–43	90	41	2
M. fremontii	Utah	—	—	—	—	—	—	93	42	1+
M. haematocarpa	—	—	—	—	—	—	—	227	103	1
M. nervosa	Clackamas Co., Oregon	39	43*	—	—	—	—	51	23	1
	Pacific Northwest	—	—	—	—	—	—	66	30	2
M. nevinii	California	—	—	—	—	—	—	126	57	1
M. repens	Basin, Montana; & Utah	—	—	—	—	119–157	54–71	136	62	2

Source: Rudolf (1974).
* Data are for berries without stems; data for other species are for berries with stems.

Table 5—*Mahonia*, Oregon-grape: stratification periods, germination test conditions, and percentage germination

Species	Cold stratification* (days)	Daily light (hrs)	Germination test conditions Medium	Temp (°C) Day	Temp (°C) Night	Days	Germination rate Amount (%)	Germination rate Days	Percent germination Avg (%)	Percent germination Samples	Purity (%)	Soundness (%)
M. aquifolium	90	8	Sand or perlite	30	20	30	22	12	25	1	95	99
M. fremontii	0	—	—	—	—	—	—	—	85	2+	90	90+
M. nevinii	90	—	Soil	—	—	95	—	—	77	1	—	—
M. repens	196‡	—	Wet paper	21	21	10	62†	150	74	*1*	*90*	—

Sources: Heit (1968a&b), McLean (1967), Mirov and Kraebel (1939), Morinaga (1926), Plummer and others (1968), Rafn and Son (nd), Rudolph (1974), Swingle (1939), Vines (1960).
* Cold stratification temperatures ranged from –1 to 5 °C.
† Maximum germination was obtained with 4 months of warm stratification at 20 °C, followed by 4 months of cold stratification at 2 to 4 °C (Dirr and Heuser 1987).
‡ Successive stratification periods were 30 days at 1 °C, 60 days at 21 °C, and 196 days at 1 °C. During the final cold period, 62% of the seeds germinated. An additional 12% germinated after the temperature was again raised to 21 °C for a total of 74%.

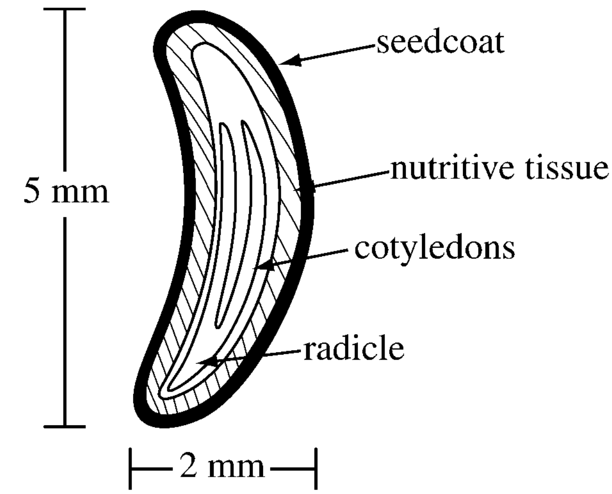
M

the distal end, and incubating in 1% TZ for 18 hrs at 30 °C. All tissues should stain in viable seeds. For the closely related Japanese and common barberries, the Association of Official Seed Analysts (AOSA 1993) recommends germination of excised embryos in covered petri dishes at temperatures of 18 to 22 °C for 10 to 14 days. This method may also be satisfactory for species of Oregon-grape.

Nursery practice. Whole berries or (preferably) cleaned seeds may be sown in the fall, or stratified seeds may be sown in the spring. Injury from molds is more likely if whole berries are used (Chadwick 1936). Fall-sown beds should be mulched until germination begins (NBV 1946). The seeds should be covered with 0.3 to 1.3 cm ($^1/_8$ to $^1/_2$ in) of soil plus 0.6 cm ($^1/_4$ in) of sand (Rudolf 1974). Germination is epigeal (Terabayashi 1987).

Oregon-grapes can be propagated from rooted stem cuttings. Many species root best when hardwood cuttings are collected in the autumn or winter (Dirr and Heuser 1987). They should be treated with indole-butyric acid (IBA) rooting hormone in talc or in solution.

Figure 3—*Mahonia repens*, Oregon-grape: longitudinal section through a seed.



References

Ahrendt T. 1961. *Berberis* and *Mahonia*: a taxonomic revision. Journal of the Linnean Society of London, Botany 57(369): 1–410.

AOSA [Association of Official Seed Analysts]. 1993. Rules for testing seeds. Journal of Seed Technology 16(3): 1–113.

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

Baskin CC, Baskin JM, Meyer SE. 1993. Seed dormancy in the Colorado plateau shrub *Mahonia fremontii* (Berberidaceae) and its ecological and evolutionary implications. Southwestern Naturalist 38(2): 91–99.

Chadwick LC. 1936. Improved practices in propagation by seed. American Nurseryman 62(8): [3]–4; (9): 5–6; (10): 7–8; (12): [3]–9.

Decker SR, Pekins PJ, Mautz WW. 1991. Nutritional evaluation of winter foods of wild turkeys. Canadian Journal of Zoology 69(8): 2128–2132.

Dirr MA. 1990. Manual of woody landscape plants: their identification, ornamental characteristics, culture, propagation, and uses. 4th. ed. Champaign, IL: Stipes Publishing Co. 1007 p.

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

Heit CE. 1967. Propagation from seed: 8. Fall planting of fruit and hardwood seeds. American Nurseryman 126(4): 12–13, 85–90.

Heit CE. 1968a. Propagation from seed: 15. Fall planting of shrub seeds for successful seedling production. American Nurseryman 128(4): 8–10, 70–80.

Heit CE. 1968b. Thirty-five year's testing of tree and shrub seeds. Journal of Forestry 66(8): 632–634.

Hitchcock CL, Cronquist A, Ownbey M, Thompson JW. 1964. Vascular plants of the Pacific Northwest: 2. Salicaeae to Saxifragaceae. Seattle: University of Washington Press. 597 p.

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

Kern FD. 1921. Observations of the dissemination of the barberry. Ecology 2: 211–214.

Kostalova D, Hrochova V, Tomko J. 1986. Tertiary alkaloids of *Mahonia aquifolium* (Pursh) Nutt. III. Chemical Papers 40(3): 389–394.

LHBH [Liberty Hyde Bailey Hortorium]. 1976. Hortus third: a concise dictionary of plants cultivated in the United States and Canada. New York: Macmillan. 1290 p.

Loiseau J. 1945. Les arbres et la forêt. Paris: Vigot Freres. 204 p.

McLean A. 1967. Germination of forest range species from southern British Columbia. Journal of Range Management 20(5): 321–322.

McMinn HE. 1951. An illustrated manual of California shrubs. Berkeley: University of California Press. 663 p.

Millet B. 1976. Kinetic study of the curve of *Mahonia aquifolium* (Pursh) Nutt. stamens electrically stimulated. Annales Scientifiques de l'Universite de Besancon Botanique 3(17): 75–80 [Biological Abstracts 68(5): 3095, Ref. 31123].

Millet B. 1977. A scanning electron microscope survey of the surface of the staminal filament in some Berberidaceae: Comparison with other sensitive organs. Comptes Rendu des Seances de la Societe de Biologie, et de Ses Filiales 171(3): 580–584 [Biological Abstracts 65(8): 4336, Ref. 44154].

Minore D. 1994. Personal observation. Corvallis, OR: Pacific Northwest Research Station.

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

Morinaga T. 1926. Effect of alternating temperatures upon the germination of seeds. American Journal of Botany 13: 141–158.

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

Ohwi J. 1965. Flora of Japan. Washington, DC: Smithsonian Institution. 1067 p.

Plummer AP, Christensen DR, Monsen SB. 1968. Restoring big-game range in Utah. Pub. 68-3. Salt Lake City: Utah Division of Fish and Game. 182 p.

Radford AE, Ahles HE, Bell CR. 1964. Guide to the vascular flora of the Carolinas. Chapel Hill: University of North Carolina Book Exchange. 333 p.

Rafn J and Son. No date. Skovfrökontoret's Fröanalyser gennem 40 Aar, 1887–1927. Copenhagen: Udfört paa Statsfrökontrollen i Köbenhavn. 5 p.

Rehder A. 1940. Manual of cultivated trees and shrubs hardy in North America. 2nd. New York: Macmillan. 996 p.

Rudolf PO. 1974. *Berberis*, barberry, mahonia. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 247–251.

Schlosser WE, Blatner KH, Zamora B. 1992. Pacific Northwest forest lands potential for floral greenery production. Northwest Science 66(1): 44–55.

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

Terabayashi S. 1987. Seedling morphology of the Berberidaceae. Acta Phytotaxonica Geobotanica 38(0): 63–74 [Biological Abstracts 85(7): AB-121, Ref. 65180].

USDA NRCS [USDA Natural Resources Conservation Service]. 1999. The PLANTS database [website available at http://plants.usda.gov/plants]. Baton Rouge, LA: USDA National Resources Conservation Service, National Plant Data Center.

Van Dersal WR. 1938. Native woody plants of the United States: their erosion control and wildlife values. Misc. Pub. 303. Washington, DC: U.S. Department of Agriculture. 362 p.

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

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

Wyman D. 1947. Seed collection dates of woody plants. Arnoldia 7(9): 53–56.

Zhao TF, Wang XK, Rimando AM, Che CT. 1991. Folkloric medicinal plants: *Tinospora sagittata* var. *cravaniana* and *Mahonia bealei*. Planta Medica 57: 5, 505.

Rosaceae—Rose family

Malus Mill.

apple

Paul D. Anderson and John A. Crossley

Dr. Anderson is a plant physiologist at the USDA Forest Service's Pacific Northwest Research Station, Corvallis, Oregon; Mr. Crossley retired from the USDA Forest Service's Northeastern Forest Experiment Station

Growth habit, occurrence, and use. The apple genus—*Malus* Mill.—includes about 25 species of deciduous trees or shrubs native to the temperate regions of North America, Europe, and Asia. Taxonomic classification of the native North American apples is the subject of active debate (Green 1996; Yanny 1996). Rehder (1940) recognized 9 native species—*M. angustifolia, M. bracteata, M. coronaria, M. fusca, M. glabrata, M. glaucescens, M. ioensis, M. lancifolia, and M. platycarpa.* Fiala (1994) suggests that, based on chromosome number, there are 3 distinct native species—M. coronaria, M. fusca, and M. ioensis. Other taxonomic structures having intermediate numbers of species have proponents (Green 1996). The nomenclature and occurrence of commonly recognized species are presented in table 1.

Native apples and planted cultivars occur throughout much of North America. In general, apple performs best in full sunlight in deep, well-drained soils. Growth and vigor are best in rich sandy loams, but apple will grow well in heavier clay soils as long as they are well-drained (Fiala 1994). Ideal soil pH ranges from 5.5 to 6.5, but soils with pH in the range of 5.0 to 7.5 will support apple species (Fiala 1994).

The Oregon crab apple, the only native apple in western North America, occurs along the Pacific Coast from northern California to Alaska, occupying mesic to wet habitats at less than 800 m elevation (Hickman 1993). In California and Oregon, it occurs in open forests of the coast ranges and the foothills of the Cascade Range (Hickman 1993). In British Columbia and southern Alaska, its range includes coastal climatic regions as well as zones of gradual transition to continental climate (Pojar 1996; Vierdeck and Little 1972). Oregon crab apple occurs as an early seral species occupying gaps within old-growth forests, as a component of estuarian and riparian complexes in major river valleys, and in upland Sitka spruce–red cedar swamps having locally perched water tables. In tidal marshes, it can form thickets as the dominant canopy species in association with grasses and forbs. It also occurs in the coastal fringe forest as scattered, slow-growing individuals on rocky shorelines and inland passages where it is protected from wind and salt spray. Oregon crab apple is somewhat tolerant of brackish water and short-term inundation.

In the upper mid-West of the United States, prairie and Great Lakes crab apples occur in open areas, on well-drained soils, near forest margins, in abandoned pastures, in oak savannahs, and at prairie margins (Kromm 1996; Little 1980; Yanny 1996). Common associates include shrubs of hawthorn (*Crataegus* spp.) and bur (*Quercus macrocarpa*) and black (*Q. velutina)* oaks. In southeastern Wisconsin, the native crab apples occur with greater frequency on clay and loam soils than on sandy soils. However, in contrast to Oregon crab apple, neither prairie or Great Lakes crab apples occur in wet areas (Kromm 1996).

In the southeastern United States, southern crab apple occurs at low altitudes on moist soils of valley bottoms and lower slopes. It is found in abandoned fields, along fence rows, and at forest margins, often forming dense thickets (Little 1980).

Native apples have served as a supply of food for both wildlife and humans. Indigenous peoples in both the eastern and western regions of North America have consumed crab apples (Pojar 1996; Vierdeck and Little 1972; Yarnell 1964). The occurrence of crab apples may be locally abundant in areas traditionally inhabited by indigenous peoples, but it is not known whether the trees were cultivated or grew from discarded fruit remains (Pojar 1996).

Consumption of fruit by birds and mammals is common. Known consumers include grouse (*Bonasa umbellus*), pheasant (*Phasianus colchicus*), rabbits (*Sylvilagus* spp.), squirrels *(Sciurus* spp.*)*, opossum (*Didelphis virginiana*), raccoon (*Procyon lotor*), skunks (*Conepattus* spp.) and foxes (*Vulpes vulpes*) (Little 1980). The abundance of crab apples along fencelines and riparian areas is thought to reflect dispersal by wildlife. However, the large fruit size and retention of the stem upon falling make transport by

Table 1— *Malus*, apple: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***Malus angustifolia* (Ait.) Michx.**	**southern crab apple,** narrow-leaf crab apple	SE US from Virginia to Florida & W to Mississippi
***Malus baccata* (L.) Borkh.** *Pyrus baccata* L.	**Siberian crab apple**	Asia; planted extensively in US
***M. coronaria* (L.) Mill.** *P. bracteata* Baily; *P. coronaria* L. *M. bracteata* (Baily) Rehd.	**American crab apple,** wild sweet crab apple, garland-tree	E US; New York to Alabama, W to E Indiana
***M. coronaria* var. *dasycalyx* Rehd.** *P. coronaria* var. *dasycalyx* (Rehd.) Fern. *P. coronaria* var. *lancifolia* (Rehd.) Fern. *P. lancifolia* (Rehd.) Baily *M. coronaria* var. *lancifolia* (Rehd.) C.F. Reed *M. lancifolia* Rehd.	**Great Lakes crab apple**	S Ontario to Ohio & Indiana
***M. floribunda* Sieb. ex Van Houtte** *M. pulcherrima* (Sieb.) Makino	**Japanese flowering crab apple**	Japan; planted extensively in E US
***M. fusca* (Raf.) Schneid.** *P. rivularis* Dougl. ex Hook. *P. fusca* Raf. *M. diversifolia* (Bong.) M. Roemer	**Oregon crab apple**, Pacific crab apple, western crab apple, wild crab apple	Pacific Coast region from N California to S Alaska
***M. glabrata* Rehd.**	**Biltmore crab apple**	SE US; North Carolina to Alabama
***M. glaucescens* Rehd.** *P. glaucescens* (Rehd.) Baily	**Dunbar crab apple**	E US; New York to North Carolina & W into Alabama
***M. ioensis* (Wood) Britt.** *P. ioensis* (Wood) Baily	**prairie crab apple**, Iowa crab apple, midwest crab apple	Minnesota & Wisconsin to Nebraska & Kansas & to Texas & Louisiana
***M. pumila* P. Mill.** *P. pumila* (P. Mill.) Borkh. *M. communis* Poir *M. domestica* (Borkh.) Borkh.	**common apple,** apple, paradise apple	Europe & W Asia; cultivated horticulturally and agriculturally in US
***M. x robusta* (Carr.)** Rehd. *M. baccata x (M. prunifolia* (Willd.) Borkh.	**red Siberian crab apple**	Asia
***M. sargentii* Rehd.**	**Sargent apple**	Japan
***M. sylvestris* P. Mill.** *P. malus* L. *M. malus* (L.) Britt.	**European crab apple,** apple	Europe & W Asia

Sources: Crossley (1974), Fiala (1994), Little (1980).

most species of frugivorous birds unlikely (Snow and Snow 1988). Observations suggest that deer may be the principal dispersal agent of crab apples in Europe (Snow and Snow 1988) and in southern Wisconsin (Kromm 1996).

Members of the apple genus have traditionally been some of our most important fruit bearers and ornamentals (table 1). Siberian crab apple has been used in shelterbelts. Larger stems of southern crab apple have been used to make tool handles. More recently, propagation of native crab apples has become increasingly important for habitat restoration (Callahan 1996) and apple cultivars have been considered for use in revegetation of minespoil (Brown and others 1983). Seedling propagation of native prairie crab apple as an ornamental is increasing in the mid-West as a means of avoiding the poorly adapted plants that can arise as sprouts from non-native rootstock following shoot girdling or browsing (Yanny 1996). Many cultivated varieties have been developed from the common or cultivated apple and from the Siberian crab apple, but these varieties are usually propagated vegetatively. Common apple and European crabapple are most often used as the rootstock for cultivars of crab apple (Fiala 1994).

Flowering and fruiting. The pink to white perfect flowers appear in the spring with or before the leaves. Flowering time varies among species from March to June (table 2). The fruit is a fleshy pome in which 3 to 5 carpels, usually 5, are embedded. Each carpel contains 2 seeds or 1 by abortion (figure 1) (Sargent 1965). Seeds have a thin lining of endosperm (figure 2), except in the cultivated, or common, apple, which has almost no endosperm (Martin 1946). Depending upon species, fruits ripen as early as August or as late as November (table 2). The fruits drop to the ground soon after ripening. Color of ripe fruit varies among the species (table 2).

Good crops of fruits and seeds generally occur every 2 to 4 years (Crossley 1974); however, good seed production

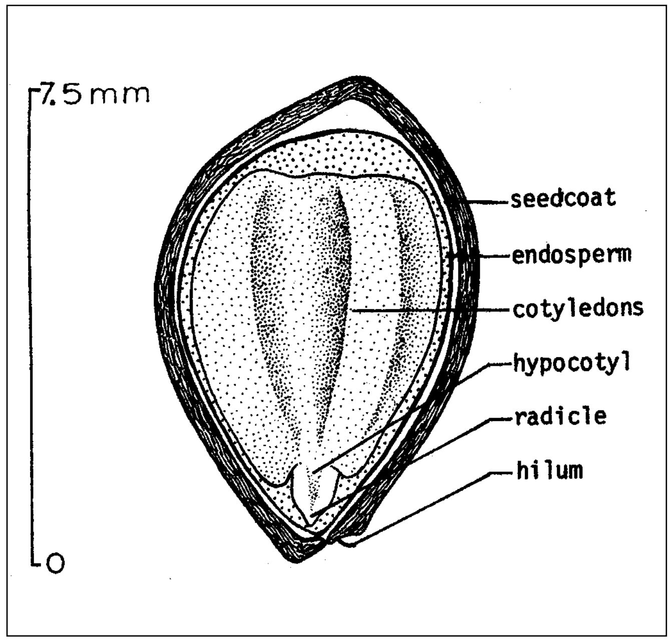
Table 2—*Malus*, apple: phenology of flowering and fruiting, color of ripe fruit, and height of mature trees

Species	Flowering	Fruit ripening	Color of ripe fruit	Height of mature trees (m)	Year first cultivated
M. baccata	May	Aug–Oct	Red or yellow	12.2	1784
M. coronaria	Mar–May	Sept–Nov	Yellow-green	9.2	1724
M. floribunda	May	—	Red or yellow	3.6–10.0	1862
M. fusca	—	Oct–Nov	Green-yellow to yellow & red	8–12.2	1836
M. ioensis	May–June	Sept–Oct	Greenish waxy	—	1885
M. pumila	May	Aug–Oct	Yellow to red	15.4	Ancient times
M. x robusta	Apr–May	—	Red or yellow-green	—	1815
M. sargentii	—	—	Red	1.8–2.5	—

Sources: Callahan (1996), Crossley (1974), Fiala (1994), Krüssmann (1960), Nielsen (1988), Rehder (1940), Sudworth (1908), Van Dersal (1938).

Figure 1—*Malus pumila*, common apple: seeds.

Figure 2—*Malus coronaria*, American crab apple: longitudinal section through a seed.



has been observed annually for select stands of prairie crab apple in Wisconsin (Kromm 1996) and for many crab apple cultivars (Fiala 1994). Seed production may be negatively affected by late-spring frosts. The severity of frost effect on seed production depends on the stage of fruit development at the time of frost. Late-flowering cultivars of apple are less susceptible to fruit damage by late frosts than early and medium flowering cultivars (Nybom 1992). Cultivars of apple exposed to freezing temperatures during the pink to early-bloom stages of fruit development demonstrated seed abortion and fruit pedicle damage, but they continued to produce a smaller, but economically significant fruitcrop (Simons and Doll 1976). A similar phenomenon has been observed in a wild stand of prairie crab apple, where a normal crop of crab apples were produced, yet the fruits bore no seeds (Kromm 1996).

Biennial bearing is a problem for commercial apple production (Williams 1989). Alternate-year fruit production arises from competitive effects of vegetative production, fruit development, and flowering. Trees bearing fruit with a large complement of seeds tend to initiate fewer flowers. Chemical methods, including the post-bloom application of thinning agents or growth regulators, have been used in manipulating fruit set and fruit quality (shape, firmness, russeting, and seed set) in commercial cultivars of apple (Greene 1989; Looney and others 1992; Williams 1989).

Collection of fruits; extraction and storage of seed. Ripe apples may be collected either by picking the fruits from the tree or by gathering fallen fruits from the ground (Crossley 1974). In contrast to domesticated varieties of apples, crab apples may persist in good condition on the ground for 2 to 3 weeks. Fruits from wild trees need to be collected soon after they ripen, for wildlife may rapidly forage and deplete crops in the wild. Large amounts of seeds from domesticated apple cultivars may be extracted from cores obtained at food-processing plants (Richardson 1966). Seeds from cider mills, however, are often damaged (Crossley 1974) and may have a very low germinative capacity.

Accepted methods for seed extraction from the ripe fruits are cumbersome procedures involving combinations of after-ripening, mashing, and separation of pulp and seeds. After-ripening is the partial fermentation of the fruit. This can be done in a large container where the fruits are maintained at 10 to 18 °C for 2 to 4 weeks to soften (Callahan 1996; Nielson 1988). The softened fruits are then covered with water and mashed. The seeds may be sieved or left to settle out while the pulp is floated over the top with running water (Richardson 1966). Care should be taken to avoid high temperatures or excessive fermentation, as this may injure or kill the seeds (Heit 1967). Seeds may also be extracted by putting the fruits through a mechanical macerator (blender) with water, floating off the pulp, and then screening out the seeds (Nielson 1988). Mechanical macerators or presses must be used with caution, as the seedcoats of apple species are thin and easily damaged, resulting in loss of germinative capacity. Extraction may be enhanced by carefully slitting the endodermis of the fruit before mashing (Yanny 1996). Wisconsin native populations of prairie and Great Lakes apples yield 1 to 2 and 3 to 4 viable seeds per fruit, respectively (Kromm 1996). The numbers of seeds per weight of fruit for various species are listed in table 3.

Seeds extracted in the above fashion can be sown immediately. If there is a need for overwintering, the seeds can be air-dried at room temperature for 3 months and then placed in refrigerator in a 50:50 sand and peat mixture for an additional 3 months. As with seeds of commercial varieties of apple, seeds from native crab apples may germinate in cold storage, resulting in difficult sowing.

Apple seeds are orthodox in storage behavior; long-term storage of seeds can be accomplished by drying the seedlot to lower moisture contents. Seeds dried to a moisture content less than 11% have been stored in a sealed container at 2 to 10 °C for over 2 years without loss of germinative capacity or seedling vigor (Solovjeva and Kocjubinskaja 1955). Decline in seed viability as a function of storage temperature and seed moisture content has been modeled for cultivars of cultivated apple (Dickie and Bowyer 1985). They determined that seedlots dried to 14.5% moisture content (fresh-weight basis) and stored at 6 °C lose half their viability in 323 days. With further drying to 5%, the estimated storage life increases to 37 years at –5 °C storage temperature or 100 years at –18 °C storage temperature (Dickie 1986).

Germination. Apple seeds display dormancy which has been overcome by cold stratification (table 4). Stratification is achieved by placing the seeds in a moist medium and storing at a temperature of 2 to 5 °C. A minimum of about 30 days under stratification conditions is required to remove embryonic dormancy (Zhang and Lespinasse 1991). After stratification, apple seeds exposed to diurnally alternating day/night temperatures of 30/20 °C, germinated in 30 to 60 days (table 4). Germination is epigeal (figure 3).

The application of growth-regulating chemicals, including gibberellin A_3 (GA_3), ethephon (E), and benzylaminopurine (BAP), has been used to obtain germination from non-stratified seeds (AOSA 1965; Litvinenko 1959; Sinska 1989; Zhang and Lespinasse 1991). Chemical treatments often involve soaking excised embryos in growth regulator solutions for periods of 1 to 24 hours. Variations in the concentration of growth substance and duration of soaking have

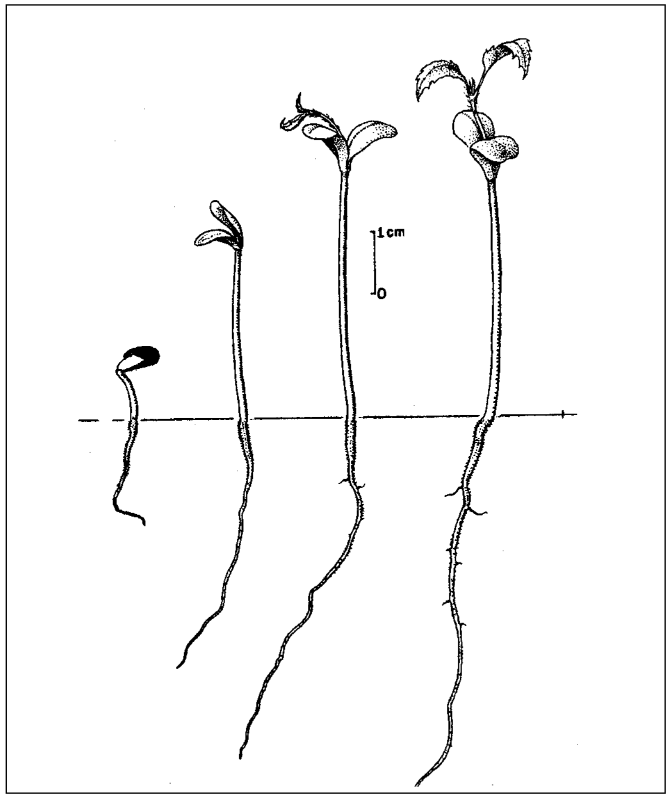
Table 3—*Malus*, apple: seed yield data

Species	Seeds/fruit wt /100 kg	Seeds/fruit wt /100 lb	Cleaned seeds/fruit weight: Range /kg	Range /lb	Average /kg	Average /lb	Samples
M. bacatta	1.2	2.5	10,850–42,000	22,000–85,000	30,000	66,000	5
M. coronaria	0.5	1	—	—	6,350	14,000	1
M. fusca	1.2	2.4	—	—	24,500	54,000	1
M. floribunda	—	—	—	—	26,800	59,000	—
M. ioensis	—	—	—	—	13,600	30,000	1
M. pumila	0.4	0.75	3,460–13,300	7,000–27,000	9,100	20,000	5+
M. x robusta	—	—	—	—	7,700	17,000	—

Sources: Crossley (1974), Swingle (1939).

significant impacts on both the percentage embryo germination and the quality of the resulting plants. Germination of nearly 100% of non-stratified embryos has been obtained with GA_3 applied at concentrations of 12.5 to 50.0 mg/liter for periods of 1 to 24 hours and with BAP applied at 12.5 to 100 mg/liter for periods of 6 to 24 hours. Such treatments have resulted in 50 to 60% germination in less than 10 days and nearly 100% germination in 30 days (Zhang and Lespinasse 1991). Some plants produced from treated embryos demonstrate reduced growth, abnormally thick stems, or poorly developed roots. The percentage of abnormal plants produced tends to increase with increasing growth regulator concentration or increasing period of soaking. Successful application of growth regulator treatments as a substitute for stratification requires careful attention to protocol and is beyond the needs of most propagators as germination percentages of 90% or greater are commonly achieved using the relatively simple cold stratification process.

Figure 3—*Malus coronaria*, American crab apple: seedling development at 1, 3, 9, and 16 days after germination.



Nursery practice. Seedlings for use in landscape restoration or as apple rootstocks are often grown from seeds in nurseries (Richardson 1966; Callahan 1996). Untreated seeds have been sown in late fall (Bakke and others 1926; Callahan 1996; Kromm 1996; Yanny 1996) and stratified seeds have been sown in the spring (Crossley 1974; Yanny 1996). In a Washington nursery, seeds are stratified by first soaking them in water for 5 to 7 days, then placing sacks of seeds between layers of ice in a sawdust pit for 6 to 8 weeks. Seeds are subsequently dried only enough to flow freely through a mechanical planter (Crossley 1974). Seeds are sown in rows 20 cm (8 in) wide and 106 cm (42 in) apart (Davis 1940), 1.25 to 2.5 cm ($^1/_2$ to 1 in) deep on loose friable soil. A thin sawdust mulch aids seedling emergence on soils that form a crust after watering. Seedlings may be sprayed weekly with a fungicide to control powdery mildew. By the end of the growing season most of the seedling stems should be pencil-thick and about 38 cm (15 in) high (Richardson 1966). A height of 23 cm (9 in) is regarded as minimum size for grafting (Davis 1940). Most commercial varieties are propagated by budding or grafting onto seedling rootstocks (Crossley 1974; Fiala 1994; Richardson 1966; Solovjeva and Kocjubinskaja 1955).

In Wisconsin, crab apples for landscape use have been produced from seeds sown in the fall at a density of 270/m^2 (5/ft^2) and covered with 2.5 cm (1 in) of sand. Apple seeds are among the first to germinate in the spring, often while

Table 4—*Malus*, apple: effects of cold stratification and germination test conditions on germination results

Species	Cold stratification (days)	Germination conditions Temp (°C) Day	Night	Days	Germinative energy %	days	Germinative capacity (%)	Samples
M. bacatta	30	30	20	30	48	8	54	2
M. coronaria	120	10	10	30	93	19	96	1
M. fusca	90	—	—	—	—	—	—	—
M. floribunda	60–120	—	—	—	—	—	—	—
M. ioensis†	60	30	20	10	48	4	58	1
M. pumila	60	30	20	60	—	—	65	1+
M. x robusta	60–120	—	—	—	—	—	—	—

Sources: Crossley (1974), Heit (1967), Kallio (1962).
* In a moist medium at temperatures of 2 to 5 °C.
† In another test, fresh seeds from slightly green fruit were sown in a nurserybed without pretreatment and germinated 100%.

soil temperatures are less than 4.5 °C, and the seedlings are generally hardy with respect to spring frost. Seedlings may be grown for 2 years without undercutting, reaching a size of 30 to 60 cm (1 to 2 ft) in height and a caliper of 1.25 cm ($^1/_2$ in) (Kromm 1996).

References

AOSA [Association of Official Seed Analysts]. 1965. Rules for testing seed. Proceedings of the Association of Official Seed Analysts 54(2): 1–112.

Bakke AL, Riches NW, Reeves K. 1926. Germination and storage of apple seeds. Iowa Agricultural Experiment Station Research Bulletin 97: 243–255.

Brown JE, Maddox JB, Splittstoesser WE. 1983. Performance of trees, shrubs, and forbs seeded directly in the fall on minespoil and silt loam soil. Journal of Environmental Quality 12: 523–525.

Callahan F. 1996. Personal communication. Central Point, OR: Callahan Seed.

Crossley JA. 1974. *Malus* Mill., apple. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 531–533.

Davis LL. 1940. Germination and growth of crab apple seedlings as influenced by fungicidal treatment. Proceedings of the American Horticultural Society 37: 359–360.

Dickie JB. 1986. A note on the long-term storage of apple seeds. Plant Genetic Resources Newsletter 65: 13–15.

Dickie JB, Bowyer JT. 1985. Estimation of provisional seed viability constants for apple (*Malus domestica* Borkh. cv. Greensleeves). Annals of Botany 56: 271–275.

Fiala JL. 1994. Flowering crabapples: the genus *Malus*. Portland, OR: Timber Press.

Green T. 1996. Personal communication. Macomb, IL: Western Illinois University.

Greene DW. 1989. CPPU influences 'McIntosh' apple crop load and fruit characteristics. HortScience 24: 94–96.

Heit CE. 1967. Propagation from seed: 11. Storage of deciduous tree and shrub seeds. American Nurseryman 126(10): 12–13, 86–94.

Hickman JC. 1993. The Jepsen manual: higher plants of California. Berkeley: University of California Press.

Kallio TK. 1962. Seed stratification with special reference to apples. Puntarha 65: 62–63 [Horticultural Abstracts 32(4277), 1962].

Kromm D. 1996. Personal communication. Reeseville, WI: Reeseville Ridge Nursery.

Krüssmann G. 1960. Handbuch der Laubgeholze. Volume 1, 495 p.; volume 2, 608 p.

Little EL Jr. 1980. The Audubon Society field guide to North American trees: eastern region. New York: Knopf. 714 p.

Litvinenko SN. 1959. [in Russian: The Ukrainian gibberellin, an effective growth stimulant]. Doklady Akademii Nauk SSSR [Horticultural Abstracts 30(73), 1960].

Looney NE, Granger RL, Chu CL, Mander LN, Pharis RP. 1992. Influences of giberellins A_4, A_4+7 and A_4+iso-A_7 on apple fruit quality and tree productivity: 2. Other effects on fruit quality and importance of fruit position within the tree canopy. Journal of Horticultural Science 67: 841–847.

Martin AC. 1946. The comparative internal morphology of seeds. American Midland Naturalist 36: 513–660.

Neilson KK. 1988. Dormancy in seeds from different positions on individual plants. Acta-Hortica 1 (226): 255-261.

Nybom H. 1992. Freeze damage to flower buds of some apple cultivars. Journal of Horticultural Science 67: 171–177.

Pojar J. 1996. Personal communication. Smithers, BC: British Columbia Ministry of Forests.

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

Richardson BD. 1966. Raising apple seedling rootstock. Tasmanian Journal of Agriculture 37: 15–19.

Sargent CS. 1965. Manual of the trees of North America. New York: Dover. 934 p.

Simons RK, Doll CC. 1976. Morphological and anatomical response of apples to late spring frost in relation to stage of fruit development. Journal of the American Society of Horticultural Science 101: 315–320.

Sinska I. 1989. Interaction of ethephon with cytokinen and gibberellin during the removal of apple seed dormancy and germination of embryos. Plant Science 64: 39–44.

Snow B, Snow D. 1988. Birds and berries: a study of an ecological interaction. Calton, UK: T & D Poyser. 268 p.

Solovjeva MA, Kocjubinskaja VN. 1955. [in Russian: Effect of storage conditions of seed on germination and yield of standard root stocks.] Sadi Ogorod 9: 53–55 [Horticultural Abstracts 26(149), 1956].

Sudworth GB. 1908. Forest trees of the Pacific Slope. Washington, DC: USDA Forest Service. 441 p.

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

Van Dersal WR. 1938. Native woody plants of the United States: their erosion-control and wildlife values. Misc. Pub. 303. Washington, DC: USDA. 165 p.

Viereck LA, Little EL Jr. 1972. Alaska trees and shrubs. Agric. Handbk. 410. Washington, DC: USDA Forest Service. 265 p.

Williams MW. 1989. Control of flowering, fruit set, and seed development in apple (*Malus domestica* Borkh.) with chemical growth regulators. Acta Horticulturae 240:221–228.

Yanny M. 1996. Personal communication. Menomonee Falls, WI: Johnson Nursery.

Yarnell RA. 1964. Aboriginal relationships between culture and plant life in the upper Great Lakes region. Anthropol. Pap. 23. Ann Arbor: University of Michigan, Museum of Anthropology.

Zhang YX, Lespinasse Y. 1991. Removal of embryonic dormancy in apple (*Malus* x *domestica* Borkh) by 6-benzylaminopurine. Scientia Horticulturae 46: 215–223.

Meliaceae—Mahogany family

Melia azedarach L.

chinaberry

Franklin T. Bonner

Dr. Bonner is a scientist emeritus at the USDA Forest Service's Southern Research Station
Mississippi State, Mississippi

Other common names. chinatree, bead tree, Indian lilac, pride-of-India, umbrella chinaberry, umbrella-tree, *paráiso.*

Growth habit, occurrence, and use. Chinaberry—*Melia azedarach* L.—is a short-lived deciduous tree, native to southern Asia and Australia, that has been cultivated and naturalized in tropical, subtropical, and warm temperate regions throughout the world. It has naturalized locally in the southeastern United States from Virginia and Oklahoma south to Florida and Texas. It can also be found in California, Hawaii, Puerto Rico, and Virgin Islands (Little 1979). The tree reaches a maximum height of 15 m in the United States, where it is planted as an ornamental, yet has some value for timber and wildlife food. In India the wood is used for furniture, agricultural implements, and the manufacture of writing and printing paper (Guha and Negi 1965). Extracts of the leaves and fruits have insecticidal properties (Al-Sharook and others 1991; Atwal and Pajni 1964), and the fruits are valuable livestock and game food. Birds and animals are common seed dispersal agents (Vines 1960).

