

Areaceae—Palm family

Sabal Adans.
palmetto

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Growth habits, occurrence, and use. Palmettos—genus *Sabal*—are native to the Western Hemisphere and are distributed from the Bermuda Islands and the South Atlantic and Gulf States through the West Indies to Venezuela and Mexico (Sargent 1965). Five species inhabit the southeastern United States, Puerto Rico, and the Virgin Islands (table 1). Cabbage palmetto has tree form and attains a height at maturity of 12 to 27 m (Sargent 1965); it is found from North Carolina to south Florida, in low flatwoods and on offshore islands in the north, and becoming common throughout the lower part of the Florida peninsula. Cabbage palmetto has few commercial uses but is used extensively by rural residents for a variety of purposes—the trunk for timber, the bud for food, and the leaves for craft weaving. Cabbage palmetto has been planted widely as an ornamental. It has no forage value and only limited usefulness for wildlife. Scrub palmetto has a low, spreading form and attains a height at maturity

of about 1.3 m (Bailey 1939; McCurrach 1960). It has a restricted range in the dry pinelands and scrub of central Florida (Small 1933). The bud is eaten as a salad vegetable, and the fruits are eaten by animals and birds.

Flowering and fruiting. The perfect white flowers of cabbage palmetto measure about 6 mm in diameter and are borne in drooping clusters 1.3 to 1.8 m long from June to August, depending upon latitude (Sargent 1965; Snyder 1952; West and Arnold 1947). The flowers are pollinated by insects (Knuth 1906). The fruit is a berry, subglobose or slightly obovoid, about 8 mm in diameter. The fruit is dark brown to black and ripens in late autumn or winter (Bailey 1939). Each fruit contains 1 light brown seed about 6 mm in diameter (Sargent 1965). Fruits and seeds of scrub palmetto are slightly larger (figure 1). Embryos are minute (figure 2).

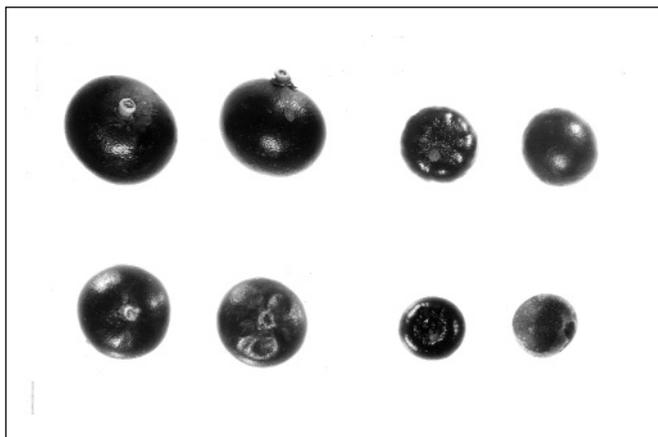
Collection, cleaning, and storage. The fruits of these palms may be picked from the plants when ripe, and the

Table 1—*Sabal*, palmetto: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
<i>Sabal causiarum</i> (O.F. Cook) Becc.	Puerto Rico palmetto, Puerto Rico hat palm	Puerto Rico & the Virgin Islands
<i>Sabal etonia</i> Swingle ex Nash <i>S. miamiensis</i> Zona	scrub palmetto, etonia palmetto	Florida
<i>Sabal mexicana</i> Mart. <i>S. exul</i> (O.F. Cook) Bailey <i>S. texana</i> (O.F. Cook) Becc. <i>Inodes exul</i> O.F. Cook; <i>Inodes texana</i> O.F. Cook	Rio Grande palmetto Mexican palmetto, Oaxaca palmetto	Texas
<i>Sabal minor</i> (Jacq.) Pers. <i>S. deeringiana</i> Small <i>S. glabra</i> Sarg., non P. Mill. <i>S. louisiana</i> (Darby) Bomhard <i>Corypha minor</i> Jacq.	dwarf palmetto, Sonoran palmetto	Florida and Louisiana, N to North Carolina, W to Oklahoma, Arkansas, & Texas
<i>Sabal palmetto</i> (Walt.) Lodd. ex J.A. & J.H. Schultes <i>S. jamesiana</i> Small <i>Inodes schwarzii</i> O.F. Cook <i>Corypha palmetto</i> Walt.	cabbage palmetto, cabbage palm, palmetto	Florida, Georgia to Louisiana, North Carolina, & South Carolina

Source: Wasson (2001).

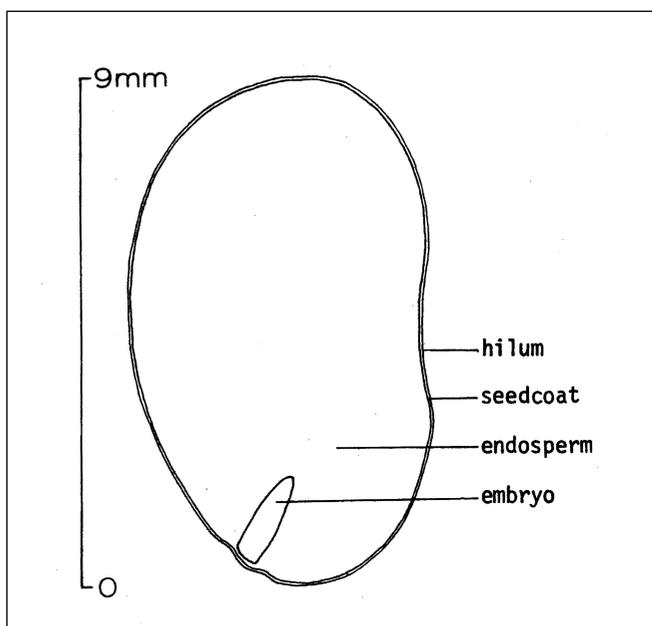
Figure 1—*Sabal*, palmetto: fruits (left) and seeds (right) of *S. etonia*, scrub palmetto (top) and *S. palmetto*, cabbage palmetto (bottom).



seeds separated from the pulp by running them through a macerator or rubbing them on hardware cloth. The purity of seed samples was 100% for seedlots used to determine seed weight (table 2) (Olson and Barnes 1974). Palmetto seeds are orthodox in storage behavior. Cabbage palmetto seeds have been stored successfully at 5 °C for up to 8 weeks (Carpenter 1987). Seeds of Rio Grande palmetto were found to tolerate desiccation, a prerequisite to dry, cold storage (Dickie and others 1993). Seeds of seamberry—*S. parviflora* Becc.—have survived dehydration to 12% moisture content and submersion in liquid nitrogen, indicating that this species, and possibly others in the genus, could be stored either under conventional freezer storage or liquid nitrogen (Becwar and others 1983).

Germination tests. The seeds of palmetto require no pretreatment to break dormancy, but 30 days of stratification in moist sand at 4 °C increases the speed of germination. For example, the average germinative capacity of 4 samples of fresh, unstratified cabbage palmetto seeds was 91% in 120 days (Olson and Barnes 1974). Four samples of stratified seeds had an average germinative capacity nearly as high (89%) in half the time (Olson and Barnes 1974). The tests were carried out at an alternating night–day temperature regime of 20 to 30 °C with 8 hours of daylight. Germination tests were conducted for cabbage palmetto in south Florida on seeds that had the micropyle caps removed and on untreated seeds (Olson and Barnes 1974). The germination percentage was 84 to 95% in 4 days with the micropyle cap removed and only 36% in 100 days for untreated seeds. Carpenter (1987) germinated cabbage palmetto at a constant

Figure 2—*Sabal etonia*, scrub palmetto: longitudinal section through a seed.



soil temperature of 30 °C in a greenhouse and found that 7 days of water soaking at 35 °C boosted germination significantly, from 65 to 85%. Speed of germination was also improved by this water soaking. Unstratified seeds of scrub palmetto averaged 72% germination in 82 days at a constant temperature of 22 °C, and only 64% in the same period with alternating 20/30 °C for 16 and 8 hours, respectively (Olson and Barnes 1974). Carpenter (1988) found, in a series of constant-temperature studies of scrub palmetto, that 30 °C was optimal for both germination percentage and speed of germination. This optimal temperature is substantially higher than that reported by Olson and Barnes (1974). The benefit in speed of germination from prechilling seeds reported by the latter authors might be explained by the fact that they reported on germination at about 7 degrees below the optimum. Slow germination has been reported for Puerto Rico, Rio Grande, and dwarf palmettos. Germination of untreated seeds of the first 2 species took from 6 to 18 weeks for completion, whereas dwarf palmetto needed 7 to 24 months of moist prechill before germination at 25 °C (Ellis and others 1985).

Nursery practice. Seeds should be planted 13 to 25 mm ($1/2$ to 1 in) deep in light textured soil, soon after collection (Jordann 1949). The seeds should not be permitted to dry.

Table 2—*Sabal*, palmetto: seed data

Species	Cleaned seeds/weight				Samples	Moisture content (%)
	Range		Average			
	/kg	/lb	/kg	/lb		
<i>S. etonia</i>	—	—	1,280	581	8	9.8
<i>S. palmetto</i>	758–763	1,668–1,682	1,675	7,600	2	19.3

Sources: Olson and Barnes (1974).

References

- Bailey LH. 1939. The standard cyclopedia of horticulture. New York: Macmillan. 3639 p.
- Becwar MR, Stanwood PC, Leonhardt KW. 1983. Dehydration effects on freezing characteristics and survival in liquid nitrogen of desiccation-tolerant and desiccation-sensitive seeds. *Journal of the American Society of Horticultural Science* 108(4): 613–618.
- Carpenter WJ. 1987. Temperature and imbibition effects on seed germination of *Sabal palmetto* and *Serenoa repens*. *HortScience* 22(4): 660.
- Carpenter WJ. 1988. Temperature affects seed germination of four Florida palm species. *HortScience* 23(2): 336–337.
- Dickie JB, Balick MJ, Linington IM. 1993. Studies on the practicality of ex situ preservation of palm seeds. *Princeps* 37(2): 94–98 [Seed Abstracts 1996; 9(4): 1304].
- Ellis RH, Hong TD, Roberts EH. 1985. Handbook of seed technology for genebanks. Volume 2, Compendium of specific germination information and test recommendations. Rome: International Board for Plant Genetic Resources. 667 p.
- Jordann AC. 1949. Observations on the propagation of palms. *Florida State Horticulture Society Proceedings* 62: 240–242.
- Knuth P. 1906–09. Handbook of flower pollination. Oxford: Clarendon Press.
- McCurrah JC. 1960. Palms of the world. New York: Harper Bros.
- Olson DF, Barnes RL. 1974. *Sabal*, palmetto. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 744–745.
- Sargent CS. 1965. Manual of trees of North America (exclusive of Mexico). 2nd ed., corrected and reprinted. New York: Dover: 934 p.
- Small JK. 1933. Manual of southeastern flora. New York: J.K. Small.
- Snyder E. 1952. Florida trees. 2nd ed. Sanibel, FL: E. Snyder.
- Wasson E, ed. 2001. Trees and shrubs: illustrated A–Z of over 8000 plants. Willoughby, NSW, Australia: Global Book Publishing: 692.
- West E, Arnold LE. 1947. The native trees of Florida. Gainesville: University of Florida Press. 212 p.

Salicaceae—Willow family

Salix L.
willow

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Growth habit, occurrence and use. The willow genus—*Salix*—includes 350 to 400 species (Argus 1996). The majority are in the Northern Hemisphere, from arctic through temperate latitudes (table 1). Three species are native south of Mexico (Dorn 1976) and 67 found in the contiguous 48 United States, where tree and shrub forms predominate. The 39 species found in Alaska are mostly tall to medium shrubs; prostrate growth forms are mostly on the tundra. Shrub and prostrate shrub forms constitute a dominant portion of the vegetation of the Circumpolar Arctic (defined as north of the treeline) and include about 29 species in the North American Arctic (Argus 1996). These tundra species are segregated into a variety of habitats (Argus 1973; Viereck and Little 1972). General information on the genus worldwide can be found in Warren-Wren (1972) and Newsholme (1992); the taxonomy and distribution of American species is covered by Argus (1973, 1986, 1995), Dorn (1976), MacKinnon and others (1992), and Viereck and Little (1972). General reviews of ecological characteristics and effects of fire on more than 20 species are available in the Fire Effects Information System Database (Fisher 1992). Seed characteristics of poplar (*Populus*, the other North American genus in the Salicaceae) are very similar to those of willows, and information for poplar is applicable to willow (Schreiner 1974; Zasada and Wyckoff 2002). The uniformity in seed characteristics, particularly germination, in the Salicaceae is remarkable considering that the family comprises several hundred species.

The importance of willows as a component of regional vegetation varies geographically and with the mix of habitat types within the region (Fisher 1992). In particular, willows become more important with increasing latitude in North America. In the boreal forests of northern Canada and Alaska, willows are the most common tall and intermediate shrubs; they fill niches occupied by hazel (*Corylus* spp.), maple (*Acer* spp.), and cherry and plum (*Prunus* spp.) in more southern parts of the boreal forest. In the tundra,

willows are often the only woody species present; in riparian areas, they are, along with alder (*Alnus* spp.), the largest plants in these important tundra habitats.

Willows have a variety of growth forms (Brinkman 1974; Newsholme 1992; Viereck and Little 1972; Warren-Wren 1972). The tallest attain heights of 30 m, whereas prostrate tundra willows attain heights of a few centimeters to little more than 30 cm. Crown spread and shape is variable; the weeping willow is a popular ornamental tree. "Diamond" willow wood (of various species), named for the diamond-shaped stem lesions that expose the heartwood, is sought after in some areas for making furniture, walking canes, and lamp bases, and for ornamental woodwork.

In natural regeneration, the relative importance of seed versus vegetative propagation varies between species and between locations for a given species (for example, feltleaf willow) (Bliss and Cantlon 1957; Moore 1982; Walker and others 1986). Under appropriate moisture conditions, seeds germinate and seedlings establish in riparian and upland habitats (Densmore and Zasada 1983; Krasny and others 1988; McBride and Strahan 1984; McLeod and McPherson 1972; Walker and others 1986; Zasada and others 1983). Mineral soil is the most suitable substrate because of its water-holding characteristics, but other substrates are adequate if water is available. After seedling establishment, some species (coyote willow and related species) develop clones by suckering from root systems and others by downward bending and layering of stems and branches; however, most species capture space by crown expansion from a multiple-stemmed clump (Douglas 1989; Krasny and others 1988; Ottenbreit and Staniforth 1992). Some species are important colonizers in early stages of primary succession on floodplains, whereas others colonize in later stages of floodplain succession (Argus 1973; Viereck 1970; Viereck and Little 1972; Walker and others 1986).

The majority of species reproduce vegetatively. The most common form of vegetative regrowth is sprouting from

Table 1—*Salix*, willow: nomenclature and occurrence

Scientific name & synonym(s)	Common name	Occurrence
<i>S. alaxensis</i> (Anderss.) Coville	feltleaf willow	Throughout Alaska, Yukon Territory, & N British Columbia; scattered E across Canadian Arctic & S in Rocky Mtns. to Jasper National Park
<i>S. amygdaloides</i> Anderss.	peachleaf willow	S Quebec, W to SE British Columbia, S to E Washington, Nevada, & Arizona, E to Kentucky & Pennsylvania
<i>S. arctica</i> Pallas	arctic willow	Alaska E to Quebec, S to California, N Europe, & Asia
<i>S. babylonica</i> L.	weeping willow	China; naturalized from s Quebec, S Ontario, & S Vermont SW to Missouri, Georgia, & South Carolina
<i>S. bebbiana</i> Sarg.	Bebb willow	Newfoundland, W to Hudson Bay & Alaska, S to New Mexico, N to Montana & E to Iowa, Maryland, & New England
<i>S. boothii</i> Dorn.	Booth willow	British Columbia to Alberta, S through Washington & Montana to New Mexico, Arizona, & California
<i>S. caroliniana</i> Michx.	coastal plain willow	Maryland to E Kansas, S to E Texas & E to S Florida; also in Cuba
<i>S. discolor</i> Muhl.	pussy willow	Labrador W to central British Columbia, S to Idaho, E to Delaware & in mtns. S to E Tennessee
<i>S. eriocephala</i> Michx.	cordate willow	S Newfoundland to E Saskatchewan & Montana, S to Kansas, E to Virginia
<i>S. cordata</i> Muhl.; <i>S. rigida</i> Muhl.		
<i>S. exigua</i> Nutt.	coyote willow	Montana, Alberta to British Columbia & Washington, S to S California, E to W Texas & W South Dakota
<i>S. geyerana</i> Anderss.	Geyer willow	Montana W to British Columbia, S to California & Arizona; also Colorado & Wyoming
<i>S. glauca</i> L.	white willow	Alaska, S to British Columbia & in Rocky Mtns to New Mexico & W Texas; also N Mexico
<i>S. interior</i> Rowlee	sandbar willow	E Quebec, W to central interior Alaska, S to E Colorado & New Mexico, E to Louisiana, Tennessee, & Maryland; also N Mexico
<i>S. lasiolepis</i> Benth.	arroyo willow	Idaho & Washington, S to S California, SE Arizona & W Texas; also N Mexico
<i>S. lucida</i> Muhl. [incl. <i>S. lasiandra</i> Benth.]	Pacific willow	Saskatchewan to interior Alaska, S to S California; scattered E to New Mexico & N to Wyoming & Idaho
<i>S. lutea</i> Nutt.	yellow willow	Manitoba & Saskatchewan, w to Yukon & British Columbia, S to E Washington & E Oregon & to S California, Arizona, & New Mexico; also E Nebraska & North Dakota
<i>S. nigra</i> Marsh.	black willow	Maine to E Minnesota, S to E Kansas & S Texas, E to N Florida; also in N Mexico, Arizona, & California
<i>S. petiolaris</i> Sm.	meadow willow	New Brunswick W to Alberta; scattered S to Colorado & E to New Jersey
<i>S. planifolia</i> Pursh.	diamondleaf willow	Throughout Alaska & Yukon Territory, N British Columbia
<i>S. repens</i> L.	creeping willow	Wet areas in Europe & Asia
<i>S. scouleriana</i> Barratt ex Hook.	Scouler willow	E Manitoba to S Alaska, S to S California; scattered E to New Mexico & N to Montana

Sources: Argus (1973, 1975), Brinkman (1974), Cooper and Van Havern (1994), Hillier and sons (1989), Little (1979), MacKinnon and others (1992), Newsholme (1972, 1992), Viereck (1987), Viereck and Little (1972), Vogel (1990).

buds located at the base of the stem. Other types of vegetative regeneration found in a limited number of species include sprouting from roots, layering of stems, and rooting of broken stem and branch segments. In riparian areas, whole plants are sometimes dispersed by water after being washed out by erosion. Artificial regeneration can be achieved by seeding or by planting seedlings and stem cuttings. Willows regenerate quickly after natural disturbances such as flooding (Krasny and others 1988; Shafroth and others 1994; Viereck 1970) and fire (Lyon and Stickney 1976; Viereck and Dyrness 1979; Zasada and others 1983; Zedler and Sheid 1988). They also regenerate on sites dis-

turbed by humans, including mine tailings (Chose and Shetron 1976; Holmes 1982); thermally polluted lands (McLeod and Sherrod 1981); and construction sites (Bishop and Chapin 1989). Willows are used to artificially revegetate areas of natural and human disturbance such as those indicated above and for dune stabilization (Fisher 1992; Westoby 1975).

Hybridization occurs in willows but the extent to which it is present is not well established (Argus 1973, 1974; Mosseler and Zsuffa 1989). Hybridization experiments by Argus (1974), Mosseler and Zsuffa (1989), and Mosseler (1987, 1990) conducted with North American willows have

confirmed that hybridization occurs among some native species. Barriers to natural hybridization include phenological differences in flowering times, differences in pollen morphology, and other pre- and post-pollination limitations (Kim and others 1990; Mosseler 1987, 1990; Mosseler and Papadopol 1989).

Uses of willows include wood and fiber production, watershed and soil stabilization, habitat and food for wildlife, environmental restoration, landscaping, basketry and furniture making (MacKinnon and others 1992; Newsholme 1992; Viereck and Little 1972; Warren-Wren 1972). Because of the ease of rooting of stem cuttings, rapid early growth and biomass production, and prolific coppicing following cutting, willows are used in short-rotation forestry (Mitchell and others 1992; Sennerby-Forse 1986; Siren and others 1987; Zsuffa and others 1993). Willows were used by Native Americans and Eskimos for medicinal purposes and construction materials (Fisher 1992; MacKinnon and others 1992; Meeker and others 1993; Viereck 1987; Vogel 1990).

Flowering and fruiting. Willows are dioecious (figure 1). The sex ratio in natural populations is often female-biased, with ratios as high as 4:1 (Alliende and Harper 1989; Begin and Payette 1991; Crawford and Balfour 1983, 1990; Fox 1992; Kaul and Kaul 1984; Kay and Chadde 1992; Moore 1982). Because of irregular flowering, at least several years may be required to accurately assess the sex of individual shrubs and determine sex ratios in natural populations; this is particularly true on less productive sites. There

Figure 1—*Salix bebbiana*, Bebb willow: male (**right**) and female (**left**) catkins, which consist of a varying number of flowers depending on sex of the flower and species. The mature female flower produces a capsule (**see figure 3**) containing variable numbers of seeds depending on species, pollination success, and post-pollination predation.



is no definitive biochemical test or molecular genetics technique available for distinguishing male and female plants.

Mosseler (1987) and Mosseler and Zsuffa (1989) found highly skewed sex ratios resulting from controlled inter- and intraspecific crosses. Sex ratios in naturalized exotic species—for example, *S. × rubens* Schronk (pro spp.) and *S. alba* spp. *vitellina* (L.) Arcang. in riparian areas in Colorado—are often highly skewed toward one sex because of vegetative reproduction (Shafroth and others 1994).

There have been reports of differences in vegetative characteristics and growth rate between male and female plants, but these differences are not well-established (Alliende and Harper 1989; Crawford and Balfour 1983, 1990). Male plants usually produce more flowers per unit of crown area than female plants (Kay and Chadde 1992; Zasada 2000).

Although the dioecious trait is universal across the genus, hermaphrodite plants (individuals with separate male and female flowers) and catkins (male and female flowers on the same catkin) have been observed in a number of species (Alliende and Harper 1989; Crawford and Balfour 1983; Mosseler and Zsuffa 1989). Mosseler and Zsuffa (1989) observed hermaphroditic plants in both natural populations and in controlled inter- and intraspecific crosses. Plants that are hermaphroditic initially sometimes become completely male as they mature sexually (Mosseler and Zsuffa 1989).

Seed-bearing age in willows depends on species and site conditions. Following disturbances such as fire and logging, willows of vegetative origin (for example, stump sprouts developing from the basal bud bank) flower sooner than plants of seed origin. Sprouts often produce seeds 1 to 2 years after a fire that kills the mature plant, whereas seedlings of the same species require 5 to 10 years before the first seeds are produced. In controlled environments, Mosseler and Zsuffa (1989) reported that coyote willow plants flowered several months after germination in a controlled environment and Mosseler (1996) found that 6 of 7 native willows flowered within 2 years of germination. Zasada (2000) has also observed flowering in 1-year-old creeping willow seedlings.

Catkins bearing several to many staminate or carpellate flowers (figure 1) appear before or after leaf appearance, depending on the species (Mosseler 1987; Viereck and Little 1972). Each carpellate flower contains 2 carpels. The number of ovules per carpel may vary considerable within and among species. Argus (1996) observed the following variation in ovules per carpel: feltleaf willow, 6 to 9; peachleaf willow, 8 to 11; arctic willow, 6 to 7; Bebb willow, 3 to 8;

Booth willow, 6 to 9; pussy willow, 3 to 9; coyote willow, 6 to 15; Geyer willow, 3 to 6; Pacific willow, 16 to 20; yellow willow, 3 to 9; meadow willow, 3. Hand-pollination can significantly affect seed production (it increases the number of flowers producing seeds and the number of fertilized ovules per flower), suggesting that insufficient pollination is common in natural populations (Fox 1992). Species vary in their dependence on insect- or wind-pollination, though the former predominates across the genus (for example, Argus 1974; Mosquin 1971; Vroege and Stelleman 1990). The female catkin, when adequately pollinated, produces several to many capsules (fruits) with multiple seeds (figures 2 and 3 and table 2). Moore (1982) observed that 24, 38, 67, and 62% of the capsules (flowers) matured and produced viable seeds in feltleaf willow. Zasada (2000) found that between 80 to 90% of the capsules in creeping willow produced seeds. Jones (1995) found that between 28 to 88% of capsules on arctic willow catkins produced seeds.

Primary dispersal of willow seeds is by wind. The hairs or “cotton”—which give the seeds great buoyancy—develop on the seedcoat as opposed to being a modification of the seedcoat, as is the case with the wings and other structures that facilitate dispersal in other species (Bewley and Black 1994). The seed separates easily from the hairs. Although willows have the potential to travel great distances (many kilometers), depending on wind and weather conditions, large quantities are deposited under the plant (Zasada 2000). Seeds can also be carried long distances over water, either by the wind or by the water itself. Measuring seed-rain for willows is not as easy as in other species because of the nature of the dispersal unit and the short life of the seeds. Various sized containers filled with water or a soil mix in which germination occurs have been used successfully (Walker and others 1986; Zasada and Densmore 1979) and

sticky traps are also effective in catching and hold seeds. Water and wet soil appear to be particularly good media for catching and holding the dispersal unit.

Flowering and fruiting can be reduced significantly by biotic and abiotic factors. Zasada (2000) observed mortality due to frost of 0 to 38% for female flowers and 0 to 68% for males. Herbivores—for example, moose (*Alces alces*) and elk (*Cervus elphus*)—can reduce flower production by browsing twigs, and birds such as ptarmigan (*Lagopus leucurus*) specifically eat flower buds. Kay and Chadde (1992) found essentially no catkins outside of exclosures protected from elk browsing, whereas inside exclosures there were an average of 1,445 (137/ft²), 583 (55/ft²), 694 (66/ft²), and 1336 (126/ft²) catkins/m² of canopy for Bebb, Booth, yellow, and Geyer willows, respectively. Insect galls in arroyo willow reduced reproductive bud production by 43% compared to unaffected stems and seed production potential of individual clones by 10 to 50% (Sacchi and others 1988).

Collection of fruits and seeds. There are 2 broad groups of willows relative to seed dispersal patterns—those with seeds that are dispersed in late spring or summer and those with seeds that are dispersed in the fall, mainly after leaves have been shed (Chmelar and Meusel 1979; Densmore and Zasada 1983; Junttila 1976; Lautenschlager 1984; Poptsov and Buc 1957; Toepfer 1915; Viereck and Little 1972; Zasada and Densmore 1980; Zasada and

Figure 3—*Salix*, willow: capsule at various stages of opening (a–e) and the dispersal unit at different stages; **f** = hairs in capsule; **g** = hairs fully deployed and separated from the seed. When seeds land on water, hairs may remain attached to the seed, giving it buoyancy; based on Lautenschlager (1984) and Lautenschlager and Lautenschlager (1994).

Figure 2—*Salix glauca*, white willow: catkin just beginning to open.

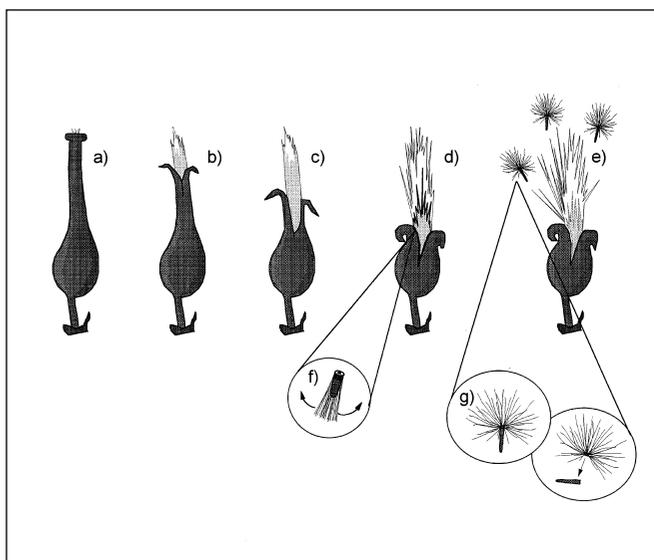


Table 2—*Salix*, willow: seed quantity in catkins

Species	Location	Capsules in catkin with seeds	Seeds/capsule	Seeds/catkin
<i>S. alaxensis</i>	Alaskan Arctic Slope			
	Site 1	45 (35–61)	8 (7–8)	333 (245–427)
	Site 2	71 (61–80)	9 (8–10)	673 (488–800)
	Site 3	119 (92–137)	10 (8–11)	1,174 (736–1,280)
	Site 4	98 (82–109)	7 (6–8)	600 (492–763)
<i>S. amygdaloides</i>	Ontario, Canada	—	16 (14–18)	—
<i>S. arctica</i>	Canadian high Arctic—Ellesmere Island			
	Dry site (year 1)	24 (8–40)	18 (10–25)	432
	Dry site (year 2)	65 (60–70)	9 (8–10)	595
	Wet site (year 1)	7 (2–12)	12 (5–18)	84
<i>S. bebbiana</i>	Yellowstone National Park	37 (24–48)	6 (5–7)	218 (144–311)
<i>S. boothii</i>	Yellowstone National Park	64 (43–79)	6	400 (286–427)
<i>S. discolor</i>	Ontario, Canada	—	10 (8–12)	—
<i>S. exigua</i>	Ontario, Canada	—	25 (15–36)	—
<i>S. geeyeriana</i>	Yellowstone National Park	18 (12–29)	5 (4–6)	81 (42–171)
<i>S. lucida</i>	Ontario, Canada	—	17 (12–20)	—
<i>S. lutea</i>	Yellowstone National Park	74 (69–78)	11 (11–12)	841 (754–925)
<i>S. petiolaris</i>	Ontario, Canada	—	3 (2–5)	—
<i>S. repens</i>	Newborough, Warren, North Wales	4 (3–4)	22 (19–25)	82 (50–110)

Sources: Jones (1995), Kay and Chadde (1992), Moore (1982), Mosseler (1987), Zasada (2000).
Note: Values are means with ranges in parentheses.