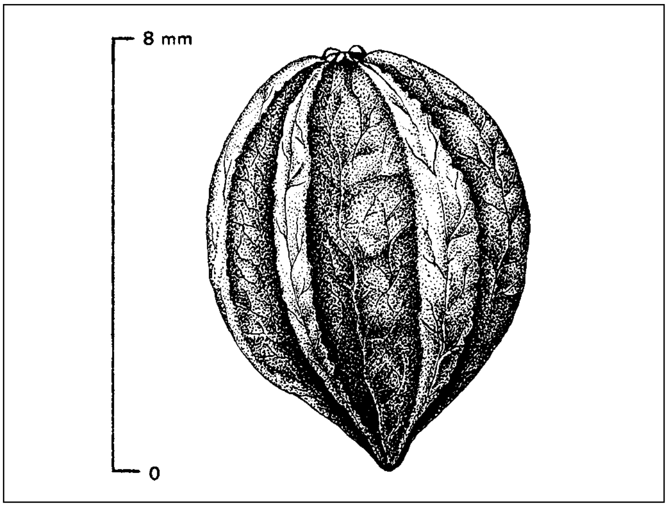
Flowering and fruiting. The flowering habit is either perfect or polygamo-dioecious (Nair 1959). The pretty, lilac-colored perfect flowers are borne in axillary panicles 10 to 15 cm long in March to May. The fruit is a subglobose, fleshy, round, drupe, 13 to 19 mm in diameter, that ripens in September and October and persists on the tree well into winter (Vines 1960). It turns yellow and wrinkled as it ripens (figure 1). Inside the fleshy mesocarp is a single, fluted, light brown or yellowish stone that contains 3 to 5 pointed, smooth, black seeds (figures 2 and 3). Abundant seed crops are borne almost annually.

Collection, extraction, and storage of seeds. Fruits can be collected by hand after the leaves have fallen in late autumn or early winter. Some seeds will germinate when the fruit coats are still green, but it is best to wait until they turn yellow for collection (Moncur and Gunn 1990). The pulp should be removed from the fruits before storage or planting. This can easily be done in mechanical macerators with water, with the pulp floated off or screened out (Amata-Archachai and Wasuwanich 1986). There are about 1,400 fruits/kg (640/lb) (7 samples). Chinaberry is an oily seed of the tropics and subtropics, yet several tests suggest that they are orthodox in storage behavior (Bonner and Grano 1974; Moncur and Gunn 1990). Under refrigerated, dry conditions fruits may be stored for at least a year without loss of viability. Additional research on storage of this species is needed.

Figure 1—*Melia azedarach* L., chinaberry: fruit and stone (**lower left**).

Germination tests. Pregermination treatments are not necessary (Bonner and Grano 1974), but germination is usually improved if the fruit pulp is removed (Moncur and Gunn 1990). In nature, the epigeous germination usually occurs during the spring following dispersal. One fruit may produce up to 4 seedlings. Suggested germination test conditions are 21 °C (night) to 30 °C (day) for 60 days with 200 seeds/test in sand flats. Fresh stones from southeastern Arkansas had a germinative capacity of 81% at 90 days in sand flats in a greenhouse; germination rate was 54% at 30 days (Bonner and Grano 1974). Seeds from tropical sources

Figure 2—*Melia azedarach* L., chinaberry: stone (**left**) and seeds (**right**).



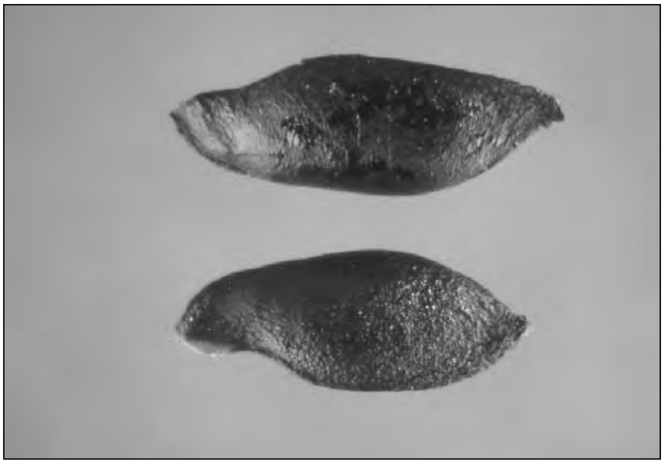
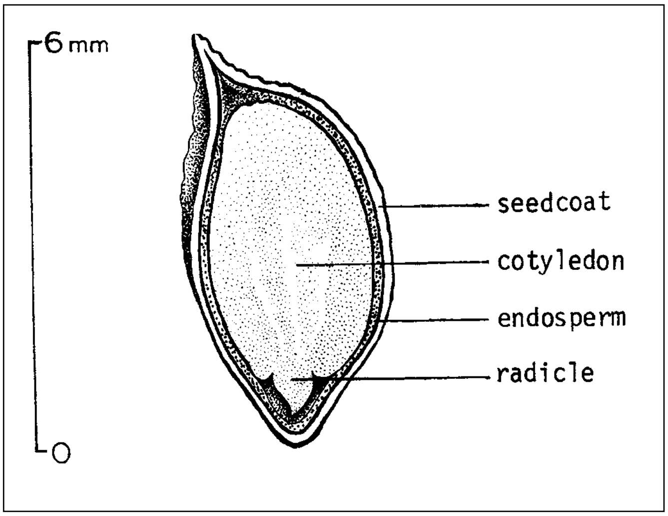


Figure 3—*Melia azedarach* L., chinaberry: longitudinal section through a seed.



seem to require higher temperatures for germination. Moncur and Gunn (1990) reported very little germination below a regime of 30 to 35 °C for Australian collections

Nursery practice. Stones are usually sown intact immediately after collection in the fall or in the following spring. They should be sown 5 to 7 cm (2 to 3 in) apart in drills and covered with about 2.5 cm (1 in) of soil. Germination takes place about 3 weeks after a spring sowing. As planting stock, 1-year-old seedlings are preferred. Older stock should be top-and-root pruned. Chinaberry may also be propagated from cuttings and root suckers and by direct seeding (Bonner and Grano 1974; Dirr and Heuser 1987).

References

Al-Sharook Z, Balan K, Jiang Y, Rembold H. 1991. Insect growth inhibitors from two tropical Meliaceae: effects of crude seed extracts on mosquito larvae. Journal of Applied Entomology 111: 425–430.

Amata-Archachai P, Wasuwanich P. 1986. Mechanical extraction and cleaning of nuts of some tropical species. Embryon 2(1): 1–8.

Atwal AS, Pajni HR. 1964. Preliminary studies on the insecticidal properties of drupes of *Melia azedarach* against caterpillars of *Pieris brassicae* L. (Lepidoptera: Pieridae). Indian Journal of Entomology 26: 221–227.

Bonner FT, Grano CX. 1974. *Melia azedarach* L., chinaberry. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 535–536.

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

Guha SRD, Negi JS. 1965. Writing and printing paper from *Melia azedarach* Linn. (Persian lilac). Indian Forester 91: 867–869.

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

Nair NC. 1959. Studies of Meliaceae: 2. Floral morphology and embryology of *Melia azedarach* Linn.—a reinvestigation. Journal of the Indian Botanical Society 38: 367–378.

Moncur MW, Gunn BV. 1990. Seed development and germination responses of *Melia azedarach* var. *australasica*. In: Turnbull JW, ed. Tropical tree seed research. 1989 August 21–24; Gympie, Australia. AICAR Proc. 28. Canberra: Australian Centre for International Agricultural Research: 24–28.

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

M

Menispermaceae—Moonseed family

Menispermum canadense L.

common moonseed

Kenneth A. Brinkman and H. M. Phipps*

Drs. Brinkman and Phipps retired from the USDA Forest Service's North Central Research Station

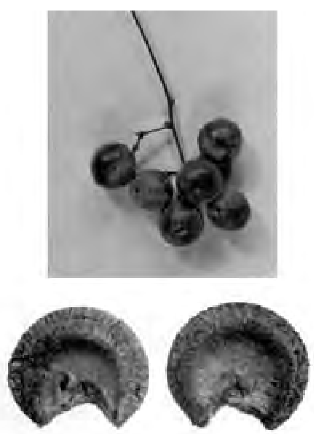
Growth habit, occurrence, and use. Common moonseed—*Menispermum canadense* L.—is a climbing woody vine growing to a height of 3.6 m (Rehder 1940) that is capable of spreading from underground stems (Wyman 1949). It is native from Quebec and western New England to southeastern Manitoba, south to Georgia, Alabama, and Oklahoma (Fernald 1950). The plants are seldom eaten by livestock (Van Dersal 1938), but the fruits are of value to wildlife, although reportedly poisonous to humans (Kingsbury 1964). This species has been cultivated since 1646 for its attractive foliage and fruit (Rehder 1940).

Flowering and fruiting. The dioecious flowers appear from May to July and the bluish-black drupes ripen from September to November (Grimm 1966; Redher 1940). The seeds are flattened stones in the form of a crescent or ring (figures 1 and 2).

Collection of fruits and seed extraction. Fruits may be collected from September to November (Rehder 1940). Seeds may be extracted by washing the macerated fruits in water. One sample showed 16,758 seeds/kg (7,600/lb) (Brinkman and Phipps 1974).

Germination. Stratification of one seedlot at 5 °C for 60 days resulted in 65% germination in 11 days and 98% in 26 days. An unstratified seedlot showed germination of 83% in 28 days and 92% in 60 days (Brinkman and Phipps 1974). Germination was tested in sand under light at alternating temperatures of 30 (day) and 20 °C (night).

Figure 1—*Menispermum canadense* L., common moonseed: fruit (**top**) and seeds (**bottom**).



Nursery practice. Common moonseed is propagated readily by seeds stratified and sown in the spring or planted as soon as ripe (Bailey 1935). Vegetative propagation also is possible from cuttings.

References

Bailey LH. 1935. The nursery manual, a complete guide to the multiplication of plants. 22nd ed. New York: Macmillan. 456 p.

Brinkman KA, Phipps HM. 1974. *Menispermum*, common moonseed. In: Schopmeyer CS, tech coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 537–538.

Fernald ML. 1950. Gray's manual of botany. 8th ed. New York: American Book Co. 1632 p.

Grimm WC. 1966. Recognizing native shrubs. Harrisburg, PA: Stackpole Books. 319 p.

Kingsbury JM. 1964. Poisonous plants of the U.S. and Canada. Englewood Cliffs, NJ: Prentice-Hall. 626 p.

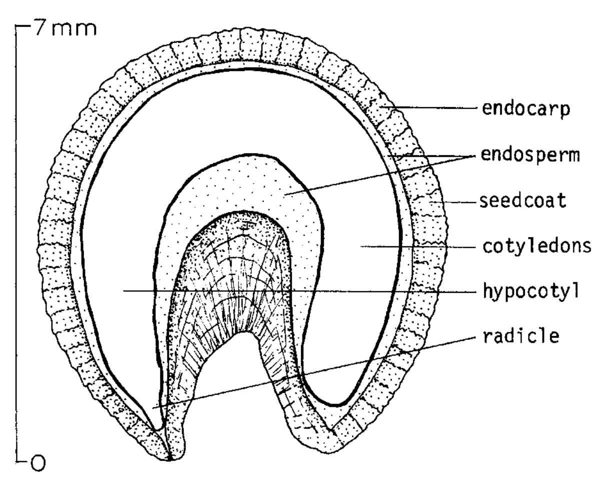
Rehder A. 1940. Manual of cultivated trees and shrubs. 2nd ed. New York: Macmillan. 2996 p.

Van Dersal WR. 1938. Native woody plants of the United States: their erosion-control and wildlife values. Misc. Pub. 303. Washington, DC: USDA Forest Service. 362 p.

Wyman D. 1949. Shrubs and vines for American gardens. New York: Macmillan. 442 p.

*Note: Review of the literature by Jill R. Barbour, germination specialist at the USDA Forest Service's National Seed Laboratory, Dry Branch, Georgia, found no new information.

Figure 2—*Menispermum canadense* L., common moonseed: longitudinal section through a seed.



Oleaceae—Olive family

Menodora scabra Gray

rough menodora

Stanley L. Krugman and John C. Zasada

Dr. Krugman retired from the World Bank and the USDA Forest Service's Research and Development National Office, Washington, DC; Dr. Zasada retired from the USDA Forest Service's North Central Research Station

Growth habit, occurrence, and use. Rough menodora—*Menodora scabra* Gray—is a low herbaceous to woody shrub 0.2 to 0.8 m in height. It is native to dry rocky areas and desert grasslands from 462 to 2,155 m in southern California, Arizona, New Mexico, western Texas, Colorado, and Utah (Munz and Keck 1965; Vines 1960). It provides browse for livestock and game animals (Krugman 1974). Due to the type of habitat in which it is usually found, it should grow on strip-mined land (Sabo and others 1979). The genus *Menodora* is represented by 14 species in North America (Turner 1991). Rough menodora is recommended for use as a rock garden plant.

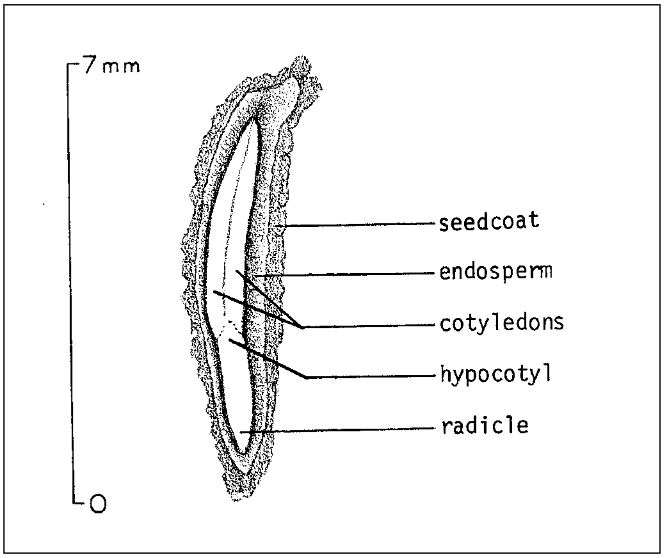
Flowering and fruiting; seed collection and storage. The yellow, often showy flowers of rough menodora appear from May through August (Krugman 1974; Vines 1960). The fruit, a bispherical thin-walled capsule with 2 seeds in each cell, ripens in September to November. Seeds are dispersed during October and November (Krugman 1974; Munz and Keck 1965; Vines 1960). Seeds should be collected from September to November (Krugman 1974). The mature seeds are about 4 to 5 mm in length and 3 mm wide, flat greenish to brownish with a yellowish narrow wing (figures 1 and 2) (Munz and Keck 1965; Vines 1960).

Good seedcrops of rough menodora usually occur annually (Krugman 1974). The number of cleaned seeds per weight in 2 samples was 224,000 and 246,000/kg (102,000 and 112,000/lb). Vines (1960) reported that purity of seedlots was 41% and soundness 98%. Storage in a dry place at room temperature has been satisfactory.

Germination. Sabo and others (1979) reported that germination occurred at alternating and constant temperatures between 14 to 40 °C. The best germination (about 80%) was under alternating temperature regimes of 24 °C for 8 hours and 17 °C for 16 hours and 17 °C for 8 hours and 24 °C for 16 hours. The mean day of germination varied from to about 6 to 10 days under these temperature regimes. Light was not required for germination. Percentage and rate of germination of showy menodora—*M. longiflora* Gray—a

Figure 1—*Menodora scabra*, rough menodora: seed.

Figure 2—*Menodora scabra*, rough menodora: longitudinal section through a seed.



M

related sub-shrub, was improved by acid scarification. However, at a temperature regime of 30/20 °C, 60% of unscarified seeds germinated. Germination rate of scarified seeds increased with increasing temperature up to 30/20 ·°C but declined at warmer temperatures. Seeds of showy menodora germinated in the dark, but both germination rate and germination percentage were greater in a light regime with 12 hours light (Fulbright and Flenniken 1986).

References

Fulbright TE, Flenniken KS. 1986. Effects of temperature and presowing treatments on showy menodora seed germination. Journal of Range Management 39(4): 310–313.

Krugman SL. 1974. *Menodora scabra* A. Gray, rough menodora. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States: Agric. Handbk. 450. Washington, DC: USDA Forest Service: 539.

Munz PA, Keck DD. 1965. A California flora. Berkeley: University of California Press. 1681 p.

Sabo DG, Johnson GV, Martin WC, Aldon EF. 1979. Germination requirements of 19 species of arid land plants. Res. Pap. RM-210. Fort Collins, CO: USDA Forest Service. 23 p.

Turner BL. 1991. An overview of the North American species of *Menodora*. Phytologia 71(5): 340–356.

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

M

Taxodiaceae—Redwood family

Metasequoia glyptostroboides Hu & W.C. Cheng

dawn-redwood

John P. Sloan and LeRoy C. Johnson

Mr. Sloan is at the USDA Forest Service's Lucky Peak Nursery, Boise, Idaho; Mr. Johnson retired from the USDA Forest Service's Pacific Southwest Forest and Range Experiment Station

Growth habit, occurrence, and use. Dawn-redwood—*Metasequoia glyptostroboides* Hu & W.C. Cheng—is the only known living example of its genus (Hu and Cheng 1948). It is often called a "living fossil" because until 1946 it was known only from the fossil record (Hu 1948; Merrill 1945; Shao 1982). The natural range is quite restricted: a few trees are found near the village of Mo-tao-chi in eastern Szechuan Province and the bulk of the native groves are found in Shui-hsa-pa Valley (south of Mo-tao-chi) in the northwestern corner of Hupeh Province, People's Republic of China (Chu and Cooper 1950; Shao 1982). It has been introduced to many other parts of China, as well as the United States and Europe, for a total of 50 other countries (Shao 1982).

Since its introduction into the United States in 1948, this deciduous conifer has mostly been planted as an ornamental, especially at museums and in arboreta. The wood is soft, weak, and brittle, so it has little value as a source of lumber (Wyman 1968), although it is used for building timbers in China (Shao 1982). Pulping characteristics are similar to, and its fibers are stronger than, southern pines (Wyman 1968). In the United States, Wyman (1968) reported height growth was as much as 18 m in 20 years. In China, Shao (1982) described 4-year-old dawn-redwood trees averaging 7 m tall and 11 cm dbh. In its natural range, dawn-redwood grows in the submontane zone at elevations between 100 and 1500 m. The species is hardy in Massachusetts, where the winter temperatures may drop to -34 °C, and thrives in Placerville, California, where summer temperatures often exceed 35 °C and there is usually no summer rainfall (Johnson 1974).

Geographic races. Although great phenotypic diversity exists between planted trees, no geographic races are known to exist. Several cultivars have been described (Broekhuizen and Zwart 1967; DeVos 1963). Of the 6 trees growing at the USDA Forest Service's Institute of Forest Genetics at Placerville, California, half are of the normal single-stemmed conifer shape and the others are bush-shaped with no single branch showing dominance. Johnson (1974) speculates that some of the seeds may have come from self-pollinated trees. According to Shao (1982), dawn-redwood shows a strong apical dominance and produces a straight stem.

Flowering and fruiting. Dawn-redwood is monoecious. Trees that produce female cones begin to do so several years before trees of the same age produce male cones (Em 1972; Li 1957; Wyman 1968). Female trees do not begin to produce seeds until they are 25 to 30 years old and bear heavily until they are 40 to 60 years old, when production diminishes (Shao 1982).

Male cone buds form in leaf axis or on branch tips and become visible in the fall just prior to leaf drop. At this time, they are about 2.5 mm long. Female cones are borne singly, opposite along branches (rarely terminal). Male and female buds begin to grow in late January and are readily seen by early- or mid-February. Pollination takes place in March before the tree puts on needles (Hwa 1945, 1948). This early emergence of the cones makes them susceptible to late winter frosts, which can destroy the cone crop.

Male cone buds are 4 to 6 mm long when closed and 6 to 10 mm long when expanded and shedding pollen. Each staminate strobilus has 20 to 30 distichously arranged microsporophylls with 3 microsporangia per sporophyll. Pollen grains are wingless and covered with a sticky substance that causes them to clump together in masses (Johnson 1968). Female cones have 16 to 26 distichously arranged scales, with 5 to 8 seeds per scale. Mature cones are pendulous (with a 10- to 30-mm peduncle), subquadrangular, and shortly cylindrical; they ripen the same year they are pollinated. Cones ripen in early December and shed their seeds in late December and early January.

Collection, extraction, and storage. Mature cones are light brown, but color is not a good indication of ripeness. Cones should be collected late in the year just before they begin to open. Cones picked when they first turn from green to light brown do not open and the scales must be pried apart. But cones picked when the scales naturally begin to separate will readily open with 1 to 2 weeks of drying at room temperature. Tumbling is necessary because some seeds are firmly welded to the scales. Because seed wings are minute, de-winging is unnecessary (Johnson 1974).

Seedcoats of dawn-redwood are thin and fragile. Seeds with wings attached are light brown, 5 to 6 mm long, 2 to 4 mm wide, obovate (rarely orbicular-oblong), and notched at the apex (figure 1) (Johnson 1974; Nakai and Furuno 1974). Wings are adnate and appear as tegumentary extensions of the seed (Sterling 1949). Average weight per seed is 8 mg (0.0003 oz) (Nakai and Furuno 1974). Nakai and Furuno (1974) found an average of 70 to 90 seeds per cone, with a range of 50 to 110. One kilogram of cones contains 430,00 to 560,000 seeds (1 lb contains 195,000 to 254,000 seeds) (Shao 1982). Dawn-redwood often produces a high proportion of hollow seeds (CDF 1977). Presumably, seeds can be stored in the same manner as those of other genera in Taxodiaceae such as redwood (*Sequoia*) and arborvitae (*Thuja*). Storage of dry seeds in airtight containers at 1 to 4 °C has been satisfactory for these genera (Johnson 1974).

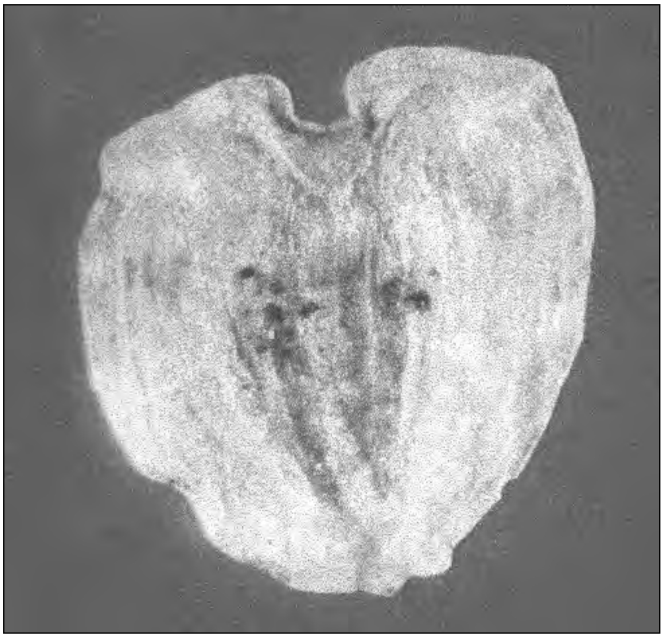
Mechanical separation of seeds is not recommended. Hollow (figure 1) and filled seeds can be identified with x-radiography, but a simpler and more efficient method is to use a light table. The seeds should be scattered 1-layer thick on a light table and then back-lit with the room lights off. The hollow seeds can be picked out with tweezers. However, this method is feasible only on a small scale. If large quantities of seeds become available, all seeds should be stored and then sown, making allowances for seed-fill when the seeding rate is calculating (Johnson 1974).

Germination and nursery practice. Seeds of dawn-redwood do not require chilling (Johnson 1968; Shao 1982; Smith 1950). Germination takes 4 to 8 days (Nakai and Furuno 1974) and is epigeal. After germination, the seedcoat sheds in 3 to 5 days, exposing the cotyledons (Johnson 1974). There are no official testing prescriptions for this species.

Seeds sown directly on soil and mulched with fine sand or Sponge Rok® begin germinating within 5 days (Johnson 1968). During the first 5 weeks of growth, the tender succulent seedlings are particularly susceptible to damping-off (Johnson 1974; Shao 1982). Losses can be minimized by sowing on heat-sterilized or fumigated soil. Young seedlings thrive in high humidity like that found in a greenhouse equipped with automatic overhead sprinklers. In hot climates the young seedlings should be shaded during the first growing season (Johnson 1974).

Because seeds of dawn-redwood are scarce, the species is often propagated from cuttings. Although cuttings are very easy to root (Johnson 1968; Mirov and Blankensop 1955; Shao 1982), growing stock can be produced faster from seeds than from cuttings (Johnson 1974). Cuttings root best when they are taken in early summer through late fall. Rooting is promoted by treatment with 50 ppm of α-naphthalene acetic acid (NAA). Rooting capability of cuttings decreases with increasing age of the mother plant (Shao 1982).

Figure 1—*Metasequoia glyptostroboides*, dawn-redwood: filled seed.



References

Broekhuizen JT, Zwart FN. 1967. A contribution to the knowledge of *Metasequoia glyptostroboides* [English summary]. Agric. Comm. 10. Wageningen, The Netherlands: University of Wageningen Institute of Forest Resources: 439–463.

CDF [China Department of Forestry, Nanking College of Forest Products]. 1977. A preliminary observation on the flowering and seed development of *Metasequoia glyptostroboides* Hu et Cheng. Acta Botanica Sinica 19(4): 252–256.

Chu K, Cooper WS. 1950. An ecological reconnaissance in the native home of *Metasequoia glyptostroboides*. Ecology 31(2): 260–275.

DeVos F. 1963. *Metasequoia glyptostroboides* 'National'. American Horticulture Magazine 42(3): 174–177.

Em H. 1972. *Metasequoia glyptostroboides* and its growth in the Skopje basin. Sumarstvo 24:5–15.

Hu H. 1948. How *Metasequoia*, the "living fossil," was discovered. Journal of the New York Botanical Garden 49(585): 201–207.

Hu H, Cheng W. 1948. On the new family Metasequoiaceae and on *Metasequoia glyptostroboides*, a living species of the genus *Metasequoia* found in Szechuan and Hupeh. Bulletin of Fan Memorial Institute of Biology NS1(2): 153–161.

Hwa CT. 1945. UCB. M 186893. [Herbarium Specimen] *Metasequoia glyptostroboides*. Shui-hsa-pa Valley, 3550 ft. March 10, 1945.

Hwa CT. 1948. UCB. M 186884. [Herbarium Specimen] *Metasequoia glyptostroboides*. In ravine; tree. Li-Chuan, Shui-hsa-pa Valley, 3500 ft. Hupeh Province. March 10, 1948.

Johnson LC. 1968. Crossability of *Metasequoia glyptostroboides*. Genetics Res. File 36105. Placerville, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Institute of Forest Genetics.

Johnson LC. 1974. *Metasequoia glyptostroboides* Hu and Cheng, dawn redwood. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 540–542.

Li H. 1957. The discovery and cultivation of *Metasequoia*. Morris Arboretum Bulletin 5(4): 49–53.

Merrill ED. 1945. *Metasequoia*, another "living fossil." Arnoldia 5(1): 1–5.

Mirov NT, Blankensop CM. 1955. A note on rooting cuttings of dawn redwood. Journal of the California Horticulture Society 20(1): 9–10.

Nakai I, Furuno T. 1974. Flowering and fruiting in *Metasequoia*. Journal of Japanese Forestry Society (Nihon Ringakkai Shi) 56(8): 294–296.

Shao QH. 1982. Silviculture of some important trees species in China. Allgemeine Forst Zeitschrift 11: 314–315.

Smith CM. 1950. Notes on seeds and seedlings of *M[e]tasequoia glyptostroboides*. New Zealand Journal of Forestry 6(2): 145–148.

Sterling C. 1949. Some features in morphology of *Metasequoia*. American Journal of Botany 36(6): 461–471.

Wyman D. 1968. *Metasequoia* after twenty years in cultivation. Arnoldia 25(10/11): 113–123.

Rubiaceae—Madder family

Mitchella repens L.

partridgeberry

Kenneth A. Brinkman, G. G. Erdmann, and Jill R. Barbour

Drs. Brinkman and Erdmann retired from the USDA Forest Service's North Central Forest Experiment Station; Ms. Barbour is a germination specialist at the USDA Forest Service's National Seed Laboratory, Dry Branch, Georgia.

Growth habit, occurrence, and use. Partridgeberry—*Mitchella repens* L., also called two-eyed berry or running-fox—is an evergreen vine or herb with fruit valuable as food for birds, raccoons (*Procyon lotor*), and red foxes (*Vulpes vulpes*) (Van Dersal 1938). The natural range is from Texas to Florida, north to southwest Newfoundland, and west to Ontario and Minnesota (Fernald 1950). This attractive plant was introduced into cultivation in 1761 and is often used in rock gardens (Rehder 1940).

Flowering and fruiting. The distylous flowers appear from June to August and can be separated into 2 genetic compatibility groups (Rehder 1940). Plants with short-styled flowers ("thrums") have exserted stamens 15 mm above the ovary and stigmas 10 mm above the ovary; whereas plants with long-styled flowers ("pins") have stamens 11 mm above the ovary and exserted stigmas 16 mm above the ovary (Ganders 1975). The only pollinations that are compatible are those between anthers and stigmas of the same height, that is, between pin and thrum and thrum and pin. The genetic control is by a single gene (S), with thrums the heterozygotes (Ss) and pins the recessive homozygotes (ss) (Allard 1960). Thrums contribute more than three-quarters of all genes transmitted through ovules, and pins more than three-quarters of all genes transmitted through pollen (Hicks and others 1985). Pins and thrums contribute almost equally to gene flow via pollen and ovules.

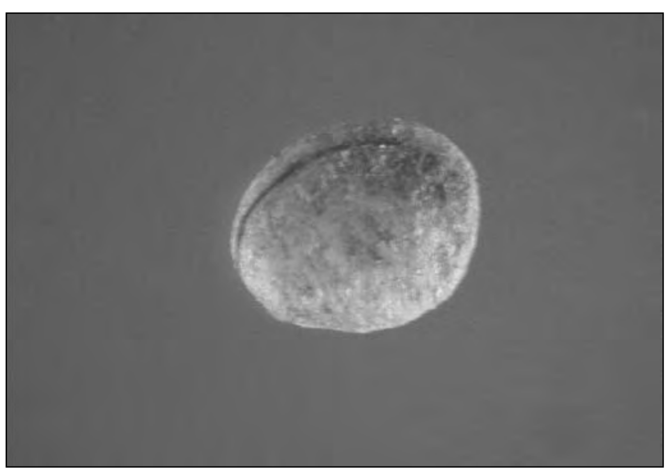
The flowers occur in pairs on a short peduncle with the base of the calyces fused. Each flower has 1 style and 4 stamens (Fernald 1950). Fruit-set occurs when both flowers of a pair have been pollinated. Bumble bees (*Bombus* spp.) are the principal pollinators of partridgeberry. They fly around a patch of partridgeberry for a mean of 2.3 ± 2.3 minutes, visiting 34 ± 43 inflorescences per minute (Hicks and others 1985).

Fruits are scarlet drupaceous berries 7 to 10 mm wide that ripen in July but usually persist overwinter (Petrides 1958). The maximum number of seeds that a single full berry may contain is 8 (Hicks and others 1985). The level of natural fruit-set is near 100% for both pins and thrums. In a flowering study in North Carolina, the overall fruit-set level for pins and thrums was 100%, whereas in New York, the fruit-set was 96.1% for pins and 86.5% for thrums (Hicks and others 1985). A Massachusetts study revealed fruit-set values of 96.8% for pins and 96.3% for thrums (Keegan and others 1979).

Collection of fruits; extraction and storage of seeds. Partridgeberry fruits may be picked in late fall. Fruits should be macerated in water and screened to remove the seeds (figures 1 and 2). About 45 kg (100 lb) of fruit yield about 5.4 kg (12 lb) of cleaned seeds (Swingle 1939). Two samples averaged 427,770 seeds/kg (194,000/lb); 98% of the seeds were sound after cleaning (Brinkman and Erdmann 1974; Swingle 1939). Seeds are orthodox in storage behavior and can be stored for some time in sealed containers at low temperature.

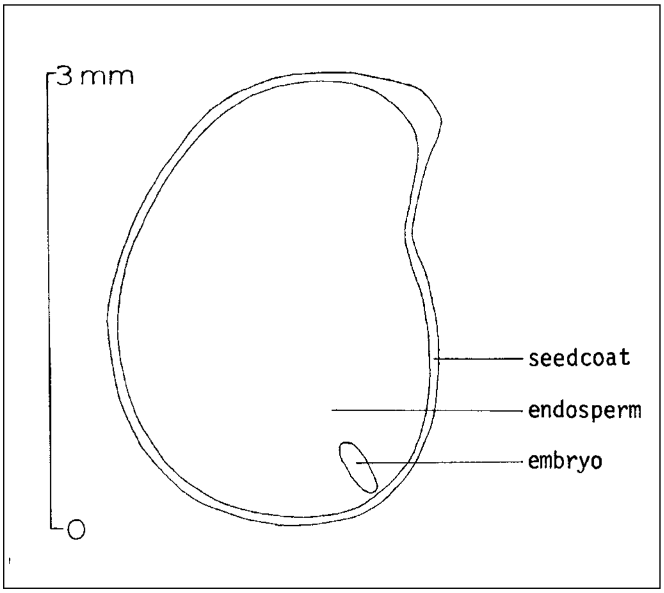
Germination tests. Partridgeberry seeds have internal dormancy, but this can be overcome by 150 to 180 days of stratification at 5 °C (Barton and Crocker 1945). No data are available on results of germination tests.

Figure 1—*Mitchella repens*, partridgeberry: seed.



Nursery practice. Seeds of many other species exhibiting embryo dormancy germinate satisfactorily when sown in the fall, so partridgeberry probably can be handled in the same way. Mulching overwinter should reduce drastic temperature changes and maintain adequate moisture.

Figure 2—*Mitchella repens*, partridgeberry: longitudinal section through a seed.



References

Allard RW. 1960. Principles of plant breeding. New York: John Wiley and Sons. 485 p.

Barton LV, Crocker W. 1945. Twenty years of seed research. London: Faber and Faber. 148 p.

Brinkman KA, Erdmann GG. 1974. *Mitchella repens* L., partridgeberry. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 543.

Fernald ML. 1950. Gray's manual of botany. 8th ed. New York: American Book Co. 1632 p.

Ganders FR. 1975. Fecundity in distylous and self-incompatible homostylous plants of *Mitchella repens* (Rubiaceae). Evolution 29(1): 186–188.

Hicks DJ, Wyatt R, Meacher TR. 1985. Reproductive biology of distylous partridgeberry, *Mitchella repens*. American Journal of Botany 72(10): 1503–1514.

Keegan CR, Voss RH, Bawa KS. 1979. Heterostyly in *Mitchella repens* (Rubiaceae). Rhodora 81: 567–573.

Petrides GA. 1958. A field guide to trees and shrubs. Boston: Houghton Mifflin. 431 p.

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

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

Van Dersal WR. 1938. Native woody plants of the United States: their erosion-control and wildlife values. Misc. Pub. 303. Washington, DC: USDA. 362 p.

Moraceae—Mulberry family

Morus L.

mulberry

Jill R. Barbour, Ralph A. Read, and Robert L. Barnes

Ms. Barbour is a germination specialist at the USDA Forest Service's National Seed Laboratory, Dry Branch, Georgia; Dr. Read retired from the USDA Forest Service's Rocky Mountain Research Station; Dr. Barnes retired from the USDA Forest Service's Southeastern Forest Experiment Station

Growth habit, occurrence, and use. The mulberry genus—*Morus*—comprises about 12 species of deciduous trees and shrubs native to temperate and subtropical regions of Asia, Europe, and North America (Rehder 1956). Seeds of 2 native species and 2 naturalized species are described here (table 1). White (sometimes called "Russian") mulberry was introduced to the United States by Mennonites from Russia in 1875. The United States Prairie States Forestry Project planted an average of over 1 million trees of this species annually from 1937 through 1942 for windbreaks in the Great Plains from Nebraska to northern Texas (Read and Barnes 1974). The high drought resistance of white mulberry makes it well suited for shelterbelt planting (Read and Barnes 1974).

There are 2 mulberries indigenous to North America. Littleleaf mulberry occurs in Arizona, New Mexico, Oklahoma, Texas, and Mexico and has not been cultivated (table 1). Red mulberry has a wide range that covers most of the eastern United States, Great Lakes region, and the southern Great Plains. Though once common, red mulberry is decreasing over its range, possibly because of an unidentified bacterial disease (Moore and Thomas 1977). Its place is being taken by the introduced and naturalized white mulberry (Core 1974).

White mulberry is highly prized in Asia for its leaves, which are eaten by the silkworm—*Bombyx mori* L. The 7 or more forms and varieties of white mulberry differ in their relative drought resistance and in chromosome number and may be climatic races. Both white and red mulberry are diploids ($2n=2x=28$), but black mulberry has a high polyploidy level ($2n=22x=308$) (Ottman 1987).

Mulberries are valuable as food for birds and animals. Up to 18 bird species have been recorded eating the fruit in northeastern Kansas, with catbirds (*Dumetella carolinensis*) and robins (*Turdus migratorius*) consuming the most fruit (Stapanian 1982). Opossums (*Didelphis virginiana*), raccoons (*Procyon lotor*), fox squirrels (*Sciurus niger*), and eastern gray squirrels (*S. carolinensis*) eat the fruit in appreciable amounts, and cottontail rabbits (*Sylvilagus floridanus*) feed on the bark in winter (Core 1974).

All the mulberry species have white sap that contains latex (Hora 1981). The heartwood is durable, making it

Table 1—*Morus*, mulberry: nomenclature and occurrence

Scientific name & synonyms	Common name(s)	Occurrence
***M. alba* L.** *M. alba* var. *tatarica* (L.) Ser.	**white mulberry,** Russian mulberry, silkworm mulberry	China; naturalized in Europe & North America
***M. microphylla* Buckl.**	**littleleaf mulberry,** Texas mulberry, mountain mulberry	Arizona, New Mexico, Oklahoma, Texas, & Mexico
***M. nigra* L.**	**black mulberry,** Persian mulberry	Iran; widely cultivated in Europe
***M. rubra* L.**	**red mulberry**	Vermont & Massachusetts to New York, extreme S Ontario, Michigan, & Wisconsin, SE Minnesota, SE Nebraska, central Kansas, W Oklahoma, central Texas, E to S Florida

Sources: Core (1974), Read and Barnes (1974), Wasson (2001).

usable for fenceposts. Other specialty products include farm implements, cooperage, furniture, interior finish, and caskets (Burns and Honkala 1990).

Flowering and fruiting. Mulberry plants are normally dioecious, but they can also be monoecious on different branches of the same plant. The pendulous pistillate (female) and staminate (male) catkins are arranged on spikes and appear in April and May (Rehder 1956). The pistillate catkins in white mulberry are 0.5 to 2 cm long and staminate catkins are 2.5 to 4 cm long (FNAEC 1997; Radford and others 1968). The pistillate catkins in red mulberry are 1 to 3 cm long and the staminate catkins are 3 to 5 cm long (Radford and others 1968).

The green, female flowers have 4 sepals, 1 pistil that is 2-parted at the top, and a 2-locular ovary positioned above the floral organs. The ovary is about 2 mm long (Radford 1968). The style in white mulberry is red-brown and 0.5 to 1 mm long; the styles in red and littleleaf mulberries are whitish and about 1.5 mm long (FNAEC 1997). All mulberries have hairy stigmas. On the average, 44% of the pistillate inflorescences are parthenocarpic, with seedless fruits being somewhat smaller than seeded fruits (Griggs and Iwakiri 1973). Some varieties—such as Illinois everbearing mulberry, a cross between red and white mulberries—do not produce seeds (Reich 1992).

The male flowers are green tinged with red and have 4 sepals and 4 stamens; the filiform filaments vary from 2.7 mm in white mulberry to 3 to 3.5 mm in red mulberry (FNAEC 1997). The anthers open longitudinally (Fernald 1970). The sepals are pubescent and vary from 1.5 mm long in white mulberry to 2 to 2.5 mm in red mulberry (FNAEC 1997).

According to Griggs and Iwakiri (1973), the mulberry ovary is similar to that of other fleshy drupaceous fruits both morphologically and in growth pattern; therefore, the seed should be classified as a drupelet rather than an achene or nutlet. In the development of the mulberry fruit, the calyx adheres to the ovary and becomes an accessory part of the drupelet.

The multiple fruit is composed of many small, closely appressed drupelets (figure 1). Cultivated fruits are about 2 cm long, but fruits from native-grown trees are usually less than 1 cm long and have a cylindrical shape (Hora 1981). White mulberry fruits measure 1.5 to 2.5 × 1 cm, littleleaf mulberry fruits, 1 to 1.5 cm long, and red mulberry fruits, 1.5 to 6 × 1 cm (FNAEC 1997).

Red mulberry bears on the average 50 multiple fruits per branch and yields about 8.6 fruits/g or 8,600 fruits/kg (3,900 fruits/lb) (Burns and Honkala 1990; Griggs and Iwakiri

Figure 1—*Morus*, mulberry: fruit and leaves of *M. alba*, white mulberry (**left**) and *M. rubra*, red mulberry (**right**).

1973; Halls 1973). Mature trees can produce about 3.7 hl (10 bu) of fruit (Reich 1992). Open-grown trees produce up to about 7 times the amount of fruits per plant than do trees growing in the understory (Halls 1973).

Each fruit contains a dozen or more small drupelets (figures 2 and 3) that have thin, membranous coats and endocarps (stones) (Griggs and Iwakiri 1973). White mulberry yields about 10.7 to 32.0 drupelets per fruit, whereas red mulberry yields 10.7 to 30.0 drupelets per fruit (Stapanian 1982). Red mulberry seeds ("stones") are 2.8 mm long and 1.8 mm wide, white mulberry seeds are 2 to 3 mm long, and littleleaf mulberry seeds are about 2 mm long (FNAEC 1997). Red and littleleaf mulberry seeds are yellowish, whereas white mulberry seeds are light brown. Seed yield is up to 22 g/tree for open-grown plants and up to 3 g/tree for understory plants (Halls 1973). Seed embryos are curved, with cotyledon tips nearly touching the radicle (figure 3).

Fruits ripen and drop from the trees during the months of June to August (table 2), though they are often dispersed by birds and animals. Fruiting season can be extended by applying plenty of water during the summer months (Reich 1992). Varieties differ in size and color of ripe fruit (figure 1 and table 3) and vary in taste from insipid to sweet. The fruits stain everything they touch, so that planting mulberries along patios, sidewalks, driveways, and parking lots is NOT recommended (Reich 1992). Large fruit crops appear nearly every year on white mulberry in the Great Plains (Read and Barnes 1974) (table 3). Seed bearing begins at about 5 years of age for white mulberry, 2 years for open-grown red mulberry, and 4 years for red mulberry in the understory (table 3) (Halls 1973). In forest stands, optimum

Figure 2—*Morus alba*, white mulberry: longitudinal section through a seed.

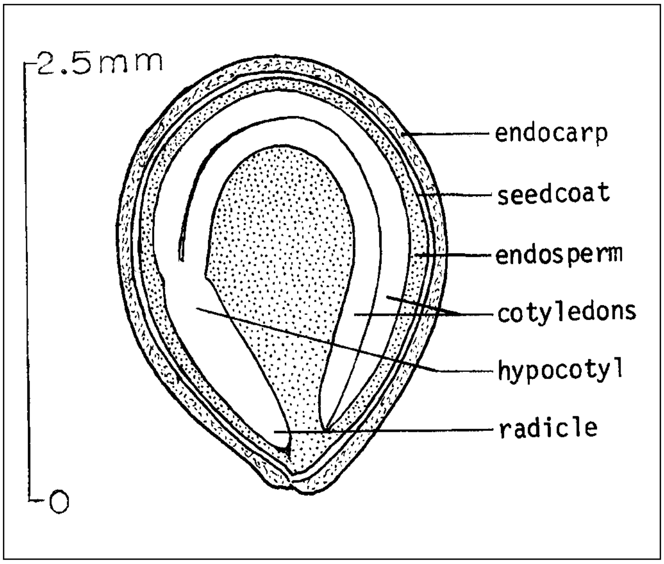
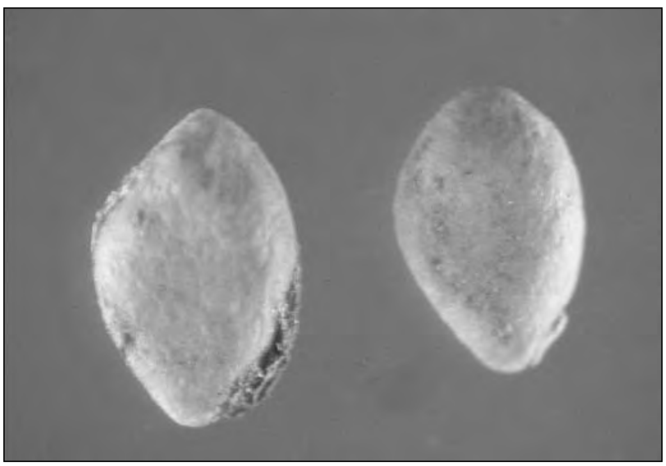


Figure 3—*Morus rubra*, red mulberry: cleaned seeds.



seed-bearing age is 30 to 85 years; the maximum being 125 years (Lamson 1990).

Collection of fruits. Before the fruits are collected, fruits from every tree should be sampled and checked, because mulberry fruits can develop without seeds. Ripe mulberry fruits may be collected by stripping, shaking, flailing, or waiting for them to fall from the tree onto a ground cloth. Fruits should be collected as soon as most are ripe to avoid loss to birds and animals. Seedlots of red mulberry fruits collected 4 to 5 days after falling yielded 89% germination, whereas seeds from fruits collected 1 to 2 weeks after falling reduced germination to 73% (Huffman 1996). Soaking red mulberry seeds in water for 48 and 72 hours reduced germination to 56 and 33%, respectively, making it advisable to not soak seeds for more than 24 hours (Huffman 1996). Seedlots from white mulberry fruits collected in early July that were cleaned and sown immediately showed 75% germination (Dirr and Heuser 1987). Fresh fruits, placed in tubs, can be stored in a cooler at 3 to 5 °C for up to 2 weeks without harming the seeds. Forty-five kilograms (100 lb) of fresh fruit of either species yields from 0.9 to 1.4 kg (2 to 3 lb) of clean seeds (Read and Barnes 1974) (table 4).

Extraction and storage of seeds. Fresh fruits are usually soaked in water and run through a macerator, where pulp and empty seeds are skimmed or floated off. If the fruits are not sufficiently ripe, soaking them in water for 24 hours will aid in the maceration. Fermentation at moderate indoor temperatures for 1 to 2 days before maceration facilitates extraction and improves viability of white mulberry seeds (Taylor 1941). A more efficient method is to spread the fruits on a clean floor, allow them to soften at room temperature for 4 to 5 days and then run them through a seed macerator with the water adjusted so that only the pulp goes through (the plate should be adjusted to 4 mm) (Engstrom

Table 2—*Morus*, mulberrry: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening
M. alba	E US	May	July–Aug
	Nebraska	May	June–Aug
	Oklahoma	Apr	Late May–June
M. microphylla	SW US	Apr–May	June–Aug
M. rubra	E US	Apr–May	June–Aug

Sources: Engstrom (1969), FNAEC (1997), Little and Delisle (1962), Read and Barnes (1974), Rehder (1956).

Table 3—*Morus*, mulberry: height, seed-bearing age, seedcrop frequency, and fruit ripeness criteria

	Height at maturity (m)	Year first cultivated	Minimum seed-bearing age (yr)	Years between large crops	Fruit ripeness criteria: Preripe color	Fruit ripeness criteria: Ripe color
M. alba	3–14	1700s	5	—	White	White, pinkish, or purplish
M. microphylla	7.5	—	—	—	Dark green	Red, purple, or black
M. nigra	10	1548	—	Yearly	Greenish red	Purple to black
M. rubra	12	1629	10	2–3	—	Dark red, dark purple to black

Sources: Little and Delisle (1962), Read and Barnes (1974), Rehder (1956), Sargent (1940), Small (1933).

1969). The now-clean seeds remain. Small samples may be cleaned by rubbing the fruits gently through a 2.4-mm (#6) round-hole screen and floating off the pulp (Read and Barnes 1974). A 1% lye solution can be used to remove any sticky pulp left on the seeds after maceration.

Cleaned seeds should be spread to air-dry in the shade, then cleaned by fanning before storage or use. Lightweight trash and seeds can be removed with a gravity table (Myatt and others 1991). Subfreezing temperatures of –23 to –18 °C are recommended for storage of dry mulberry seeds (Engstrom 1969). Numbers of seeds per weight are listed in table 4.

Pregermination treatments. Germination of untreated seeds in the laboratory may vary greatly because part of each collection may consist of seeds with dormant embryos and impermeable seedcoats (Read and Barnes 1974). Engstrom (1969) found that some seeds that had no pretreatment—but were extracted from fruits that were fermented before the seeds were extracted—did germinate completely under light at low night and high day temperatures. Fresh seeds sown in the fall are usually not pretreated (Lamson 1990). For spring-sowing, stratification in moist sand at 0.6 to 5 °C for 30 to 120 days has improved germination (Afanasiev 1942; Core 1974; Lamson 1990; Read and Barnes 1974; Taylor 1941).

Germination tests. The International Seed Testing Association (ISTA 1999) recommends testing mulberry seeds on top of moist blotters for 28 days at diurnally alternating temperatures of 30 °C (day) for 8 hours and 20 °C (night) for 16 hours. No pretreatment is stipulated in the rules. Germination is epigeal. Red mulberry requires light to germinate under laboratory conditions (Dirr and Heuser 1987). Germination values of red mulberry seedlots obtained from official laboratory tests vary greatly. The germination after 30 days of cold moist stratification was 88% with 95% full seeds; germination after 60 days of cold moist stratification was 1 to 66% and after 90 days it was 3 to 68% (USDA FS 2002).

Tests on pretreated seeds run on wet absorbent paper, wet sand, and mixtures of sand and peat at the same temperature regime for 15 to 45 days with a daily light period of 8 to 16 hours resulted in germination ranging from 20 to 92% (Heit 1968; Read and Barnes 1974; Taylor 1941). In a laboratory study of seeds planted in sand, red mulberry seeds exhibited very high seedling emergence at 25 °C under moderate moisture conditions (4 to 20%) but did not germinate at 5 or 10 °C (Burton and Bazzaz 1991). Seedling emergence was calculated as 75% of the final emerging seedlings divided by the number of days required to achieve 75% emergence (Burton and Bazzaz 1991).

Nursery practice. In fall or spring, properly pretreated mulberry seeds mixed with sand may be broadcast or sown in drills. Rows can be drilled 20 to 30 cm (8 to 12 in) apart, with 164 seeds/m (50/ft) of row, and barely covered with soil. In Oklahoma, white mulberry is sown with 65 to 82 viable seeds/m (20 to 25/ft) in a 7.5- to 10-cm (3- to 4-in) band to produce 33 usable seedlings/m (10/ft) (Engstrom 1969). One Nebraska nursery uses a seedling density of 197 to 262/m of drill (60 to 80/ft) (Korves 1969). Freshly harvested and processed white mulberry seeds have been successfully hand-sown in July at 312 seeds/m^2 (29 seeds/ft^2), lightly raked, rolled, and then covered with straw mulch: germination occurred 2 weeks later (Peaslee 2002).

Beds should be mulched with straw, leaves, or burlap and kept moist until germination begins. Beds should be half-shaded for a few weeks after germination, which usually begins 1 to 2 weeks after spring-sowing (Dirr and Heuser 1987). Twelve to 50% of the seeds of white mulberry should produce usable seedlings. One-year-old seedling stock is used for field planting; seedlings should be dug about 25 cm (10 in) deep with a very sharp blade—main roots are rather stout and tough (Engstrom 1969).

Bacterial canker can be serious threat to white mulberry seedlings in the southern Great Plains; however, treatment of soil with formaldehyde solution before seeding has provided

M

Table 4—*Morus*, mulberry: seed yield data

	Seeds (x1,000)/weight				
	Range		Average		
Species	/kg	/lb	/kg	/lb	Samples
M. alba	286–770	130–350	517	235	18+
M. rubra	440–1,100	200–500	792	360	4

Sources: Engstrom and Stoeckler (1941), Read and Barnes (1974), Swingle (1939).

adequate control. Mulberry seedbeds should not be located near older mulberry trees (Davis and others 1942). Damping-off may occasionally be a problem, but losses are usually minimal, probably due to nursery cultural methods presently used (Wright 1944). Fungal leaf-spot caused by *Cercospora* spp. and *Mycosphaerella mori* (Fuckel.) E.A. Wolf, as well as bacterial leaf-spot caused by *Pseudomonas mori* (Boy. & Lamb.) Stev. may cause damage.

Mulberries are easy to root from summer softwoods; June and July are optimum months (Dirr and Heuser 1987). When mid-July cuttings were treated with 8,000 ppm IBA in talc and stuck into sand, 100% rooted in 3 weeks (Dirr and Heuser 1987).

References

Afanasiev M. 1942. Propagation of trees and shrubs by seed. Circ.C106. Oklahoma Agricultural Experiment Station. 43 p.

Burton PJ, Bazzaz FA. 1991. Tree seedling emergence on interactive temperature and moisture gradients and in patches of old-field vegetation. American Journal of Botany 78(1): 131–149.

Core EL. 1974. Red mulberry, *Morus rubra* L. In: Gill JD, Healy WM, comp. Shrubs and vines for northeastern wildlife. Gen. Tech. Rep. NE-9. Upper Darby, PA: USDA Forest Service, Northeastern Forest Experiment Station: 106–107.

Davis WC, Wright E, Hartley C. 1942. Diseases of forest-tree nursery stock. For. Pub. 9. Washington, DC: USDA Civilian Conservation Corps. 79 p.

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

Dirr MA. 1998. Manual of woody landscape plants: their identification, ornamental characteristics, culture, propagation and uses. 5th ed. Champaign, IL: Stipes Publishing. 1187 p.

Engstrom A. 1969. Personal communication. Oklahoma City: Oklahoma Department of Agriculture, Forestry Division.

Engstrom HE, Stoeckler JH. 1941. Nursery practice for trees and shrubs suitable for planting on the Prairie-Plains. Misc. Pub. 434. Washington, DC: USDA. 159 p.

Fernald ML. 1970. Gray's manual of botany. 8th ed. New York: Van Nostrand Co. 1632 p.

FNAEC [Flora of North America Editorial Committee]. 1997. Flora of North America North to Mexico. Volume 3, Magnoliophyta: Magnoliidae and Hamamelidae. New York: Oxford University Press: 390–392.

Griggs WH, Iwakiri BT. 1973. Development of seeded and parthenocarpic fruits in mulberry (*Morus rubra* L.). Journal of Horticultural Science 48: 83–97.

Halls LK. 1973. Flowering and fruiting of southern browse species. Res. Pap. SO-90. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 10 p.

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

Hora B, ed. 1981. The Oxford encyclopedia of trees of the world. Oxford, UK: Oxford University Press. 288 p.

Huffman GR. 1996. Seed handling and propagation of hardwood trees and shrubs at Oklahoma Forestry Services' Forest Regeneration Center. In: Landis TD, South DB, tech coords. National Proceedings, Forest and Conservation Nursery Associations. Gen. Tech. Rep. PNW-389. Portland, OR: USDA Forest Service, Pacific Northwest Research Station: 43–48.

ISTA [International Seed Testing Association]. 1999. International rules for testing seeds: rules 1999. Seed Science and Technology 27 (Suppl.) 333 p.

Korves T. 1969. Correspondence. Fremont, NE: Plumfield Nursery.

Lamson NI. 1990. *Morus rubra* L., red mulberry. In: Burns RM, Honkala BH. tech. coords. Silvics of North America. Volume 2, Hardwoods. Agric. Handbk 654. Washington, DC: USDA Forest Service: 470–473.

Little EL Jr, Delisle AL. 1962. Time periods in development: forest trees, North American. In: Altman PL, Dittmer DS, eds. Growth including reproduction and morphological development. Washington, DC: Federation of American Societies for Experimental Biology: 382–386.

Myatt A, Huffman G, Odell J. 1991. Seed processing manual. Washington, OK: Oklahoma Department of Agriculture, Forestry Division, Forest Regeneration Center.

Moore DM, Thomas WP. 1977. Red mulberry, *Morus rubra* L. In: Halls LK, ed. Southern fruit-producing woody plants used by wildlife. Gen. Tech. Rep. SO-16. New Orleans: USDA Forest Service, Southern Forest Experiment Station: 55–56.

Ottman Y. 1987. Rediscovering the realm of fruiting mulberry varieties. Fruit Varieties Journal 41(1): 4–7.

Peaslee A. 2002. Personal communication. Jackson, NJ: New Jersey Forest Tree Nursery.

Radford AE, Ahles HE, Bell CR. 1968. Manual of the vascular flora of the Carolinas. Chapel Hill: University of North Carolina Press. 1183 p.

Read RA, Barnes RL. 1974. *Morus* L., mulberry. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk 450. Washington, DC: USDA Forest Service: 544–547.

Rehder A. 1956. Manual of cultivated trees and shrubs hardy in North America. 2nd ed. New York: Macmillan. 996 p.

Reich L. 1992. Native American fruits. Organic gardening 39(2): 52, 54–57.

Sargent CS. 1940. Manual of the trees of North America (exclusive of Mexico). 2nd ed., corrected and reprinted. New York: Dover. 934 p.

Small JK. 1933. Manual of the southeastern flora. New York: J.K. Small. 1554 p.

Stapanian MA. 1982. A model for fruiting display: seed dispersal by birds for mulberry trees. Ecology 63(5): 1432–1443.

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

Taylor CA. 1941. Germination behavior of tree seeds. Washington, DC: USDA Forest Service, Prairie States Forestry Project. 64 p.

USDA FS [USDA Forest Service]. 2002. Unpublished data. Dry Branch, GA: National Tree Seed Laboratory.

Wasson E. 2001. Trees and shrubs: illustrated A–Z of over 8500 plants. Willoughby, NSW, Australia: Global Book Publishing: 483–484.

Wright E. 1944. Damping-off in broadleaf nurseries of the Great Plains region. Journal of Agricultural Research 69: 77–94.

Myricaceae—Bayberry family

Myrica L. and *Morella* Lour.

bayberry

Jason J. Griffin and Frank A. Blazich

Dr. Griffin is assistant Professor at Kansas State University's Department of Horticulture, Forestry, and Recreation Resources, Manhattan, Kansas; Dr. Blazich is alumni distinguished graduate professor of plant propagation and tissue culture at North Carolina State University's Department of Horticultural Science, Raleigh, North Carolina

Synonyms and common names. Considerable disagreement exists regarding taxonomy of the Myricaceae, particularly the number and classification of genera within the family. Inclusion of the genera *Myrica* and *Comptonia* L'Hér. ex Aiton in the Myricaceae appears to be universal (Bornstein 1997; Kartesz 1994; Radford and others 1968; Small 1933; Weakley 2000; Wilbur 1994). However, species within the genus *Myrica* and its division into 2 separate genera are still being debated (Bornstein 1997; Weakley 2000; Wilbur 1994). If the Myricaceae are divided into 3 genera, sweet gale *(M. gale* L.*)* and Sierra sweet-bay *(M. hartwegii* S. Wats.*)* are the only species that remain in the genus *Myrica* (Weakley 2000; Wilbur 1994). The other species formerly in the genus *Myrica* are grouped under a third genus which, depending on the authority, is either *Morella* Lour. (Weakley 2000; Wilbur 1994) or *Cerothamnus* Tidestrom (Small 1933). Radford and others (1968) also divide *Myrica* into 2 genera. However, in their view, sweet gale is removed from *Myrica* and placed in the genus *Gale* Adanson.

The newly standardized plant nomenclature of USDA (the PLANTS database of the National Resources Conservation Service), which is being followed in this publication, places the former *Myrica* species into 2 genera—*Myrica* and *Morella.* Both genera are included in this chapter on *Myrica* because the *Morella* nomenclature is not widely known (table 1). The reader should be aware that further division of *Myrica* is possible in the future and the above cited references should be consulted for more information.

Occurrence, growth habit, and uses. Bayberries—both *Myrica* and *Morella*—include about 35 to 50 species of

Table 1—*Morella* and *Myrica,* bayberry and wax-myrtle: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
Morella californica **(Cham. & Schlecht.) Wilbur** *Myrica californica* Cham. & Schlecht.	**California wax-myrtle,** California bayberry, Pacific bayberry	Pacific Coast from Washington to California
Morella cerifera **(L.) Small** *Myrica cerifera* L. *Myrica pusilla* Raf. *Cerothamnus ceriferus* (L.) Small *C. pumilus* (Michx.) Small *Morella pumila* (Michx.) Small	**southern wax-myrtle,** southern bayberry waxberry, candleberry	New Jersey to S Florida, W to Texas & N to Arkansas (swampy or sandy soils with low pH)
Morella faya **(Ait.) Wilbur** *Myrica faya* Ait.	**candleberry-myrtle**	Canary Islands, Madeira, & Portugal
Morella pensylvanica **(Mirbel) Kartesz** *Myrica pensylvanica* *Cerothamnus pensylvanica* (Mirbel) Moldenke *M. caroliniensis* auct. non Mill.	**northern bayberry** bayberry, candleberry	Alaska to Newfoundland, S to Pennsylvania, W to Wisconsin, Washington, & Oregon; isolated areas of Tennessee & North Carolina (swampy soils) Coastal plain from Newfoundland & Nova Scotia S to North Carolina
Myrica gale **L.** *Gale palustris* Chev. *Myrica palustris* Lam.	**sweet gale,** bog-myrtle, meadow-fern	

deciduous or evergreen shrubs and trees (Bornstein 1997; Huxley 1992; LHBH 1976). Six are native to North America; of these only California wax-myrtle, southern wax-myrtle, sweet gale, and northern bayberry are of any horticultural significance. Another species—candleberry-myrtle, which is native to the Canary and Madeira Islands—was introduced into Hawaii and has achieved considerable ecological impact (Walker 1990).

The evergreen California wax-myrtle and southern wax-myrtle can be maintained as shrubs or allowed to grow to 10.5 m in height, whereas candleberry-myrtle, also evergreen, matures at a shorter height of 7.5 m. The deciduous sweet gale and the deciduous or semi-evergreen, multi-stemmed northern bayberry are species that attain heights of 1.5 and 2.7 m, respectively (LHBH 1976).

Species of bayberry have both ecological and landscape significance. Their ability to associate with symbiotic nitrogen-fixing bacteria—*Frankia* Brunchorst spp.—makes them well adapted for land-reclamation efforts. California wax-myrtle, candleberry-myrtle, and northern bayberry have been used for this purpose, as they establish and grow well in near-sterile soils (Everett 1981; Walker 1990). Candleberry-myrtle performs so well under these conditions that it is now considered a noxious weed in Hawaii, becoming a co-dominant species in areas of the Hawaii Volcanoes National Park (Walker 1990). Southern wax-myrtle and northern bayberry are well suited to coastal marine environments because they will tolerate soils high in salt that may be saturated with water or prone to drought (Bir 1992). Both species are extremely versatile and can be used as shrubs or trained to grow as attractive multi-stemmed small trees.

Bayberries are valued also for their ornamental attributes. California wax myrtle has lustrous dark green foliage and attractive purple fruits (Everett 1981). The foliage of southern wax-myrtle and northern bayberry is pleasantly aromatic when crushed. Birds are attracted to the wax-covered fruits of these species, and the wax is used to scent candles and soaps (Fordham 1983). Medicinal properties as well as ornamental characteristics were the rationale for introducing candleberry-myrtle into Hawaii (Walker 1990). Sweet gale also has been used for medicinal purposes, as well as flavoring beer in Europe (Everett 1981).

Geographic races and hybrids. Individual plants of southern wax-myrtle, which inhabit dry, sandy soils, tend to be more rhizomatous and ultimately attain a smaller size with smaller morphological characteristics than individuals growing in fertile soils (Bornstein 1997). These plants are commonly referred to as *Morella cerifera* var. *pumila* Michx. (*M. pusilla* Raf.) and are usually < 1 m in height; they occur on dry, sandy pinelands and prairies from Texas to North Carolina and Florida (Elias 1971). However, it is uncertain if these differences are genetic or environmentally influenced, and therefore assignment of varietal status is uncertain (Bornstein 1997). Leaf pubescence of sweet gale can be quite variable and is reflected in 2 varieties—*M. gale* var. *subglabra* (Chev.) Fern. and *M. gale* var. *tomentosa* C. DC. (Elias 1971; Kartesz 1994). Other authors, however, do not recognize these as valid varieties (Bornstein 1997). Few selections of particular species have been reported in the literature. However, one—*Morella cerifera* 'Emperor'—is distinguished by elongated, deeply serrate leaves (Brackin 1991).

Flowering and fruiting. Flowers of bayberries are small and inconspicuous. Time of flowering is variable, depending on the species (table 2). Male inflorescences consist of catkins usually < 2 cm long; female inflorescences are ovoid and sessile up to 1 cm in length (Huxley 1992). Fordham (1983) reported that southern wax-myrtle, sweet gale, and northern bayberry are all dioecious. However, there are reports of monoecious forms of sweet gale. Even more interesting is the phenomenon that individual plants of sweet gale have been observed altering their sex from year to year (Everett 1981). Plants of California wax-myrtle are monoecious (Krochmal 1974). Fruit maturation generally occurs in late summer to fall (table 2). Fruits are small spherical drupes usually covered with a wax coating (figures 1 and 2) that ranges in color from gray-green to purple (Huxley 1992). Fruits of sweet gale, however, are surrounded by 2 wing-like bracts and form a catkin by clustering around a central axis (Fordham 1983).

Figure 1—*Morella cerifera*, southern wax-myrtle: wax-coated drupe (**left**) and cleaned drupe (**right**).

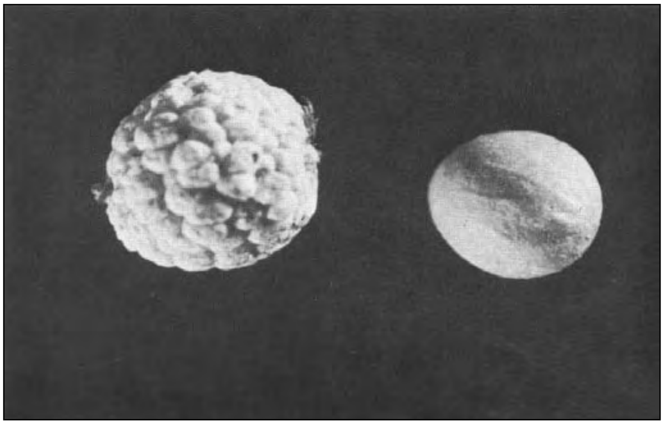
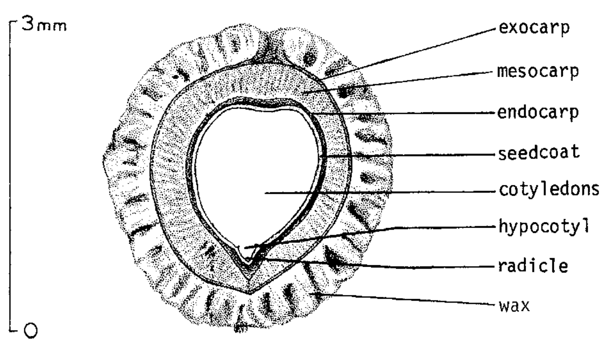


Table 2—*Morella* and *Myrica,* bayberry and wax-myrtle: flowering and fruiting characteristics

Species	Flowering	Fruit ripening	Color of ripe fruit	Diam of ripe fruit (mm)	Cleaned seeds/wt /kg	Cleaned seeds/wt /lb
Morella californica	May–June	Sept	Brownish purple with grayish white wax	6	48,000	22,000
Morella cerifera	Mar-June	Aug–Oct	Light green with pale blue wax	3	185,000	84,000
Morella faya	Variable	Aug–Nov	Red to purple	5	—	—
Myrica pensylvanica	Apr–July	Sept–Oct	Covered with grayish white wax	4	121,000	55,000
Myrica gale	Mar–Apr	Oct	Lustrous & dotted with resin	3	—	—

Sources: Fordham (1983), Huxley (1992), Krochmal (1974), Krüssmann (1984), Schwintzer and Ostrofsky (1989), Walker (1990).

Figure 2—*Morella cerifera*, southern wax-myrtle: longitudinal section of a drupe.



Collection of fruits, seed extraction and cleaning. Ripe drupes can be harvested by stripping branches by hand or shaking them from the branches onto ground sheets. After harvest, they should be handled as seeds (Krochmal 1974). Therefore, seed extraction and cleaning are often unnecessary except as mentioned below.

Seed storage. Fordham (1983) suggested that drupes should be stored intact to avoid desiccation of their seeds; drupes of northern bayberry stored in this manner remained viable for 9 months at room temperature (Krochmal 1974). Most evidence, however, suggests that bayberry seeds are orthodox and should be dried to low moisture contents and stored at low temperatures. Dirr and Heuser (1987) recommend that wax be removed before long-term (10 to 15 years) dry storage at 1 to 3 °C. Seeds of sweet gale air-dried at room temperature for 28 days following collection and stored dry at 5 °C remained viable for 6 years (Schwintzer and Ostrofsky 1989). Optimum moisture contents for storage of bayberry seeds are not known, but similar seeds of other orthodox species store well at 6 to 10% moisture.

Pregermination treatments and germination tests. All species of bayberry discussed herein require pregermination treatments for optimum germination. Those species with wax-covered drupes require that the wax be removed. This can be accomplished by abrasion with a screen or with a warm water soak (Fordham 1983). Following wax removal, stratification (moist-prechilling) for approximately 90 days at 5 °C is necessary to overcome dormancy. However, stratification is ineffective if wax remains (Fordham 1983). Fruits of sweet gale, which lack a wax coating, will germinate in low percentages without stratification. However, best germination occurs following 6 weeks stratification at 5 °C (Schwintzer and Ostrofsky 1989). Seeds of candleberry-myrtle also germinate without any pregermination treatments. However, a fleshy mesocarp and stony endocarp are inhibitory to germination. Removal of the mesocarp and scarification of the endocarp will significantly increase germination (Walker 1990).

Fordham (1983) investigated seed germination of southern wax-myrtle. Seeds were subjected to 4 treatments: no stratification with no wax removal; stratification at 5 °C for 90 days with no wax removal; no stratification with wax removal; and stratification with wax removal. Germination for the first 3 treatments was very poor (6, 17, and 6%, respectively), whereas that for the fourth treatment was significant (data not available).

Schwintzer and Ostrofsky (1989) conducted an extensive study on seed germination of sweet gale. Among factors investigated were the effects of stratification, light, and gibberellic acid (GA) treatment. Some germination (38%) was noted with no stratification or GA treatment. However, stratification for 3, 6, or 12 weeks at 5 °C significantly increased germination with the highest (66%) occurring following 6 weeks of stratification. Without stratification, GA treatment at 500 ppm (0.05%) stimulated germination (48%).

However, germination was reduced when GA was used in combination with stratification. Seeds did not germinate in the dark. Germination was about 12% when seeds were exposed to light for a single 16-hour photoperiod (80 $\mu mol/m^2/sec$) and then placed in darkness for 28 days. Maximum germination (about 35%) occurred following exposure to 4 such photoperiods.

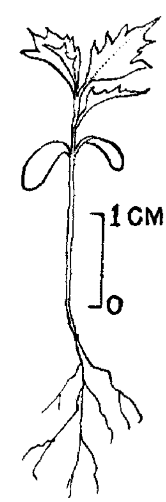
Hamilton and Carpenter (1977) investigated effects of scarification, stratification, and exogenous growth regulator treatment on seed germination of northern bayberry. After their wax was removed, seeds were either scarified with coarse sandpaper or not. Seeds were then soaked in 0, 100 (0.01%), 500 (0.05%), or 900 ppm (0.09%) GA_3 or 6-furfurylamino purine (kinetin) at 0, 25 (0.0025%), or 100 ppm (0.01%) for 24 hours at 22 °C. Following scarification and growth regulator treatments, seeds were sown in flats containing a 1:1 peat/perlite (v/v) medium. Then, flats were placed in sealed polyethylene bags for stratification at 5 °C for 0, 15, or 30 days. After stratification, flats were removed from the bags and placed in a greenhouse at 25 °C for germination periods of 20, 40, 60, or 80 days. Kinetin had no effect on germination unless seeds were scarified and stratified for 30 days. When seeds were scarified and stratified, germination after 80 days was 4, 20, and 28% for seeds treated with 0, 25, or 100 ppm kinetin. Highest germination of scarified seeds followed by stratification for 0 or 15 days was 4 and 8%, respectively. GA_3 proved more effective in promoting germination. Germination after 80 days for scarified seeds was 8, 25, 69, and 65% for seeds treated with 0, 100, 500, or 900 ppm GA_3, respectively. Reducing the length of stratification significantly decreased germination. Germination of nonscarified seeds was similar to scarified seeds following 0 or 15 days of stratification. However, germination was enhanced provided seeds were scarified followed by stratification for 30 days.

Walker (1990) studied the effects of various environmental factors on germination of candleberry-myrtle. He found that storage periods >10 weeks at 20 °C significantly reduced germination. He also noted that germination of seeds collected after passage through the digestive tract of birds (normal method of dissemination) did not differ significantly in comparison to seeds collected directly from trees. Irrigating seeds with water steeped with litter of native woody species and candleberry-myrtle (leachate), densely shading seeds (>55% shade), and covering sown seeds with 0.5 cm of medium all reduced germination. Germination was promoted by removal of the fleshy mesocarp.

Nursery practice and seedling care. For field production, seeds can be sown in fall or spring. Fall-sowing should be sufficiently late to avoid germination before winter, and seedbeds should be mulched. Spring-sowing should follow a period of stratification at 5 °C for 90 days (Krochmal 1974). If container production is desired, seeds may be sown indoors in early spring, and the seedlings repotted before moving outdoors for further growth. Germination is epigeal (figure 3) (Young and Young 1992).

Asexual propagation has been successful to varying degrees depending on species. Blazich and Bonaminino (1984) reported that terminal stem cuttings of southern wax-myrtle, in a transitional growth stage between softwood and semi-hardwood, rooted in high percentages. Cuttings treated with solutions of indolebutyric acid (IBA) at 0, 1,000 (0.1%), 2,000 (0.2%), or 4,000 ppm (0.4%) resulted in rooting of 87, 97, 87, and 90%, respectively. Cutting propagation of northern bayberry is more challenging. However, softwood cuttings can be rooted successfully when treated with a solution of 5,000 ppm (0.5%) IBA (Dirr and Heuser 1987). Most bayberry species produce root suckers and can be propagated by division as well as by root cuttings (Dirr and Heuser 1987).