Viereck 1975). Fall-dispersers comprise about 11% and about 20% of the species in North America and Alaska, respectively. Fall-dispersers are most common in the tundra regions of Alaska and Canada, but some species occur in the boreal forest (Argus 1973; Densmore and Zasada 1983; MacKinnon and others 1992; Viereck and Little 1972).

The seeds of the summer-dispersers live up to about 8 weeks; the rate at which seeds lose viability differs among species and is related to ambient temperature and relative humidity. No seeds in this group have been observed to overwinter and germinate the year after dispersal (Densmore 1979; Densmore and Zasada 1983; Ebersole 1989; Martens and Young 1992; Moss 1938). The rapid loss of viability is a critical consideration when collecting and handling fruits and seeds.

Catkins should be collected as close to the time of seed dispersal as possible. Timing of collection can be based on catkin color and condition of the capsule. Catkin color changes from green to yellow or yellow-brown at maturity. It is best to wait until the capsules begin to open (figure 3), as collection at this stage usually results in the most rapid opening of capsules and the most efficient seed extraction. One note of caution: insect-damaged capsules may appear to be dispersing seeds but are often still green and capsules are not opening normally (figure 3). There can be variation of a month or more in timing of dispersal for a species with

a wide altitudinal or elevational range (table 3). Once capsules are ripe and begin to open, the rate of seed dispersal is determined by weather conditions: under warm, dry, windy conditions all seeds may be dispersed within a few days. Under wetter, cooler conditions, dispersal may be spread out over a month. If a small amount of seeds is all that is required, stems with immature catkins can be collected and placed in a greenhouse in water; seeds can then be collected when the capsules open (Marten and Young 1992).

After catkins have been removed from the plant they should be placed in a paper bag that allows the catkin-drying process to continue during transport. Catkins should not be packed tightly because air circulation may be restricted. Bags containing catkins must be kept out of direct sunlight.

To obtain seeds from a specific inter- or intraspecific cross, dormant stem cuttings (50 cm or less in length) with reproductive buds should be obtained from female and male plants in late winter (Mosseler 1987). These cuttings should then be placed in a greenhouse or growth chamber, where they will flower within 2 weeks. Male clones are often forced to flower before females and the pollen stored until the females are ready for pollination. This avoids pollination from unwanted sources. Willow pollen may be frozen for 1 to 2 months without losing its viability. There is a period of 3 to 6 days, depending on species, during which flowers can be pollinated (Mosseler 1987). Catkins will produce viable

Table 3—*Salix*, willow: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal
<i>S. alaxensis</i>	Alaska—Brooks Range	May–June	June–July	July–Aug
	Alaska—Tanana River	Apr–May	May	May–June
	Alaska—central Interior*	May–June	June–July	July–Aug
<i>S. amygdaloides</i>	NE Minnesota	May–June	—	—
<i>S. arctica</i>	Canadian high Arctic— Ellesmere Island	July	Aug–Sept	—
	Interior Alaska	June–July	July–Aug	Aug–Sept
<i>S. bebbiana</i>	—	Apr–June	May–June	May–June
<i>S. caroliniana</i>	North & South Carolina	Mar–April	Mar–Apr	—
<i>S. discolor</i>	N Ontario & British Columbia	May	—	—
	Rocky Mtns, USA	Mar–April	Apr–May	Apr–May
<i>S. eriocephala</i> (as <i>S. rigida</i>)	NE Minnesota & N Ontario	Apr–June	June	June–July
<i>S. exigua</i>	—	May–July	June–July	June–July
<i>S. fragilis</i>	US & Europe	Apr–May	May–June	May–June
<i>S. glauca</i>	Alaska—Brooks Range	June–July	July–Aug	Sept–Nov
	Alaska—mid-boreal forest	May–June	July–Aug	Sept–Nov
	Alaska—Denali National Park	June–July	July–Aug	Sept–Nov
<i>S. interior</i>	N Ontario	—	Aug 13	—
<i>S. lucida</i> †	Idaho	Apr–May	June–Aug	June–Aug
<i>S. nigra</i>	In north	Feb–April	Apr–May	Apr–May
	In south	May–June	June–July	June–July
<i>S. petiolaris</i>	General	May–June	June–July	June–July
<i>S. scouleriana</i>	General	Apr–June	May–July	May–July

Sources: Brinkman (1974), Densmore and Zasada (1983), Jones (1995), Viereck and Little (1972).

* High elevation. † As *S. lasiandra*.

seeds within 3 to 5 weeks using these procedures. It may be necessary to remove some catkins from the branch in order to assure that enough water and other resources are available for complete development of some catkins. Stems can be kept in aerated or unaerated water; water should be changed 2 to 3 times per week. At each change of water, 1 to 2 cm of stem should be trimmed from the base to expose fresh xylem to assure efficient water uptake. Stems of some species will root readily under these conditions (Densmore and Zasada 1978; Haissig 1970; Mosseler 1987). Mosseler (1987) reported that stem cuttings that rooted were more likely to produce seeds.

The seeds of the fall-dispersers are not as short-lived as summer-dispersers and thus there is more leeway in collecting catkins and handling seeds (Zasada and Densmore 1977). Seeds of fall-dispersers may disperse quickly during warm weather in September, but it is often possible to find seeds in late fall after the first snowfall.

To estimate the number of catkins necessary for a desired quantity of seed, it is important to know the seed yield per catkin (table 2). As in other genera with multiple-seeded fruits, seed yield per catkin varies among species,

among sites for a species, among years, and with condition of the catkin (for example, amount of insect infestation or disease).

Although willows generally produce seeds annually, the variation among years is not well-documented. Moore (1982) found that some female fettleaf willows produced relatively large numbers of catkins (200 to 500) over a 2-year period, whereas others of the same age and stature produced no catkins in either year. Within Moore's 3 study areas, 22 of 66% of the mature shrubs did not produce flowers. Jones (1995) found that annual variation in seed production occurred on both wet and dry sites during 2 years of study and that no seeds were produced on their wet site in one of the years. Walker and others (1986) observed similar levels of willow seed production on riparian sites in Alaska during a 2-year period. In addition to genetic and physiological factors that control flowering and seed production, animal browsing, insects, and disease can significantly affect annual variation in seed availability (Kay and Chadde 1992). Though some level of variation in seed production should be expected among years, it is usually possible to find some individuals of a species with a collectible seedcrop in a given year on most sites.

Extraction and storage of seeds. Simak (1980) stated that the following conditions were key for extraction and storage of Salicaceae seeds: (1) placement in proper conditions as soon as possible (catkins cannot necessarily be stored at ambient air or room temperatures and be expected to have viable seeds); (2) separation of seeds from the cotton using methods that minimize mechanical damage to seeds; (3) pre-drying to about 6 to 10% of dry weight and storage in sealed containers that will maintain a constant humidity; and (4) storage of seeds at subfreezing temperatures to maintain seed viability for time periods of 6 months or more.

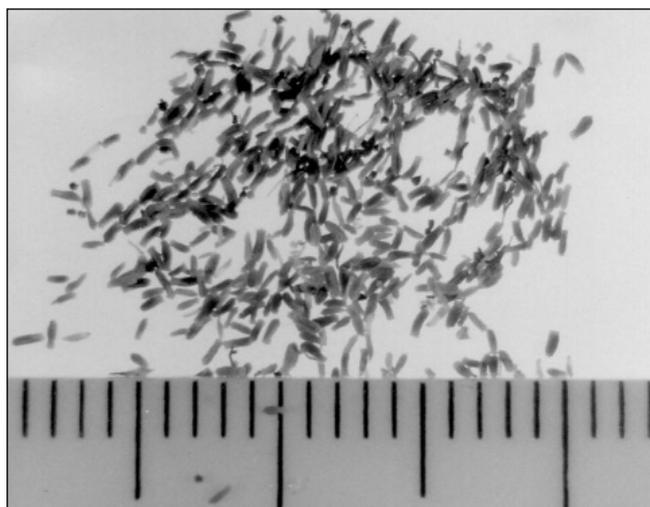
There is some difference of opinion regarding the need to separate seeds from the cotton (figure 4) (Martens and Young 1992; Simak 1980). We agree with Simak (1980) that seeds should be separated because doing so reduces the bulk of the material to be stored. There is some indication that storage with the cotton may reduce viability, particularly in the summer-dispersing species (Simak 1980).

Small- to medium-sized lots of seeds can be cleaned according to the following steps:

- Catkins should be placed in a single layer in screen-covered boxes in a relatively warm, dry area, with temperature at 20 to 24 °C and relative humidity at 25 to 35%. Air should be able to circulate around the catkins to allow rapid drying. If capsules are beginning to open when collected, opening will be completed in 2 to 3 days. Green catkins open more slowly and incompletely and seed recovery is low.
- Then, the catkins and cotton-containing seeds should be placed in a container so that material can be shaken or tumbled in an airstream or tumbled as in a cement mixer (Einspahr and Schlafke 1957; Fung and Hamel 1993). The seeds separate easily from the cotton (figure 4) under these conditions.
- Seeds can be separated from coarser and finer residue by passing the mixture through a screen or sieve.
- Seeds extracted in this way have a moisture content very close to the 6 to 8% recommended by Simak (1980).

Seeds should be stored at temperatures from –5 to –40 °C immediately after cleaning. They can be stored for up to 6 months at 1 to 5 °C but not for longer. Storage in containers with a desiccant such as calcium chloride (CaCl₂) does not appear to prolong seed life (Martens and Young 1992; Simak 1980). However, storage with a desiccant appears to provide long-term benefit for poplar (*Populus* spp.) (Zasada and Wyckoff 2003) and additional work is

Figure 4—*Salix alaxensis*, feltleaf willow: seeds, divisions on scale each = 1 mm.



needed on use of desiccants for storing willow seeds. The longest periods of successful storage reported are 44 months at –20 °C (Simak 1980) and 36 months at –10 °C (Zasada and Densmore 1980). Viability of poplar seeds with characteristics similar to summer-dispersing willows has been maintained for 10 to 12 years when stored at –10 to –20 °C (Wyckoff and Zasada 2003). The small seed size (figure 5 and table 4) makes it easy to store very large quantities of seeds in a limited space.

Germination tests. Willow seeds are very small, usually 1 to 2 mm long and less than 1 mm wide (figures 5 and 6). The seedcoat is transparent and the green cotyledons are readily visible. The seeds appear to contain a functional photosynthetic system, with the following levels (chlorophyll a, 1.45 mg/g, and chlorophyll a:b, about 2.4 mg/g) for dormant seeds of white willow, a fall-disperser (Zasada and Coyne 1975). Green color is an indicator of potential seed viability.

Germination requirements differ for summer and fall dispersers (figure 7) (Densmore and Zasada 1983; Juntilla 1976; Poptsov and Buch 1957; Zasada and Viereck 1975). Under natural conditions, seeds of summer dispersers germinate in 12 to 24 hours after dispersal with adequate moisture (figure 7). Seeds will even germinate underwater (Densmore and Zasada 1983; Moore 1982). Germination may be reduced on substrates with a substantial content of salt (Jackson and others 1990; Krasny and others 1988). All tested species—from climates as different as the Arctic, coastal rain forest, and plains areas of the western United States—appear to exhibit a similar response to temperature and do not exhibit any signs of dormancy (Densmore and Zasada 1983; Juntilla 1975; Krasny and others 1988; Martens and

Table 4—*Salix*, willow: cleaned seed data

Species	Place collected	Cleaned seeds (x 1,000)/weight		Samples
		/kg	/lb	
<i>S. amygdaloides</i>	Minnesota	5,720	2,600	1
<i>S. bebbiana</i>	Idaho (770 m)	5,500	2,500	2
<i>S. caroliniana</i>	South Carolina	18,260	8,300	1
<i>S. exigua</i>	Washington (615 m)	22,000	10,000	1
<i>S. fragilis</i>	Minnesota	7,040	3,200	1
<i>S. lasiandra</i>	Idaho (770 m)	25,300	11,500	1
<i>S. petiolaris</i>	Minnesota	1,100	500	1
<i>S. scouleriana</i>	Idaho (770 m)	14,300	6,500	1

Source: Brinkman (1974).

Figure 5—*Salix*, willow: seed; there is no endosperm and the seed is attached to the hairs at the radicle end. Viable seeds are green due to the presence of chlorophyll; the shade of green is determined by the species, seed water content, and length of time in storage (Simak 1980).

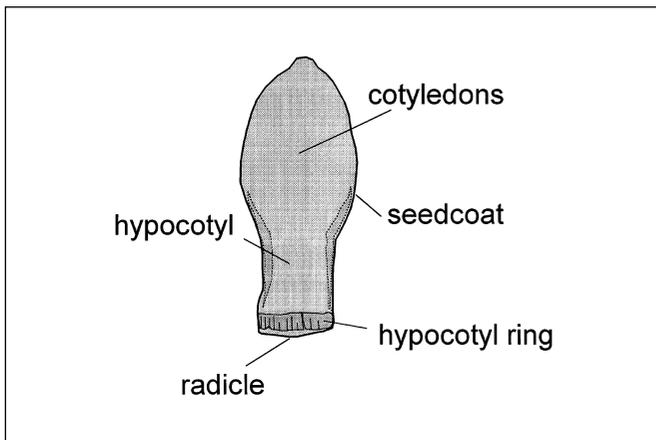
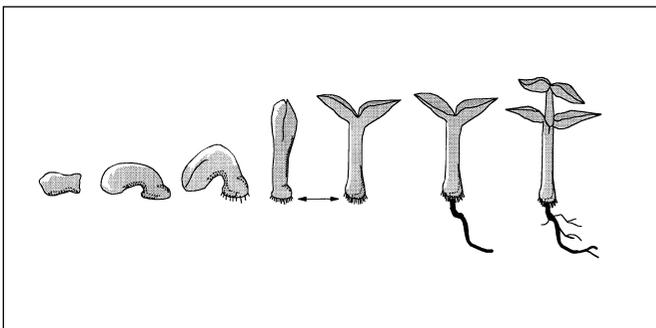


Figure 6—*Salix*, willow: seeds; note development of hypocotyl hairs (arrow) from the hypocotyl ring (see figure 5); adapted from Simak (1980).