Figure 3—*Morella californica*, California wax-myrtle: 1-month-old seedling.



References

Bir RE. 1992. Growing and propagating showy native woody plants. Chapel Hill: University of North Carolina Press. 192 p.

Blazich FA, Bonaminio VP. 1984. Propagation of southern waxmyrtle by stem cuttings. Journal of Environmental Horticulture 2(2): 45–48.

Bornstein AJ. 1997. Myricaceae. In: Flora of North America Editorial Committee, eds. Flora of North America north of Mexico. Volume 3, Magnoliophyta: Magnoliidae and Hamamelidae. New York: Oxford University Press: 429–434.

Brackin RL. 1991. Wax myrtle named Lane. United States Plant Patent 7555.

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

Elias TS. 1971. The genera of Myricaceae in the southeastern United States. Journal of the Arnold Arboretum 52(2): 305–318.

Everett TH. 1981. The New York Botanical Garden illustrated encyclopedia of horticulture. Volume 7. New York: Garland Publishing: 2131–2492.

Fordham AJ. 1983. Of birds and bayberries: seed dispersal and propagation of three *Myrica* species. Arnoldia 43(4): 20–23.

Hamilton DF, Carpenter PL. 1977. Seed germination of *Myrica pensylvanicum* L. HortScience 12(6): 565–566.

Huxley A, ed. 1992. The new Royal Horticultural Society dictionary of gardening. Volume 3. New York: Stockton Press. 790 p.

Kartesz JT. 1994. A synonymized checklist of the vascular flora of the United States, Canada, and Greenland. 2nd ed. Volume 1. Portland, OR: Timber Press. 622 p.

Krochmal A. 1974. *Myrica*, bayberry. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 548–550.

Krüssmann G. 1984. Manual of cultivated broad-leaved trees and shrubs. Volume 1. Portland, OR: Timber Press. 624 p.

LHBH [Liberty Hyde Bailey Hortorium]. 1976. Hortus third: a concise dictionary of plants cultivated in the United States and Canada. 3rd ed. New York: Macmillan. 1290 p.

Radford AE, Ahles HE, Bell CR. 1968. Manual of the vascular flora of the Carolinas. Chapel Hill: University of North Carolina Press. 1183 p.

Schwintzer CR, Ostrofsky A. 1989. Factors affecting germination of *Myrica gale* seeds. Canadian Journal of Forest Research 19(9): 1105–1109.

Small JK. 1933. Manual of the southeastern flora. Chapel Hill: University of North Carolina Press. 1554 p.

Walker LR. 1990. Germination of an invading tree species (*Myrica faya*) in Hawaii. Biotropica 22(2): 140–145.

Weakley AS. 2000. Flora of the Carolinas and Virginia: working draft of 15 May 2000. Chapel Hill, NC: Nature Conservancy, Southeast Regional Office, Southern Conservation Science Department [available in draft from the author].

Wilbur RL. 1994. The Myricaceae of the United States and Canada: genera, subgenera, and series. SIDA 16(1): 93–107.

Young JA, Young CG. 1992. Seeds of woody plants in North America. Portland, OR: Timber Press. 407 p.

Hydrophyllaceae—Waterleaf family

Nama lobbii Gray
woolly nama

Eamor C. Nord and Andrew T. Leiser

Dr. Nord (deceased) retired from the USDA Forest Service's Pacific Southwest Forest and Range Experiment Station; Dr. Leiser is professor emeritus at the University of California's Department of Horticulture Davis, California

Other common names. Lobb fiddleleaf.

Growth habit, occurrence, and use. There are 2 perennial species in this genus, both low-growing, suffruticose plants native to California, Nevada, and Utah. Only the sub-shrub woolly nama—*Nama lobbii* Gray—has potential for revegetation use, as it can provide a rather persistent, dense groundcover. The other species—Rothrock fiddleleaf, *N. rothrockii* Gray—furnishes only a sparse cover that dies back to the roots each year.

Woolly nama is native to the Sierra Nevada and Cascade ranges in east central and northern California, and western Nevada at elevations of 1,220 to 2,100 m within ponderosa (*Pinus ponderosa* Dougl. ex Laws.) or Jeffrey (*P. jeffreyi* Grev. & Balf.) pine and California red fir (*Abies magnifica* A. Murr.) forests. It occurs in sunny, exposed locations with slightly to moderately acid soils derived mostly from volcanic mud flows and decomposed granites. Plants 15 to 60 cm tall are generally sparse and widely scattered (McDonald and Oliver 1984). However, where the tree or associated shrub overstory is removed, such as by logging or other mechanical means, woolly nama spreads rapidly to form dense crowns up to 1.5 m in diameter on individual plants (McDonald and Fiddler 1995). Fast-growing roots that extend up to 5 m or more in a single year contain a profusion of adventitious buds that sprout to form new plants.

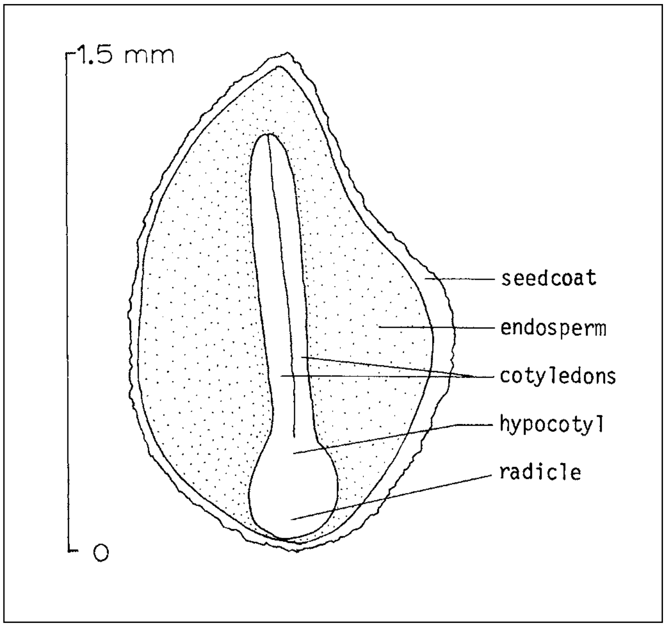
Woolly nama has many characteristics that make it desirable for revegetation on adapted sites. The low growth habit helps reduce fire hazards in brush-cleared areas, and its abundant, aggressive sprouting habit together with dense foliage provides good groundcover. It is known to offer strong competition and thus reduce growth of young conifers within plantations (McDonald and Oliver 1984). Although it is not regarded as a serious weed pest in areas where it occurs naturally, care should be exercised to prevent introduction and possible spread of this plant into cultivated croplands, mainly because of its aggressive rooting habits, which enable the plant to withstand cultivation.

Flowering and fruiting. The numerous small purple flowers are borne in reduced terminal cymes or in axillary angles along slightly erect stems; they appear from May to September. The fruit is a capsule containing 10 to 12 oval, angular, very dark brown seeds up to 1.5 mm long (figures 1 and 2). The capsules mature in late August, September, and October. In a test of a cleaned seedlot, seeds measured 1 to 1.3 mm in diameter; 85% of the seeds in the lot were filled and there were about 2,000 seeds/g (56,875/oz).

Collection, extraction, and storage. Mature seeds may be hand-stripped or flailed directly into containers, or seed heads together with some foliage may be harvested mechanically during late September and thereafter until snow covers the ground. One means is to use a rotary lawn-mower equipped with a collection bag and set at maximum height that clips and gathers the material, which is later dried and threshed. The seeds may be extracted by threshers or hammermills, and cleaned with aspirators or air-screen cleaners. A collection made in the Tahoe basin, using this type of equipment, yielded over 1.8 kg (4 lb) of clean seeds from about 59 kg (130 lb) of dry clippings (Nord and Leiser 1974). Only half of the total number of seeds was released from capsules during clipping and drying, and the remaining seeds had to be extracted and separated by a hammermill and South Dakota Seed Blower. No precise data are available on longevity of woolly nama seeds, but they are presumed to be orthodox in storage behavior and should remain

Figure 1—*Nama lobbii*, woolly nama: seed.

Figure 2—*Nama lobbii*, woolly nama: longitudinal section through a seed.



viable for a number of years when stored dry at low temperatures.

Germination. Woolly nama seeds exhibit what apparently is seedcoat dormancy. Stratification has no effect, but when the seedcoats are removed, up to 60% of the seeds will germinate. The dormancy may be due to a chemical that is found in the seedcoat. Extracts of the colored leachate obtained from seeds kept under intermittent mist contained an anionic polyphenol that may inhibit germination (Nord and Leiser 1974). Leaching woolly nama seeds for 3 days under intermittent mist for 3 seconds at 2-minute intervals, followed by soaking in 200 ppm gibberellic acid, yielded 39% germination. Other treatments in which gibberellic acid was used yielded as much as 30% total germination, but sulfuric acid, thiourea, hydrogen peroxide, and hot water treatments were not effective in improving germination. In laboratory tests , the first observed germination was at 12 days and germination continued intermittently thereafter throughout a 4-month period (Nord and Leiser 1974).

Because of the very low and slow germination, it is most unlikely that woolly nama can establish itself satisfactorily from direct field seeding unless seeds are treated in some manner to break dormancy. This appears to be the case even in native stands, where seedling plants are rarely found; presumably most natural establishment or spread of this species comes from root segments transported during some form of soil disturbance.

Nursery and field practice. The best method known to prepare the seeds for sowing calls for leaching the seeds under intermittent mist or running water for 2 to 3 days, soaking in gibberellic acid that is constantly agitated, and air-drying thoroughly. The seeds should not be rinsed or washed. Soaking for 2 hours in 200 ppm or stronger gibberellic acid solution is suggested if seeds are to be sown within a few days after treatment. If seeding is to be delayed for more than about 10 days and soil moisture conditions are unpredictable, stronger solutions and longer soak times (probably up to 500 ppm for periods up to 24 hours) should be used to reduce risks of leaching should rains occur before seeds germinate. Seeding should be done in the late fall or very early spring to take advantage of the most favorable moisture conditions for germination and seedling establishment. Seeds may be sown separately or mixed with rice hulls as a diluent and carrier at a depth of about 12 mm ($^1/_2$ in) on properly prepared, firm seedbeds where competing vegetation has been previously removed.

The plant makes its best development on medium-textured, well-drained soils that are neutral to moderately acid in reaction. The plants are susceptible to gopher damage to the roots in southern California, but they appear to be immune from damage to the foliage by animals, including rabbits, which often damage or destroy many other shrub or herbaceous species.

Rooting either stem cuttings or root sections of woolly nama has not been too successful. In several trials, only 30% of stem cuttings rooted, and none survived when transplanted into pots. Root cuttings failed to regenerate new plants, although some fresh shoots became green and grew slightly (Nord and Goodin 1970).

References

McDonald PM, Fiddler GO. 1995. Development of a mixed shrub–ponderosa pine community in a natural and treated condition. Res. Pap. PSW-224-web. Albany, CA: USDA Forest Service, Pacific Southwest Research Station. 19 p.

McDonald PM, Oliver WW. 1984. Woody shrubs retard growth of ponderosa pine seedlings and saplings. In: Proceedings, 5th Annual Forest Vegetation Management Conference; 1983 November 2–3; Redding, CA. Redding, CA: Forest Vegetation Management Conference: 65–89.

Nord EC, Goodin JR. 1970. Rooting cuttings of shrub species for plantings in California wildlands. Res. Note PSW-213. Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. 4 p.

Nord EC, Leiser AT. 1974. *Nama lobbii* Gray, woolly nama. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 551–552.

N

Berberidaceae—Barberry family

Nandina domestica Thunb.

nandina

Laura G. Jull and Frank A. Blazich

Dr. Jull is assistant professor at the University of Wisconsin's Department of Horticulture, Madison, Wisconsin; Dr. Blazich is alumni distinguished graduate professor of plant propagation and tissue culture at North Carolina State University's Department of Horticultural Science, Raleigh, North Carolina

Other common names. heavenly-bamboo, sacred-bamboo, *nanten*.

Occurrence, growth habit, and uses. *Nandina* is a monotypic genus indigenous from India to central China (Huxley and others 1992; Krüssmann 1985; Ohwi 1984). It was introduced into Japan from China before the sixteenth century (Coats 1992). The species is a broadleaf evergreen, upright, flat-topped shrub reaching a height of 1.5 to 2.4 m with a spread of 1.0 to 1.5 m that can spread by root suckers into large colonies (Dirr 1990; Whitcomb 1996). Plants are characterized by numerous, unbranched stems with horizontal branches. However, with age, they tend to become leggy and open, unless pruned properly (Flint 1997). The species is hardy to USDA Zone 6 (Dirr 1990) and will remain evergreen in USDA Zones 7–8. It becomes deciduous when exposed to colder temperatures (Gibson 1982).

In Japan, nandina is called *nanten*, "sacred-bamboo," as fruiting twigs are sold in winter to decorate altars, both in temples and private homes (Coats 1992; Krüssmann 1985; Richards and Kaneko 1988). There, nandina is planted close to the entrances of homes because the plant is used to comfort family members who have bad dreams. The wood is aromatic and very close grained; it is considered by the Japanese to be flavorful and suitable for toothpicks (Coats 1992). The plant is reputed to have medicinal properties effective in treatment of various ailments (Ikuta 1994).

Nandina is cultivated commonly in the United States because of several desirable landscape attributes. The new, finely dissected leaves are bronze to red, becoming blue-green with age, and turning a dull purple to bright red in winter (Flint 1997). Flowers occur in large panicles held above the foliage and are followed in the fall by showy, bright red berries produced in clusters that persist throughout the winter. The stems give the appearance of bamboo (Flint 1997). Plants are adaptable to many different soils; they tolerate sun, shade, and drought; and they are pest free (Dirr 1990; Whitcomb 1996).

Geographic races and hybrids. Nandina has been in cultivation for centuries. China and Japan are considered as sources of dwarf selections. Cultivars with fern-like foliage, distorted branchlets, and white, yellow, or crimson fruits occur in the nursery trade (Dirr 1990).

Flowering and fruiting. Nandina will flower and produce fruit in heavy shade to full sun (Dirr 1990). Plants fail to set fruit if planted singly, so it is best to plant groupings of several plants to ensure cross pollination (Gibson 1982). Inflorescences are erect, terminal, 20- to 38-cm-long white panicles that appear from May to June. Individual flowers are perfect, 6 to 13 mm across, and pinkish in bud, opening to white with yellow anthers. The fruits are globular, bright red berries that are 8 mm in diameter with 2 seeds; they ripen in the fall and persist through the winter (Dirr 1990).

Collection of fruits, seed extraction, and cleaning. Fruits should be harvested when mature in the fall. Removal of the fleshy pulp is recommended and is accomplished easily by maceration (Dirr and Heuser 1987; Gibson 1982). After fruits are soaked in water for 24 hours and macerated, the seeds (figures 1 & 2) can be separated from the fleshy pulp (Newman 1991).

Seed storage. Due to the presence of a rudimentary embryo, seeds should be stored under slightly moist conditions at 4 °C, then sown in late spring or summer to obtain uniform and rapid germination (Dehgan 1984; Hartmann and others 1997). Seeds held in cold storage for 9 to 10 months germinate as well as those sown immediately after seed extraction and do so without appreciable loss in viability (Afanasiev 1943; Dirr and Heuser 1987).

Pregermination treatments. Seeds exhibit delayed germination due to a rudimentary embryo and slow rate of embryo development (Dirr and Heuser 1987). The rudimentary embryo is formed after flowering in August and September and during fruit enlargement in winter. However, further development is arrested during spring and summer months (Afanasiev 1943), although embryo maturation can

Figure 1—*Nandina domestica*, nandina: seeds.

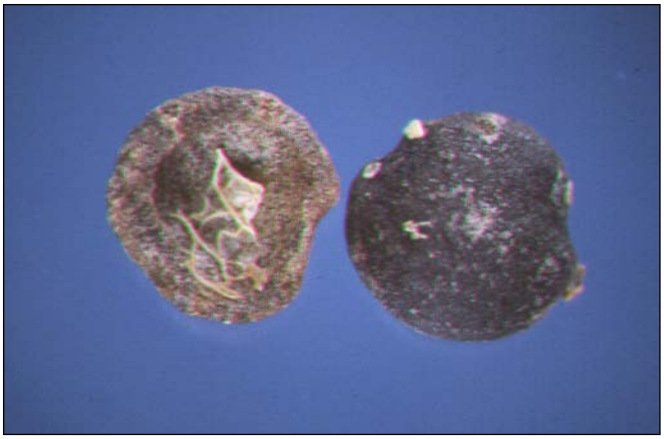
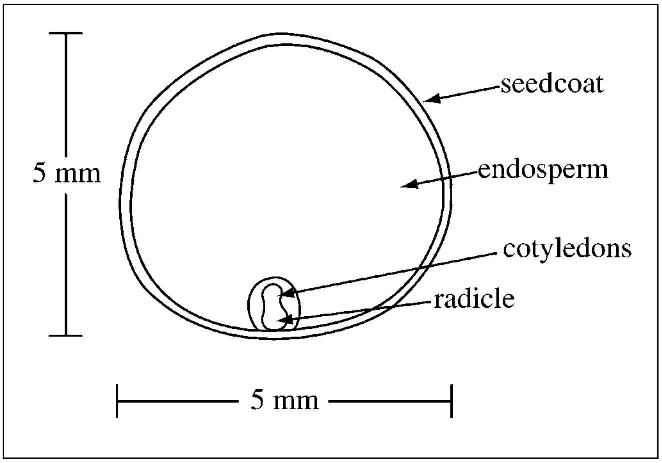


Figure 2—*Nandina domestica*, nanadina: longitudinal section of a seed.



occur during cold storage (Hartmann and others 1997). Embryo development also can occur regardless of whether seeds are stored at high or low temperatures or in moist or dry environments (Dirr and Heuser 1987).

Seeds of nandina have a tendency to germinate only during late fall or early winter, regardless of the sowing date (Afanasiev 1943; Hartmann and others 1997). Attempts to overcome this response—by cold stratification, treatment with various chemical compounds, increased oxygen pressure during germination, or varying the time of planting—have all been unsuccessful (Afanasiev 1943). Afanasiev concluded that cold stratification neither hastened embryo development nor improved germination. To speed embryo development, Dirr and Heuser (1987) recommend warm stratification of seeds for several months, followed by cold stratification for several months. In contrast, Hartmann and others (1997) reported that cold stratification was not necessary for seed germination.

Dehgan (1984) further investigated seed germination of nandina. Seeds were placed under dry or moist conditions at 4 or 30 °C for 0, 6, or 12 weeks. Another group of seeds was first treated with 1,000 ppm (0.1%) gibberellic acid (GA_3) for 24 or 48 hours followed by cold stratification at 4 °C or warm stratification at 30 °C for 0, 6 or 12 weeks. Results demonstrated that cold stratified seeds sown in a greenhouse in February had the greatest germination (78%) with the shortest germination time (3 weeks). Seeds that were cold-stratified for 12 weeks germinated more rapidly and uniformly compared to those stratified for 6 weeks. Neither GA_3 treatment nor warm stratification (30 °C) resulted in greater germination than nontreated seeds. Alternating periods of cold–warm, warm–cold, or warm stratification alone had little effect on increasing germination.

Germination tests. At present, optimum conditions for seed germination of nandina have not been defined. Two years are required for germination if seeds are sown in the fall (Dirr 1990). Dirr and Heuser (1987) reported 65% germination of seeds sown immediately following collection. However, time of actual germination was not reported.

Nursery practice. Although seeds can be germinated, commercial propagation of nandina is typically accomplished by vegetative means. If sexual propagation is desired, nandina seeds should be sown 6 mm ($^1/_4$ in) deep in a moist, sterile medium at 21 °C. The medium needs to be covered with polyethylene film and the container placed in bright light. Germination tends to be slow and generally occurs in about 60 days (Gibson 1982; Hartmann and others 1997). Seedlings tend to be relatively uniform (Whitcomb 1996).

Stem cuttings can be rooted anytime of year (except during the spring flush) with success rates of 80 to 90% (Barr 1987; Hartmann and others 1997). Auxin treatment of cuttings is beneficial (Barr 1987; Dirr and Heuser 1987). However, rooting tends to be slow (Bean 1976). Once stems have hardened, which is indicated by a reddening of the foliage, they become more difficult to root (Dirr and Heuser 1987; Gwaltney 1983). In addition, division of side shoots and removal of suckers that appear at the bases of plants have been successful, especially on dwarf cultivars (Dirr and Heuser 1987; Gwaltney 1983; Hartmann and others 1997). This is best accomplished in spring before growth begins.

Micropropagation protocols for nandina are currently being used commercially (Briggs and McCulloch 1983; Dirr 1990). *In vitro* techniques have been used to eliminate viruses from nandina (Smith 1983).

N

References

Afanasiev M. 1943. Germinating *Nandina domestica* seeds. American Nurseryman 78 (9): 7–8.

Barr B. 1987. Propagation of dwarf nandina cultivars. Combined Proceedings of the International Plant Propagators' Society 37: 507–508.

Bean WJ. 1976. Trees and shrubs hardy in the British Isles. 8th ed. Volume 3. London: John Murray Co. p. 1.

Briggs BA, McCulloch SM. 1983. Progress in micropropagation of woody plants in the United States and western Canada. Combined Proceedings of the International Plant Propagators' Society 33: 239–248.

Coats AM. 1992. Garden shrubs and their histories. New York: Simon and Schuster. 223 p.

Dehgan B. 1984. Germination of *Nandina domestica* seed as influenced by GA_3 and stratification. Proceedings of the Florida State Horticultural Society 97: 311–313.

Dirr MA. 1990. Manual of woody landscape plants: their identification, ornamental characteristics, culture, propagation, and uses. 4th ed. Champaign, IL: Stipes Publishing Co. 1007 p.

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

Flint HL. 1997. Landscape plants for eastern North America: exclusive of Florida and the immediate Gulf Coast. 2nd ed. New York: John Wiley and Sons. 842 p.

Gibson G. 1982. The bamboo alternative. American Horticulturist 61(10): 4, 7–10, 36.

Gwaltney T. 1983. Propagation of dwarf nandina cultivars. Combined Proceedings of the International Plant Propagators' Society 33: 624–628.

Hartmann HT, Kester DE, Davies Jr FT, Geneve RL. 1997. Plant propagation: principles and practices. 6th ed. Upper Saddle River, NJ: Prentice Hall. 770 p.

Huxley A, Griffiths M, Levy M. 1992. The new Royal Horticultural Society dictionary of gardening. Volume 3. London: Macmillan. 790 p.

Ikuta A. 1994. *Nandina domestica* (heavenly bamboo): *in vitro* culture and the production of jatrorrhizine, berberine, and other alkaloids. In: Bajaj YPS, ed. Biotechnology in agriculture and forestry: Medicinal and aromatic plants VI. Volume 26. Berlin: Springer-Verlag: 259–268.

Krüssmann G. 1985. Manual of cultivated broad-leaved trees and shrubs. Volume 2. Portland, OR: Timber Press. 624 p.

Newman SE. 1991. Germination of doubly dormant woody ornamental seeds. Combined Proceedings of the International Plant Propagators' Society 41: 359–364.

Ohwi J. 1984. Flora of Japan. Washington, DC: Smithsonian Institution. 1067 p.

Richards BW, Kaneko A. 1988. Japanese plants: know them and use them. Tokyo: Shufunotomo Co.: 98–99.

Smith RH. 1983. *In vitro* propagation of *Nandina domestica*. HortScience 18(3): 304–305.

Whitcomb CE. 1996. Know it and grow it: 3. A guide to the identification and use of landscape plants. Stillwater, OK: Lacebark Publications and Research. 802 p.

Aquifoliaceae—Holly family

Nemopanthus mucronatus (L.) Loes.

mountain-holly

John C. Zasada and C. S. Schopmeyer

Dr. Zasada retired from the USDA Forest Service's North Central Research Station; Dr. Schopmeyer (deceased) retired from the USDA Forest Service's Research National Office

Growth habit, occurrence, and use. Mountain-holly is a deciduous, branchy shrub occasionally attaining small tree stature that occurs in swamps, bogs, and poor fens from Newfoundland to Minnesota and south to Virginia and Indiana. Heights at ages 5, 10, 20, 30, and 40 years for plants in a shrub-dominated peatland in New York were 1.4, 2.0, 3.5, 4.0, and 4.5 m, respectively (LeBlanc and Leopold 1992). It is regarded as an obligate wetland species: 99% of the plants grow in wetlands (Begin and others 1990; Curtis 1959; Reed 1988; Vitt and Slack 1975). It is typically found on acidic to mildly acidic soils in the shrub zone adjacent to bog mats (Cram 1988).

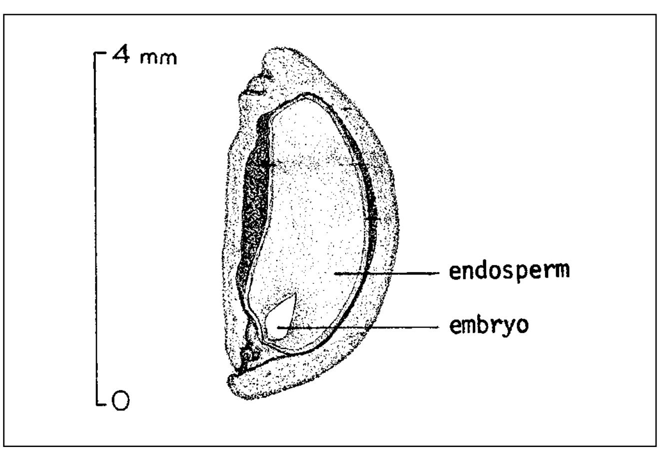
Nemopanthus is a monospecific genus and is closely related to *Ilex* spp. Similarities between *Ilex* and *Nemopanthus* in anatomical characteristics provide a basis for combining the 2 genera, but at this time it is maintained as a separate genus (Baas 1984). Information from Bonner (1974) for *Ilex* seeds is relevant to *Nemopanthus*. The species was introduced into cultivation in 1802.

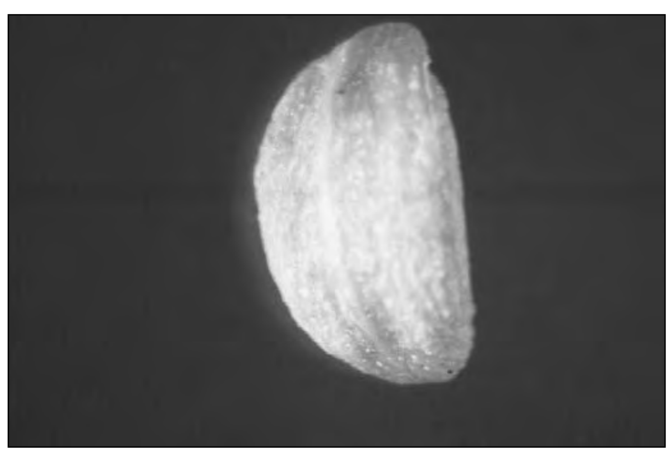
Flowering, fruiting, and seed collection. This species is mainly dioecious, with some monecious individuals (Farrar 1995). Flowering occurs in early May to June; fruits ripen as early as July, continuing into August; animals disperse the seeds (Gorchov 1990). The fruit is a scarlet, dull-red berrylike drupe, 0.6 to 2.5 cm in diameter, containing 4 to 5 bony nutlets (Rehder 1940), although Gorchov (1990) found a mean of 2.9 seeds/fruit. The latter are somewhat crescent shaped and are bone colored, with 1 rib on the back (figure 1). Because the fruits are somewhat persistent, they may be collected as late as mid-October (Schopmeyer 1974).

Extraction and cleaning of seeds. Seeds in small lots can be prepared by rubbing the fruits through a #10 soil screen (0.7mm) and then floating off the pulp and empty seeds. There are about 1,600 berries in 0.45 kg (1 lb) of fruit. The number of cleaned seeds per weight (3 samples) ranged from 68,355/kg (31,000 to 66,000/lb), with an average of 99,225/kg (45,000/lb). Seed purity in one sample was 96% and average soundness in 4 samples was 80% (Schopmeyer 1974).

Germination. Seeds are doubly dormant and require a period of after-ripening before the immature embryo will develop (figure 1) (Dirr and Heuser 1987). Consequently, germination is very slow. In 3 tests, germination began several months after sowing and continued for about 2 years, when germination capacities of 14 to 66% were observed

Figure 1—*Nemopanthus mucronatus*, mountain-holly: longitudinal section through a nutlet showing small immature embryo (**left**) and nutlet (**right**)





N

(Adams 1927; Schopmeyer 1974). Cold stratification alone did not increase germination rate (Adams 1927; Nichols 1934). Dirr and Heuser (1987) recommended 5 months of warm followed by 3 months of cold stratification. Propagation by greenwood cuttings is feasible (Bailey 1937; Dirr and Heuser 1987).

References

Adams J. 1927. The germination of the seeds of some plants with fleshy fruits, American Journal of Botany 14: 415–425.

Baas P. 1984. Vegetative anatomy and the taxonomic status of *Ilex collina* and *Nemopanthus* (Aquifoliaceae). Journal of the Arnold Arboretum 65: 243–250.

Bailey LH. 1937. The standard cyclopedia of horticulture. 3 vol. New York: Macmillan. 3639 p.

Begin J, Belanger L, Pfalzgraf J, Pineau M. 1990. Qualite de production dans les erablieres rouges de la plaine Drummondville, Quebec. Forestry Chronicle 66(4): 377–386.

Bonner FT. 1974. *Ilex* L., holly. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington DC: USDA Forest Service: 450–453.

Curtis JT. 1959. The vegetation of Wisconsin: an ordination of plant communities. Madison: University of Wisconsin Press: 655 p.

Cram H. 1988. A focus on peatlands and peat mosses. Ann Arbor: University of Michigan Press. 306 p.

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

Farrar JL. 1995. Trees in Canada. Markham, ON: Fitzhenry and White. 502 p.

Gorchov DL. 1990. Pattern adaptation and constraint in fruiting synchrony within verterbrate dispersed woody plants. Oikos 58: 169–180.

LeBlanc CM, Leopold DJ. 1992. Demography and age structure of a central New York shrub-carr 94 years after fire. Bulletin of the Torrey Botanical Club 119(1): 50–64.

Nichols GE. 1934. The influence of exposure to winter temperatures upon the seed germination in various native American plants. Ecology 15: 364–373.

Reed PB JR. 1988. National list of plant species that occur in wetlands. Biol. Rep. 88 (26.1), Northeast Region (region 1). Washington DC: USDI US Fish and Wildlife Service, Northeast Region.

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

Schopmeyer CS. 1974. *Nemopanthus mucronatus* (L.) Trel., mountain holly. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington DC: USDA Forest Service: 553.

Vitt DH, Slack NG. 1975. An analysis of the vegetation of sphagnum-dominated kettle-hole bogs in relation to environmental gradients. Canadian Journal of Botany 53: 332–359.

Nyssaceae—Sour-gum family

Nyssa L.

tupelo

Franklin T. Bonner

Dr. Bonner is a scientist emeritus at the USDA Forest Service's Southern Research Station, Mississippi State, Mississippi

Growth habit and use. The 4 deciduous, arboreal species of tupelo—the genus *Nyssa*—native to North America (table 1) are valued for pulp, veneer, specialty wood products, wildlife food, and honey production. Water tupelo, black tupelo, and swamp tupelo were cultivated in North America before 1750 (Bonner 1974; Brown and Kirkman 1990).

Flowering and fruiting. The minute, greenish white flowers that appear in spring (table 2) may be either perfect or staminate and pistillate; flowers may be borne separately on different trees. Fruits of the tupelos are thin-fleshed, oblong drupes about 10 to 38 mm long (figure 1). Their colors range from red to blue-black when they ripen in the autumn (table 2). Each fruit contains a bony, ribbed, usually 1-seeded stone (figures 2 and 3). Seeds of water tupelo range in color from white to dark brown or gray, and some are pinkish white. Seeds of all colors have germinated equally well (Bonner 1974). Trees of Ogeechee tupelo will bear fruit when they are about 5 years old (Kossuth and Scheer 1990), and 2-year-old stump sprouts of both swamp

Table 1—*Nyssa,* tupelo: nomenclature, occurrence, and height

Scientific name & synonym(s)	Common name(s)	Occurrence	Height at maturity (m)
N. aquatica **L.** *N. uniflora* Wangenh.	**water tupelo,** tupelo-gum, sourgum, cotton-gum, swamp tupelo	Coastal Plain from Virginia to N Florida & Texas N to Missouri & S Illinois	24–30
N. biflora **Walt.** *N. sylvatica* var. *biflora* (Walt.) Sarg. *N. sylvatica* var. *ursina* (Small) Wen & Stuessy	**swamp tupelo,** blackgum, swamp, black-gum	Coastal Plain, chiefly from Delaware to S Florida & E Texas, N to W Tennessee	40
N. ogeche **Bartr. ex. Marsh**. *N. acuminata* Small	**Ogeechee tupelo,** Ogeechee-lime, sour tupelo, sour tupelo-gum, white tupelo	Coastal Plain from South Carolina to NW Florida	12–15
N. sylvatica **Marsh.**	**black tupelo,** blackgum, sourgum, tupelo-gum, pepperidge	Maine W to Michigan & Missouri, S to E Texas & S Florida	15–18

Source: Little (1978).

Table 2—*Nyssa,* tupelo: phenology of flowering and fruiting

Species	Flowering	Fruit ripening	Color of ripe fruits	Fruit drop
N. aquatica	Mar–Apr	Sept–Oct	Dark purple	Oct–Dec
N. biflora	Apr–June	Aug–Oct	Blue-black	Sept–Dec
N. ogeche	Mar–May	July–Aug	Red	Nov–Dec
N. sylvatica	Apr–June	Sept–Oct	Blue-black	Sept–Nov

Sources: DeBell and Hook (1969), Kossuth and Scheer (1990), Radford and others (1964), Vande Linde (1964).

N

Figure 1—*Nyssa*, tupelo: fruits of *N. aquatica*, water tupelo (**upper left**); *N. sylvatica*, black tupelo (**upper right**); *N. ogeche*, Ogeechee tupelo (bottom).

Figure 2—*Nyssa,* tupelo: stones (seeds) of *N. aquatica*, water tupelo (**upper left**); *N. ogeche*, Ogeechee tupelo (**upper right**); *N. sylvatica*, black tupelo (**lower right**); *N. biflora*, swamp tupelo (**lower right**).

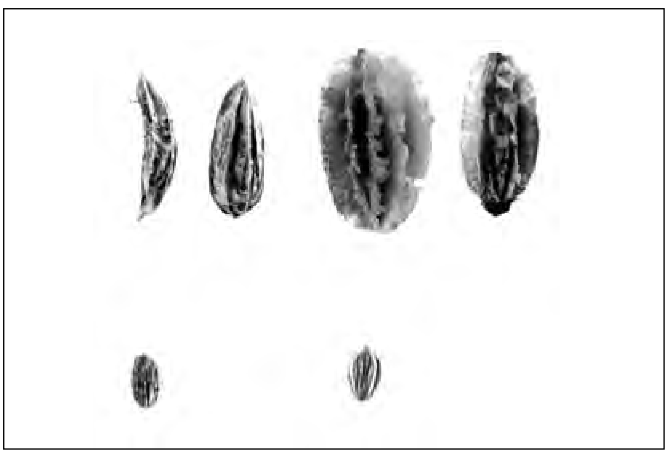
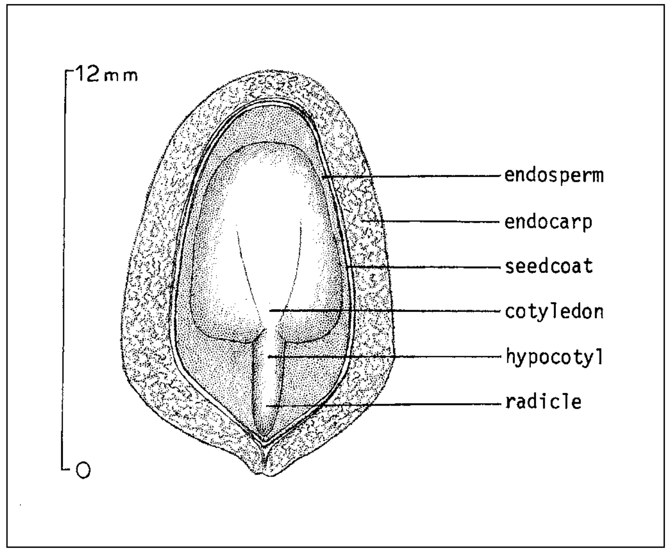


Figure 3—*Nyssa sylvatica*, black tupelo: longitudinal section through a seed.



tupelo and water tupelo have produced viable seeds (Priester 1979). Major seed production can be expected when trees reach a dbh of about 20 cm, and all of the tupelos typically fruit abundantly each year (Johnson 1990; Kossuth and Scheer 1990; McGee and Outcalt 1990).

Collection, extraction, and storage. Ripe tupelo fruits may be picked from the ground, from standing trees, or from freshly felled logging tops. Newly shed fruits of water tupelo with exocarps intact will float for as long as 100 days, and they may be skimmed from the top of the water or picked from drift piles (Johnson 1990; Schneider and Sharitz 1988). Ogeechee tupelo fruits that are partially dried may float also (Kossuth and Scheer 1990), but fruits of the other tupelos do not (McGee and Outcalt 1990). External fruit color is the best index of maturity in the field (table 2). To extract the seeds, the fruits should be run through a macerator with running water to float off the pulp. Small samples may be de-pulped by rubbing the fruits over a large-meshed screen, such as hardware cloth. For water tupelo, observed numbers of fruits per weight have been from 340 to 600/kg (155 to 270/lb). Fifty kilograms (100 lb) of black tupelo fruits should yield 12 kg (25 lb) of cleaned seeds (Bonner 1974). Seed weights are listed in table 3.

Water tupelo seeds are orthodox in storage behavior. They can be stored for at least 30 months in polyethylene bags at either 3 or –10 °C, if seed moisture contents are <20% or <10%, respectively (Bonner and Kennedy 1973). Seeds of black tupelo can be stored satisfactorily over 1 winter in cold, moist stratification in sand or in just cold storage (Vande Linde 1964). Removal of the pulp did not appear to be essential for retention of viability in either condition. There are no published storage data for other tupelo species, but it is probable that the same methods would be successful for them also.

Pregermination treatment. Tupelo seeds exhibit moderate embryo dormancy, and they benefit from cold, moist stratification. Treatment in moist sand and in plastic bags without medium have been used successfully (Bonner 1974; DeBell and Hook 1969). Good germination has been reported after only 30 days of stratification, but periods up to 120 days may be needed for some seedlots (Bonner 1974; DuBarry 1963).

Germination tests. Official seed testing prescriptions for tupelos in North America (AOSA 1993) call for a temperature regime of 8 hours at 30 °C in light and 16 hours at 20 °C in the dark. Testing should be on moist blotters or creped cellulose wadding for 21 days (water tupelo) or 28 days (black tupelo). Stratification for 28 to 30 days should precede the test. Germination of stratified seeds has been tested in several other media (table 4), and each of these probably would be satisfactory for seeds of all tupelo species.

Nursery practice. Although untreated seeds may be sown in the fall (Heit 1967) spring-sowing of stratified seeds is recommended, particularly in the South. They may be broadcast or drilled in rows, with 50 seeds/m (15/ft) for water tupelo. Seeds should be planted 12 to 25 mm ($^1/_2$ to 1 in) deep or sown on the bed surface and rolled into the soil and mulched (Bonner 1974; Vande Linde 1964). Mulching with 2 to 3.5 cm (.8 to 1.4 in) of sawdust is recommended for water tupelo and with 6 mm ($^1/_2$ in) of sawdust or 1 cm (.4 in) of pine straw for swamp tupelo. After sowing, the seeds and mulch must not be allowed to dry excessively.

Table 3—*Nyssa,* tupleo: seed weights

		Cleaned seeds/weight				
		Range		Avg		
Species	Collection place	/kg	/lb	/kg	/lb	Samples
N. aquatica	—	—	—	1,000	456	—
N. biflora	South Carolina	—	—	5,320	2,415	10
N. ogeche	—	2,300–3,100	1,040–1,420	2,700	1,230	2
N. sylvatica	—	4,100–8,820	1,850–4,000	7,280	3,300	5
	North Carolina	5,750–8,500	2,610–3,860	7,450	3,380	10
	Midwest	—	—	5,500	2,492	2+

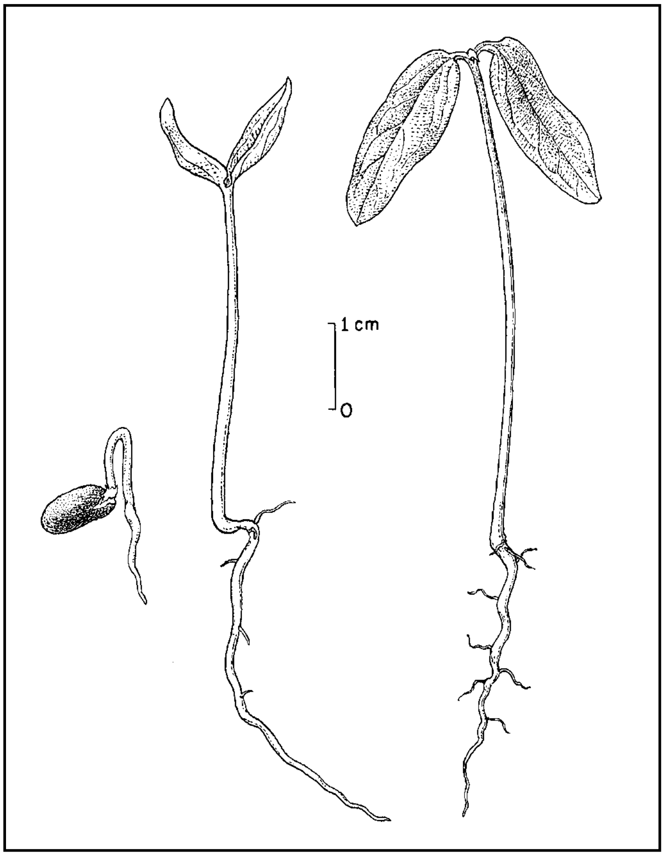
Sources: Bonner (1974), Earle and Jones (1969).

Table 4—*Nyssa,* tupelo: germination test conditions and results on stratified seeds

	Daily	Germination test conditions				Germination rate		Germination %		
	light		Temp (°C)			Amt		Avg		Purity
Species	(hr)	Medium	Day	Night	Days	(%)	Days	(%)	Samples	(%)
N. aquatica	8	Kimpak	30	20	27	87	18	97	5	100
	0	Water in petri dish	29	29	28	57	14	79	24	—
N. biflora	ND	Sand	—	—	60	—	—	51	—	—
N. ogeche	8	Kimpak	30	20	70	69	12	85	1	—
N. sylvatica var. *sylvatica*	8	Kimpak	30	20	27	—	—	71	8	99

Sources: Bonner (1974), Debell and Hook (1969).
ND = natural daylength in a greenhouse.

Figure 4—*Nyssa sylvatica*, black tupelo: seedling development at 1, 4, and 39 days after germination.



Shading with tobacco shade cloth can help keep beds moist and aid the newly emerged seedlings (Vande Linde 1964). Germination is epigeal (figure 4). Desirable seedbed densities for water and black tupelos are 100 to 150 seedlings/m^2 (9 to 14/ft^2) (Williams and Hanks 1976. Vegetative propagation of tupelos is possible by softwood cuttings and grafting (Dirr and Heuser 1987).

References

AOSA [Association of Official Seed Analysts]. 1993. Rules for testing seeds. Journal of Seed Technology 16(3): 1–113.

Bonner FT. 1974. *Nyssa* L., tupelo. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 554–557.

Bonner FT, Kennedy HE Jr. 1973. Storage of water tupelo seeds. Tree Planters' Notes 24(4): 7–8.

Brown CL, Kirkman LK. 1990. Trees of Georgia and adjacent states. Portland, OR: Timber Press. 292 p.

DeBell DS, Hook DD. 1969. Seeding habits of swamp tupelo. Res. Pap. SE-47. Asheville, NC: USDA Forest Service, Southeastern Forest Experiment Station. 8 p.

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

DuBarry AP Jr. 1963. Germination of bottomland tree seed while immersed in water. Journal of Forestry 61: 225–226.

Earle FR, Jones Q. 1962. Analyses of seed samples from 113 plant families. Economic Botany 16: 221–250.

Heit CE. 1967. Propagation from seed: 8. Fall planting of fruit and hardwood seeds. American Nurseryman 126 (4): 12–13, 85–90.

Johnson RL. 1990. *Nyssa aquatica* L., water tupelo. In: Burns RN, Honkala BH, tech. coords. Silvics of North America. Volume 2, Hardwoods. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 474–478.

Kossuth SV, Scheer RL. 1990. *Nyssa ogeche* Bartr. ex Marsh., Ogeechee tupelo. In: Burns RM, Honkala BH, tech. coord. Silvics of North America. Volume 2, Hardwoods. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 479–481.

Little EL Jr. 1978. Checklist of United States trees (native and naturalized). Agric. Handbk. 541. Washington, DC: USDA Forest Service. 375 p.

McGee CE, Outcalt KW. 1990. *Nyssa sylvatica* Marsh., black tupelo. *N. sylvatica* Marsh. var. *sylvatica*; black tupelo (typical), *N. sylvatica* var. *biflora* (Walt.) Sarg., swamp tupelo. In: Burns RM, Honkala BH, tech. coords. Volume 2, Hardwoods. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 482–489.

Priester DS. 1979. Stump sprouts of swamp and water tupelo produce seeds. Southern Journal of Applied Forestry 3: 149–151.

Radford AE, Ahles HE, Bell CR. 1964. Guide to the vascular flora of the Carolinas. Chapel Hill: University of North Carolina Book Exchange. 1183 p.

Schneider RL, Sharitz RR. 1988. Hydrochory and regeneration in a bald cypress–water tupelo swamp forest. Ecology 69: 1055–1063.

Vande Linde F. 1964. Nursery practices for southern oaks and gums. Tree Planters' Notes 65: 24–26.

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

Rosaceae—Rose family

Oemleria cerasiformis (Torr. & Gray ex Hook. & Arn.) Landon

osoberry

William I. Stein

Dr. Stein is a forest ecologist emeritus at the USDA Forest Service's Pacific Northwest Research Station, Corvallis, Oregon

Other common names. Indian plum, squaw-plum, Indian peach.

Growth habit, occurrence, and uses. The genus *Oemleria* contains a single species—osoberry, *Oemleria cerasiformis* (Torr. & Gray ex Hook. & Arn.) Landon. Osoberry was described originally as *Nuttalia cerasiformis,* then identified for decades as *Osmaronia cerasiformis* (Hunt 1970) until an earlier legitimate name was rediscovered about 30 years ago (Landon 1975).

Osoberry is a deciduous, generally multiple-stemmed shrub that is 1.5 to 5 m or taller and sometimes develops into a small tree (Abrams 1944; Hitchcock and others 1961). A plant may have 10 or more stems and can produce new stems throughout its lifetime. Individual stems 7 m tall and 50 years of age have been observed (Allen and Antos 1993). Osoberry's native range is from the Pacific Coast eastward into the Cascade Mountains and the Sierra Nevada from southwest British Columbia southward to California, extending to Tulare County in the Sierras and northern Santa Barbara County in the coastal ranges (Hitchcock and others 1961; McMinn 1970). It is most widely distributed from the Willamette Valley northward to Vancouver Island on stream terraces, alluvial soils, and other moist to moderately dry locations, especially in Oregon white oak (*Quercus garryana* Dougl. ex Hook.) woodlands and open Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests. Based on a sampling of osoberry stands at 56 locations, Antos and Allen (1990b) concluded that its geographical distribution is related to (1) a fairly mild maritime climate, (2) moist areas over much of its range, (3) an inability to tolerate low light levels or wet soils, and (4) a need for disturbance to allow seedling establishment. It is most common at elevations below 250 m but occurs up to 1,700 m in the southern part of its range (Antos and Allen 1990b; Munz and Keck 1959). Two varieties were described in 1905—*lancifolia* in British Columbia and *nigra* in Washington (Hitchcock and others 1961)—but their recognition is now uncertain.

Ripening osoberry fruits are highly attractive to birds such as cedar waxwings (*Bombycilla cedrorum*), and ripe fruits are readily eaten by both birds and mammals (Dayton 1931; Dimock and Stein 1974). The fruits were eaten in small quantities fresh, cooked, or dried by Native American peoples in the Pacific Northwest; twigs and bark were used for several medicinal purposes (Gunther 1945; Mitchem 1993; Pojar and Mackinnon 1994). Flavor of the fruits apparently varies by locality, from sweet to bitter (Dayton 1931). Its attractiveness as an ornamental includes flushing of light green leaves and white flowers much earlier than other plant associates, handsome variegated appearance as scattered leaves throughout the crown turn yellow in early summer, and colorful clusters of fruit (figure 1) that soon disperse or are eaten by wildlife.

Figure 1—*Oemleria cerasiformis*, osoberry: ripe and near-ripe fruits; their color changes from reddish to purple when fully ripe.

Flowering and Fruiting. Anatomical and natural population studies have confirmed strongly that osoberry is dioecious, with male and female plants similar in size, growth form, morphology of vegetative structures, and microhabitats occupied (Allen and Antos 1988, 1993, 1999; Antos and Allen 1990a; Sterling 1964). Flowering period in osoberry is relatively short and varies with latitude and elevation from January to May concurrent with leaf development (Allen 1986; Haskin 1967; Hitchcock and others 1961; McMinn 1970). Both male and female plants flower frequently except in low light; male plants are generally more abundant and may have up to 3 times as many flowers as female plants (Allen 1986; Allen and Antos 1988, 1993). Male plants start flowering earlier than female plants but reach peak abundance and finish flowering later (Allen 1986). First flowering has occurred 2 years after germination on male plants raised from seed (Allen and Antos 1993). The 5-petaled flowers are white, fragrant, and borne on drooping racemes (figure 2). Osoberry pollen is sculptured and distinctive among Rosaceae pollens studied in western Canada (Hebda and others 1991).

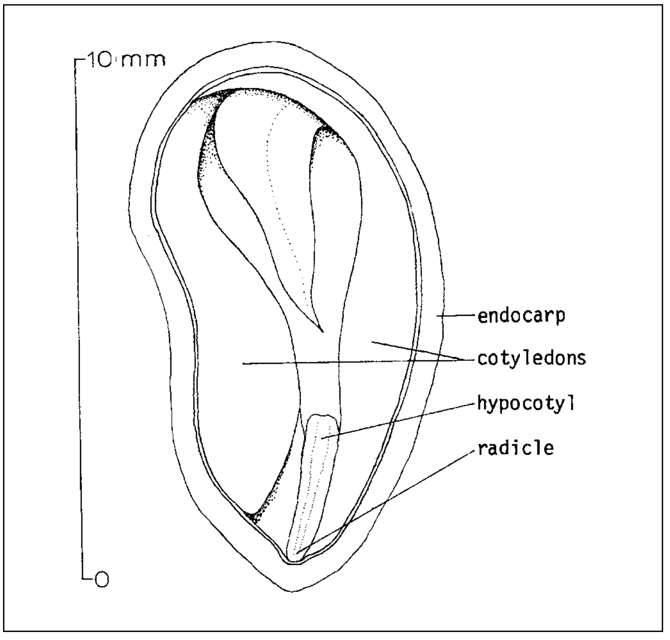
Pistillate flowers may yield up to 5 thin-fleshed, single-seeded drupes per flower, but generally fewer than 60% of pistils on a plant bear fruit; production from 10 to 20 of pistils has been reported (Antos and Allen 1994, 1999). Higher light levels favorably influence fruit set; exposure to light is gained by early flowering before deciduous associates leaf out (Allen and Antos 1988). Fruits develop and ripen in 10 to 12 weeks near Victoria, British Columbia (Antos and Allen 1994). Developing fruits become peach colored, then reddish, and finally deep blue-black under a whitish bloom when ripe (figure 1). In the Pacific Northwest, dispersal by gravity, birds, and mammals may begin in May and be nearly finished in July (Dimock and Stein 1974), substantially earlier than the August 1 to September 15 collection period listed for California by Mirov and Kraebel (1939).

Figure 2—*Oemleria cerasiformis*, osoberry: white flowers are borne on drooping racemes.

Collection, extraction, and storage. Clusters of the ripe 1-seeded drupes can be stripped readily from the shrubs by hand. Fruits in small collections are de-pulped easily by rubbing them against a submerged screen or by running them through a macerator followed by repeated washings to float off the loosened pulp. Fruit biomass is about half pulp and half seed (ovendry weight); the seeds have a much higher nitrogen concentration (Antos and Allen 1990a, 1994). Osoberry seeds have a bony endocarp (Abrams 1944) and lack endosperm (figures 3 and 4). Air-drying is needed to minimize molding in cool dry storage.

Figure 3—*Oemleria cerasiformis*, osoberry: seeds have a bony endocarp.

Figure 4—*Oemleria cerasiformis*, osoberry: longitudinal section through a seed shows folded cotyledons



About 11 kg (25 lb) of seeds (cleaned and air-dried for 24 hours) can be obtained from 45 kg (100 lb) of fresh drupes, based on 7 samples (Dimock and Stein 1974). Cleaned seeds air-dried for 4 weeks averaged 10.2/g (4,630/lb) for 12 samples from western Washington. Heavier seed weights have been reported from other parts of the osoberry's range—4.0/g (1,800/lb) in California (Mirov and Kraebel 1939) and 9.2/g (4,175/lb) in British Columbia (Antos and Allen 1994). Seeds generally are full, 98 to 100% in 4 samples (Dimock and Stein 1974).

Pregermination treatments and germination tests. Lengthy cold moist stratification is needed to overcome dormancy in fresh osoberry seeds (Dimock and Stein 1974; Mirov and Kraebel 1939). In a comparison of stratification periods at 3.3 °C in peat moss followed by 21 days at alternating 30 to 20 °C day/night temperatures, Dimock and Stein (1974) found that 60 days of stratification barely triggered germination, whereas 120 days were required for nearly complete germination. Osoberry seeds are capable of germinating at 3.3 °C during lengthy stratification—84% of total germination in 120 days, full germination in 180 days (table 1). Over 90% germination is obtainable from good seeds. Germination is epigeal (figure 5).

Nursery practice. Osoberry was introduced to cultivation by Theodor Hartweg in 1848 (Hunt 1970). It has been propagated primarily from seeds but also from suckers and cuttings. It lacks rhizomes or stolons, but some layering occurs naturally when woody debris presses stems to the ground (Antos and Allen 1990b). Tips of branches have been propagated vegetatively in a frame with bottom heat (Mirov and Kraebel 1939).

Though fruits ripen and are disseminated naturally by early summer, the seeds rarely, if ever, germinate within the year of dispersal (Dimock and Stein 1974). However, in the following year, they may germinate as early as mid-February. Seeds collected in July, cleaned, and stored at room temperature until sown outdoors in flats in late December began germinating in March in Victoria, British Columbia; second-year germination started in early February and varied from 0 to 70% of total germination for individual seedlots (Allen and Antos 1995). Total germination ranged from 1 to 96% among the 25 lots of 100 seeds each representing 5 plants at each of 5 collection areas in British Columbia and Washington.

Figure 5—*Oemleria cerasiformis*, osoberry: seedlings at 40 and 120 days after germination.

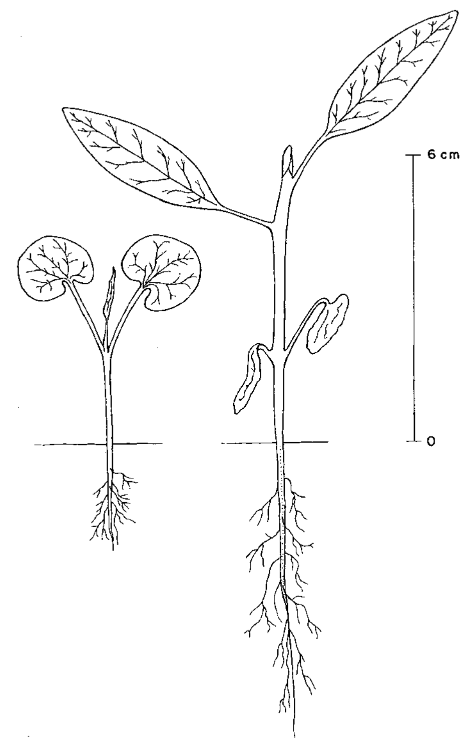


Table 1—*Oemleria cerasiformis*, osoberry: effect of stratification on germination

Stratification at 3.3 °C (days)	Germination during stratification (%)	Additional germination during 21 days at 30/20 °C (%)	Total germination (%)
60	0	1	1
90	21	37	58
120	80	14	94
160	94	0	94
180	95	0	95

O

References

Abrams L. 1944. Illustrated flora of the Pacific States. Stanford, CA: Stanford University Press. Volume 2. 635 p.

Allen GA. 1986. Flowering pattern and fruit production in the dioecious shrub *Oemleria cerasiformis* (Rosaceae). Canadian Journal of Botany 64: 1216–1220.

Allen GA, Antos JA. 1988. Relative reproductive effort in males and females of the dioecious shrub *Oemleria cerasiformis*. Oecologia 76: 111–118.

Allen GA, Antos JA. 1993. Sex ratio variation in the dioecious shrub *Oemleria cerasiformis*. American Naturalist 141: 537–553.

Allen GA, Antos JA. 1995. Personal communication. Victoria, BC: University of Victoria.

Antos JA, Allen GA. 1990a. A comparison of reproductive effort in the dioecious shrub *Oemleria cerasiformis* using nitrogen, energy, and biomass as currencies. American Midland Naturalist 124: 254–262.

Antos JA, Allen GA. 1990b. Habitat relationships of the Pacific Coast shrub *Oemleria cerasiformis* (Rosaceae). Madroño 37: 249–260.

Antos JA, Allen GA. 1994. Biomass allocation among reproductive structures in the dioecious shrub *Oemleria cerasiformis*—a functional interpretation. Journal of Ecology 82: 21–29.

Antos JA, Allen GA. 1999. Patterns of reproductiive effort in male and female shrubs of *Oemleria cerasiformis*: a six-year study. Journal of Ecology 87: 77–84.

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

Dimock EJ II, Stein WI. 1974. *Osmaronia* (Torr. & Gray) Greene, osoberry. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 561–563.

Gunther E. 1945. Ethnobotany of western Washington. Seattle: University of Washington Press. 61 p.

Haskin LL. 1967. Wild flowers of the Pacific Coast. Portland, OR: Binfords and Mort. 408 p.

Hebda RJ, Chinnappa CC, Smith BM. 1991. Pollen morphology of the Rosaceae of western Canada: 4. *Luetka, Oemleria, Physocarpus, Prunus*. Canadian Journal of Botany 69: 2583–2596.

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

Hunt DR. 1970. *Osmaronia cerasiformis*, Rosaceae. Curtis's Botanical Magazine NS 178(1): Tab. 582.

Landon JW. 1975. A new name for *Osmaronia cerasiformis* (Rosaceae). Taxon 24: 200.

McMinn HE. 1970. An illustrated manual of California shrubs. Berkeley: University of California Press. 663 p.

Mitchem, CM. 1993. Short notes on *Oemleria*. Plantsman 14(4): 252–255.

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

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

Pojar J, Mackinnon A, eds. 1994. Plants of the Pacific Northwest Coast. Redmond, WA: Lone Pine Publishing. 527 p.

Sterling C. 1964. Comparative morphology of the carpel in the Rosaceae: 2. Prunoideae: *Maddenia, Pygeum, Osmaronia*. American Journal of Botany 51: 354–360.

Oleaceae—Olive family

Olea europaea L.

olive

George C. Martin

Dr. Martin is professor of pomology emeritus at the University of California, Davis, California

Growth habit. Olive is a member of the Oleaceae, the family that contains the genera *Fraxinus* (ash), *Forsythia* (golden bell), *Forestiera (F. neomexicana*, the California "wild-olive"), *Ligustrum (*privet), and *Syringa* (lilac) as well as *Olea* (olive). Commercial olives belong to the species *Olea europaea* L. There are about 20 species of *Olea* found in tropical and subtropical regions of the world, but only *O. europaea* L. produces edible fruit.

Olive is a long-lived evergreen tree; some specimens have been reported to live for 1,000 years. The wood resists decay, and when the top of the tree is killed by mechanical damage or environmental extremes, new growth arises from the root system. Whether propagated by seed or cuttings, the root system generally is shallow, spreading to 0.9 or 1.2 m even in deep soils. The above-ground portion of the olive tree is recognizable by the dense assembly of limbs, the short internodes, and the compact nature of the foliage. Light does not readily penetrate to the interior of an olive tree unless the tree is well managed and pruned to open light channels toward the trunk. If unpruned, olives develop multiple branches with cascading limbs. The branches are able to carry large populations of fruit on terminal twigs, which are pendulous and flexible—swaying with the slightest breeze.

Olive leaves are thick, leathery, and oppositely arranged. Each leaf grows over a 2-year period. Leaves have stomata on their lower surfaces only. Stomata are nestled in peltate trichomes that restrict water loss and make the olive relatively resistant to drought. Some multicellular hairs are present on leaf surfaces. Olive leaves usually abscise in the spring when they are 2 or 3 years old; however, as with other evergreens, leaves older than 3 years are often present.

Flower bud inflorescences are borne in the axil of each leaf. Usually the bud is formed on the current season's growth and begins visible growth the next season. Buds may remain dormant for more than a year and then begin growth, forming viable inflorescences with flowers a season later than expected. When each leaf axil maintains a developing inflorescence, there are hundreds of flowers per twig. Each inflorescence contains between 15 and 30 flowers, depending on developmental processes for that year and the cultivar.

The flowers are borne on the inflorescence and are small, yellow-white, and inconspicuous. Each contains a short, 4-segmented calyx and a short-tubed corolla containing 4 lobes. The 2 stamens are opposite on either side of the 2-loculed ovary that bears a short style and capitate stigma. Two types of flowers are present each season: perfect flowers, containing stamen and pistil, and staminate flowers, containing aborted pistils and functional stamens. The proportion of perfect and staminate flowers varies with inflorescence, cultivar, and year. Large commercial crops occur when 1 or 2 perfect flowers are present among the 15 to 30 flowers per inflorescence. As a rule, more staminate flowers than pistillate flowers are present.

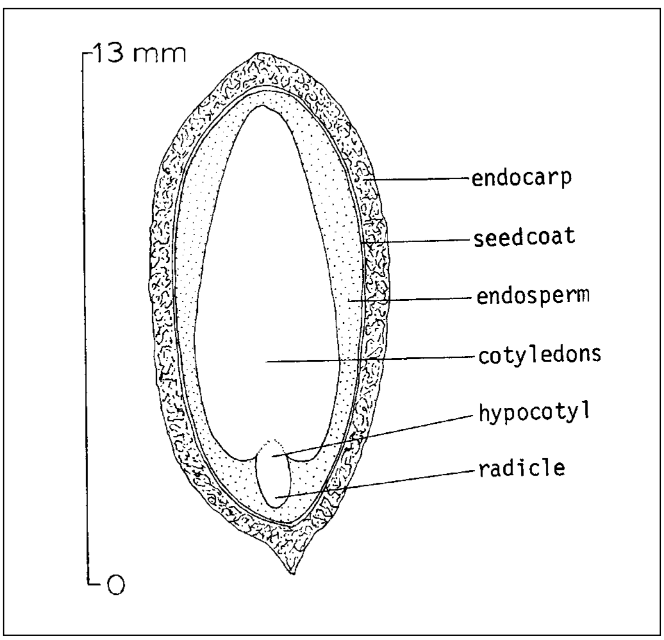
The perfect flower is evidenced by its large pistil, which nearly fills the space within the floral tube. The pistil is green when immature and deep green when open at full bloom. Staminate flower pistils are tiny, barely rising above the floral tube base. The style is small and brown, greenish white, or white, and the stigma is large and plumose as it is in a functioning pistil.

The olive fruit is a drupe, botanically similar to almond, apricot, cherry, nectarine, peach, and plum fruits. The olive fruit consists of carpel, and the wall of the ovary has both fleshy and dry portions. The skin (exocarp) is free of hairs and contains stomata. The flesh (mesocarp) is the tissue eaten, and the pit (endocarp) encloses the seed. Fruit shape and size and pit size and surface morphology vary greatly among cultivars.

The mature seed (figure 1) is covered with a thin coat that covers the starch-filled endosperm (figure 2). The latter surrounds the tapering, flat leaflike cotyledons, short radicle

Figure 1—*Olea europaea,* olive: stone.

Figure 2—*Olea europaea*, olive: longitudinal section through a stone.



(root), and plumule (stem). Seed size and absolute shape vary greatly with cultivar.

The seed undergoes most of its development starting in July and ending in about September. The fruit is horticulturally mature in September or October (ready for the California black-ripe or green-ripe process), and physiologically mature in January or February. The seed is horticulturally mature by October, and if harvested and stratified at that time it will achieve maximum germination (Lagarda and others 1983a). When the fruit is physiologically mature by January, seed germination is greatly reduced.

Occurrence. The origin of olive is lost in prewritten history. The wild olives *Olea chrysophylla* Lam. and *O. europaea* L. var. *oleaster* most probably yielded the domesticated form *O. europaea* L. These wild types are known to have existed in the region of Syria about 6,000 years ago (Zohary and Spiegal-Roy 1975). From the eastern Mediterranean, olive trees were spread west throughout the Mediterranean area and into Greece, Italy, Spain, Portugal, and France. In 1560, the Spanish Conquistadors carried olive cuttings and seeds to Peru. From there or independently, olive was found in Mexico at Jesuit missions. The Franciscan padres carried olive and other fruits from San Blas, Mexico, into California. Sent by Jose de Galvez, Father Junipero Serra established Mission San Diego de Acala in 1769. Though oil production began there in the next decade, the first mention of oil was written in the records of Mission San Diego de Alcala in 1803 as described by Father Lasuen.

Use. By the late 1800s, olive oil production in California was sufficient to supply markets outside of California. By the 1900s, California olive oil production had met the competition from imported olive oil and American vegetable oil and, in an effort to survive, the canning olive industry was born. During the 20th century, the California canning olive occupied a strong market position in America, with olive oil as a salvage industry. Currently, a renewed emphasis in health benefits of monosaturated olive oil has lead to a resurgence of olive oil production in California.

The olive tree has been used widely for shade around homes and as a street tree in cities. Its distribution is only limited by cold weather in the winter, as temperatures below –9.4 °C are lethal (Denney and others 1993).

Varieties. Several hundred varieties of olive are known and can be found at the World's Olive Variety Collection in Cordoba, Spain (del Rio and Caballero 1994). A smaller collection exits at the United States Germplasm Repository at Winters, California. Varieties differ by features of the tree shape, leaves, and fruit. Canning varieties possess larger fruit than do oil varieties. Any of the varieties are useful for landscape purposes. The varieties grown in California for canning are 'Manzanillo', 'Mission', 'Sevillano', 'Ascolano', and 'Barouni'.

Flowering and fruiting. Floral initiation occurs by November (Pinney and Polito 1990), after which, flower parts form in March. Unlike deciduous fruits with a short induction-to-initiation cycle, induction in olive may occur as early as July (about 6 weeks after full bloom), but initiation is not easily seen until 8 months later in February. Complex microscopic and histochemical techniques reveal evidence of floral initiation by November, but the process of developing all the flower parts starts in March. Some olive cultivars, such as those grown in Crete, southern Greece, Egypt, Israel, and Tunisia, bloom and fruit heavily with very little winter chilling; whereas those originating in Italy, Spain, and California require substantial chilling for good fruiting.

In experiments with the cultivars grown in California, optimum flowering occurred when the temperature fluctuated daily between 15.5 to 19 °C maximum and 2 to 40 °C minimum. Trees held at a constant temperature of 13 °C also bloomed profusely but had poor pistillate flower formation. If temperatures did not rise above 7.5 °C or fall below 15.5 °C, trees did not bloom. At 13 °C, both chilling and warmth are sufficient for flowering but not for complete flower development. In contrast to flower buds, vegetative buds of olive seem to have little if any dormancy, growing whenever the temperatures are much above 21 °C. In addition to winter chilling, inflorescence formation requires leaves on the fruiting shoots. Therefore, it is important to prevent defoliation. The occasional occurrence of hot, dry winds during the blooming period has been associated with reduced fruit set. Winds or heat increase the amount of natural abscission.

Prolonged, abnormally cold weather during April and May, when the olive flower buds should be developing rapidly, can have a detrimental effect on subsequent flowering, pollination, and fruit set. Such weather occurred in California in the spring of 1967, delaying bloom by several weeks and leading to flower abnormalities and a crop of only 14,000 tons, the lightest in modern California history. In California, fruit on the tree by July 1, as a rule, continue on to maturity.

At full bloom, flowers are delicately poised for pollination, when some 500,000 flowers are present in a mature tree; a commercial crop of 7 metric tons/ha (3 tons/ac) or more can be achieved when 1 or 2% of these flowers remain as developing fruit. By 14 days after full bloom, most of the flowers destined to abscise have done so. By that time, about 494,000 flowers have abscised from a tree that started with 500,000 flowers.

Olives are polygamo-monoecious. The flowers are born axially along the shoot in panicles. The panicles of 'Barouni', 'Manzanillo', 'Mission', and 'Sevillano' carry an average of 12 to 18 flowers; 'Ascolano' average 20 flowers. Perfect flowers, those with both pistillate and staminate parts, normally consist of a small calyx, 4 petals, 2 stamens and filaments supporting large pollen-bearing anthers, and a plum-green pistil with a short thick style and a large stigma. Perfect flowers are borne apically in an inflorescence, and within the typical triple-flower inflorescence the middle flower is generally perfect. Imperfect flowers are staminate, with the pistil either lacking or rudimentary. Flowers with abortive anthers also occur and are common in 'Sevillano'.

Cultivars vary, but most abscission occurs soon after full bloom and final fruit set nearly always occurs within 6 weeks of full bloom. Further fruit abscission can result from pest infestation and environmental extremes. When trees have an inflorescence at nearly every leaf axil a commercial crop occurs with 1 to 2% fruit set; with a small population of inflorescence, a commercial crop may require 10% fruit set.

"Shotberries" (parthenocarpic fruits) occur randomly and for reasons not clearly understood. When shotberries occur, they may be seen in clusters on each inflorescence. Here the interfruit competition for raw materials differs from that of normal olive fruits. Shotberries mature much earlier than normal fruit and may be more prevalent when conditions favor a second large crop in succession.

The endocarp (pit) enlarges to full size and hardens by 6 weeks after full bloom. At that time, the endosperm begins to solidify and embryo development takes place, leading to embryo maturity by September. The mesocarp (flesh) and exocarp (skin) continue their gradual growth. The fruits begin changing from the green color to yellow-white (straw) and accumulate anthocyanin from the distal or base end. The purple to black color eventually bleeds into the mesocarp, signaling fruit overmature for the California black-ripe or green-ripe processing. As has been reported for most other fruit crops, trees with few fruits mature their crops earlier than trees with many fruits.

Collection, extraction, storage, and germination of seeds. For seed production, the fruits should be harvested when ripe, but before they turn black. This period extends from late September to mid-November, depending on the cultivar (Largarda and others 1983a&b). Pits are removed from the flesh of the fruit with macerators. Pits can be stored in a dry place for years or planted directly, but germination is slow and uneven. Pregermination treatments are designed to overcome both seedcoat (mechanical) and embryo dormancies. Mechanical or chemical scarification is used to treat mechanical dormancy. In scarification, the endocarp can be cracked mechanically or clipped at the radicle end, with care taken not to damage the embryo. Clipping just the cotyledonary end of the endocarp does not improve germination. Good germination results can be obtained using a seed cracking device before subsequent handling procedures (Martin and others 1986). Pits may be soaked in concentrated sulfuric acid to soften the endocarp. Soaking time depends on the thickness of the endocarp; typical soaking times for 'Manzanillo' are between 24 and 30 hours. The

O

Table 1—*Olea europaea,* olive: fruit and seed data

	Fruits/wt		Seed wt/metric ton of fruit		Seeds/weight	
	/kg	/lb	kg	lb	/kg	/lb
Small	706	320	778	353	4,410	2,000
Medium	198	90	584	265	1,654	750
Large	99	45	485	220	992	450

acid bath is followed by 1 to 2 hours of rinsing in water (Crisosto and Sutter 1985).

The pits can be planted directly after the endocarp treatments. Pits should be planted at a depth about 2 to 3 times their diameter. Seeds planted outdoors in December do not germinate until the following spring. Pits can also be planted in pots or seedbeds in a greenhouse maintained at a 21 to 24 °C daytime temperature. Germination takes up to 3 months. It is critical that the seeds do not dry out after germination begins. The number of fruits and seeds per weight for 3 commercial size classes are listed in table 1.

Germination is quicker and more uniform when treatments to overcome internal dormancy are carried out in addition to scarification. The most successful of these treatments on a commercial scale is stratification. Pits are scarified as described above and then soaked in water at room temperature for 24 hours. The pits are mixed with moist sand or vermiculite and then placed in the dark in a controlled environment. The temperature is kept at 15 °C for 30 days. Stratification is thought to reduce abscisic acid (which inhibits germination) within the embryo or seedcoat. After stratification, pits can be planted outdoors if the weather is suitable; severe weather can cause losses. Pits can be planted in a greenhouse maintained at a 21 to 27 °C daytime temperature. Bottom heat is necessary. Germination should occur within 1 month. Transplanting seedlings from the greenhouse to the nursery should include steps to harden the seedlings, such as partial shade provided by a lathhouse. Adequate irrigation and fertilization are recommended to ensure continued rapid growth.

Nursery practice and seedling care. Virtually all olive trees are produced from rooted cuttings. Seed handling difficulties, low germination percentage, and slow initial seedling growth rate make seedling production impractical.

References

Crisosto C, Suffer EG. 1985. Improving 'Manzanillo' olive seed germination. HortScience 20: 100–102.

del Rio C, Caballero JM. 1994. Preliminary agronomical characterization of 131 cultivars introduced in the Olive Germplasm Bank of Cordoba in March 1987. Acta Horticulturae 356: 110–115.

Denney JO, Martin GC, Kammereck R, Ketchie DO, Connell JH, Krueger WH, Osgood JW, Sibbeft GS, Nour GA. 1993. Freeze damage and coldhardiness in olive: findings from the 1990 freeze. California Agriculture 47: 1–12.

Lagarda A, Martin GC, Kester DE. 1983a. Influence of environment, seed tissue and seed maturity on 'Manzanillo' olive seed germination. HortScience 18: 868–869.