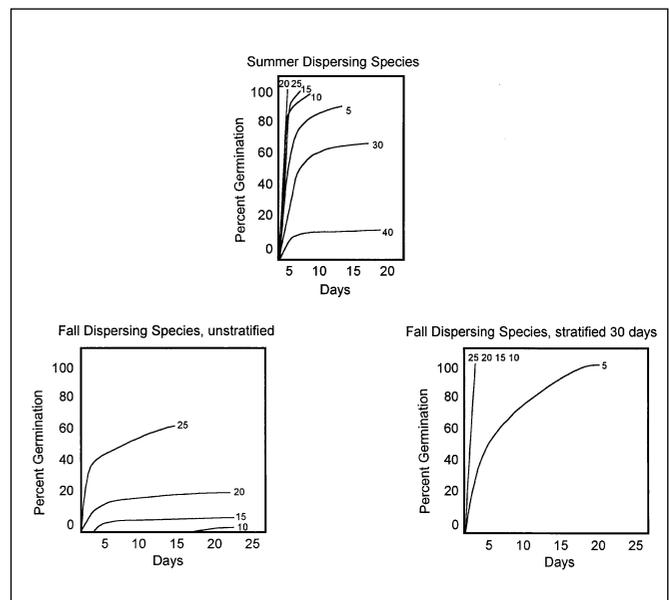


Young 1992; Zasada and Viereck 1975). Germination is complete between 5 to 30 °C but declines rapidly at temperatures above 30 °C. Temperatures of 20 to 25 °C appear to be optimum (figure 7). Germination may be tested on a variety of substrates (Brinkman 1974). Seeds germinate completely in the dark, but rate of germination may be higher in the light (Densmore and Zasada 1983; Zasada and Viereck

1975). Official seed testing recommendations call for a 14-day test on moist blotter paper with alternating temperatures of 20 to 30 °C, and light during the 8 hours at 30 °C; no pretreatments are needed (ISTA 1993).

Fall-dispersers exhibit seed dormancy (figure 7). Under natural conditions, seeds overwinter and germinate quickly following snowmelt (Densmore 1979; Densmore and Zasada 1977). Germination of unstratified seeds occurs between 5 to 30 °C, with the highest germination at the warmest temperatures. Stratification widens the range of temperatures over which seeds germinate and increases the rate of germination (Densmore 1979; Densmore and Zasada 1977; Juntilla 1976; Zasada and Viereck 1975; Zasada and Densmore 1983). After 30 days of stratification, the germination pattern at all temperatures resembles that of summer dispersers (Densmore and Zasada 1983). The length of strat-

Figure 7—*Salix*, willow: generalized patterns of temperature and stratification effects on germination of seeds of summer- and fall-dispersing willows; numbers indicate germination temperatures (°C).



ification required for complete germination increases prior to the onset of dispersal, reaching a maximum as dispersal begins in the fall, and declining in seeds dispersed late in the fall (Densmore 1979; Densmore and Zasada 1983; Zasada and Viereck 1975). The International Seed Testing Association (1993) did not consider fall-dispersed seeds in their testing rules.

Willow germination, though epigeal, does not follow the usual pattern. Hypocotyl hairs attach the seedling to the substrate and the radicle shows delayed development. Simak (1980) has proposed appropriate criteria for evaluating willow germinant quality (figure 7).

Nursery practice. Contrary to earlier beliefs (Brinkman 1974), seeds can be sown after being stored. Although seed viability may decline during 3 to 4 years of storage, vigorous seedlings can be produced with seeds stored for at least this long. Seedlings can be produced as

bareroot stock or in containers and much of the information for poplars applies to willows (Schreiner 1974; Wyckoff and Zasada 2002). Although opened capsules containing seeds and cotton can be broadcast on well-prepared beds, seedling density and distribution can be better controlled if the cotton is removed.

After sowing, seeds can be gently pressed into the soil. Seeds should not be buried, however, as a soil covering of 2 to 4 mm (0.09 to 0.2 in) will significantly reduce seedling emergence (McDonough 1979; Zasada 2000). Seedbeds must be kept moist until the seedlings are well-established; a fine spray of water is preferable. To conserve moisture and maintain a high relative humidity near the bed surface, close shading often is provided with slats and burlap. These covers should be removed as soon after germination as possible, for willows grow best under full light. Seedling growth is relatively rapid, and plantable container seedlings can be produced in 1 growing season.

References

- Alliende MC, Harper JL. 1989. Demographic studies of a dioecious tree: I. Colonization, sex and age structure of a population of *Salix cinerea*. *Journal of Ecology* 77: 1029–1047.
- Argus GW. 1973. The genus *Salix* in Alaska and the Yukon. *Pub. Bot.* 2. Ottawa: National Museum of Natural Sciences.
- Argus GW. 1974. An experimental study of hybridization and pollination in *Salix* (willow). *Canadian Journal of Botany* 52(7): 1613–1619.
- Argus GW. 1986. The genus *Salix* (Salicaceae) in the southeastern United States. *Systematic Botany Monographs* 9: 1–170.
- Argus GW. 1995. Salicaceae, part 2: *Salix*. *Journal of the Arizona–Nevada Academy of Science* 29(1): 39–61.
- Argus GW. 1996. Personal communication. Ottawa: Canadian Museum of Nature.
- Begin Y, Payette S. 1991. Population structure of lakeshore willows and ice-push events in subarctic Quebec, Canada. *Holarctic Ecology* 14: 9–17.
- Bewley JD, Black M. 1994. Seeds: physiology, development, and germination. New York: Plenum Press. 445 p.
- Bishop SC, Chapin FS. 1989. Establishment of *Salix alaxensis* on a gravel pad in arctic Alaska. *Journal of Applied Ecology* 26: 575–583.
- Bliss LC, Cantlon JE. 1957. Succession on river alluvium in northern Alaska. *American Midland Naturalist* 58(2): 454–469.
- Brinkman KA. 1974. *Salix* L., willow. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. *Agric Handbk.* 450. Washington DC: USDA Forest Service: 746–750.
- Chmelar J, Meusel W. 1979. *Die Weiden Europas*. Wittenberg, Germany: A. Ziemsen Verlag. 143 p.
- Chosa JA, Shetron SG. 1976. Use of willow cuttings to revegetate the 'slime' areas of iron mine tailings basins. *Res. Note* 21. Houghton: Michigan Technological University. 6 p.
- Cooper DJ, Van Haveren. 1994. Establishing feltleaf willow from seed to restore Alaskan, U.S.A. floodplains. *Arctic and Alpine Research* 26(1): 42–45.
- Crawford RMM, Balfour J. 1983. Female predominant sex ratios and physiological differentiation in arctic willows. *Journal of Ecology* 71: 149–160.
- Crawford RMM, Balfour J. 1990. Female-biased sex ratios and differential growth in arctic willows. *Flora* 184: 291–302.
- Densmore R. 1979. Aspects of the seed ecology of woody plants of the Alaskan taiga and tundra [PhD thesis]. Durham, NC: Duke University. 285 p.
- Densmore R, Zasada JC. 1978. Rooting potential of Alaska willow cuttings. *Canadian Journal of Forest Research* 8: 477–479.
- Densmore R, Zasada JC. 1983. Seed dispersal and dormancy patterns in northern willows: ecological and evolutionary significance. *Canadian Journal of Botany* 61: 3207–3216.
- Dorn RD. 1976. A synopsis of American *Salix*. *Canadian Journal of Botany* 54: 2769–2789.
- Douglas DA. 1989. Clonal growth of *Salix setchelliana* on glacial river gravel bars in Alaska. *Journal of Ecology* 77: 112–126.
- Ebersole JJ. 1989. Role of the seed bank in providing colonizers on a tundra disturbance in Alaska. *Canadian Journal of Botany* 67: 466–471.
- Einspahr DW, Schlafke D. 1957. A method for aspen and cottonwood seed extraction. *Tree Planters' Notes* 28: 10.
- Fisher WC, comp. 1992. The Fire Effects Information System [database]. Missoula, MT: USDA Forest Service; Intermountain Research Station [includes literature reviews on more than 20 willow species].
- Fox JF. 1992. Pollen limitation of reproductive effort in willows. *Oecologia* 90: 283–287.
- Fung MYP, Hamel BA. 1993. Aspen seed collection and extraction. *Tree Planters' Notes* 44: 98–100.
- Haissig BW. 1970. Preformed adventitious root initiation in brittle willow grown in a controlled environment. *Canadian Journal of Botany* 48: 2309–2312.
- Hillier and Sons. 1989. Hillier's manual of trees and shrubs. 5th ed. Newton Abbot, UK: David and Charles Publishing.
- Holmes KW. 1982. Natural revegetation of gold dredge tailings at Fox, Alaska [MS thesis]. Fairbanks: University of Alaska. 197 p.
- ISTA [International Seed Testing Association]. 1993. International rules for seed testing: rules 1993. *Seed Science and Technology* 21 (Suppl.): 1–259.
- Jackson J, Ball JT, Rose MR. 1990. Assessment of the salinity tolerance of eight sonoran and desert riparian trees and shrubs. *Final Rep. USBR Contr.* 9-CP-30-07170. Reno: University of Nevada, Desert Research Institute.
- Jones MH. 1995. Experimental investigations into effects of climate change on high arctic plants [PhD thesis]. Edmonton: University of Alberta. 121 p.
- Junttila O. 1976. Seed germination and viability in five *Salix* species. *Astarte* 9: 19–24.
- Kaul RB, Kaul MN. 1984. Sex ratios of *Populus deltoides* and *Salix amygdaloides* (Salicaceae) in Nebraska. *Southwestern Naturalist* 29(3): 265–269.
- Kay CE, Chadde S. 1992. Reduction of willow seed production by ungulate browsing in Yellowstone National Park. In: Clary WP, McArthur ED, Bedunah D, Wambolt CL, comps. *Proceedings, Symposium on Ecology and Management of Riparian Shrub Communities*; 1991 May 29–31; Sun Valley, ID. *Gen. Tech. Rep. INT-289*. Ogden, UT: USDA Forest Service Intermountain Research Station: 92–99.

- Kim KH, Zsuffa L, Kenny A, Mosseler A. 1990. Interspecific and intraspecific variation in pollen morphology in four species of *Salix*. *Canadian Journal of Botany* 68: 1497–1501.
- Krasny ME, Vogt KA, Zasada JC. 1988. Establishment of four Salicaceae species on river bars in interior Alaska. *Holarctic Ecology* 11: 210–219.
- Lautenschlager E. 1984. Keimungsbeobachtungen bei einigen Weidenspecies. *Bauhinia* 8(1): 31–35.
- Lautenschlager FI, Lautenschlager E. 1994. Die Weiden von Mittel- und Nordeuropa. Berlin: Birkhäuser Verlag. 171 p.
- Little EL Jr. 1979. Checklist of United States trees (native and naturalized). *Agric. Handbk.* 541. Washington, DC: USDA Forest Service: 255–267.
- Lyon LJ, Stickney PF. 1976. Early vegetal succession following large northern Rocky Mountain wildfires. *Proceedings of the Annual Tall Timbers Fire Ecology Conference* 14: 355–373.
- MacKinnon A, Pojar J, Coupe R. 1992. *Plants of northern British Columbia*. Edmonton, AB: Lone Pine Publishing. 345 p.
- Martens E, Young JA. 1992. Seed germination data for yellow willow at a Nevada riparian site. In: Clary WP, McArthur, Bedunah D, Wambolt CL, comps. *Proceedings, Symposium, Ecology and Management of Riparian Shrub Communities*; 1991 May 29–31; Sun Valley ID. Gen. Tech. Rep. INT-289. Ogden, UT: USDA Forest Service Intermountain Research Station: 142–144.
- McBride JR, Strahan J. 1984. Establishment and survival of woody riparian species on the gravel bars of an intermittent stream. *American Midland Naturalist* 112(2): 102–110.
- McDonough WT. 1979. Quaking aspen: seed germination and early seedling growth. *Res. Pap. INT-234*. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 13 p.
- McLeod KW, McPherson JK. 1972. Factors limiting the distribution of *Salix nigra*. *Bulletin of the Torrey Botanical Club* 100(2): 102–110.
- McLeod KW, Sherrod C Jr. 1981. Bald cypress seedling growth in thermally altered habitats. *Canadian Journal of Botany* 68(7): 918–923.
- Meeker JE, Elias JE, Heim JA. 1993. *Plants used by the Great Lakes Ojibwa*. Odanah, WI: Great Lakes Indian and Wildlife Commission. 440 p.
- Mitchell CP, Ford-Robertson JB, Hinckley T, Sennerby-Forsse L, eds. 1992. *Ecophysiology of short rotation forest crops*. New York: Elsevier. 308 p.
- Moore NJ. 1982. *Pioneer Salix alaxensis communities along the Sagavanirktok River and adjacent drainages [MS thesis]*. Fairbanks: University of Alaska. 189 p.
- Mosquin T. 1971. Competition for pollinators as a stimulus for the evolution of flowering time. *Oikos* 22(3): 398–402.
- Moss EH. 1938. Longevity of seed and establishment of seedlings in species of *Populus*. *Botanical Gazette* 99: 529–542.
- Mosseler AJ. 1987. *Interspecific hybridization and reproductive barriers between some North American willow species [PhD thesis]*. Toronto: University of Toronto. 266 p.
- Mosseler A, Papadopol CS. 1989. Seasonal isolation as a reproductive barrier among sympatric *Salix* species. *Canadian Journal of Botany* 67: 2563–2570.
- Mosseler A, Zsuffa L. 1989. Sex expression and sex ratios in intra- and inter-specific hybrid families of *Salix* L. *Silvae Genetica* 38: 12–17.
- Mosseler A. 1990. Hybrid performance and species crossability relationships in willows (*Salix*). *Canadian Journal of Botany* 68(11): 2329–2338.
- Mosseler A. 1996. Personal communication. Fredericton, NB: Canadian Forest Service.
- Newsholme C. 1992. *Willows, the genus Salix*. London: BT Batsford Ltd. 224 p.
- Ottensbreit KA, Staniforth RJ. 1992. Life cycle and age structure of ramets in an expanding population of *Salix exigua* (sandbar willow). *Canadian Journal of Botany* 70: 1141–1146.
- Poplar Research Institute. 1986. *Poplars and willows in Yugoslavia*. Novi Sad, Yugoslavia: Poplar Research Institute. 295 p.
- Poptsov AV, Buch TG. 1957. Ukazaniya po khraneniyo semyan ivy I topolya [Directions for storing seeds of willow and poplar]. *Byulleten Glavnogo Botanicheskogo Sada Akademii Nauk SSSR* 27: 110–112 [Biological Abstracts 33: 7373].
- Sacchi CF, Price PW, Craig TP, Itami JK. 1988. Impact of shoot gall attack on sexual reproduction in the arroyo willow. *Ecology* 69(6): 2021–2030.
- Schreiner EJ. 1974. *Populus* L., poplar. In: Schopmeyer CS, tech. coord. *Seeds of woody plants in the United States*. *Agric. Handbk.* 450. Washington, DC: USDA Forest Service: 645–655.
- Sennerby-Forsse L, ed. 1986. *Handbook for energy forestry*. Uppsala: Swedish University of Agricultural Sciences, Department of Ecology and Environmental Research.
- Shafroth PB, Scott ML, Friedman JM. 1994. Establishment, sex structure, and breeding system of an exotic riparian willow, *Salix × rubens*. *American Midland Naturalist* 132: 159–172.
- Simak M. 1980. Germination and storage of *Salix caprea* L. and *Populus tremula* L. seeds. In *Proceedings, International Symposium on Forest Tree Seed Storage*; 1980 September 23–27; Chalk River, ON. Ottawa: Canadian Forestry Service: 142–160.
- Siren G, Sennerby-Forsse L, Ledin S. 1987. Energy plantations: short rotation forestry in Sweden. In: Hall DE, Overend RP, eds. *Biomass*. London: John Wiley and Sons: 119–143.
- Toepfer AD. 1915. *Salices Bavariae, Versuch einer Monographie der bayerischen Weiden*. *Berichte der Bayerischen Botanischen Gesellschaft zur Erforschung der Heimischen Flora* 15.
- Viereck LA, Little EL Jr. 1972. *Alaska trees and shrubs*. *Agric. Handbk.* 410. Washington, DC: USDA Forest Service. 265 p.
- Viereck LA. 1970. Forest succession and soil development adjacent to the Chena River in interior Alaska. *Arctic and Alpine Research* 2: 1–26.
- Viereck LA, Dymess CT, eds. 1979. *Ecological effects of the Wickersham Dome fire near Fairbanks, Alaska*. Gen. Tech. Rep. PNW-90. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station.
- Viereck EG. 1987. *Alaska's wilderness medicines: healthful plants of the far north*. Edmonds, WA: Northwest Publishing Company. 107 p.
- Vogel VJ. 1990. *American Indian medicine*. Norman: University of Oklahoma Press. 578 p.
- Vroege PW, Stellemen P. 1990. Insect and wind pollination in *Salix repens* L. and *Salix caprea* L. *Israel Journal of Botany* 39(1/2): 125–132.
- Walker LR, Zasada JC, Chapin FS. 1986. The role of life history processes in primary succession on an Alaskan floodplain. *Ecology* 67(5): 1243–1253.
- Warren-Wren SC. 1972. *Willows*. Newton Abbot, UK: David and Charles Publishers. 179 p.
- Westoby JC. 1975. China uses trees to halt sands. *World Wood* 16(13): 20–22.
- Wyckoff G, Zasada JC. 2005. *Populus* L., poplar. In: Bonner F, tech. coord. *Woody plant seed manual*. *Agric. Handbk.* 727. Washington, DC: USDA Forest Service: 856–871.
- Zasada JC. 2000. Unpublished data. Grand Rapids, MN: USDA Forest Service, North Central Research Station.
- Zasada JC, Pi, Coyne 1975. Unpublished data. Grand Rapids, MN: USDA Forest Service, North Central Research Station.
- Zasada JC, Densmore RA. 1977. Changes in viability during storage for selected Alaskan Salicaceae. *Seed Science and Technology* 5: 509–518.
- Zasada JC, Densmore R. 1979. A trap to measure *Populus* and *Salix* seed-fall. *Canadian Field-Naturalist* 93(1): 77–79.
- Zasada J[C], Densmore R[A]. 1980. Alaskan willow and balsam poplar seed viability after 3 years' storage. *Tree Planters' Notes* 31: 9–10.
- Zasada JC, Viereck LA. 1975. The effect of temperature and stratification on germination in selected members of the Salicaceae in interior Alaska. *Canadian Journal of Forest Research* 5: 333–337.
- Zasada JC, van Veldhuizen RM, Norum RA, Teutsch CE. 1983. Artificial regeneration of trees and tall shrubs in experimentally burned upland black spruce/feathermoss stands in Alaska. *Canadian Journal of Forest Research* 13(5): 903–913.
- Zedler PH, Scheid GA. 1988. Invasion of *Carpobrotus edulis* and *Salix lasiolepis* after fire in a coastal chaparral site in Santa Barbara county. *Madrono* 35(3): 196–201.
- Zsuffa L, Sennerby-Forsse L, Weisgerber H, Hall RB. 1993. Five strategies for clonal forestry with poplars, aspens, and willows. In: Ahuja MR, Libby WJ, eds. *Clonal forestry*. Volume 2, Conservation and Application. Berlin: Springer-Verlag.

Lamiaceae—Mint family

Salvia L.

sage

Susan E. Meyer

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Growth habit, occurrence, and use. The sage genus—*Salvia* contains about 700 species of annual and perennial herbs and shrubs and is worldwide in distribution. There are perhaps 20 woody species in the United States, principally in the Southwest and California (table 1) (Correll and Johnson 1970; Munz and Keck 1959). They are intricately branched, rounded or sprawling shrubs or subshrubs with often leathery, opposite, leaves. The foliage is usually strongly aromatic. Members of the sage genus are used medicinally and as culinary herbs; many of the native species have been locally adopted for these uses. Native sages are often fast-growing and freely reseed themselves onto disturbed lands (Keeley and Keeley 1984). They could be useful in the stabilization of disturbed land. Several California species are dominant components of coastal sage scrub communities and are also significant in chaparral. They also head the list of wild California bee plants for honey production (Jepson 1951). In addition, sages are showy in flower and have interesting foliage, giving them great potential as ornamentals for low-water-use landscaping (ANPS 1990). Most are native to warm winter areas, but Dorr sage occurs throughout the Great Basin and is quite cold hardy.

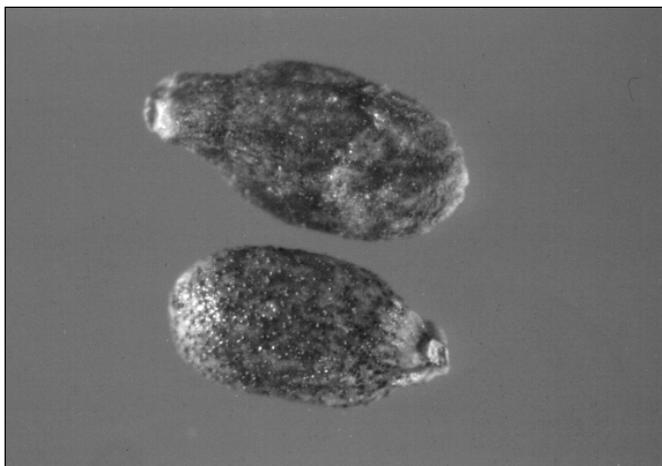
Flowering and fruiting. Sages tend to flower after the principal rainy season. Thus, California and Mojave Desert species are spring-flowering, whereas Sonoran and Chihuahuan Desert species are usually late-summer-flowering. The flowers are often large and showy, borne in interrupted spikes or terminal heads, and attractive to many native bees and other pollinators. The corollas are strongly 2-lipped and range from white through red, blue, or violet in color, depending on the species. The superior ovary is deeply 4-lobed, and after fertilization it develops into 4 easily separable nutlets that ripen within the papery calyx cup. Fruits toward the base of each inflorescence ripen first, perhaps 2 to 3 weeks earlier than those at the upper end (Nord and Gunter 1974). The nutlets usually ripen about 6 weeks after full flower. Each nutlet contains a single seed (figures 1 and 2). The ripened nutlets are shaken from the plant by wind or raindrops. Once on the ground they may be eaten by ants, rodents, or birds. They have no special mode of dispersal.

Seed collection, cleaning, and storage. The procedures of Nord and Gunter (1974) for the harvest, cleaning, and storage of Sonoma sage could probably be applied to most shrubby species. The seeds are harvested by clipping, hand-stripping, or beating into containers as soon as nutlets

Table 1—*Salvia*, sage: nomenclature, habit, habitat, and geographic distribution

Scientific name	Common name(s)	Habit	Habitat	Distribution
<i>S. apiana</i> Jepson	white sage	Subshrub	Coastal sage scrub, chaparral, ponderosa pine forest, warm desert shrub margins	Coastal & cis-montane S California S to Baja California
<i>S. dorrii</i> (Kellogg) Abrams	Dorr sage, purple sage	Shrub	Warm & cold desert shrub communities, piñon-juniper woodland	W Washington to SE California, Arizona, Utah, & Idaho
<i>S. mellifera</i> Greene	black sage	Subshrub	Coastal sage scrub, chaparral, warm desert shrub margins	Coastal & cis-montane central California S to Baja California
<i>S. sonomensis</i> Green	creeping sage	Mat-forming suffrutescent	Chaparral, oak woodland, ponderosa pine forest	Coastal & cis-montane California, mostly in N

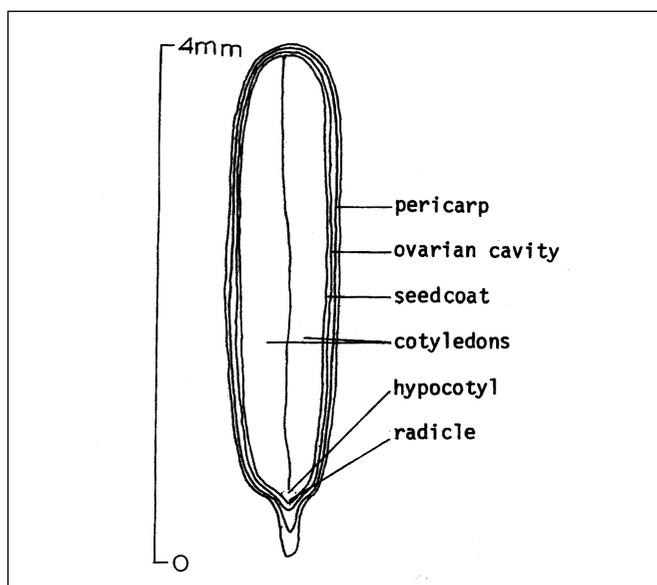
Source: Munz and Keck (1959).

Figure 1—*Salvia sonomensis*, creeping sage: nutlets.

can be dislodged from the lower parts of the inflorescences. These early seeds are apparently larger and of better quality than those produced later in the season. If harvesting is delayed, most of the crop could be “stormed-off” and lost. The harvested material should be thoroughly dried and passed through a hammermill or barley debearder. Small lots may be handrubbed. The seeds may then be cleaned-out by screening or with a fanning mill. For creeping sage, a #1 (1-mm) screen retained a high proportion of filled nutlets while allowing most unfilled nutlets to pass through. The optimal screen size for this purpose will depend on species and possibly on the seedlot (table 2). Fill percentage can be increased by blowing or screening out smaller nutlets, so that this value is somewhat an artifact of the cleaning procedure. The importance of high fill depends on the intended use of the seedlot. The reported weights for individual nutlets of different species vary from 0.8 to 2.4 mg, and number of seeds per weight varies from 416,750 to 1,250,230/kg (189,000 to 567,000/lb) (table 2).

Sage species may form persistent seedbanks in the field (Keeley and Keeley 1984; Malanson and O'Leary 1982), so it is likely that they remain viable for considerable periods in dry storage (orthodox behavior). Kay and others (1988) reported that seeds of Doff and white sages showed little loss of viability during 5 to 7 years of sealed warehouse or 4 °C storage, whereas in unsealed warehouse storage (where moisture levels were allowed to fluctuate) some loss of viability was observed. Nord and Gunter (1974) reported no loss of viability for seeds of creeping sage stored at 4 °C for over 2 years.

Germination and seed testing. Seeds of shrubby sage species are generally relatively easy to germinate (table 3). Seed collections of cis-montane California and desert

Figure 2—*Salvia sonomensis*, creeping sage: longitudinal section through a seed.

species generally contain a readily germinable fraction (Kay and others 1988; Keeley 1986, 1987)), whereas seeds of other species, such as creeping sage, may have a chilling requirement (Nord and Gunter 1974). A desert population of black sage showed increased germination in the light in response to heat-shock treatments (1 or 5 hours at 70 °C or 5 minutes at 115 °C) that may have simulated summer soil heating (Keeley 1986). Seeds of desert populations of the related annual species chia—*S. columbariae* Benth.—are known to have an after-ripening requirement that is met more quickly at high temperatures (Capon and others 1978). White sage is also reported to respond positively to heat shock (Keeley 1987, 1991). Coastal sage scrub and chaparral populations of black sage germinated well in light without pretreatment but required a charate stimulus (a leachate made from charred wood) to germinate in the dark (Keeley 1986). This response is apparently an adaptation that permits seedlings to germinate and establish from persistent seedbanks after wildfire (Keeley 1986). Chilling and alternating temperature regimes sometimes increased germination percentages for black sage, but the results were inconsistent (Keeley 1986). Kay and others (1988) reported that a seedlot of Doff sage germinated to 28% at 15 °C in the dark after a summer of warehouse storage and that its germination increased to 53% after 5 years in storage, suggesting that seeds of this species also have a dry after-ripening requirement. They obtained a similar increase (from 19% to 43%) for seeds of white sage during a single year of warehouse storage. Sage seed dormancy that is overcome in nature by

Table 2—*Salvia*, sage: seed weights and maximum germination percentages

Species	Seed weight		Seeds/weight		Max germination %
	mg	oz	/kg	/lb	
<i>S. apiana</i>	1.4	.05	714,400	324,000	42
	1.9	.07	511,600	233,000	43
<i>S. dorrii</i>	2.4	.08	416,800	189,000	53
<i>S. mellifera</i>	1.1	.04	911,000	413,000	69
<i>S. sonomensis</i>	1.5	.05	685,800	311,000	90
	0.8	.03	1,212,800	550,000	70

Source: Kay and others (1988), Keeley (1986, 1987), Nord and Gunter (1974).

Table 3—*Salvia*, sage: seed germination responses to pretreatments and incubation conditions

Species	Light	Alternating temp	Chilling	Heat shock	Dry storage	Charate	GA
<i>S. apiana</i>	+	+	+	+	+	nd	+
<i>S. mellifera</i>	+	+	+	+	nd	+	nd
<i>S. sonomensis</i>	nd	nd	+	nd	nd	nd	+

Sources: Emery (1988), Kay and others (1988), Keeley (1986, 1987), Nord and Gunter (1974).