Largarda A, Martin GC, Polito VS. 1983b. Anatomical and morphological development of 'Manzanillo' olive seed in relation to germination. Journal of the American Society of Horticultural Science 108: 741–743.

Martin GC, Kuniyuki AH, Mehlschau JJ, Whisler J. 1986. Semi-automated pit cracking machine for rapid seed removal. HortScience 21: 535–536.

Pinney J, Polito VS. 1990. Flower initiation in 'Manzanillo' olive. Acta Horticulturae 286: 203–205.

Zohary D, Spiegal-Roy P. 1975. Beginnings of fruit growing in the world. Science 187: 319–327.

Fabaceae—Pea family

Olneya tesota Gray

olneya

Robert Becker

Mr. Becker retired from the USDA Agricultural Research Service's Western Regional Research Center

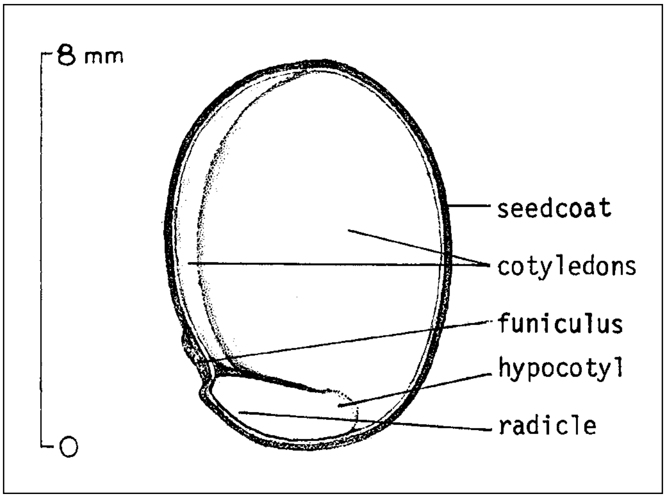
Other common names. ironwood, desert ironwood, *palo fierro, tesota*.

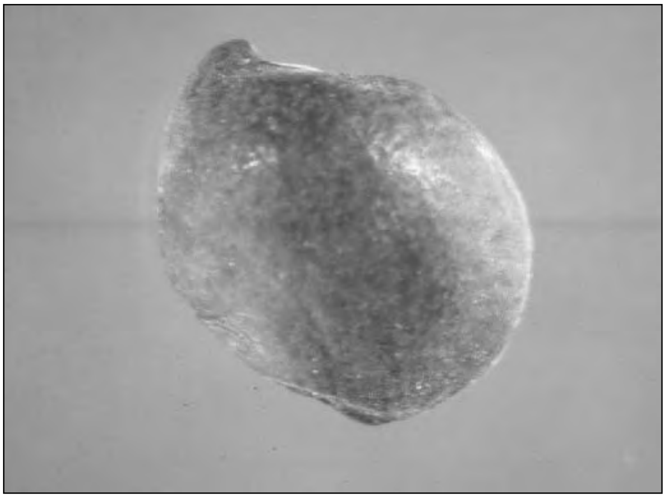
Growth habit, occurrence, and uses. Olneya is a long-lived, multi-trunked, broad-crowned, deciduous tree, 5 to 10 m high, that is commonly found at elevations below 600 m in desert washes and valleys of the Sonora Desert in California, Arizona, Baja California, Baja California Sur, and Sonora (Munz 1974; Shreve and Wiggins 1964). It will grow in areas receiving less water than is required to support mesquite (*Prosopis* spp.) (Felker 1981), has a frost tolerance similar to that of citrus, and will nodulate and fix nitrogen (Felker and Clark 1981). Olneya provides browse for cattle and habitat for native animals; it serves as a nurse plant for cacti and other plants (Nabhan and Carr 1994; Suzan and others 1994). It was also a food source for early cultures of Native Americans (Felger and Moser 1985). The seeds contain large amounts of canavanine, an arginine analog that is a potent growth inhibitor (Becker 1983). The wood is very dark, used for carvings, and will not float, its density being 1.22. The tree is threatened by introduced pasture grasses, urbanization, and illegal harvesting for charcoal and artists' wood.

Flowering and fruiting. Flowering occurs from April to June (Munz 1984; Shreve and Wiggins 1964). The pinkish to pale rose-purple flowers, 8 to 9 mm long, produce a legume (pod) that may contain 1 to 2, or sometimes 3 or 4 or more seeds. The legume is light brown, rounded, and hairy, and measures 4 to 6 cm in length (Munz 1984; Shreve and Wiggins 1964). The seeds are chestnut brown to blackish, shiny, ovoid, and 8 to 9 mm long (figure 1) (Irving and Becker 1985).

Collection and storage of fruits. Legumes on the tree may be picked in June or July or fallen legumes and seeds may be hand-gathered. The legumes dehise easily (Felker 1981). Many seeds are infested with insect larvae when collected, so the seeds should be stored cold or fumigated. Seed

Figure 1— *Olneya tesota*, olneya: longitudinal section through a seed (**left**) and exterior view (**right**).





counts on 2 samples were 4,400 and 4,850 seeds/kg (2,000 and 2,200/lb) (Krugman 1974), with a reported yield of 8 kg (17.6 lbs) of seeds/tree (Felker 1981).

Germination and nursery practice. Fresh seeds germinate readily when soaked for 12 to 24 hours in water; stored seeds may require longer soaking. Mild scarification before soaking is often helpful (Emery 1964; Krugman 1974). Seeds can be broadcast sown in the spring and covered with 6 mm (1/2 in) of soil or sand. Small seedlots can be germinated in planting flats or small containers and then transplanted. Seeds will rot easily, so extra care must be taken in watering (Everett 1957; Krugman 1974). Initial germination is prompt when soaked or watered, often occurring within 18 to 24 hours of sowing (Everett 1957; Krugman 1974). Seedlings appear within 6 days after sowing (Krugman 1974).

References

Becker R. 1983. Nutritional evaluation and chemical composition of seeds from desert ironwood *Olneya tesota*. International Tree Crops Journal 2 (3/4): 297–312.

Emery D. 1964. Seed propagation of native California plants. Leaflet. Santa Barbara Botanical Garden 1(10): 81–96.

Everett PC. 1957. A summary of the culture of California plants at the Rancho Santa Ana Botanic Garden 1927–1950. Claremont, CA: Rancho Santa Ana Botanical Garden. 223 p.

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

Felker P. 1981. Uses of tree legumes in semiarid regions. Economic Botany 35(2): 174–186.

Felker P, Clark PR. 1981. Nodulation and nitrogen fixation (acetylene reduction) in desert ironwood (*Olneya tesota*). Oecologia 48(2): 292–293.

Irving DW, Becker R. 1985. Seed structure and composition of potential new crops. Food Microstructure 4(1): 43–53.

Krugman SL. 1974. *Olneya tesota*, tesota. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 560.

Munz PA. 1974. A flora of Southern California. Berkeley: University of California Press. 1086 p.

Nabhan GP, Carr JL, eds. 1994. Ironwood: an ecological and cultural keystone of the Sonoran Desert. Occ. Pap. 1. Washington DC: Conservation International. 92 p.

Shreve F, Wiggins IL. 1964. Vegetation and flora of the Sonoran Desert. Volume 1. Stanford, CA: Stanford University Press. 840 p.

Suzan H, Nabhan GP, Patten DT. 1994. Nurse plant and floral biology of a rare night-blooming cereus *Peniocereus striatus* (Brandegee) f. Buxbaum. Conservation Biology 8(2): 461–470.

Betulaceae—Birch family

Ostrya virginiana (P. Mill.) K. Koch

eastern hophornbeam

William B. Leak and Franklin T. Bonner

Dr. Leak is a silviculturist at the USDA Forest Service's Northeastern Research Station, Durham, New Hampshire; Dr. Bonner is a scientist emeritus at the USDA Forest Service's Southern Research Station, Mississippi State, Mississippi

Other common names. hophornbeam, American hophornbeam, hornbeam, leverwood, ironwood.

Growth habit, occurrence, and uses. Three of the 8 species of the hophornbeam genus—*Ostrya*—are native to the United States; of these, eastern hophornbeam is the most common (Little 1979). It is a small deciduous tree that attains a maximum height of about 18 m and occurs throughout the eastern half of North America, ranging from Nova Scotia and southeastern Manitoba in Canada south to eastern Texas and northern Florida. It also occurs in the mountains of Mexico, El Salvador, and Honduras (Little 1979). Small trees often occur in the understory on a wide variety of sites ranging from deep, moist soils to dry and gravelly or rocky slopes (Metzger 1990).

The heavy, hard, durable wood has been used for fence posts, tool handles, and other specialty items (Schopmeyer and Leak 1974). Eastern hophornbeam also provides food and cover for many birds and some mammals. The seeds are a preferred food for sharp-tailed grouse (*Pedioecetes phasianellus*) and wild turkey (*Meleagris gallopavo*), and the buds and catkins are important winter foods for ruffed grouse (*Bonasa umbellus*) (Metzger 1990). This tree is sometimes planted as ornamental because of its attractive foliage and fruit clusters (Brown and Kirkman 1990), but it does not grow very rapidly. It was first cultivated in 1690 (Rehder 1940).

Flowering and fruiting. The flowers are monoecious. Staminate catkins, 2.5 to 4 cm in length, develop on the branch tips in late summer and overwinter in a dormant state. Pistillate catkins are small, inconspicuous, and 6 mm long; they appear with the leaves in the spring. Both flowers mature and open in March and April in the South and May and June in the North (Brown and Kirkman 1990; Metzger 1990). The fruit is a strobile, usually 2.5 to 7.5 cm long (figure 1), consisting of involucres that each enclose a single nut (figure 2) about 7 mm long and 4 mm in diameter (Brown and Kirkman 1990; Sargent 1965). The fruits ripen from the end of August in Michigan to October in the South. Nuts are dispersed after ripening when the strobiles fall apart. The buoyancy of the papery sacs aids dispersal by wind (Metzger 1990). Trees do not produce seeds abundantly until they are about 25 years old (Schopmeyer and Leak 1974). Seed production in the northern part of the range has averaged 124,000 seeds/ha (50,200/ac) (Metzger 1990).

Figure 1—*Ostrya virginiana*, eastern hophornbeam: strobile

Collection, extraction, storage. The strobiles may be hand-picked from the trees when they are a pale greenish brown in color. At this stage, they are not yet dry enough to fall apart. When completely ripe, they are light gray to greenish brown (Schopmeyer and Leak 1974). The fruits should be thoroughly dried before seeds are extracted by thrashing or rubbing the dried fruits over screens. Seeds can be separated from the chaff with air-screen cleaners or fractionating aspirators or by fanning. One hectoliter of fruit will yield about 2.5 kg of seed (1 bu yields 2 lb). The number of seeds per weight (5 samples) ranged from 55,100 to 77,200/kg (25,000 to 35,000/lb), with an average of 66,100/kg (30,000/lb). Purities (percentages) in the high 90s are easily obtained with good cleaning. The proportion of sound seeds will vary widely, especially due to insect dam-

O

Figure 2—*Ostrya virginiana*, eastern hophornbeam: longitudinal section through a seed (**left**) and intact seeds (**right**).

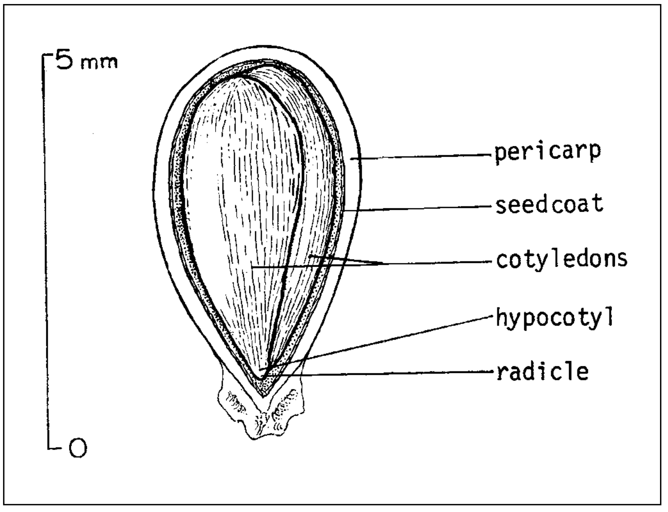
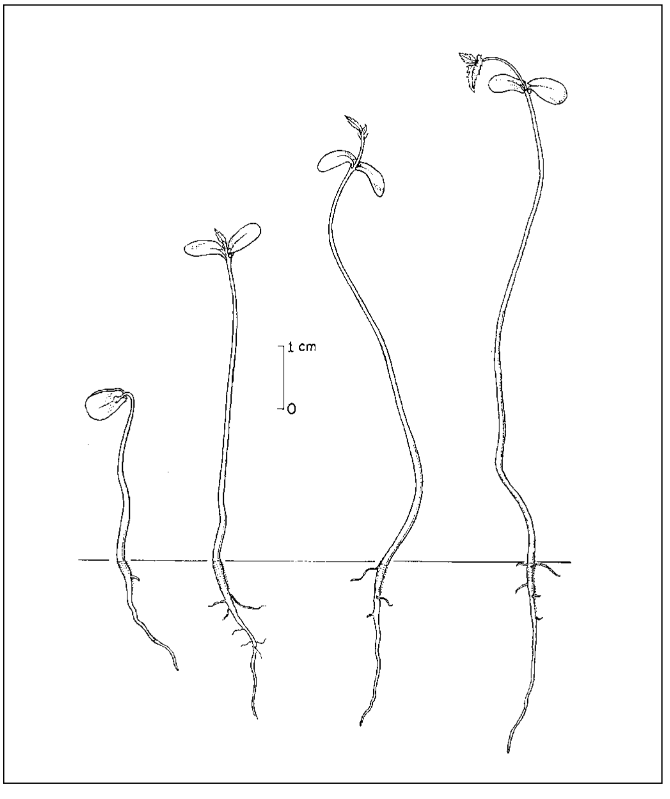


Figure 3—*Ostrya virginiana*, eastern hophornbeam: seedling development at 2, 4, 23, and 27 days after germination.



age, but 80% has been reported (Schopmeyer and Leak 1974). There are no storage test data for eastern hophornbeam, but the seeds have the ability to survive at least 1 year in the soil and should have good storage potential.

Pregermination treatments and germination tests. Seeds have a hard seedcoat and an internal dormancy that is difficult to overcome. Warm incubation, followed by cold stratification may be best. Three months of warm, followed by 3 to 5 months of cold produced germination of 81 to 92% (Dirr and Heuser 1987). Germination is epigeal (figure 3). Tetrazolium staining can be used to estimate viability. Official seed testing organizations do not include eastern hophornbeam in their recommendations.

Nursery practice. Either fall- or spring-sowing is feasible, but fall-sowing should take place soon after seeds are collected. In Iowa, seeds collected when they were slightly immature (August) and sown immediately germinated 100% the following spring (Titus 1940). Seeds should be covered with 6 mm ($^{1}/_{4}$ in) of firmed soil. Fall-sown beds should be covered with burlap, straw, or other suitable mulch, and uncovered when germination begins. Stratified seeds may be sown in the spring as soon as the soil can be worked, and the beds should be mulched or watered to keep them moist until germination starts (Schopmeyer and Leak 1974).

References

Brown CL, Kirkman LK. 1990. Trees of Georgia and adjacent states. Portland, OR: Timber Press. 292 p.

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

Little EL Jr. 1979. Checklist of United States trees (native and naturalized). Agric. Handbk. 451. Washington, DC: USDA Forest Service. 375 p.

Metzger FT. 1990. *Ostrya virginiana* (Mill.) K. Koch, eastern hophornbeam. In: Burns RM, Honkala BH, tech. coord. Silvics of North America. Volume 2, Hardwoods. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 490–496.

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

Sargent CS. 1965. Manual of the trees of North America (exclusive of Mexico). 2nd ed., corrected and reprinted. New York: Dover. 934 p.

Schopmeyer CS, Leak WB. 1974. *Ostrya virginiana* (Mill.) K. Koch, eastern hophornbeam. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 564–565.

Titus GR. 1940. So-called 2-year seeds germinated 1st year. American Nurseryman 72(11): 22.

Ericaceae—Heath family

Oxydendrum arboreum (L.) DC.

sourwood

Frank A. Blazich and Mark C. Starrett

Dr. Blazich is alumni distinguished graduate professor of plant propagation and and tissue culture at North Carolina State University's Department of Horticultural Science, Raleigh, North Carolina; Dr. Starrett is associate professor at the University of Vermont's Department of Plant and Soil Science, Burlington, Vermont

Synonym. *Andromeda arboreum* L.

Other common names. sorrel-tree, lily-of-the-valley tree.

Growth habit, occurrence, and uses. Sourwood is a medium-sized, deciduous tree that develops a graceful, pyramidal shape when mature (Dirr 1990). The plant typically grows 9 to 15 m tall in the wild but seldom attains such height outside its native range (DeWolf 1987). This species is indigenous to the eastern United States, extending from Pennsylvania southward into northern Florida, and west to Indiana and Louisiana (Rehder 1986). Sourwood often is found on ridges of gravelly soil adjacent to streams and is hardy to USDA Zone 5 (Dirr 1990). The species has several attributes that create an outstanding specimen plant. It has slender, drooping branches of dark green foliage that contrast sharply with pendulous terminal panicles of white flowers in mid-summer, when few other plants are flowering. In addition, the brilliant scarlet fall foliage is without comparison amongst plants indigenous to the United States (DeWolf 1987). Sourwood should be grown in full sun to attain maximum flower production and the most vibrant fall color. However, the tree will also grow in partial shade (DeWolf 1987). Sourwood prefers an acidic (pH 4.0 to 5.5), moist, well-drained soil high in organic matter (DeWolf 1987; Dirr 1990). Sourwood is best suited for suburban or rural landscapes, as it will not tolerate air pollution occurring in urban areas (DeWolf 1987). Lastly, sourwood honey is highly prized, as is the wood, which is used for tool handles and in crafts (Duncan and Duncan 1988).

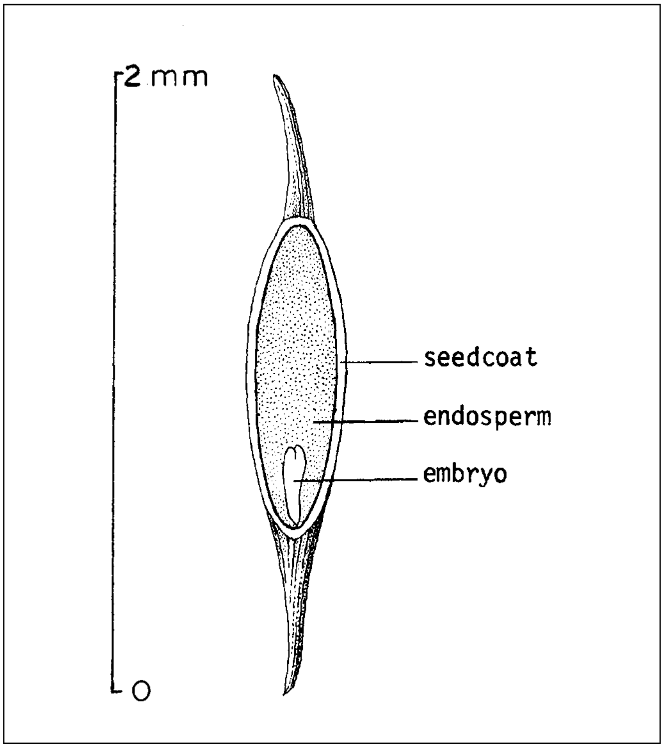
Geographic races and hybrids. Sourwood is monotypic, that is, the only species of its genus. No hybrids are described in the literature.

Flowering and fruiting. Fragrant, 6-mm-wide, white, urn-shaped flowers are borne profusely on 15- to 25-cm, pendulous, terminal panicles (Bridwell 1994; Dirr 1990). Flowers open in late June or July and provide a dramatic, mid-summer show. The floral display can completely shroud the dark green foliage in a white, lacy veil (Dirr 1990). Fruits are ovoid-pyramidal, dry, 5-chambered, dehiscent capsules, borne in clusters, each capsule about 5 to 7 mm long (Bailey 1977; Dirr 1990; Radford and others 1968). Seeds are 2 mm long, 0.5 mm wide, and gray to brown when mature (figure 1) (Olson and Barnes 1974).

Collection of fruits, seed extraction, cleaning, and storage. Capsules and seeds ripen in September and October and can be collected at that time (Olson and Barnes 1974). Capsules are removed from the plant, lightly beaten, and then rubbed to open them completely (Dirr and Heuser 1987). Next, seeds are shaken from the capsules. Viability can be poor if seeds are not graded rigorously. Use of an air-column blower is recommended to remove chaff and empty seeds (Barton and Bonaminio 1986). Lots of cleaned, pure seeds average 8,200 seeds/g (230,000/oz) (Olson and Barnes 1974). The seeds are apparently orthodox in storage behavior and may remain viable for several years if stored dry in a sealed container at 4.5 °C (Blazich 1996).

Pretreatment and germination tests. Seeds germinate readily after harvest and no pretreatments are necessary (Dirr and Heuser 1987; Fordham 1960). Germination is epigeal (figure 2). Seeds of sourwood require light for maximum germination (Barton and Bonaminio 1985). A 30-day test of seeds collected in Yadkin Co., North Carolina, demonstrated that germination in total darkness at 25 °C was minimal (5%) (Barton and Bonaminio 1985). However, a daily photoperiod of $^1/_2$ hour resulted in 29% germination and daily photoperiods $\geq$ 4 hours resulted in maximum germination (58%). In another test, seeds were placed at 20, 22.5, 25, 28 °C, or at 9/15-hour thermoperiods of 25/15 or 30/20 °C (Barton and Bonaminio 1985). Seeds received 1 hour of light daily at each temperature. After 21 days, the highest germination occurred at 25/15 °C and 30/20 °C, with germination of 50 and 64%, respectively. Germination began faster at 30/20 °C. These studies utilized cool-white fluorescent lamps as the light source, at 4.3 klux (about 55 $\mu mol/m^2/sec$). Under particular conditions, stratification (moist prechilling) also may be used to stimulate germination (Barton and Bonaminio 1986).

Figure 1—*Oxydendron arboreum*, sourwood: seeds in longitudinal section (**left**) and external view (**right**).



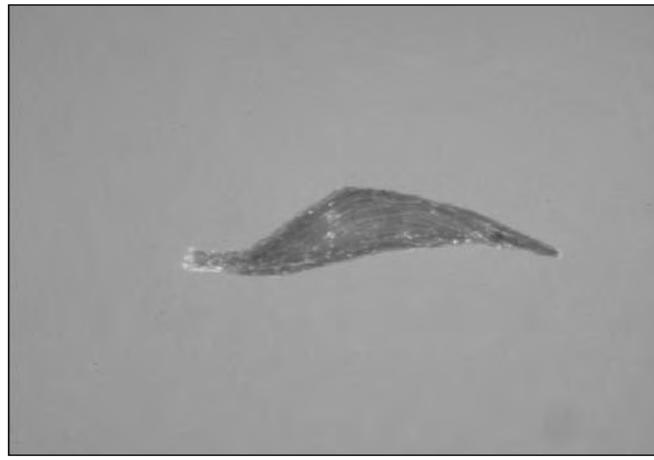
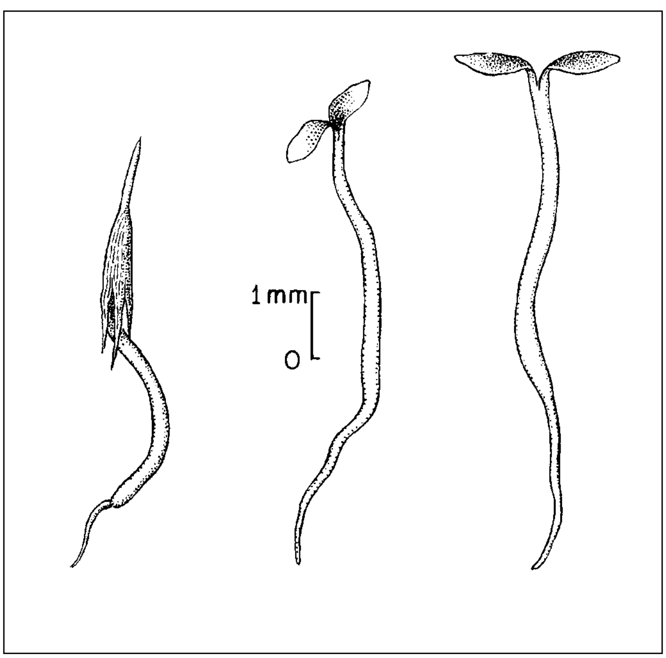


Figure 2—*Oxydendron arboreum*, sourwood: seedlings of sourwood at 2, 6, and 8 days after germination.



Nursery practice. Johnson (1978) described a commercial method for seed propagation, in which seeds are sown in November soon after harvest. Seeds are spread lightly on the surface of a flat containing fine milled sphagnum and vermiculite (1:1, by vol.) and misted. Then, the flat is wrapped in a clear plastic bag, with supports to keep the bag from touching the surface of the medium, and placed under continuous light, provided by cool-white fluorescent lamps. Typically, the germination medium is maintained at 22 °C using bottom heat. The medium surface should never be allowed to dry. Seeds germinate within 2 weeks, and seedlings develop rapidly. At the 2- to 3-leaf stage, seedlings can be transplanted into peat pots or individual containers containing an acidic, organic medium. After 6 months, seedlings can be potted into 3.8-liter (1-gal) containers containing a well-drained, acidic, organic medium. Growth of 0.6 m (2 ft) can be obtained in 9 months following this production protocol. Blazich and others (1994) reported that commercial production of seedlings of sourwood may be accelerated by utilizing a pine bark medium and a day/night cycle of 26/22 °C or 30/26 °C with long-day conditions.

Stem cuttings are reported as difficult to root (Dirr and Heuser 1987). However, sourwood can be propagated vegetatively by micropropagation (Banko and Stefani 1989).

References

Bailey LH. 1977. Manual of cultivated plants. New York: Macmillan. 1116 p.

Banko TJ, Stefani MA. 1989. In vitro propagation of *Oxydendrum arboreum* from mature trees. HortScience 24(4): 683–685.

Barton SS, Bonaminio VP. 1985. Influence of light and temperature on germination of sourwood (*Oxydendrum arboreum* (L.) DC.). Journal of Environmental Horticulture 3(3): 108–111.

Barton SS, Bonaminio VP. 1986. Influence of stratification and light on germination of sourwood (*Oxydendrum arboreum* (L.) DC.). Journal of Environmental Horticulture 4(1): 8–11.

Blazich FA. 1996. Unpublished data. Raleigh: North Carolina State University.

Blazich FA, Warren SL, Thetford M. 1994. Growth response of sourwood as influenced by temperature, photoperiod, and media. Proceedings, Southern Nurserymen's Association Research Conference, 39th Annual Report: 137.

Bridwell FM. 1994. Landscape plants: their identification, culture and use. Albany, NY: Delmar Publishers. 560 p.

DeWolf Jr. GP. 1987. Taylor's guide to trees. New York: Chanticleer Press. 479 p.

Dirr MA. 1990. Manual of woody landscape plants: their identification, ornamental characteristics, culture, propagation and uses. 4th ed. Champaign, IL: Stipes Publishing Co. 1007 p.

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

Duncan WH, Duncan MB. 1988. Trees of the southeastern United States. Athens, GA: University of Georgia Press. 322 p.

Fordham AJ. 1960. Propagation of woody plants by seed. Arnoldia 20(6): 33–40.

Johnson H. 1978. Propagation of *Oxydendrum arboreum* (L.) DC. by seed. Plant Propagator 24(2): 13.

Olson Jr DF, Barnes RL. 1974. *Oxydendrum*, sourwood. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 566–567.

Radford AE, Ahles HE, Bell CR. 1968. Manual of the vascular flora of the Carolinas. Chapel Hill: University of North Carolina Press. 1183 p.

Rehder A. 1986. Manual of cultivated trees and shrubs hardy in North America. 2nd ed. Portland, OR: Dioscorides Press. 996 p.

P

Fabaceae—Pea family

Paraserianthes falcataria (L.) I. Nielsen

peacock-plume

John A. Parrotta and Franklin T. Bonner

Dr. Parrotta is a research program leader at the USDA Forest Service's Research and Development National Office, Arlington, Virginia; Dr. Bonner is a scientist emeritus at the USDA Forest Service's Southern Research Station, Mississippi State, Mississippi

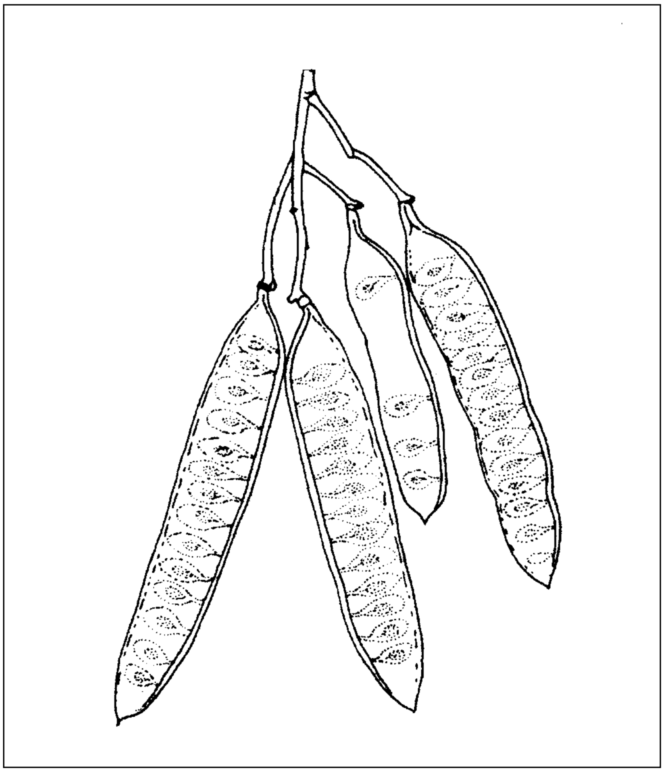
Synonyms. *Albizia falcataria* (L.) Fosberg

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

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

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

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



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

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

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

References

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

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

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

Little EL Jr, Skolmen RG. 1989. Common forest trees of Hawaii (native and introduced). Agric. Handbk. 679. Washington, DC: USDA Forest Service. 321 p.

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

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

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

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

P

Fabaceae—Pea family

Parkinsonia L.

palo verde

Kristina F. Connor, Jane E. Rodgers, and Carol Miller

Dr. Connor is a research plant physiologist at the USDA Forest Service's Southern Research Station, Auburn University, Alabama; Ms. Rodgers is now stationed at the Point Reyes National Seashore, Point Reyes, California; Ms. Miller is a former propagationist at the Joshua Tree National Park, Twentynine Palms, California

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

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

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

Table 1—Parkinsonia, palo verde: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***P. aculeata* L.**	**palo verde,** Jerusalem-thorn, horsebean, *retama, palo de ray, palo rayo*	South to trans-Pecos Texas & S Arizona; widely distributed in tropical America; Puerto Rico
***P. florida* (Benth. ex Gray) S. Wats** *Cercidium floridum* Benth. ex Gray	**blue palo verde**	SW US
***P. microphylla* Torr.** *Cercidium mycrophyllum* (Torr.) Rose & I.M. Johnston	**yellow palo verde**	SW US

Sources: Bainbridge and Virginia (1989), Little (1979), Little and Wadsworth (1964).

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

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

Some form of seed scarification is necessary in order to achieve rapid and uniform germination. Francis and Rodríguez (1993) germinated mechanically scarified seeds of palo verde on blotter paper and reported that 59% had germinated after 2 days. Everitt (1983) found that soaking seeds in concentrated sulfuric acid for 45 minutes increased germination from 1% to over 50%. Germination rose to over 87% at continuous temperatures of 15 to 35 °C, or at alternating temperatures of 10/20, 15/25, or 20/30 °C. Although percentage germination and radicle length were little affected by pH, results were enhanced if seeds were buried 1 to 7 cm (0.4 to 2 $^{3}/_{4}$ in) rather than left on the surface. Zodape (1991) reported germination of over 80% of seeds soaked in concentrated sulfuric acid. However, Bainbridge and Virginia (1989) found a negative effect of certain abrasion methods—they can create a dust on the seeds that encourages mold growth during germination.

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

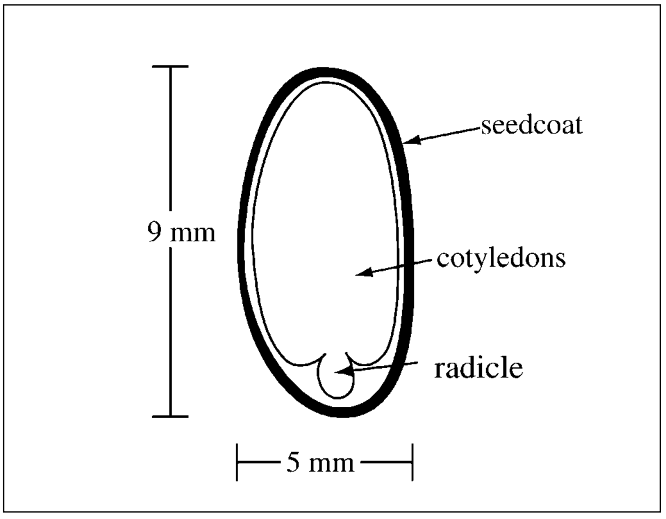
Although the seedcoat serves as a barrier to overcome when germinating, it also serves as a protective shield against insect infestation. Janzen (1977) found that the cause of mortality of larvae of the southern cowpea weevil—*Callosobruchus maculatus* F.—in palo verde seeds was not seed toxicity but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

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

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

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

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



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

References

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

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

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

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

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

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

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

Francis JK, Liogier HA. 1991. Naturalized exotic tree species in Puerto Rico. Gen. Tech. Rep. SO-82. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 12 p.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Vitaceae—Grape family

Parthenocissus Planch.

creeper

John D. Gill, Franz L. Pogge, and Franklin T. Bonner

Dr. Gill and Mr. Pogge retired from the USDA Forest Service's Northeastern Forest Experiment Station; Dr. Bonner is a scientist emeritus at the USDA Forest Service's Southern Research Station, Mississippi State, Mississippi

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

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

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

Table 1—*Parthenocissus,* creeper: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
P. quinquefolia **(L.) Planch.** *P. inserta* (Kerner) Fritsch *Pserda quinquefolia* (L.) Greene	**Virginia creeper,** woodbine	Maine to Manitoba & Florida, to Texas & Rocky Mtns, also California & Mexico
P. tricuspidata **(Sieb. & Zucc.) Planch.** *Ampelopsis tricuspidata* Sieb. & Zucc.	**Japanese creeper,** Boston ivy	Japan & Central China; escaped from cultivation in Massachusetts & Ohio

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

Table 2—*Parthenocissus,* creeper: phenology of flowering and fruiting

Species	Flowering	Fruit ripening	Fruit drop
P. quinquefolia	June–Aug	July–Oct	Aug–Feb
P. tricuspidata	June–July	Sept–Oct	—

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

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

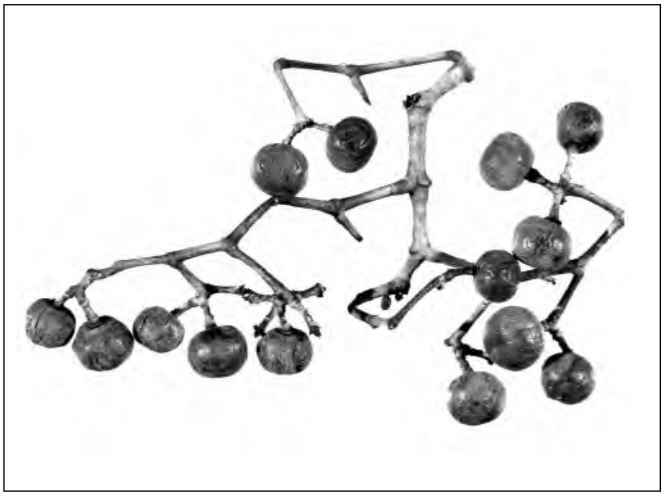


Figure 2—*Parthenocissus*, creeper: seeds of *P. quinquefolia*, Virginia creeper (**left**) and *P. tricuspidata*, Japanese creeper (**right**).

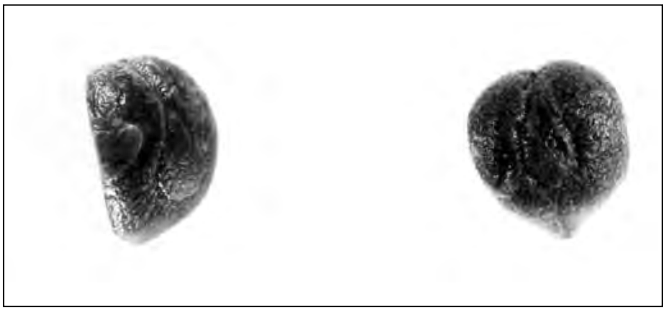
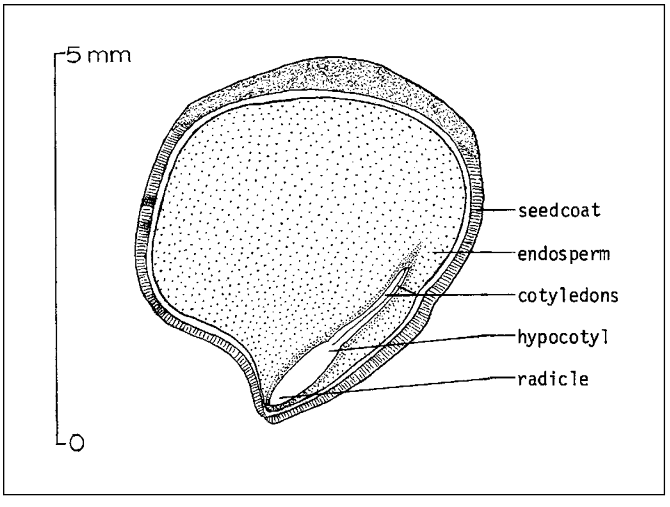


Figure 3—*Parthenocissus quinquefolia*, Virginia creeper: longitudinal section through a seed.