Notes: nd = no data; see text for details.

either dry after-ripening or chilling may be circumvented through a 1-hour soak in gibberellic acid (GA) at 100 to 500 ppm (Nord and Gunter 1974) and 400 ppm (Emery 1988). The seeds may be dried for sowing following the GA treatment.

For recently harvested seedlots of sage species, a cut test is a good indicator of viability. Tetrazolium (TZ) staining may also be used, either to evaluate the viability of ungerminated seeds at the end of a germination test or in lieu of a germination test. Belcher (1985) recommends the following procedure for the herbaceous blue sage, *S. azurea* Michx. ex Lam.: soak seeds overnight in water, clip at cotyledon end, place in 1% TZ solution for 6 hours and then slice them lengthwise for evaluation. The embryo in sage seeds is well-developed and fills the seed cavity, but the endosperm is rudimentary or absent. Until more specific recommendations can be made, a generic germination test for shrubby sage species (as recommended for blue sage) is incubation at 15/25 °C or 20/30 °C in the light, with first count at 7 days and last count at 21 days and with post-test viability evaluation as described above.

Field seeding and nursery practice. Shrubby sage species can be direct-seeded in early to late fall in winter rainfall areas such as cis-montane and coastal California (Emery 1988). Sonoran and Chihuahuan Desert species would probably best be seeded before summer rains. Sages are often early seral species adapted to disturbance and establish more readily if seeded in the absence of heavy herbaceous competition (Nord and Gunter 1974). Spring-seeding of chilled or GA-treated seeds was recommended for creeping sage, on the argument that rodent predation would be decreased and that field chilling conditions were unreliable (Nord and Gunter 1974).

Shrubby sages are readily produced from seed as container stock in a nursery setting. In California, seeds are sown outdoors in flats in early fall (Emery 1988). More dormant seedlots may be treated with GA or subjected to a chilling treatment before sowing. Seedlings are then transplanted to larger containers when at the 6- to 8-leaf stage. Sages may also be direct-seeded or planted as germlings in tube containers such as those used for conifer seedlings.

References

- ANPS [Arizona Native Plant Society]. 1990. Desert shrubs. Tucson: Arizona Native Plant Society, Urban Landscape Committee. 35 p.
- Belcher E[W Jr]. 1985. Handbook on seeds of browse-shrubs and forbs. Tech. Pub. R8-8, USDA Forest Service, Southern Region. 246 p.
- Capoh B, Maxwell GL, Smith PH. 1978. Germination responses to temperature pretreatment of seeds from ten populations of *Salvia columbariae* in the San Gabriel Mountains and Mojave Desert, California. *Aliso* 9: 365-373.
- Correll DS, Johnson MC. 1970. Manual of the vascular plants of Texas. Renner: Texas Research Foundation. 1881 p.
- Emery DE. 1988. Seed propagation of native California plants. Santa Barbara, CA: Santa Barbara Botanic Garden. 107 p.
- Jepson WL. 1951. A manual of flowering plants of California. Berkeley: University of California Press. 1238 p.
- Kay BL, Graves WL, Young JA. 1988. Long-term storage of desert shrub seed. Mojave Reveg. Notes 23. Davis: University of California Department of Agronomy and Range Science. 22 p.
- Keeley JE. 1986. Seed germination patterns of *Salvia mellifera* in fire-prone environments. *Oecologia* 71: 1-5.
- Keeley JE. 1987. Role of fire in seed germination of woody taxa in California chaparral. *Ecology* 68: 434-443.
- Keeley JE. 1991. Seed germination and life history syndromes in the California chaparral. *Botanical Review* 57: 81-116.
- Keeley JE, Keeley SC. 1984. Postfire recovery of California coastal sage scrub. *American Midland Naturalist* 111: 105-117.
- Malanson GP, OLeary JF. 1982. Post-fire regeneration strategies of California coastal sage shrubs. *Oecologia* 53: 355-358.
- Munz PA, Keck DD. 1959. A California flora. Berkeley: University of California Press. 1681 p.
- Nord EC, Gunter LE. 1974. *Salvia sonomensis* Greene, creeping sage. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 751-753.

Caprifoliaceae—Honeysuckle family

***Sambucus* L.**

elder

Kenneth A. Brinkman and W. Gary Johnson

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Mr. Johnson retired from the USDA Forest Service's National Seed Laboratory

Growth habit, occurrence and use. The elder genus—*Sambucus*—includes about 20 species of deciduous shrubs or small trees, rarely herbs, native to temperate and subtropical regions of both the Eastern and Western Hemispheres. The fruit of most species is used by birds and mammals as well as by humans, but some species have poisonous fruits. Some species have medicinal properties; others are planted for their attractive foliage and colorful fruit. Plants are often browsed by deer (*Odocoileus virginianus*) and livestock (Plummer and others 1968; Van Dersal 1938). In the United States, 3 native varieties and subspecies have potential value for wildlife and environmental plantings (table 1). American elder and blue elder have been used more than the other species for these purposes.

Flowering and fruiting. The large clusters of small, white or yellowish white, perfect flowers bloom in the spring or summer (table 2). The fruit is a berrylike drupe

(figure 1) containing 3 to 5 one-seeded nutlets or stones (figures 2 and 3). When ripe, the fruits vary from red to nearly black, depending on species (table 3). Dispersal is chiefly by birds and animals.

Geographic races. Regional floras do not agree on the taxonomy of this genus. There is great confusion on delimiting the species, subspecies, and varieties (LHBH 1976). Two varieties of blue elder have definite geographic limits and these may be climatic races. Both American and scarlet elders have developed varieties, but these do not appear to be related to climate.

Collection of fruits. Elder fruits are collected by stripping or cutting the clusters from the branches. Collection should be made as soon as the fruits ripen to reduce losses to birds. If the seeds are not to be extracted immediately, the fruits should be spread out in thin layers to prevent heating. Scarlet elder fruits can be harvested before

Table 1—*Sambucus*, elder: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
<i>S. nigra</i> spp. <i>canadensis</i> (L.) R. Bolli <i>S. canadensis</i> L.	American elder , common elder, sweet elder, elderberry, black elderberry	Nova Scotia to Manitoba, Florida to Texas
<i>S. nigra</i> spp. <i>cerulea</i> (Raf.) R. Bolli <i>S. caerulea</i> Raf.; <i>S. glauca</i> Nutt.	blue elder , blue elderberry, blueberry elder, elder blueberry	British Columbia & W Montana S to California & New Mexico
<i>S. racemosa</i> var. <i>racemosa</i> L. <i>S. callicarpa</i> Greene; <i>S. pubens</i> Michx.	scarlet elder , red elder, redberried elder	Newfoundland to Alaska, S to Georgia, W Oregon & mtns of central & S California

Table 2—*Sambucus*, elder: phenology of flowering and fruiting

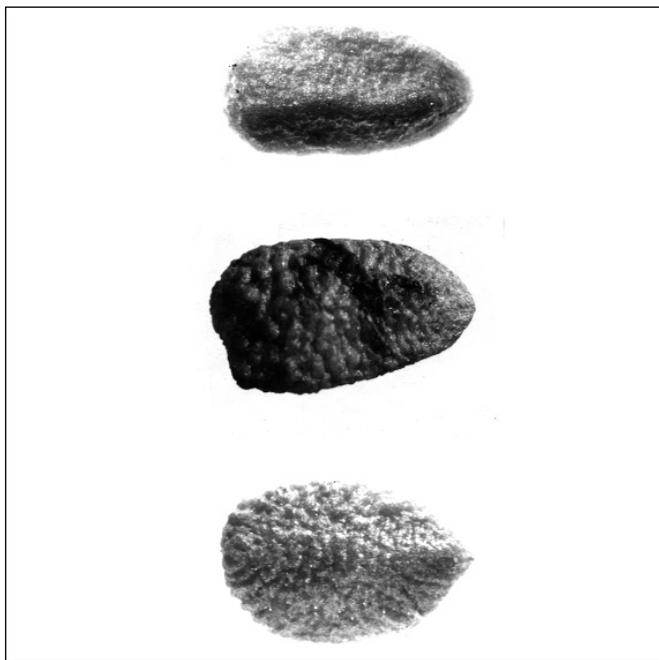
Species	Flowering	Fruit ripening	Seed dispersal
<i>S. nigra</i> spp. <i>canadensis</i>	June–July	July–Sept	Aug–Oct
spp. <i>cerulea</i>	May–July	Aug–Sept	Aug–Oct
<i>S. racemosa</i> var. <i>racemosa</i>	Apr–July	June–Aug	June–Nov

Sources: Harris (1969), Hitchcock and others (1959), LHBH (1976), Plummer and others (1968), Rehder (1940), Van Dersal (1938).

Figure 1—*Sambucus nigra* spp. *cerulea*, blue elder: fruit cluster (**top**) and single fruit (**bottom**).



Figure 2—*Sambucus*, elder: seeds of *S. racemosa* var. *racemosa*, scarlet elder (**top**); *S. nigra* spp. *canadensis*, American elder (**center**); and *S. nigra* spp. *cerulea*, blue elder (**bottom**).



maturity and the seeds will still germinate (Dirr and Heuser 1987). Cram (1982) found that seeds harvested on August 5 in Saskatchewan before the fruit was color ripe showed 95% germination after 90 days of cold stratification, whereas seeds harvested on August 25 showed only 76%. Increased dormancy or harder seedcoat may be the cause of the lower germination in the seeds harvested August 25 (Cram 1982). Specific gravity or moisture content of the fruits did not decrease during maturation but fluctuated up and down, apparently in response to rainfall (Cram 1982).

Extraction and storage of seeds. The fruits (figure 1) may be (a) dried; (b) run through a macerator with water and the pulp and empty seeds floated off (Plummer and others 1968); or (c) crushed, dried, and used without further cleaning. Commercial seedlots may consist of either dried fruits or cleaned seeds (figures 2 and 3). After a short period of drying, lots of freshly extracted seeds may be fanned or screened to remove debris. Excessive drying should be avoided. Seed yields and number of seeds per weight vary among species (table 4).

Small lots of fruit may be cleaned in a food blender (Morrow and others 1954). The berries are covered with water, the blender is run long enough to macerate them, and more water is added to float off the pulp and debris. Several changes of water will result in cleaner seeds. The seeds are separated from the last change of water in a filter-line funnel and can be dried on the filter paper.

Elder seeds may be stored dry at 5 °C for several years (Morrow and others 1954). Seeds of American elder showed

Figure 3—*Sambucus racemosa* var. *racemosa*, scarlet elder: longitudinal section through a nutlet.

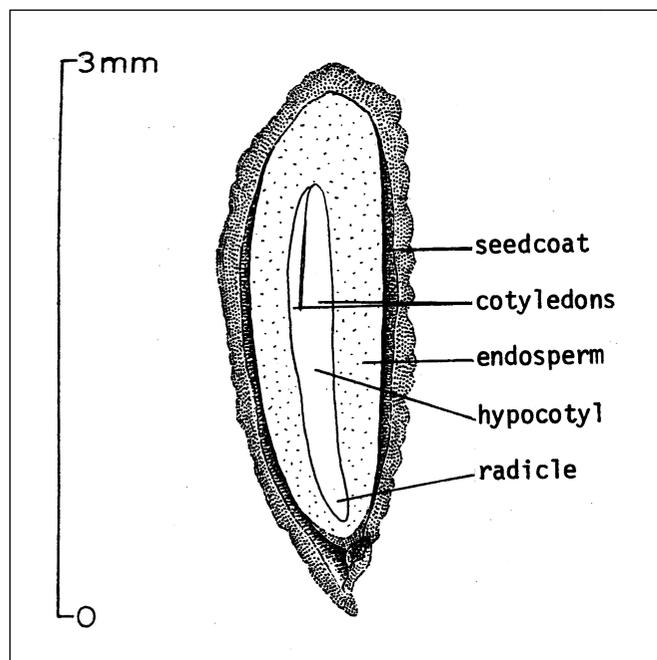


Table 3—*Sambucus*, elder: height, seedcrop frequency, and fruit ripeness criteria

Species	Height at maturity (m)	Year first cultivated	Years between large seedcrops	Ripe fruit color
<i>S. nigra</i>				
spp. <i>canadensis</i>	2.7	1761	I	Purplish black
spp. <i>cerulea</i>	9	1850	—	Blue-black
<i>S. racemosa</i> var. <i>racemosa</i>	3.0	1812	I	Scarlet, bright red

Sources: Brinkman (1974), Fernald (1950), LHBH (1976), Rehder (1940), Rydberg (1965).

Table 4—*Sambucus*, elder: seed yield data

Species	Seeds/wt of fruit		Cleaned seeds/weight				Samples
			Range		Average		
	kg /45 kg	lbs/100 lbs	/kg	/lb	/kg	/lb	
<i>S. nigra</i>							
spp. <i>canadensis</i>	3.2–8.2	7–18	385–713	175–324	510	232	14
spp. <i>cerulea</i>	2.7	6	257–570	117–259	451	205	23
<i>S. racemosa</i> var. <i>racemosa</i>	1.8	4	422–829	192–377	629	286	6

Sources: Brinkman (1974), McKeever (1938), Plummer (1968), Rydberg (1965), Swingle (1939).

little loss in viability after 2 years (Brinkman 1974). Seeds of scarlet elder have been kept satisfactorily in moist sand at 5 °C for a year, but cold, dry storage probably is adequate.

Pregermination treatments. Elder seeds are difficult to germinate because of their dormant embryos and hard seedcoats. Although response varies among species and seedlots, good germination of dried seeds usually results after warm stratification for 60 to 90 days followed by at least 90 days at 5 °C (table 5). Heit (1967) suggested that 10 to 15 minutes of soaking in sulfuric acid, followed by 2 months of chilling at 1 to 4 °C or by late summer planting, would give optimum seedling production. Some seedlots, however, germinated better when treated for 5 minutes with acid, followed by 2 days of water soaking and then by warm and cold stratification (Brinkman 1974). American elder seeds from southern sources of usually do not need acid treatment (Dirr and Heuser 1987). For blue elder, treatment with 1,000 mg of gibberellic acid per liter for 24 hours followed by 30 days of stratification at 4 °C yielded 55% germination. Combining 100 mg of ethephon (an ethylene-releasing compound) per liter with the gibberellic acid treatment and stratification resulted in a 69% germination (Norton 1986a&b).

Germination tests. Tests can be made in sand or on germination paper at alternating temperatures of 30 and 20 °C, but lower temperatures are equally successful for some species (table 6). Although most tests were made with

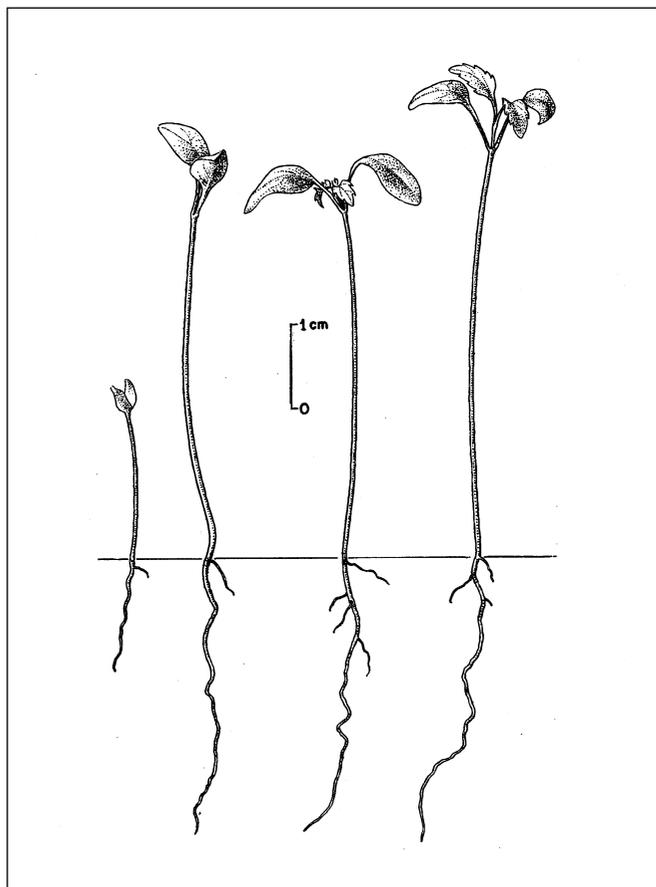
Figure 4—*Sambucus nigra* spp. *canadensis*, American elder: seedling development at 2, 20, 33, and 45 days after germination.

Table 5—*Sambucus*, elder: stratification treatments

Species	Medium	Warm period		Cold period	
		Temp (°C)	Days	Temp (°C)	Days
<i>S. nigra</i>					
spp. <i>canadensis</i>	Sand	20–30	60	5	90–150
spp. <i>cerulea</i>	Sand	Room*	450*	5	98
<i>S. racemosa</i> var. <i>racemosa</i>	Sand	20–30	30–60	5	90–150

Sources: Adams (1927), Brinkman (1974), Davis (1927), McKeever (1938).

* Dry seeds were stored, but not stratified, for 450 days at room temperature.

Table 6—*Sambucus*, elder: germination test conditions and results

Species	Germination test conditions							Purity (%)	
	Medium	Temp (°C)			Germination speed		Germination avg		
		Day	Night	Days	Percent	Days	(%) Samples		
<i>S. nigra</i>									
ssp. <i>canadensis</i>	Sand or soil	30	20	60	32	16	63	7	80
spp. <i>cerulea</i>	Sand	21	21	35	55	12	79	3	80–90
<i>S. racemosa</i> var. <i>racemosa</i>									
	Sand	30*	20*	60	50	27	47	6	97

Sources: Adams (1927), Brinkman (1974), Davis (1927), McKeever (1938), Plummer (1968).

* Day and night temperature of 77 and 50 °F were used on some samples.

at least 16 hours of light, the need for light has not been established. Germination is epigeal (figure 4).

Nursery practice. Elder seeds can be sown in the fall soon after collection, or they can be stratified and sown in the spring. In either case, germination often is not complete until the second spring. At the USDA Forest Service's nursery in Coeur d'Alene, Idaho, dried seeds of blue elder usually are soaked in water for 3 days, then stratified in vermiculite for 3 months at 1 °C before spring-sowing (Brinkman

1974). A seedling density of 375/m² (35/ft²) is sought. Seeds are sown 5 mm (1/4 in) deep in drills and covered with about 8 mm (3/8 in) of sawdust mulch. Two reported tests of American elder sown soon after collection resulted in 92 to 95% (Adams 1927) and 60 to 70% germination (Davis 1927). Fall-sown seedbeds should be mulched. One-year-old seedlings usually are large enough for field planting. Elders also can be propagated from cuttings (Dirr and Heuser 1987; LHBH 1976).

References

- Adams J. 1927. The germination of seeds of some plants with fleshy fruits. *American Journal of Botany* 14: 415–428.
- Brinkman KA. 1974. *Sambucus*, elder. In: Schopmeyer CS, tech. Coord. *Seeds of woody plants in the United States*. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 372.
- Cram WH. 1982. Seed germination of elder (*Sambucus pubens*) and honeysuckle (*Lonicera tatarica*). *Hortscience* 17(4): 618–619.
- Davis OH. 1927. Germination and early growth of *Cornus florida*, *Sambucus canadensis*, and *Berberis thunbergii*. *Botanical Gazette* 84: 225–263.
- Dirr M, Heuser C Jr. 1987. *The reference manual of woody plant propagation: from seed to tissue culture*. Athens, GA: Varsity Press. 239 p.
- Fernald ML. 1950. *Gray's manual of botany*. 8th ed. New York: American Book Co. 1632 p.
- Harris AS. 1969. Unpublished observation. Juneau, AK: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station.
- Heit CE. 1967. Propagation from seed: 7. Successful propagation of 6 hard-seeded group species. *American Nurseryman* 125(12): 10–12, 37–41, 44–45.
- Hitchcock CL, Cronquist A, Ownbey M, Thompson JW. 1959. *Vascular plants of the Pacific Northwest: 4. Ericaceae through Campanulaceae*. Seattle: University of Washington Press. 510 p.
- 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.
- McKeever DG. 1938. The effect of various methods of treatment on the germination of seeds of some plants valuable for game and erosion control purposes [unpublished master's thesis]. Moscow, ID: University of Idaho School of Forestry. 132 p.
- Morrow EB, Darrow GM, Scott DH. 1954. A quick method of cleaning berry seed for breeders. *Proceedings of the American Society of Horticultural Science*. 63: 265.

-
- Norton CR. 1986a. Low temperature and gibberellic acid stimulation of germination in *Sambucus caerulea* Raf. *Scientia Horticulturae* 28: 323–329.
- Norton CR. 1986b. Seed technology aspects of woody ornamental seed germination. In: Germination of ornamental plant seeds. *Acta Horticulturae* 202: 23–30.
- Plummer AP, Christensen DR, Monsen SB. 1968. Restoring big-game range in Utah. Pub. 68-3. Salt Lake City: Utah Department of Natural Resources, Division of Fish and Game. 182 p.
- Rehder A. 1940. Manual of cultivated trees and shrubs. 2nd ed. New York: Macmillan. 996 p.
- Rydberg PA. 1965. Flora of the prairies and plains of central North America. New York: Hafner. 969 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.
- USDA NRCS [USDA National Resources Conservation Service]. 1996. PLANTS [database]. 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.

Sapindus saponaria var. *drummondii* (Hook. & Arn.) L. Benson

western soapberry

Ralph A. Read and John C. Zasada

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Dr. Zasada retired from the USDA Forest Service's North Central Research Station

Other scientific and common names. Previously classified as *Sapindus drummondii* Hook. & Arn. Other common names include wild China-tree, soapberry, Indian soapplant, cherrioni, jaboncillo (Little 1950; Tirmenstein 1990; Vora 1989).

Growth habit, occurrence, and use. Western soapberry grows on clay soils and on dry limestone uplands from southwestern Missouri to Louisiana, and westward through Oklahoma and Texas to southern Colorado, New Mexico, southern Arizona, and northern Mexico. It is used as an indicator species for riparian habitats in parts of the southwestern United States (Tirmenstein 1990). The soapberry family comprises nearly 2,000 species, which are primarily tropical (Watson and Dallwitz 1992). Western soapberry is similar to wingleafed soapberry (*Sapindus saponaria* L. var. *saponaria*), which is found from Arizona to Florida.

Soapberry is a small to medium deciduous tree, 7.7 to 15.4 m tall (Dirr 1990; Little 1950; Phillips and Gibbs 1953). It was first introduced into cultivation in 1900. Soapberry is planted for its environmental and wildlife value and, to a small extent, for shelterbelts in the southern plains (Tirmenstein 1990; Vora 1992). It is also a useful shade and ornamental tree in dry, windy, landscape sites (Khatamian and Abuelgasim 1986). The glossy, yellow fruit and long, pinnate leaves make it especially attractive. The fruit contains about 37% saponin and was used locally in the past for making soap (Tirmenstein 1990). The heavy, strong, close-grained wood splits into thin strips that have been used in basketry (Read 1974).

Flowering and fruiting. Western soapberry is described as polygamo-dioecious. That is, individual trees in a population may be truly dioecious (having only male or female flowers) or they may contain flowers with both male and female functions (Dirr 1990). The small, white flowers, borne in rather large clusters of terminal or axillary panicles, open during May to July (Read 1974). The fruit, a yellow,

translucent, globular drupe measuring 10 to 14 mm in diameter, usually contains a single, dark brown, hard-coated seed (figures 1 and 2), but occasionally 2 or 3 seeds are present (Khatamian and Abuelgasim 1986; Preston 1940). The fruits ripen during September to October and persist on the tree until late winter or spring. Seedcrops are usually abundant each year (Engstrom and Stoeckler 1941).

Collection, extraction, and storage. Fruits may be collected any time during late fall or winter by hand-picking or flailing them from the trees onto canvas. Although fruits are fairly dry by this time, they still need to be spread in shallow layers to keep them from heating. A bushel of fresh fruits from a central Oklahoma source had a calculated weight of 18.6 kg (41 lb) (Read 1974). Seed extraction is facilitated by sprinkling the fruits with water twice daily until pulp softens. Pulp can then be removed and floated away by running the fruits through a macerator with water. After drying, the seeds are ready for storage or use (Read 1974).

Forty-five kilograms (100 lb) of fruit will yield 13.6 to 16 kg (30 to 35 lb) of clean seeds (Read 1974) with a maximum of 37.2 kg (82 lb) reported (Swingle 1939). There are 950 to 1430 fruits/kg (430 to 650/lb) (Read 1974). Clean seeds per weight (based on 8 samples) varied from 1,510 to 4,360/kg (685 to 1,980/lb) (Engstrom and Stoeckler 1941; Read 1974; Swingle 1939). A fresh collection from central Oklahoma ran 1,540 seeds/kg (700/lb), with 104% moisture (percentage of dry weight) after 7 days of water-soaking followed by a de-pulping treatment (Reed 1974). Soundness of 12 samples averaged 77% (Read 1974). No data are available on seed longevity in cold storage, but it is likely that dry storage at low temperatures would be satisfactory.

Pregermination treatments. Germination of stored seeds may be slow and delayed. The chief cause is embryo dormancy, often accompanied by an impermeable seedcoat. Some seedlots require only stratification, whereas others

Figure 1—*Sapindus saponaria* var. *drummondii*, western soapberry: fruit and seed.

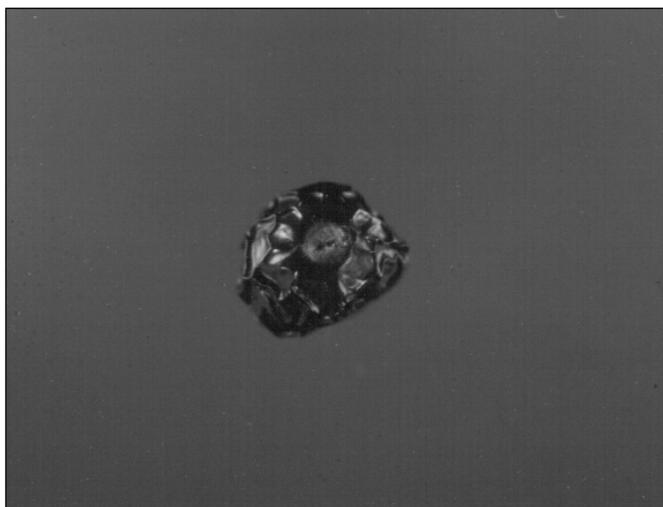
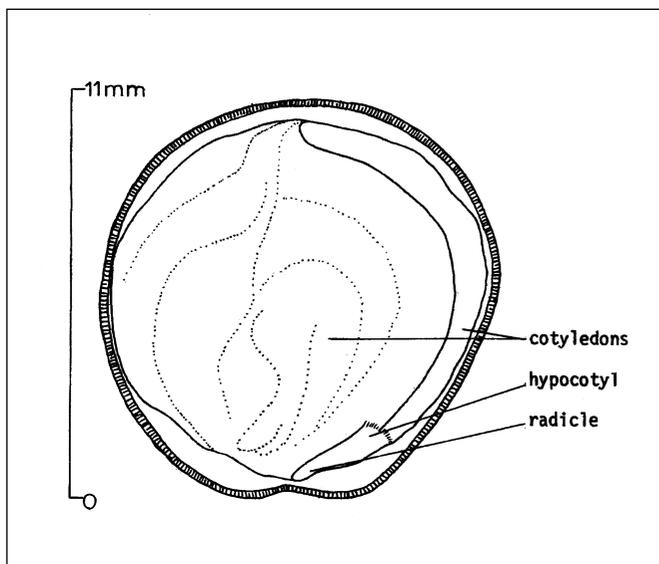


Figure 2—*Sapindus saponaria* var. *drummondii*, western soapberry: longitudinal section through a seed.



may need a prestratification treatment (Afanasiev 1942; Munson 1984; Vora 1989). Germination of western soapberry and other species in the genus may be improved by pretreatment with concentrated sulfuric acid (Munson 1984; Read 1974; Sheikh 1979; Vora 1989). The need for acid scarification can be determined by soaking a few seeds in cold water for 5 to 7 days. If the seeds swell, only stratification is needed. If the seeds remain small and hard, they should be pretreated with acid; however even seedlots responding to acid treatment contain some seeds that will germinate without treatment (Munson 1984; Vora 1989). The length of time that seeds need to be acid-scarified for maximum germination has varied among studies. Thirty to

45 minutes seems to be a minimum amount of time, with 60 to 180 minutes as times necessary for maximum germination (Munson 1984; Read 1974; Sheikh 1979; Vora 1989). Stratification following scarification may or may not improve germination. Hot water scarification and freezing seeds in conjunction with 90 days of stratification at 5 °C also improved germination but not as effectively as acid treatment with or without stratification (Munson 1984). A warm stratification of dried fruits for 6 to 10 weeks at 21 to 30 °C often has the same effect as pretreating cleaned seeds with acid. After such treatment, the pulp is decayed or partially decomposed and can be washed off without difficulty. Seedlots should then be stratified at a low temperature for 90 days (Afanasiev 1942). Freshly collected, clean seeds germinated better without pretreatment (Read 1974).