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

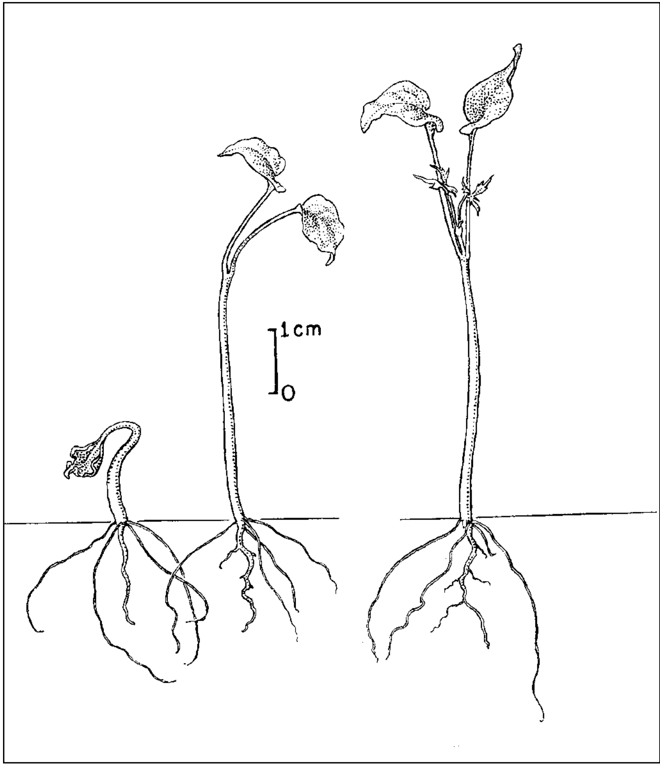
Cleaned Virginia creeper seeds range from 21,600 to 57,800/kg (9,800 to 26,200/lb) and average 36,500/kg (16,560/lb). No seed yield data on Japanese creeper are available, but they are probably similar to those for Virginia creeper.

Germination. Natural germination takes place during the first or perhaps the second spring following dispersal and is epigeal (Fisher and others 1935) (figure 4). The seeds have an internal dormancy that can be overcome by moist stratification for about 60 days at 5 °C (Gill and Pogge 1974). Outdoor stratification in winter, during which the seeds become frozen, has also increased germination (Adams 1927; Howard 1915). There are no official germination test prescriptions for creepers, but tests can be made in sand flats at alternating temperatures of 20/30 °C. About 30 days is a sufficient test length for stratified seeds, but untreated seeds may require >150 days (Gill and Pogge 1974). Results from a small number of tests suggest that germination of stratified seeds should peak at about 15 days and reach 70 to 80% by 30 days. For untreated seeds, germination was less than 5% in 4 tests, but 45% in another that ran for 595 days (Adams 1927; Howard 1915; Gill and Pogge 1974). The excised embryo method has also been used to estimate viability (Flemion 1948; Heit 1955).

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

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

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



References

Adams J. 1927. The germination of the seeds of some plants with fleshy fruits. American Journal of Botany 15 (8): 415–428.

Bailey LH. 1914. The standard cyclopedia of horticulture. 6 vol. New York: Macmillan. 3639 p.

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

Edminster FC. 1947. The ruffed grouse: its life story, ecology and management. New York: Macmillan. 385 p.

Fernald ML. 1950. Gray's manual of botany. 8th ed. New York: American Book Co. 1632 p.

Fisher PL, Briggs AH, Elkins WA, Roe EL. 1935. Propagation of game food and cover plants of the Lake States. St. Paul: USDA Forest Service, Lake States Forest Experiment Station. 81 p.

Flemion F. 1948. Reliability of the excised embryo method as a rapid test for determining the germinative capacity of dormant seeds. Contributions of the Boyce Thompson Institute 15: 229–241.

Gill JD, Pogge FL. 1974. *Parthenocissus* Planch., creeper. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 568–571.

Heit CE. 1955. The excised embryo method for testing germination quality of dormant seed. Proceedings Association of Official Seed Analysts 1955: 108–117.

Howard WL. 1915. An experimental study of the rest period in plants: seeds. Res. Bull. 17. Columbia: Missouri Agricultural Experiment Station. 58 p.

Rehder A. 1949. Manual of cultivated trees and shrubs. Rev. ed. New York: Macmillan. 1116 p.

Robinson FB. 1960. Useful trees and shrubs: reference cards [a card file of data on hardy woody plants in common use as ornamentals]. Champaign, IL: Garrard Press. 427 cards.

Swingle CF, comp. 1939. Seed propagation of trees, shrubs, and forbs for conservation planting. SCS-TP-27. Washington, DC: USDA Soil Conservation Service. 187 p.

Van Dersal WR. 1938. Native woody plants of the United States: their erosion-control and wildlife values. Misc. Pub. 303. Washington, DC: USDA. 362 p.

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

P

Scrophulariaceae—Figwort family

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

royal paulownia

Franklin T. Bonner

Dr. Bonner is a scientist emeritus at the USDA Forest Service's Southern Research Station, Mississippi State, Mississippi.

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

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

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

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

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

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

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

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

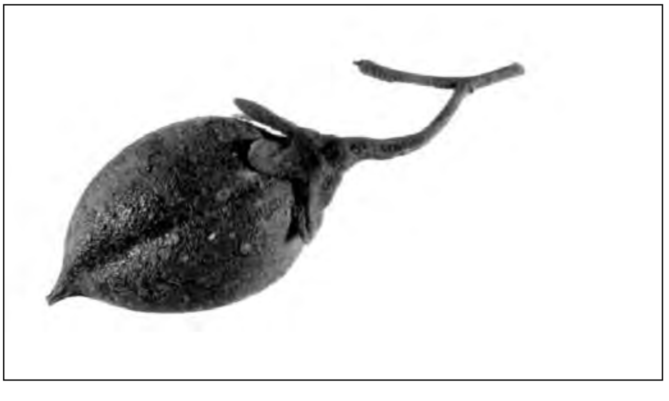
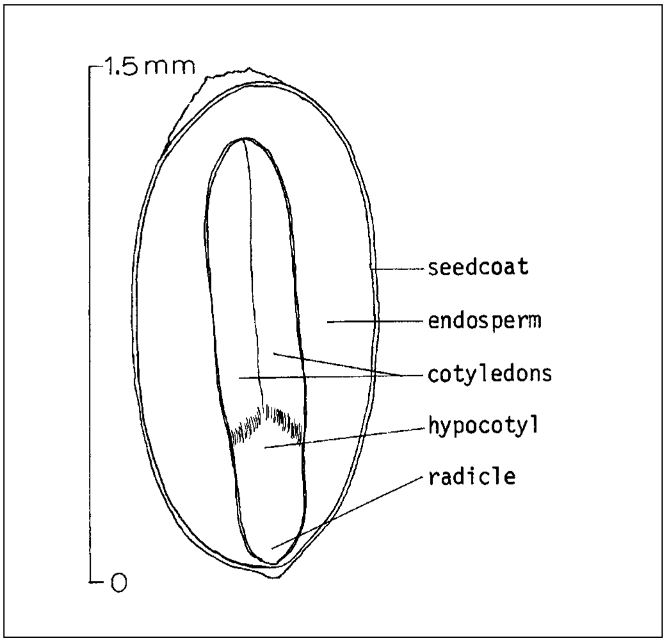


Figure 2—*Paulownia tomentosa*, royal paulownia: winged seed.

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



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

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

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

References

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

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

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

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

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

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

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

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

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

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

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

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

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

Scrophulariaceae—Figwort family

Penstemon Schmidel

penstemon, beardtongue

Susan E. Meyer

Dr. Meyer is a research ecologist at the USDA Forest Service's Rocky Mountain Research Station, Shrub Sciences Laboratory, Provo, Utah

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

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

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

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

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

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

Seed collection, cleaning, and storage. Penstemon seeds are usually harvested by hand-stripping or clipping the flowering stalks into containers. Capsules generally begin to split open from 6 to 8 weeks after the plants are in full flower, with those at the base of each stalk ripening first. Stalks can be clipped before the capsules start to open, as long as the seeds can be seen darkening through the ovary wall. If the stalks are clipped after the capsules begin to open, care must be taken to avoid excessive spillage during harvest. For most species, the window of opportunity for harvest is quite wide, as capsules are held upright on the plant and seeds are dispersed only gradually. The harvested material should be dried carefully to avoid molding, especially if it is collected when somewhat green. The capsules will open after harvest, and for small lots, the seeds can be shaken free and collected by screening. For commercial seedlots, processing with a hammermill or barley debearder, followed by a fanning mill, is the usual procedure. Seedlots can readily be cleaned to high purity (>95%).

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

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

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

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

Source: Meyer (2002).

Table 3—*Penstemon*, penstemon, beardtongue: germination data after 0 to 24 weeks of chilling*

Species	0 wk	4 wk	8 wk	12 wk	16 wk	24 wk	Samples
P. ambiguus	35	21	19	10	16	31	3
P. fruticosus	6	19	14	19	40	83	4
P. leonardii	0	1	22	82	80	80	2
P. linarioides	0	0	1	6	12	10	2
P. petiolatus	100	—	—	100	100	100	1
P. platyphyllus	1	55	66	99	97	100	7
P. rostriflorus	18	17	54	83	—	98	3
P. sepalulus	3	25	37	83	86	100	2

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

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

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

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

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

Penstemons may also be readily produced from seeds in container culture. They grow well in a coarse medium in elongated containers such as those used to produce conifer seedlings. Seeds of nondormant species may be direct-sown, whereas chilled seeds or germlings may be planted for those species with seeds that require chilling. The seedlings will be ready for hardening-off and outplanting in 3 to 4 months, but they can be held much longer if necessary. Survival of outplanted stock is usually high, as long as plants are watered-in well at the time of transplanting and care is taken to eliminate air pockets around the roots. Plants both from direct seeding and outplanting usually flower the second year, and individuals of the subshrubby species can live for 10 years or more. If seed stalks are not clipped, most plants will readily self-seed.

References

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

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

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

Kitchen SG, Meyer SE. 1991. Seed germination of intermountain penstemons as influenced by stratification and GA_3 treatments. Journal of Environmental Horticulture 9: 51–56.

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

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

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

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

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

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

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

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

Rosaceae—Rose family

Peraphyllum ramosissimum Nutt.

squaw-apple

Janene Auger and Justin G. Smith

Dr. Auger is assistant editor of Western North American Naturalist Monte L. Bean Museum, Brigham Young University, Provo, Utah; Dr. Smith retired from the USDA Forest Service's Pacific Northwest Forest and Range Experiment Station

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

Uses. Wildlife known to eat squaw-apple fruits and seeds or both in Utah include grouse and wild turkeys (family Phasianidae), deer mice (*Peromyscus maniculatus*), chipmunks (*Eutamias* spp.), ground squirrels (*Spermophilus* spp.), and American black bears (*Ursus americanus*) (Auger and others 1995). Deer (*Odocoileus* spp.) browse squaw-apple lightly during the fall and winter (Shaw and others 2004; Smith 1974), and small birds use the intricately branched shrubs as cover even when leaves are not present (Shaw and Monsen 2004). Livestock also browse squaw-apple, and opinions vary widely on its forage value. In central Utah, squaw-apple is said to be almost worthless; in western Colorado, it is considered poor to fair; in eastern Oregon and northeastern California, it is commonly considered fair to moderately good sheep and cattle browse in the spring; and finally, in southwestern Utah, squaw-apple ranks as a valuable browse (Dayton 1931; Plummer and others 1968; Smith 1974). On ranges grazed by cattle during late winter and very early spring, individual plants may be severely hedged (Smith 1974). Even though squaw-apple grows slowly, Monsen and Davies (1985) suggest that it can persist in native plant landscaping for arid environments.

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

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

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

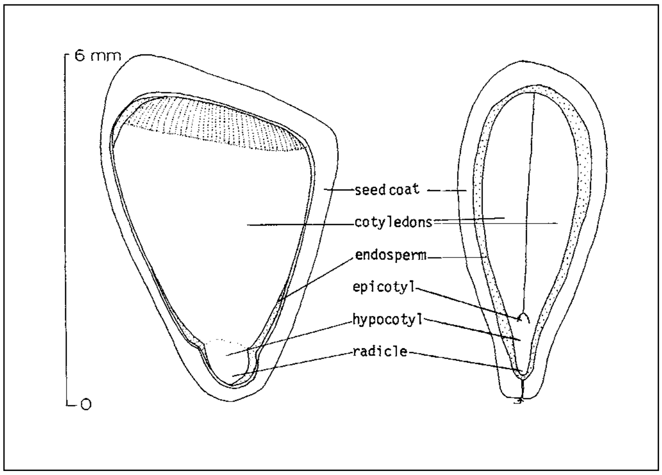
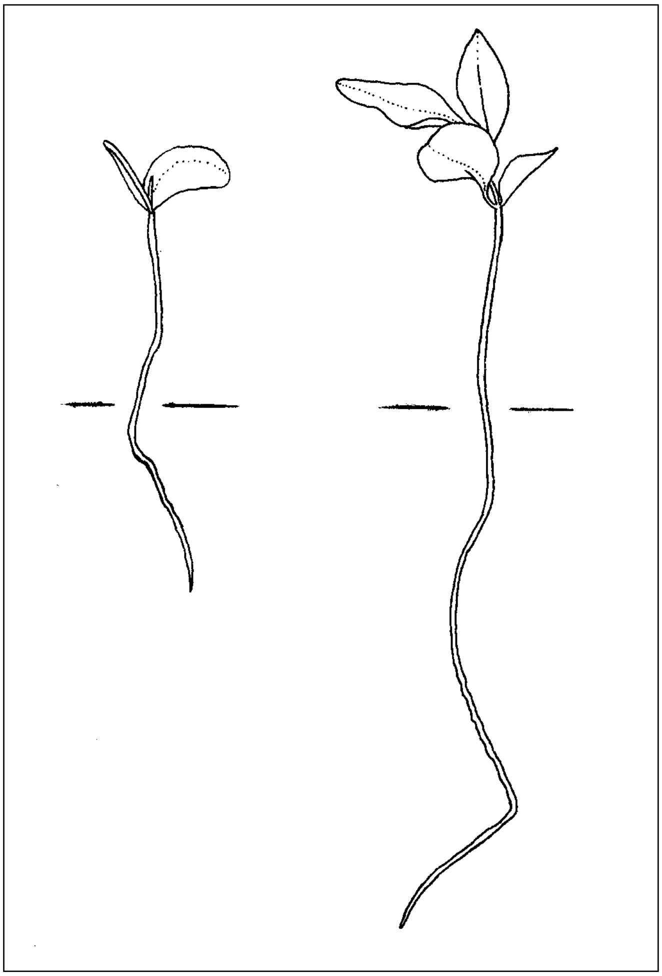


Figure 3—*Peraphyllum ramosissimum*, squaw-apple: germinating seedlings.



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

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

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

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

P

References

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

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

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

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

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

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

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

Plummer AP, Christensen DR, Monsen SB. 1968. Restoring big-game range in Utah. Pub. 68-3. Salt Lake City: Utah Department of Natural Resources, Division of Fish and Game. 183 p.

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

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

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

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

Lauraceae—Laurel family

Persea borbonia (L.) Spreng.

redbay

Franklin T. Bonner

Dr. Bonner is a scientist emeritus at the USDA Forest Service's Southern Research Station, Mississippi State, Mississippi

Other common names. shorebay, swampbay, swampbay persea.

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

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

Collection, extraction, and storage. Redbay fruits can be easily collected by hand from the branches when the exteriors of the fruits turn dark blue or purple. Even though the fruits persist for a short while on the trees, early collection may be necessary to prevent predation by birds. Removal of the fleshy exocarp should not be necessary if seeds are to be planted immediately. If they are to be stored temporarily, removal of this tissue may help avoid damage from pathogens. There are about 3,680 seeds/kg (1,670/lb) (the sample came from Mississippi). Storage data are not available for redbay, so viability retention under typical storage conditions is unknown. Avocado, however, is considered to be recalcitrant in nature and difficult to store (King and

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

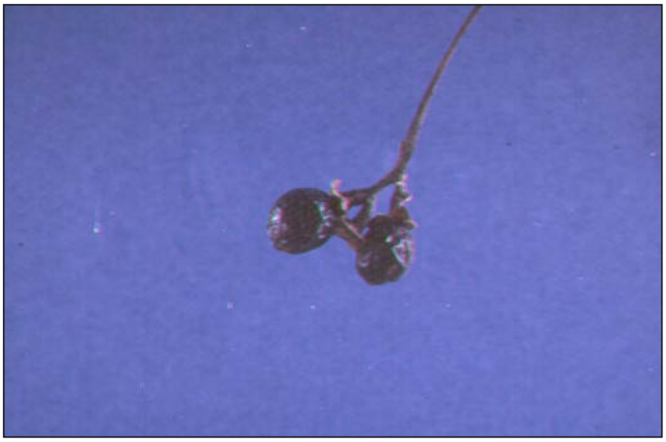
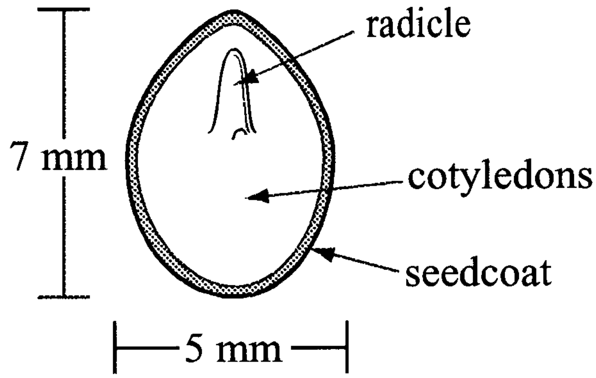


Figure 2—*Persea borbonia*, redbay: cleaned seed.

P

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



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

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

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

References

Brendemuehl RH. 1990. *Persea borbonia* (L.) Spreng., redbay. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 2, Hardwoods. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 503–506.

Brown CL, Kirkman LK. 1990. Trees of Georgia and adjacent states. Portland, OR: Timber Press. 292 p.

King MW, Roberts EH. 1980. Maintenance of recalcitrant seeds in storage. In: Chin HF, Roberts EH, eds. Recalcitrant crop seeds. Kuala Lumpur: Tropical Press: 53–89.

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

Radford AE, Ahles HE, Bell CR. 1968. Manual of the vascular flora of the Carolinas. Chapel Hill: University of North Carolina Press. 1183 p.

Sargent CS. 1965. Manual of the trees of North America (exclusive of Mexico). 2nd. Ed., corrected and reprinted. New York: Dover. 934 p.

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

Rutaceae—Rue family

Phellodendron amurense Rupr.

Amur corktree

Ralph A. Read and John C. Zasada

Dr. Read retired from the USDA Forest Service Rocky Mountain Research Station;
Dr. Zasada retired from the North Central Research Station

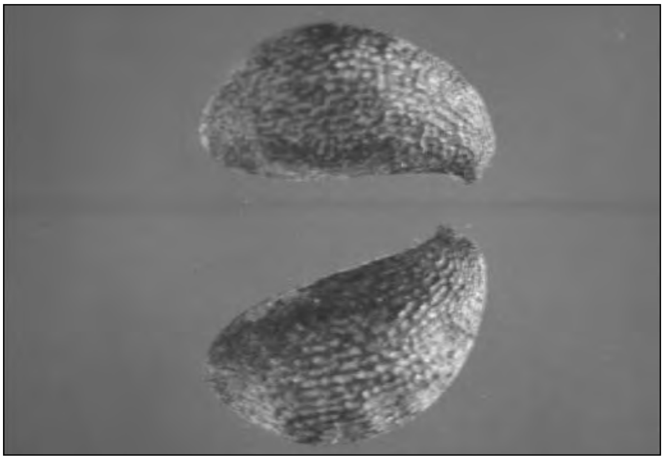
Growth habit, occurrence, and use. Amur corktree—*Phellodendron amurense* Rupr.—is native to northern China, Manchuria, Korea, and Japan. This small to medium deciduous tree—25 to 50 feet tall—has been cultivated in the Far East and eastern Europe. It was introduced into the United States around 1865,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

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

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

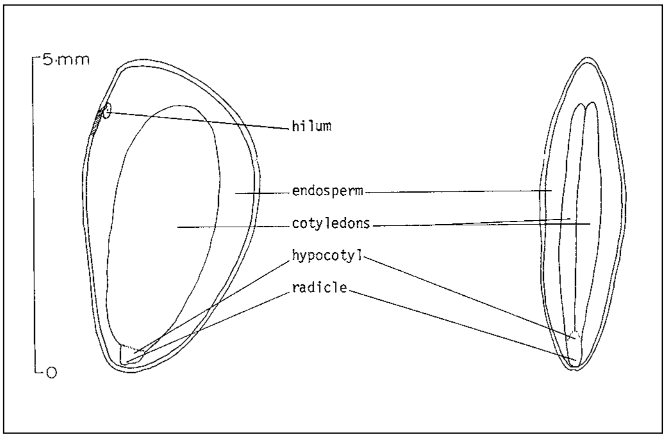
Figure 1—*Phellodendron amurense*, Amur corktree: fruit cluster.

Figure 2—*Phellodendron amurense*, Amur corktree:



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

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



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

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

Germination. Fresh seeds germinate well without pretreatment (Dirr 1990; Read 1974). However, there are a number of reports of greatly improved germination following stratification. Stratification is recommended for seeds stored any length of time (Dirr and Heuser 1987). Germination for a seedlot (for which the handling and storage history was not described) was best following cold moist, underground stratification for 166 days (Timm 1989). In another study, seeds stratified for 8 weeks had a higher germination rate and the same germination percentage as seeds stratified 4 weeks; germination of unstratified seeds was less than half that of stratified seeds (Mukai and Yokoyama 1985). Based on the information available, it is recommended that seeds be stratified if the history of collection, handling, and storage is not documented. Seeds of other *Phellodendron* spp. vary in their requirements for stratification (Dirr and Heuser 1987; Lin and others 1994).

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

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

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

References

Antonyuk ED. 1987. Growth of seedlings in a polythene greenhouse in relation to sowing times. Lesnoe Khozyaistvo 4: 36–37.

Atkimockin NG. 1960. [in Russian: Trials with *Phellodendron* spp. at the Forest-Steppe Experiment Station [abstract]. Byulleten Glavnogo Botanicheskogo Sada [Moskva] 37: 30–33.

Bailey LH. 1947. Standard cyclopedia of horticulture. 2nd ed. New York: Macmillan. 1388 p.

Blackburn BC. 1952. Trees and shrubs of eastern North America. New York: Oxford University Press. 358 p.

Dirr MA. 1990. Manual of woody landscape plants: their identification, ornamental characteristics, culture, propagation, and uses. Champaign, IL: Stipes Publishing. 1007 p.

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

Everett TH. 1964. New illustrated encyclopedia of gardening. Volume 8. New York: Greystone Press: 1455–1456.

Gorokhova GI. 1981. Fruiting of far-eastern species of plants under conditions of the forest steppe zone of western Siberia. Soviet Journal of Ecology 12 (4): 219–222 [translated and published 1982].

Gorokhova GI. 1986. Effect of drought on the seed quality of exotic plants from the Soviet East [abstract]. Byulleten Glavnogo Botanicheskogo Sada [Moskva] 139: 85–89.

Hensley DL, Wiest SC, Long CE, Pair JC, Gibbons FD III. 1991. Evaluation of 10 landscape trees for the Midwest. Journal of Environmental Horticulture 9(3): 149–155.

Hoag DG. 1965. Trees and shrubs of the northern plains. Minneapolis: Lund Press. 376 p.
Izmodenov AG. 1972. Multiple use of *Pinus koraiensis* forests [English abstract]. Moscow: Lenaya Promyshlenoost. 122 p.
Krecetova NV. 1960. [in Russian: The biology of flowering and fertilization in *P. amurense.* abstract]. Botanicheskii Zhurnal 45(9): 1336–1340.
Letkovskij AI. 1960. [in Russian: Planting *Phellodendron amurense* to increase the productivity of Scots pine forest (in Belorussia.)] Lesnaya Hortus 12(1): 36–37 [Forestry Abstracts 23: 548, 1962].
Lewis CE. 1957. American elm substitutes. American Nurseryman 106(10): 10–11, 50–51.
Lin TP, TW Hu, Leu JJ. 1979. The effect of alternating temperatures on the germination of the seed of *Phellodendron* spp. [abstract]. Bulletin of the Taiwan Forest Research Institute 322: 1–10.
Lin TP, Chen MH, Lin CH. 1994. Dormancy in seeds of *Phellodendron wilsonii* is mediated in part by abscisic acid. Plant Cell Physiology 35(1): 115–119.
Mukai Y, Yokoyama T. 1985. Effect of stratification on seed germination of *Phellodendron amurense* [abstract]. Journal of the Japanese Forestry Society 67(3): 103–104.
Necaev AD, Pelmenev VK. 1965. [in Russian: The importance of *Phellodendron amurense* as a nectar-bearing species.] Rastitel'nye Resursy [Moskva] 1(3): 419–423 [Forestry Abstracts 28: 621; 1967.
Ota M and others. 1965. [in Japanese: A study of the manufacturing conditions and properties of SIS hardboard from the inner bark of Kihada (*Phellodendron amurense* Rupr.).] Wood Industries Tokyo 20(6): 13–16 [Forestry Abstracts 27: 1475; 1966].
Read RA. 1974. *Phellodendron amurense* Rupr., Amur corktree. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 578–579.
Rehder A. 1940. Manual of cultivated trees and shrubs. 2nd ed. New York: Macmillan. 996 p.
Schechter MS. 1943. The insecticidal principle in the fruit of Amur corktree (*Phellodendron amurense*). Journal of Organic Chemistry 8: 194–197.
Soludukhin ED. 1977. Features of the regeneration of *Phellodendron amurense* [abstract]. Lesnoe Khozyaistvo 4: 32–33.
Starshova NP. 1972. The 'anthecology' of *Phellodendron amurense* in the middle Volga region: 1. Ecology of flowering. Botanicheskii Zhurnal 57(11): 1402–1412.
Swingle CF, comp. 1939. Seed propagation of trees, shrubs, and forbs for conservation planting. SCS-TP-27, Washington, DC: USDA Soil Conservation Service. 198 p.
Timm GT. 1989. Effect of stratification on the field germination rate of some tree seed. Journal of the Korean Forestry Society 78(1): 26–29.
Yerkes GE. 1945. Propagation of trees and shrubs. Farm. Bull. 1567 (rev.) Washington, DC: USDA. 54 p.

Hydrangeaceae—Hydrangea family

Philadelphus L.

mock orange

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

Dr. Shaw is a research botanist at the USDA Forest Service's Rocky Mountain Research Station, Forestry Sciences Laboratory, Boise, Idaho; Dr. Hurd and Mr. Stickney retired from the USDA Forest Service's Rocky Mountain Research Station

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

Lewis mock orange, the state flower of Idaho, was named for Captain Meriwether Lewis, who collected the plant in 1806. It is an extremely variable plant, growing from 1.5 to 3 m tall and producing leaf blades that are 25 to 75 mm long. The species is distributed from British Columbia to California and eastward into Montana (table 1). It exhibits wide ecological amplitude, growing in riparian areas and on cliffs, talus slopes, and rocky hillsides from the big sagebrush (*Artemisia tridentata* Nutt.) zone to ponderosa pine (*Pinus ponderosa* Dougl.) and lodgepole pine (*Pinus contorta* Dougl.) forests at elevations from sea level to 2,440 m (Hitchcock and others 1961; Hopkins and Kovalchik 1983).

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

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

Table 1—*Philadelphus,* mockorange: nomenclature and occurrence

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

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

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

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

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

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

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

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

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

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

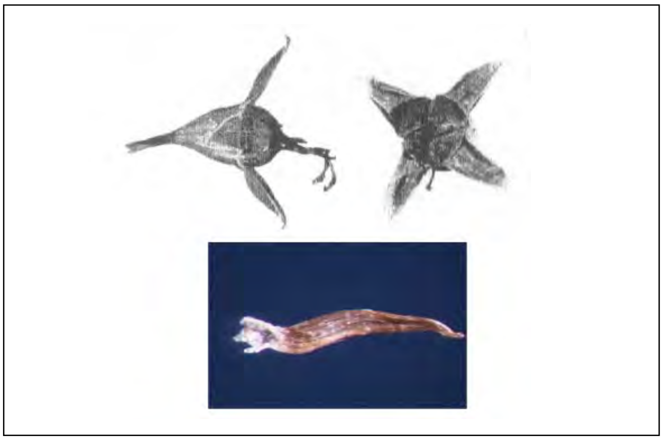
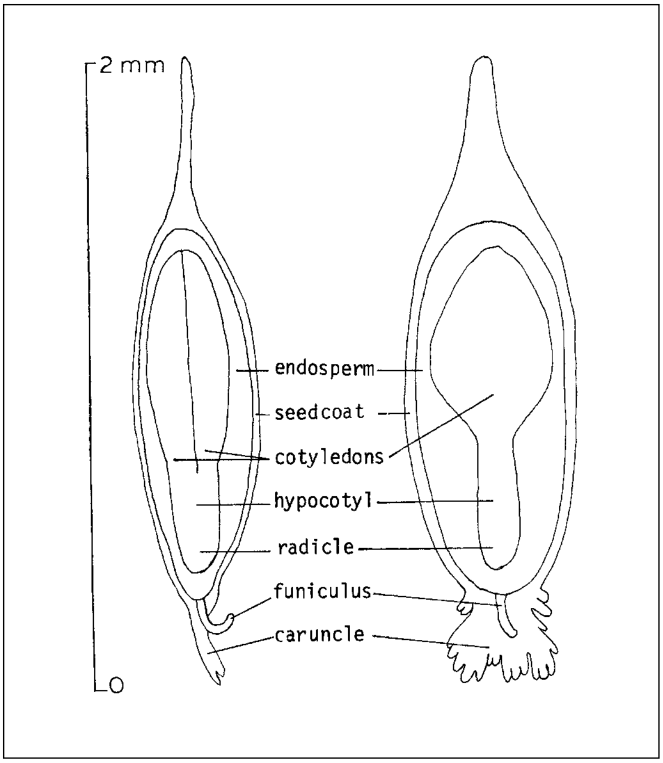


Figure 2—*Philadelphus lewisii*, Lewis mock orange: longitudinal sections of a seed.



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

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

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

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

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

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

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

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

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

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

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

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

References

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Van Dersal WR. 1938. Native woody plants of the United States: their erosion control and wildlife values. Misc. Pub. 303. Washington, DC: USDA. 362 p.

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

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

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

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

Rosaceae—Rose family

Physocarpus (Camb.) Raf.

ninebark

Andrew Youngblood, John D. Gill, and Franz L. Pogge

Dr. Youngblood is a research forester at the USDA Forest Service's Pacific Northwest Research Station, LaGrande, Oregon; Dr. Gill and Mr. Pogge retired from the USDA Forest Service's Northeastern Forest Experiment Station

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

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

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

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

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

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

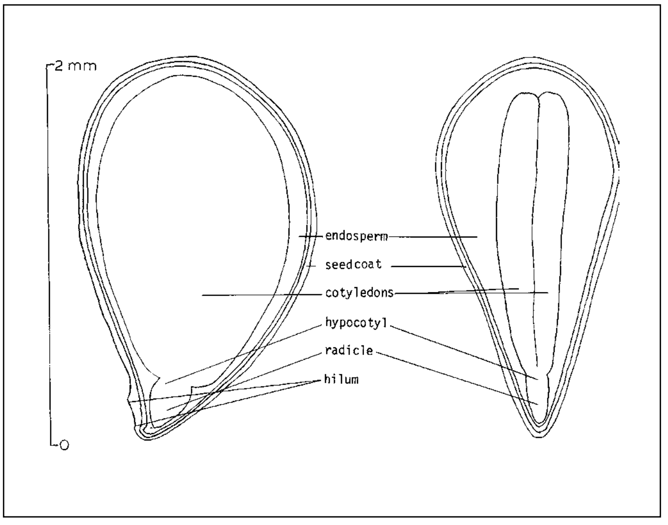
number 3 to 5 in Amur, Pacific, common, and Atlantic ninebarks. When mature, the follicles tend to be brown, reddish, or coppery in color, glabrous in common ninebark and sometimes Pacific ninebark, otherwise stellate-pubescent. Follicles burst open at both sutures when mature. They seldom fall of their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

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

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

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

Figure 2—*Physocarpus malvaceus*, mallow ninebark: longitudinal sections through a seed.



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

References

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

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

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

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

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

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

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

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

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

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

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

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

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

Pinaceae—Pine family

Picea A. Dietr.

spruce

Andrew Youngblood and Lawrence O. Safford

Dr. Youngblood is a research forester at the USDA Forest Service's Pacific Northwest Research Station, La Grande, Oregon; Dr. Safford retired from the USDA Forest Service's Northeastern Forest Experiment Station

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

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

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

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

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

Table 1—*Picea,* spruce: nomenclature and occurrence of native and cultivated species in North America

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

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

ever, especially when growing on sites with moist soils or high water tables. The conical form and dense, persistent branches of spruce species make them highly desirable for environmental plantings. All 7 North American species and the introduced Norway, Ezo, dragon, and Serbian spruces are planted as ornamentals. Many cultivars featuring variations or extremes in crown height, shape and symmetry, or thickness; rate of height growth; branch angle and degree of twig droop; and needle color exist (Everett 1981, Huxley 1992). In general, spruce species do not tolerate droughty sites but do thrive on slightly acidic and moist but well-drained soils. Of all the species, Serbian spruce may best tolerate industrial air pollution (Dallimore and Jackson 1967).

Geographic races and superior strains. The wide ranges and diverse environments to which the spruce species have adapted provide an array of individual, ecological, and geographic variations. Natural hybridization and introgression commonly occur where ranges of compatible species overlap. Hybridization between white spruce and Sitka spruce (first reported by Little 1953 as *P.* × *lutzii)*, occurs in British Columbia and throughout the Kenai Peninsula in Alaska (Copes and Beckwith 1977). This hybrid has demonstrated a genetically based resistance to attack by the Sitka spruce weevil—*Pissodes strobi* Peck—which causes severe height growth and stem form reduction in Sitka spruce (Mitchell and others 1990). Hybridization between white spruce and Engelmann spruce occurs in northern Montana and British Columbia (Daubenmire 1974). Artificial crosses of Engelmann spruce with Sitka spruce and with blue spruce suggest the close relatedness of these North American species (Fowler and Roche 1977). Electrophoresis has yet to clearly identify hybrids of Engelmann spruce and blue spruce along a 1,200-m elevational transect in the front range of the Colorado Rocky Mountains, where the species grow together. Morphological similarity between the 2 species, such as number of bud scales, number of stomatal rows, and location of resin sacs, however, suggests either convergent evolution or the influence of environmental variation on the morphological characters (Mitton and Andalora 1981). Natural introgression between the maritime Sitka spruce and the more interior complex of white and Engelmann spruces occurs in a portion of British Columbia, and the hybrid fraction was estimated by restriction fragment length polymorphisms of the nuclear ribosomal RNA genes (Sutton and others 1994). Differences in monoterpene composition from black spruce oleoresin (including α–pinene, 3-carene, and terpinolene) vary among geographic origins in an east–west pattern, except for seeds from sources in New England that have close affinity in monoterpene composition to red spruce (Chang and Hanover 1991). Natural introgression of black spruce into red spruce may result in greater height and diameter growth in New Brunswick, yet the hybrid performed unpredictably in managed stands (Fowler and others 1988).

Early crosses within the genus have provided a thorough background in potential crossability of the genus, including specimens from artificial crosses between nonsympatric species (Wright 1955). Analysis of morphological characteristics and monoterpene composition from artificial crosses between white, red, and blue spruces later verified the hybridity of the seedlings, evaluated the utility of spruce hybrids, and clarified the evolutionary relation among members of the genus (Bongarten and Hanover 1982). Height growth of Engelmann spruce × Sitka spruce hybrids proved unsuitable for reforestation purposes in the north central interior of British Columbia (Kiss 1989). Hybrids of black spruce and Serbian spruce out-performed the black spruce parents in height and diameter growth and can be produced sexually en masse in seed orchards (Fowler 1980).

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

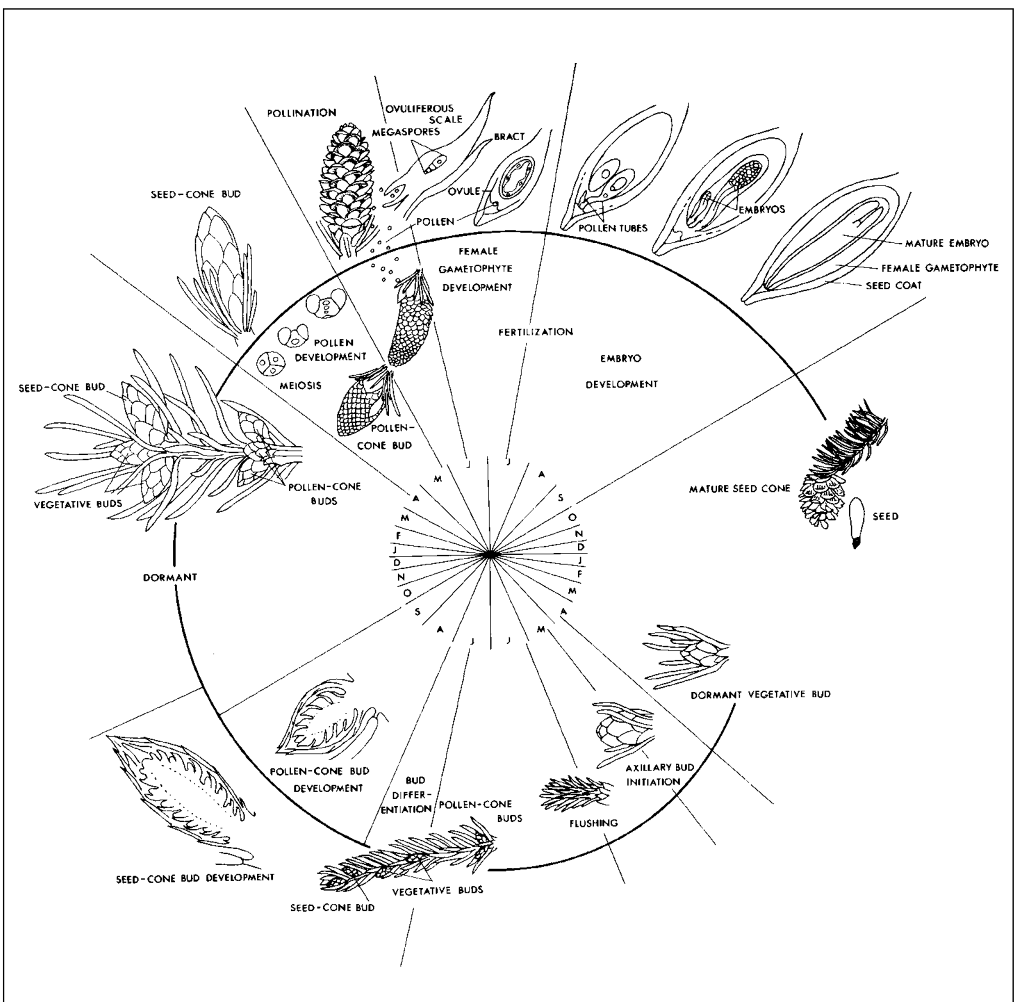
Genetic variation of Engelmann spruce may correlate with latitude and elevation; the species grows at 762 to 1,067 m in British Columbia and as high as 3,658 m in the southern Rocky Mountains (Alexander 1987). After 10 years, seedlings from more northern and lower elevation sources grew better than those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

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

Norway spruce, perhaps the most intensively studied non-native species, shows strong latitudinal and elevational gradients. Seeds from northern latitudes and higher elevations weigh less than seeds from southern latitudes and lower elevations (Heit 1968; Tyszkiewics 1968). Seed source also influences mineral nutrient content of seeds (Youngberg 1951) and early growth of seedlings in nursery beds (Heit 1968). Seed source of Serbian spruce can affect the crown shape and susceptibility to frost (Dirr and Heuser 1987).

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

Figure 1—*Picea glauca*, white spruce: reproductive cycle (from Owens and Molder 1984, used with permission of the author and publisher).



bright purple, or crimson male strobili have ovoid to cylindrical shape and uniform distribution over the crown. Each scale (microsporophyll) bears 2 pollen sacs (microsporangia) and are spirally arranged on a central axis. Male strobili dry out and fall off soon after pollen-shedding.

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

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

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

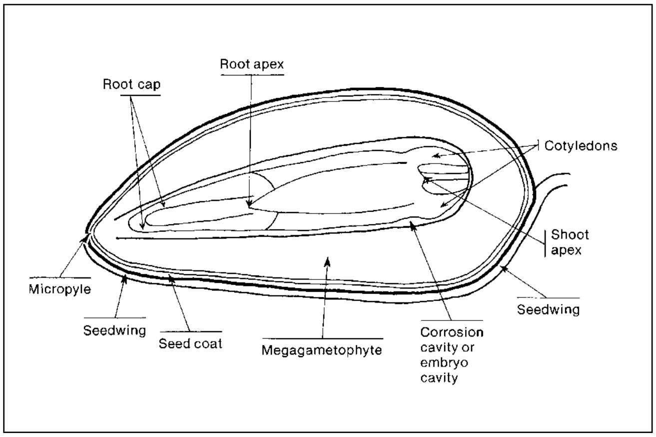
Table 2—*Picea*, spruce: height, seed-bearing age, and phenology of flowering and fruiting

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

Sources: Alden (1955), Alexander (1987), Alexander and Shepperd (1984), Edwards (1980), Fechner (1985), Nikolov and Helmisaari (1992), Safford (1974), Zasada and Viereck (1970).

* Cones of *P. mariana* are semi-serotinous and release seeds throughout the year for several years.

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



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

At maturity, the pendent cones open to shed seeds during autumn and winter (table 2). Persistent cone scales on mature cones may have rounded, pointed, irregular, notched, or reflexed ends. Most species shed cones at the end of the season, but some cones may remain on the tree throughout the next growing season. Cones should be harvested before inclement weather reduces workers' productivity or losses to squirrels increase (Curran and others 1987). Cones may be collected before they are fully ripe and, if artificially ripened, release seeds with maximal germination capacity (Edwards 1980). Cones may be collected from standing trees, slash, or animal caches, although cones that have been in contact with the forest floor may acquire seed-killing fungi. Seeds generally reach maturity before cones show their characteristic ripe color (table 2). Time of ripening varies among cones on an individual tree and among trees in a single stand (Fechner 1974; Jensen and others 1967; Zasada 1988). Various measures of estimating seed maturity have emphasized (1) physical attributes such as color and firmness of cones; (2) moisture content and specific gravity of cones; (3) color of testa and brittleness of seeds (Crossley 1953; Edwards 1980); (4) a cone moisture content of 30% or less for Norway spruce; (5) specific gravity between 0.78 and 0.95 (Winston and Haddon 1981; Zasada 1973) and a soft "spongy feel" of cones when squeezed in the fingers for white spruce; or (6) dark brown or black testa and seeds that "snap" when cut with a sharp instrument. All of these indicate that cones are sufficiently ripe for harvest.

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

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

Attempts to enhance seed yields in seed orchard programs have been hampered by the relatively long period of tree growth before flowering begins. Documented minimal seed-bearing age (table 2) for most species ranges from 10 to 60 years, although crops of sufficient quantity to warrant collection may not occur until much later. Efforts to stimulate flowering in younger trees have involved girdling of the bole, nitrogen fertilization, and root pruning. Top-pruning of grafted white spruce in seed orchards, done to maintain the cone-bearing branches at a height within reach of a short ladder, may also increase cone production and decrease the cost of cone collection (Nienstaedt 1981).

Several lines of research have attempted to define the physiological processes and procedures for large-scale stimulation of flowering to either shorten the length of breeding programs or to increase production of cones and seeds. Application of gibberellins A_4, A_7, and A_9 stimulated female cone production in grafted Norway spruce clones, although the response differed by year and clone (Dunberg 1980). Gibberellin $A_{4/7}$ applied in the top 2 branch whorls of mature Sitka spruce grafts increased female flowering and seed production (Tompsett and others 1980); girdling in combination with stem injections of gibberellin $A_{4/7}$ in grafted clones of Sitka spruce may stimulate pollen-cone production (Philipson 1985a); and top-pruning and stem injection of gibberellin $A_{4/7}$ may increase cone production in the lower crown and increase the ease of cone collection (Philipson 1985b). Heat and drought also promote flowering, although by a different induction mechanism. Potted grafts of Engelmann spruce produced high numbers of both male and female cone buds after exposure to high temperature within heated polyethylene-covered houses when the exposure occurred during the late stage of slow shoot elongation, whereas drought during the period of rapid shoot elongation after vegetative bud burst enhanced female cone production (Ross 1985). Optimal daytime temperature is 22 to 25 °C (Ross 1988a). In contrast, polyhouse temperatures that frequently exceed 30 °C during the pollination sequence of Engelmann spruce resulted in accelerated pollen shed, increased underdevelopment of pollen cones, and reduced yields of seed (Ross 1988b). These results suggest a need for a year's rest between treatments to allow time for cone maturation and vegetative replenishment of shoots. Repeated injection of gibberellin $A_{4/7}$ into container-grown grafts of Sitka spruce in a polyhouse during May and June effectively stimulated flowering (Philipson 1992). Application of gibberellin $A_{4/7}$ also stimulated flowering of white spruce (Ho 1988b; Marquard and Hanover 1984), even though white spruce has been classed as recalcitrant because of its sporadic flowering and usually nominal response to gibberellin $A_{4/7}$ alone (Pharis and others 1986). Stem injection of gibberellin $A_{4/7}$ in combination with nondestructive girdling greatly increases flowering in mature white spruce trees (Pharis and others 1986) and grafted clones (Ross 1992). Whole-tree spraying of branches at relatively high concentrations (800 mg/liter gibberellin $_{4/7}$) during May through July promoted cone production the next year (Ho 1988b). In the Great Lakes region, elongating shoots sprayed in May produced more male and female strobili than shoots sprayed in June (Cecich 1985). Flowering of white spruce responded to heat similar to that of Engelmann spruce by enhanced pollen-cone production after subjecting potted grafts to 30 °C for 10 hours, whereas seed-cone production was enhanced after 5 hours at 20 °C (Ross 1991). Seed-cone production of black spruce also has been stimulated by application of gibberellin; the greatest increase occurred with 200 mg/liter of gibberellin $A_{4/7}$ sprayed repeatedly on young grafts during the period of rapid shoot elongation (Ho 1991). Seed-cone production also may be enhanced in field-grown seed orchards by applying a foliar spray of 400 mg/liter gibberellin $A_{4/7}$ during the period before lateral shoot elongation and bud-type differentiation (Ho 1988a), and in seed orchards of seedling origin by applying a foliar spray of 200 to 800 mg/liter gibberellin $A_{4/7}$ (Hall 1988). Attempts with several species to promote male flowering preferentially by the synthetic auxin naphthalene acetic acid (NAA) have been inconclusive (Hall 1988; Ross 1992).

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

Figure 3—*Picea*, spruce: seeds with wings of *P. breweriana*, Brewer spruce; *P. engelmannii*, Engelmann spruce; *P. glauca*, white spruce; *P. mariana*, black spruce; *P. rubens*, red spruce; and *P. sitchensis*, Sitka spruce (**left to right**).

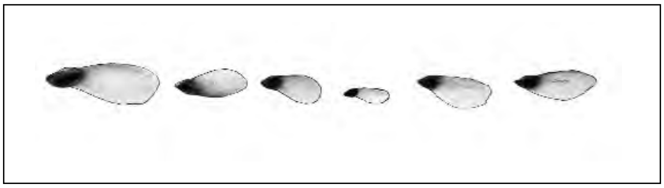


Table 3—*Picea,* spruce: common cone- and seed-damaging insects

Insect species	Common name	Damage	Affected species*
Choristoneura occidentalis Freeman	western spruce budworm	Larvae feed externally on cones	***P. engelmannii***
Dasineura canadensis Felt	spruce cone gall midge	Larvae form gall on cone scale	***P. glauca***
Dasineura rachiphaga Tripp	spruce cone axis midge	Larvae mine through scales into axis	***P. engelmannii, P. glauca***, *P. sitchensis,P. mariana*
Dioryctria abietivorella Grote	fir cone moth	Larvae mine & riddle cone	***P. mariana, P. glauca***, *P. engelmannii, P. pungens,*
Henricus fuscodorsanus Kearfott	cone cochylid	Larvae feed on scales & seeds	***P. sitchensis, P. glauca***
Hylemya anthracina Czerny	spruce cone seed maggot	Larvae tunnel around cone axis	***P. mariana, P. glauca, P. engelmannii, P. sitchensis***
Laspeyresia youngana Kerfott	spruce seed moth	Larvae feed on seeds	***P. engelmannii, P. glauca***, *P. mariana, P. pungens, P. rubens, P. sitchensis*
Mayetiola carpophaga Tripp	spruce seed midge	Larvae feed on seeds	***P. glauca***
Megastigmus atedius Walker	spruce seed chalcid	Larvae feed on seeds	All native *Picea*
Strobilomyia neanthracina Michelson	spruce cone maggot	—	***P. mariana***

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

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

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

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

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

Many species of birds consume spruce seeds. Several finches (families Fringillidae and Estrildidae) feed almost exclusively on conifer seeds, including the common (red) crossbill (*Loxia curvirostra*), the two-barred (white-winged) crossbill (*L. leucoptera*), and the pine siskin (*Carduelis pinus*). Spruce seeds often provide an important winter food source for the American goldfinch—*C. tristis*. In addition, the pine siskin and the pine grosbeak—*Pinicola enucleator*—may feed on reproductive buds (Benkman 1987; Clement and others 1993).

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

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

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

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

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

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

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

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

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

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

Sources: Dirr and Heuser (1987), Jeglum and Kennington (1993), Nikolov and Helmisaari (1992), Safford (1974), Stein and others (1986), Willan (1985).
Note: TB = top of blotters; P = petri dishes covered with blotters, filter paper, or sand.

for 14 months showed only a slight loss of percentage germination; under these conditions black spruce lost about one-third of its percentage germination and germination of all 3 species declined to about 10% of the original capacity after 27 months (MacGillivary 1955). Prechilling, or cold stratification, may widen the range of temperatures over which seeds can subsequently germinate, increase the maximal percentage germination at some temperatures, and increase the rate of germination at almost any temperature (Gosling and Rigg 1990). Prechilling of white spruce seeds at 2 to 4 °C for 6 weeks results in high percentage germination (Caron and others 1990). Other researchers have prechilled white spruce seeds by soaking them in cold running water for 24 hours, blotting them dry, and then refrigerating them at 4 °C for 3 weeks (Chanway and others 1991). Storage of cones at 5 °C for 4 weeks, however, may eliminate any subsequent need for stratification of white spruce seeds (Winston and Haddon 1981). White spruce seeds from high-latitude sites in Alaska (> 55° latitude) do not undergo dormancy, and stratification is detrimental for mature seeds (Alden 1995). Before nursery sowing, Engelmann spruce seeds need to be primed for 24 hours, then prechilled for 6 to 8 weeks at 2 °C in loosely closed polyethylene bags (Tanaka and others 1986). Unstratified seeds of black spruce incubated for 24 days at 3 or 20 °C germinated completely within18 days with 14:10 (light:dark) hours of fluorescent light, whereas moist seeds prechilled for 24 hours at 3 °C in a polyethylene bag in the dark reached 95% germination within 12 days when incubated at 5 to 30 °C, regardless of lighting regime (Farmer and others 1984). Priming black spruce seeds for 5 to 6 days in water (until the radicles nearly emerge) and surface-drying before sowing accelerated germination by about 1 week (Malek 1992). Seeds of black spruce from high latitudes in Alaska, collected and immediately extracted in the spring, will germinate in 2 to 6 days after becoming fully imbibed with water; no dormancy exists and stratification is not required (Alden 1995). Dormancy of Sitka spruce seeds is broken and 95% germination is possible after priming for 72 hours (until seeds reach 30% moisture content), then chilling for 6 weeks in loosely closed polyethylene bags at 4 °C (Gosling and Rigg 1990).

Treating seedlots with various fumigants, insecticides, fungicides, and rodent repellents in storage or before sowing may reduce germination of seeds. Germination of white spruce seeds treated with a finely ground rodent repellent mixed with graphite declined slightly from that of untreated seeds after more than 5 years of storage (Radvanyi 1980). Aluminum powder, which is used as a lubricant on Sitka and white spruce seeds in bareroot nurseries in Canada, may decrease the percentage germination of treated seeds and reduce first-year survival of seedlings (Sutherland and others 1978). Embedding black spruce seeds in pellets may discourage their consumption by small mammals, depending on the material surrounding the seeds (Martell 1981). As always, pesticide users should closely follow the manufacturer's recommended dosages.

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

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

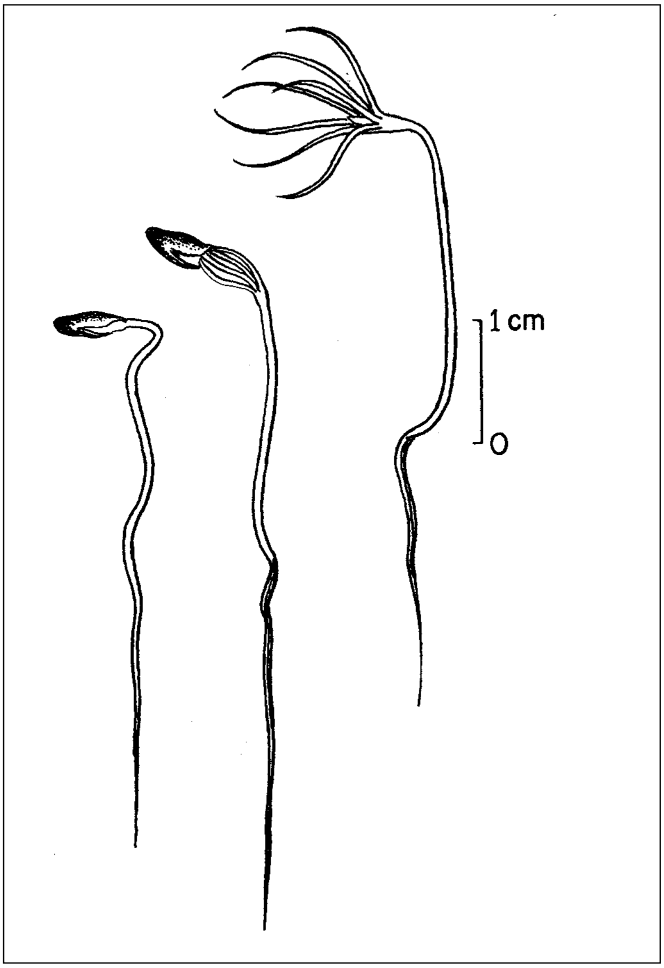
Under natural conditions, most species of spruce germinate on various media, including rotten wood, shallow duff, and mixtures of mineral and organic soil. Mineral soil makes an ideal seedbed because of greater water availability. Commercial growers raise white spruce seedlings with high stem caliper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

Seeds of most species germinate promptly and completely under a wide range of temperatures either with or without light. Once germinated, seedlings in greenhouses require extended daylength to accelerate growth and prevent dormancy. Continuous fluorescent lighting providing about 150 μmol/m^2/sec photosynthetically active radiation at 25 °C allows continuous vigorous growth of blue spruce seedlings (Young and Hanover 1978). White spruce seedlings respond favorably to photoperiodic lighting intensities of about 414 to 4,150 μmol/m^2/sec, although Engelmann spruce has a much narrower response range of about 210 to 520 μmol/m^2/sec (Arnott and Macey 1985). Seedlings of white spruce also have been grown with photosynthetically active radiation at the seedling canopy level of about 300 μmol/m^2/sec in a 16-hour photoperiod at 23 °C and a night temperature of 17 °C (Chanway and others 1991). Failure of the lighting system for only a few days reduced the effectiveness of extended or intermittent photoperiod, leading to increased root rather than shoot growth in white spruce seedlings (Arnott and Simmons 1985). Under laboratory or greenhouse conditions, newly germinated seedlings of red spruce require a light period of at least 16 hours to prevent the onset of dormancy (Safford 1974).

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

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

Figure 4—*Picea pungens*, blue spruce: seedling development at 2, 5, and 7 days after germination.



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

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

References

Ahuja MR. 1986. Storage of forest tree germplasm in liquid nitrogen (–196 °C). Silvae Genetica 35: 5–6.
Alden J. 1985. Biology and management of white spruce seed crops for reforestation in subarctic taiga forests. Bull. 69. Fairbanks: University of Alaska , School of Agriculture and Land Resources Management, Agricultural and Forestry Experiment Station. 51 p.
Alden J. 1995. Personal communication. Fairbanks: University of Alaska.
Alexander RR. 1986. Engelmann spruce seed production and dispersal, and seedling establishment in the central Rocky Mountains. Gen. Tech. Rep. RM-134. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 9 p.
Alexander RR. 1987. Ecology, silviculture, and management of the Engelmann spruce–subalpine fir type in the central and southern Rocky Mountains. Agric. Handbk. 659. Washington, DC: USDA Forest Service. 144 p.
Alexander RR, Shepperd WD. 1990. *Picea engelmannii*. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 187–203.
Arnott JT, Macey DE. 1985. Effect of supplemental light intensity on white spruce, Engelmann spruce, and mountain hemlock seedlings grown under an extended photoperiod. Canadian Journal of Forest Research 15: 295–300.
Arnott JT, Simmons CS. 1985. The effect of failure in extended and intermittent photoperiodic lighting on the growth of white spruce container seedlings. Canadian Journal of Forest Research 15: 734–737.
Bega RV, Scharpf RF. 1993. Rusts. In: Scharpf RF, tech. coord. Diseases of Pacific Coast conifers. Agric. Handbk. 521. Washington, DC: USDA Forest Service: 83–111.
Benkman CW. 1987. Food profitability and the foraging ecology of crossbills. Ecological Monographs 57: 251–267.
Blum BM. 1990. *Picea rubens*. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 250–259.
Bongarten BC, Hanover JW. 1982. Hybridization among white, red, blue, and white × blue spruces. Forest Science 28: 129–134.
Brink CH, Dean FC. 1966. Spruce seed as a food of red squirrels and flying squirrels in interior Alaska. Journal of Wildlife Management 30: 503–512.
Cameron DE, Jenkins MJ. 1988. Engelmann spruce cone losses caused by insects in northern Utah in a year of low cone production. Great Basin Naturalist 48: 508–511.
Carmichael AJ. 1958. Determination of the maximum air temperature tolerated by red pine, jack pine, white spruce and black spruce seeds at low relative humidities. Forestry Chronicle 34: 387–392.
Caron GE, Powell GR. 1989. Cone size and seed yield in young *Picea mariana* trees. Canadian Journal of Forest Research 19: 351–358.
Caron GE, Powell GR. 1992. Patterns of cone distribution in crowns of young *Picea mariana*: 1. Effect of tree age on seed cones. Canadian Journal of Forest Research 22: 46–55.
Caron GE, Wang BSP, Schooley HO. 1990. Effect of tree spacing, cone storage, and prechilling on germination of *Picea glauca* seed. Forestry Chronicle 66: 388–392.
Cecich RA. 1985. White spruce (*Picea glauca*) flowering in response to spray application of gibberellin $A_{4/7}$. Canadian Journal of Forest Science 15: 170–174.
Cerezke HF, Holmes RE. 1986. Control studies with carbofuran on seed and cone insects of white spruce. Info. Rep. NOR-X-280. Edmonton, AB: Canadian Forest Service, Northern Forest Centre. 10 p.
Chang J, Hanover JW. 1991. Geographic variation in the monoterpene composition of black spruce. Canadian Journal of Forest Research 21: 1796–1800.
Chanway CP, Radley RA, Holl FB. 1991. Inoculation of conifer seed with plant growth promoting *Bacillus* strains causes increased seedling emergence and biomass. Soil Biology and Biochemistry 23: 575–580.
Clement P, Harris A, Davis J. 1993. Finches and sparrows: an identification guide. Princeton, NJ: Princeton University Press. 500 p.
Copes DL, Beckwith RC. 1977. Isoenzyme identification of *Picea glauca, P. sitchensis*, and *P. lutzii* populations. Botanical Gazette 138: 512–521.
Croghan CF, Palmer MA, Wolosiewicz M. 1987. Stunting of white spruce (*Picea glauca* (Moench) Voss) associated with ectomycorrhizal deficiency. Tree Planters' Notes 38: 22–23.
Crossley DI. 1953. Seed maturity in white spruce (*Picea glauca*). Silviculture Research Notes [Canadian Forest Service, Research Division] 104: 1–16.
Curran WJ, Tricco P, Hall JP. 1987. Optimal dates for collection of conifer seed in central Newfoundland. Info. Rep. N-X-248. St. John's, NF: Canadian Forestry Service, Newfoundland Forestry Centre. 15 p.
Dallimore W, Jackson AB. 1967. A handbook of Coniferae and Ginkgoaceae. 4th ed. Harrison SG, rev. New York: St. Martin's Press. 729 p.
Daubenmire R. 1974. Taxonomic and ecologic relationships between *Picea glauca* and *Picea engelmannii*. Canadian Journal of Botany 52: 1545–1550.
Diebel KE, Fechner GH. 1988. Natural variation among seedlings from Colorado sources of blue spruce. Western Journal of Applied Forestry 3: 106–109.
Dirr MA, Heuser CW Jr. 1987. The reference manual of woody plant propagation: from seed to tissue culture. Athens, GA: Varsity Press. 239 p.
Dobbs RC. 1976. White spruce seed dispersal in central British Columbia. Forestry Chronicle 52: 225–228.
Dunberg A. 1980. Stimulation of flowering in *Picea abies* by gibberellins. Silvae Genetica 29: 51–53.
Edwards DGW. 1980. Maturity and quality of tree seeds: a state of the art review. Seed Science and Technology 8: 625–657.
Edwards DGW. 1986. Cone prediction, collection, and processing. In: Shearer RC, comp. Proceedings, Conifer Tree Seed in the Inland Mountain West Symposium; 1985 August 5–6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 78–102.
Eis S. 1973. Predicting white spruce cone crops. Tech. Note BC-P-7. Victoria, BC: Environment Canada, Pacific Forest Research Centre. 4 p.
Eremko RD, Edwards DGW, Wellinger D. 1989. Guide to collecting cones of British Columbia conifers. Forest Resource Development Agreement Rep. 055. Victoria, BC: Forestry Canada, British Columbia Ministry of Forestry. 114 p.
Everett TH. 1981. The New York Botanical Garden illustrated encyclopedia of horticulture. New York: Garland Publishing. 3601 p.
Farmer RE, Charrette P, Searle IE, Tarjan DP. 1984. Interaction of light, temperature, and chilling in the germination of black spruce. Canadian Journal of Forest Research 14: 131–133.
Fechner GH. 1974. Maturation of blue spruce cones. Forest Science 20: 47–50.
Fechner GH. 1985. Silvical characteristics of blue spruce. Gen. Tech. Rep. RM-117. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 19 p.
Fogal WH. 1990. White spruce cone crops in relation to seed yields, cone insect damage, and seed moth populations. In: West RJ, ed. Proceedings, Cone and Seed Pest Workshop; 1990 October 4; St. John's, NF. Info. Rep. N-X-274. St. John's, NF: Forestry Canada, Newfoundland and Labrador Region: 76–88.
Fogal WH, Alemdag IS. 1989. Estimating sound seeds per cone in white spruce. Forestry Chronicle 65: 266–270.
Fogal WH, Larocque G. 1992. Development of flowers, cones, and seeds in relation to insect damage in two white spruce communities. Forest Ecology and Management 47: 335–348.
Fowler DP. 1980. Hybridization of black spruce and Serbian spruce. Info. Rep. M-X-112. Fredericton, NB: Canadian Forestry Service, Maritimes Forest Research Centre. 30 p.

Fowler DP, Mullin RE. 1977. Upland–lowland ecotypes not well developed in black spruce in northern Ontario. Canadian Journal of Forest Research 7: 35–40.
Fowler DP, Roche L. 1977. Genetics of Engelmann spruce. Res. Pap. WO-30. Washington, DC: USDA Forest Service. 13 p.
Fowler DP, Park YS, Gordon AG. 1988. Genetic variation of red spruce in the Maritimes. Canadian Journal of Forest Research 18: 703–709.
Fraser JW. 1976. Viability of black spruce seed in or on a boreal forest seedbed. Forestry Chronicle 52: 229–231.
Furnier GR, Stine M, Mohn CA, Clyde MA. 1991. Geographic patterns of variation in allozymes and height growth in white spruce. Canadian Journal of Forest Research 21: 707–712.
Gosling PG, Rigg P. 1990. The effect of moisture content and prechill duration on the efficiency of dormancy breakage in Sitka spruce (*Picea sitchensis*). Seed Science and Technology 18: 337–343.
Haavisto VF, Fleming RL, Skeates DA. 1988. Potential and actual yields of seed from black spruce cones. Forestry Chronicle 64: 32–34.
Hall JP. 1988. Promotion of flowering in black spruce using gibberellins. Silvae Genetica 37: 135–138.
Hanover JW. 1975. Genetics of blue spruce. Res. Pap. WO-28. Washington, DC: USDA Forest Service. 12 p.
Harris AS. 1990. *Picea sitchensis*. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 260–267.
Harrison DLS, Owens JN. 1983. Bud development in *Picea engelmannii:* 1. Vegetative bud development, differentiation, and early development of reproductive buds. Canadian Journal of Botany 61: 2291–2301.
Hedlin AF. 1973. Spruce cone insects in British Columbia and their control. Canadian Entomologist 105: 113–122.
Hedlin AF, Yates HO, Tovar DC, Ebel BH, Koerber TW, Merkel EP. 1980. Cone and seed insects of North American conifers. Victoria, BC: Environment Canada, Canadian Forestry Service [with USDA Forest Service and Secretaria de Agricultura y Recuros Hidraulicos, Mexico]. 122 p.
Heit CE. 1968. Propagation from seed: 13. Some western and exotic spruce species. American Nurseryman 127: 12–13, 51–63.
Hill JA. 1976. Viability of several species of conifer seeds after long term storage. Tree Planters' Notes 27: 2–3.
Ho RH. 1988a. Gibberellin $A_{4/7}$ enhances seed-cone production in field-grown black spruce. Canadian Journal of Forest Research 18: 139–142.
Ho RH. 1988b. Promotion of cone production on white spruce grafts by gibberellin $A_{4/7}$ application. Forest Ecology and Management 23: 39–46.
Ho RH. 1991. Promotion of cone production in potted black-spruce grafts, using gibberellins, heat-treatment and root-pruning. Forest Ecology and Management 40: 261–269.
Huxley A. ed. 1992. The new Royal Horticultural Society dictionary of gardening. New York: Stockton Press. 3353 p.
Jeglum JK, Kennington DJ. 1993. Strip clearcutting in black spruce: a guide for the practicing forester. Sault Ste. Marie, ON: Forestry Canada, Ontario Region, Great Lakes Forestry Centre. 102 p.
Jensen A, Stephansen K, Løken A. 1967. Seed ripening of Norwegian coniferous trees: 2. Variation in the chemical content and germination of seeds of *Picea abies* (L.) Karst. and *Picea sitchensis* (Bong.) Carr. Forest Research Institute West Norway Report 44: 191–222.
Khalil MAK. 1984. All-range black spruce provenance study in Newfoundland: performance and genotypic stability of provenances. Silvae Genetica 33: 63–71.
Kiss GK. 1989. Engelmann × Sitka spruce hybrids in central British Columbia. Canadian Journal of Forest Research 19: 1190–1193.
Lackey M, Alm A. 1982. Evaluation of growing media for culturing containerized red pine and white spruce. Tree Planters' Notes 33: 3–7.
Landis TD, Tinus RW, McDonald SE, Barrett JP. 1989. The container tree nursery manual. Volume 4, Seedling nutrition and irrigation. Agric. Handbk. 674. Washington DC: USDA Forest Service. 112 p.
Li J, Than H, Ge J. 1990. Spruce forests in northeast China. In: Titus BD, Lavigne MB, Newton PF, Meades WJ, eds. The silvics and ecology of boreal spruces: Proceedings of the IUFRO Working Party S1.05-12 Symposium; 1989 August 12–17; St. John's, NF. Info. Rep. N-X-271. St. John's, NF: Forestry Canada: 91–95
Little EL Jr. 1953. A natural hybrid spruce in Alaska. Journal of Forestry 51: 745–747.
Little EL Jr. 1979. Checklist of United States trees (native and cultivated). Agric. Handbk. 541. Washington, DC: USDA Forest Service. 375 p.
MacGillivary JH. 1955. Germination of spruce and fir seeds following different stratification periods. Forestry Chronicle 31: 365.
Malek L. 1992. Priming black spruce seeds accelerates container stocking in techniculture single-seed sowing system. Tree Planters' Notes 43: 11–13.
Marquard RD, Hanover JW. 1984. Sexual zonation in the crown of *Picea glauca* and the flowering response to exogenous $GA_{4/7}$. Canadian Journal of Forest Research 14: 27–30.
Martell AM. 1981. Effects of pelleting and repellent coating of conifer seeds on feeding by deer mice. Info. Rep. O-X-330. Sault Ste. Marie, ON: Canadian Forestry Service, Great Lakes Forest Research Centre. 9 p.
McCaughey WW, Schmidt WC. 1987. Seed dispersal of Engelmann spruce in the Intermountain West. Northwest Science 61: 1–6.
Mitchell RG, Wright KH, Johnson NE. 1990. Damage by the Sitka spruce weevil (*Pissodes strobi*) and growth patterns for 10 spruce species and hybrids over 26 years in the Pacific Northwest. Res. Pap. PNW-434. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 12 p.
Mitton JB, Andalora R. 1981. Genetic and morphological relationships between blue spruce, *Picea pungens*, and Engelmann spruce, *Picea engelmannii*, in the Colorado Front Range. Canadian Journal of Botany 59: 2088–2094.
Morgenstern EK. 1978. Range-wide genetic variation of black spruce. Canadian Journal of Forest Research 8: 463–473.
Mullin RE. 1980. Comparison of seedling and transplant performance following 15 years of growth. Forestry Chronicle 56: 231–232.
Nienstaedt H. 1981. Top pruning white spruce seed orchard grafts. Tree Planters' Notes 32(2): 9–13.
Nienstaedt H, Zasada JC. 1990. *Picea glauca*. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 204–226.
Nikolov N, Helmisaari H. 1992. Silvics of the circumpolar boreal forest tree species. In: Shugart HH, Leemans R, Bonan GB, eds. A systems analysis of the global boreal forest. Cambridge, UK: Cambridge University Press: 13–84.
Owens JN. 1986. Cone and seed biology. In: Shearer RC, comp. Proceedings, Conifer Tree Seed in the Inland Mountain West Symposium; 1985 August 5–6; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 14–31.
Owens JN, Molder M. 1976. Bud development in Sitka spruce: 2. Cone differentiation and early development. Canadian Journal of Botany 54: 766–779.
Owens JN, Molder M. 1977. Bud development in *Picea glauca*: 2. Cone differentiation and early development. Canadian Journal of Botany 55: 2746–2760.
Owens JN, Molder M. 1984. The reproductive cycle of interior spruce. Victoria: British Columbia Ministry of Forestry, Information Services Branch. 30 p.
Park YS, Fowler DP. 1988. Geographic variation of black spruce tested in the Maritimes. Canadian Journal of Forest Research 18: 106–114.
Parker WH, Knowles P, Bennett F, Gray A, Krickl T. 1983. Habitat-dependent morphological and chemical variation in *Picea mariana* from northwestern Ontario. Canadian Journal of Botany 61: 1573–1579.
Patterson TE. 1988. A new species of *Picea* (Pinaceae) from Nuevo León, Mexico. SIDA 13(2): 131–135.
Payandeh B, Haavisto VF. 1982. Prediction equations for black spruce seed production and dispersal in northern Ontario. Forestry Chronicle 58: 96–99.
Pharis RP, Tomchuk D, Beall FD, Rauter RM, Kiss G. 1986. Promotion of flowering in white spruce (*Picea glauca*) by gibberellin $A_{4/7}$, auxin (naphthaleneacetic acid), and the adjunct cultural treatments of girdling and $Ca(NO_3)_2$ fertilization. Canadian Journal of Forest Research 16: 340–345.
Philipson JJ. 1985a. The promotion of flowering in large field-grown Sitka spruce by girdling and stem injections of gibberellin $A_{4/7}$. Canadian Journal of Forest Research 15: 166–170.
Philipson JJ. 1985b. The effect of top pruning, girdling, and gibberellin $A_{4/7}$ application on the production and distribution of pollen and seed cones in Sitka spruce. Canadian Journal of Forest Research 15: 1125–1128.
Philipson JJ. 1992. Optimal conditions for inducing coning of container-grown *Picea sitchensis* grafts: effects of applying different quantities of $GA_{4/7}$, timing and duration of heat and drought treatment, and girdling. Forest Ecology and Management 53: 39–52.
Radvanyi A. 1980. Germination of R-55 repellent treated and non-treated seeds of white spruce following prolonged cold storage. Forestry Chronicle 56: 60–63.
Ross SD. 1985. Promotion of flowering in potted *Picea engelmannii* (Perry) grafts: effects of heat, drought, gibberellin $A_{4/7}$, and their timing. Canadian Journal of Forest Research 15: 618–624.
Ross SD. 1988a. Effects of temperature, drought, and gibberellin $A_{4/7}$, and timing of treatment, on flowering in potted *Picea engelmannii* and *Picea glauca* grafts. Canadian Journal of Forest Research 18: 163–171.
Ross SD. 1988b. Pre- and post-pollination polyhouse environment effects on pollen and seed development in potted *Picea engelmannii* grafts. Canadian Journal of Forest Research 18: 623–627.
Ross SD. 1991. Effect of heat sums and of heat applied separately to shoot and roots on flowering in potted *Picea glauca* grafts. Canadian Journal of Forest Research 21: 672–679.