Germination tests. Germination tests have been run in sand flats and combinations of peat moss and vermiculite at temperatures alternating diurnally from 20 to 30 °C (Munson 1984; Read 1974; Sheikh 1979; Vora 1989). Germination varies with quality of the seedlots. In addition, there will be large variability within a seedlot depending on pretreatment. For example, germination of acid-treated seeds was 88%; hot water-treated, 65%; frozen, 58%; and untreated, 44% (Munson 1984). In another comparison, germination of untreated seeds was 17% and acid-treated seeds about 70% (Vora 1989).

Nursery practice. Because western soapberry apparently varies considerably in seed hardness and response to pregermination treatments, examination tests before nursery sowing are essential. If seeds of freshly picked and dried fruits absorb moisture during 5 to 7 days of water soaking for de-pulping, they may be sown in the fall or spring with no further treatment. If seeds remain small and hard after water-soaking, they should be scarified for 2 to 2 1/2 hours unless previous tests have shown shorter times are better (Munson 1984) and stratified (60 to 90 days) to ensure adequate germination in spring-sowing. Seeds should be sown at a density of about 211 viable seeds/m² (20 seeds/ft²) at a depth of 2 cm (3/4 inch) in a firm seedbed. Seedlings have a strong taproot, and top growth is slow in the nursery (Read 1974).

Seedlings can be grown in containers in a greenhouse environment. Davis and Whitcomb (1974) found that containers that were 6.35 cm² (2.5 in²) top area and 15 to 30 cm deep (6 to 12 in)—with volumes of 605 and 1,210 cm³ (37.5 and 75 in³), respectively—were the most promising size. Seedlings grown in containers reached a height of 25 cm (9.8 in) in 80 days. Soapberry can also be propagated from stem cuttings (Dirr 1990; Dirr and Heuser 1987; Khatamian and Abuelgasim 1986).

References

- Afanasiev M. 1942. Propagation of trees and shrubs by seed. Circ. C-106. Stillwater: Oklahoma Agricultural Experiment Station. 43 p.
- Davis RE, Whitcomb CE. 1974. Effects of propagation container size on top and root development of tree seedlings. Res. Rep. P-704. Stillwater: Oklahoma Agricultural Experiment Station: 12-13.
- Dirr MA. 1990. Manual of woody landscape plants: their identification, ornamental characteristics, culture, propagation and uses. Champaign, IL: Stipes Publishing Co. 1007 p.
- Dirr MA, Heuser CW Jr. 1987. The reference manual of woody plant propagation: from seed to tissue culture. Athens, GA: Varsity Press. 239 p.
- Engstrom HE, Stoeckeler JH. 1941. Nursery practice for trees and shrubs suitable for planting on the Prairie-Plains. Misc. Pub. 434. Washington, DC: USDA. 159 p.
- Khatamian H, Abuekgasim Z. 1986. Auxins aid soapberry cuttings. American Nurseryman 164(4): 65-72.
- Little EL. 1950. Southwestern trees. Agric. Handbk. 9. Washington, DC: USDA Forest Service. 109 p.
- Mehra PN, Khosla PK, Sareen TS. 1972. Cytogenetical studies of Himalayan Aceraceae, Hippocastanaceae, Sapindaceae and Staphyleaceae. Silvae Genetica 21: 96-102.
- Munson RH. 1984. Germination of western soapberry as affected by scarification and stratification. HortScience 19(5): 712-713.
- Phillips GR, Gibbs FJ. 1953. Forest trees of Oklahoma. Pub. 1 (rev. ed., #8). Oklahoma City: Oklahoma Planning and Resources Board, Division of Forestry. 135 p.
- Preston RJ Jr. 1940. Rocky Mountain trees. Ames: Iowa State College Press. 285 p.
- Read RA. 1974. *Sapindus drummondii* Hook. and Arn., western soapberry. In: Schopmeyer CS, comp. Seeds of woody plants in the United States. Agric. Handbk. 450. USDA Forest Service. Washington, DC: 758-759.
- Sheikh MI. 1979. Tree seeds respond to acid scarification. Pakistan Journal of Forestry 29(4): 253-254.
- 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.
- Tirmenstein DA. 1990. *Sapindus saponaria* var. *drummondii*. In: Fischer WC, comp. The Fire Effects Information System [electronic database]. Missoula, MT: USDA Forest Service, Intermountain Research Station.
- Vora RS. 1989. Seed germination characteristics of selected native plants of the lower Rio Grande Valley, Texas. Journal of Range Management 42(1): 36-40.
- Vora RS. 1992. Restoration of the native vegetation in the lower Rio Grande Valley, 1984-87. Restoration and Management Notes 10 (2): 150-157.
- Watson L, Dallwitz Mj. 1992 [onwards]. The families of flowering plants: descriptions, identification, illustrations, and information retrieval. Version 14 December 2000 [website available at <http://biodiversity.uno.edu/delta/>].

Sarcobatus vermiculatus (Hook.) Torr.

black greasewood

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Other common name. Greasewood.

Growth habit, occurrence and use. Black greasewood—*Sarcobatus vermiculatus* (Hook.) Torr.—is an erect to spreading, multi-branched, brittle, spinescent, and deciduous shrub that grows up to 2.5 m tall. It reproduces by seeds and by sprouting from its root crown and widespread root system (Branson and others 1967; Eddleman 1977; Robertson 1983). Black greasewood is widespread throughout western North America from southern Alberta, Saskatchewan, and British Columbia to Texas, northern Mexico, and eastern California (Branson and others 1967; Munz 1973; Stephens 1973; Stubbendieck and others 1994). Rickard (1982) classified this species as a phreatophytic halophyte–osmophyte. The shrub may grow on sandy soils in the northeastern part of its range (Stephens 1973), but it is most commonly associated with heavy textured soils of high salt content (0.05 to 1.6%) on flood plains that are either subject to periodic flooding or have a water table less than 10.5 m deep. Black greasewood frequently occurs in nearly pure stands in saline conditions. It also grows in nearly all the less-saline salt desert shrub types (Eddleman 1979; Robertson 1983; Romo and Eddleman 1985; Shantz and Piemeisal 1940). A narrow endemic form found in western Nevada—*S. vermiculatus* var. *Baileyi* (Cov.) Jep.—is recognized by Kartesz (1987) and Munz (1973), although it appears to integrate with the typical form.

Black greasewood is used as wood for fuel and the sharpened spines were used for painting by Native Americans (Stubbendieck and others 1994). Seeds, leaves, and new leaders are consumed by a variety of small mammals (Van Dersal 1938). It is an important browse plant and is rated from good to useless as forage for cattle, sheep, and big game animals in the winter and provides good cover and food for small mammals and birds (Blauer and others 1976). Sheep have been poisoned by rapidly consuming large amounts of new leader growth, which contains high levels of soluble oxalate (Kingsbury 1964; Stubbendieck and others 1994).

Flowering and fruiting. Black greasewood is usually monoecious, with the staminate flowers borne as catkin-like axillary spikes. Solitary green pistillate flowers are borne in leaf axils below staminate catkins (Munz 1973; Welsh 1987). Flowering occurs as early as June and as late as August (Eddleman 1979; Munz 1973; Romo 1985). The perianth is persistent, forming a circular winged coriaceous utricle containing an achene (figure 1). Achenes are composed of a thin outer membranous pericarp surrounding a coiled embryo (figure 2). Mature utricles are tan to light brown. Not all fruits ripen at the same time. Earliest maturation may be in late September; all fruits reach maturity by late November. Fruit dispersal begins in late September and may extend over the winter with a few fruit remaining on the plant in early summer the following year (Eddleman 1977, 1979; Romo 1985).

Collection, extraction, and storage of fruits. Mature fruits can be knocked from the plant with a flail. The best time for harvest is late October through November. A flail or de-winger can be used to remove the wings from well-dried fruits, which after being run through a fanning mill or seed

Figure 1—*Sarcobatus vermiculatus*, black greasewood: winged and de-winged utricles.

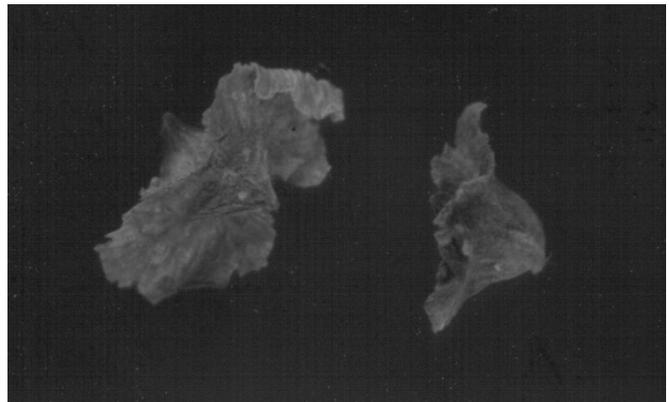
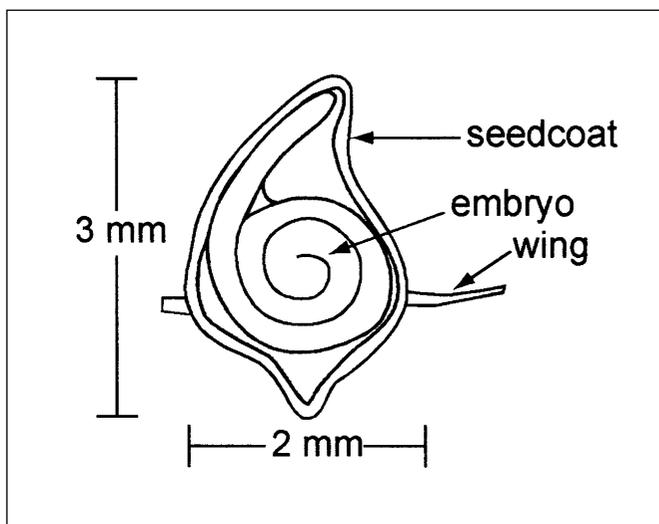


Figure 2—*Sarcobatus vermiculatus*, black greasewood: longitudinal section through a utricle with bracts removed.



blower can yield good-quality seedlots (Eddleman 1977; Romo 1985). Cleaned seeds number from 425 to 628/g (193,000 to 285,000/lb) (Blauer and others 1976; Eddleman 1977, 1979; Romo 1985).

Germination tests. Seeds germinate well at cooler temperatures and rates of germination are high (table 1). Laboratory tests have shown optimum germination temperatures range from 10 to 25 °C (Eddleman 1979; Robertson

1983; Romo and Eddleman 1985; Romo and Haferkamp 1987; Sabo and 1979). Seeds from New Mexico germinated poorly at temperatures above 19 °C; seeds from Montana germinated at temperatures ranging from 5 to 40 °C. In the latter case, high temperatures (especially those above 25 °C) reduced both germination rate and percentage germination and abnormal seedlings developed (Romo and Eddleman 1985). Seeds from an Oregon source germinated best at 20 °C (Romo and Haferkamp 1987).

Stratification does not appear to be necessary, but incubation at 4 °C for 30 or 60 days may improve percentage germination at warmer temperatures (Eddleman 1979). Seeds germinate well at 30 to 60 days following maturation. Long viability is possible: seeds stored in the laboratory for 4 years reached germination of 70% in 4 days (Eddleman 1982). Romo and Eddleman (1985) have made the distinction between viable embryos (that is, the imbibed radicle tip is white) from non-viable embryos (that is, the imbibed radicle tip is brown). It is uncertain whether removal of the bracts (wings) affects germination. These bracts contain high levels of sodium which is rapidly absorbed by the seedling, presumably as a means of adjusting its osmotic potential to cope with saline conditions during establishment (Eddleman and Romo 1987; Rickard 1982; Romo and Eddleman 1985).

Table 1—*Sarcobatus vermiculatus*, black greasewood: germination tests, conditions, and results

Seed source	Germination test conditions			Germination rate		Average % germination	Samples
	Medium	Temp (°C)	Days	Amt (%)	Days		
Montana	Kimpak	10	30	67	2	100	4
Montana	Kimpak	10	30	91	10	98	4
	—	5–25	30	—	—	80–93	4
New Mexico	Filter paper	11	25	—	—	100	—
		11	26	66	4	88	3

Sources: Eddleman (1979), Romo and Eddleman (1985), Sabo and others (1979).

References

- Blauer AC, Plummer AP, McArthur ED, Stevens R, Guinta BC. 1976. Characteristics and hybridization of important Intermountain shrubs: 2. Chenopod family. USDA Forest Service, Res. Pap. INT-177. Ogden, UT: Intermountain Forest and Range Experiment Station. 42 p.
- Branson FA, Miller RF, McQueen IS. 1967. Geographic distribution and factors affecting the distribution of salt desert shrubs in the United States. *Journal of Range Management* 20: 287–296.
- Eddleman LE. 1977. Indigenous plants of southeastern Montana: I. Viability and suitability for reclamation in the Fort Union Basin. Spec. Pub. 4. Missoula: University of Montana, Montana Forest and Conservation Experiment Station. 122 p.
- Eddleman LE. 1979. Germination in black greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.). *Northwest Science* 53: 289–294.
- Eddleman LE. 1982. Unpublished data. Corvallis: Oregon State University Department of Rangeland Resources.
- Eddleman LE, Romo JT. 1987. Sodium relations in seeds and seedlings of *Sarcobatus vermiculatus*. *Soil Science* 143: 120–123.
- Kartesz JT. 1987. A flora of Nevada [PhD dissertation]. Reno: University of Nevada. 1729 p.
- Kingsbury JM. 1964. Poisonous plants of the United States and Canada. Englewood Cliffs, NJ: Prentice-Hall. 626 p.
- Munz PA. 1973. A flora of California, with supplement. Berkeley: University of California Press. 1681 p. + 224 p.
- Rickard WH. 1982. Cation content of leaves of desert shrubs and its relationship to taxonomic and ecological classification. *American Midland Naturalist* 108: 311–316.

- Robertson JH. 1983. Greasewood (*Sarcobatus vermiculatus* (Hook.) Torr). *Phytologia* 54: 309–324.
- Romo JT. 1985. Water relations in *Artemisia tridentata* subsp. *wyomingensis*, *Sarcobatus vermiculatus*, and *Kochia prostrata* [PhD dissertation]. Corvallis: Oregon State University. 191 p.
- Romo JT, Eddleman LE. 1985. Germination response of greasewood (*Sarcobatus vermiculatus*) to temperature, water potential, and specific ions. *Journal of Range Management* 38: 117–120.
- Romo JT, Haferkamp MR. 1987. Effects of osmotic potential, potassium chloride, and sodium chloride on germination of greasewood (*Sarcobatus vermiculatus*). *Great Basin Naturalist* 47: 110–116.
- 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, Rocky Mountain Forest and Range Experiment Station. 26 p.
- Shantz HL, Piemeisel RL. 1940. Types of vegetation in the Escalante Valley, Utah, as indicators of soil conditions. Tech. Bull. 713. Washington, DC: USDA. 32 p.
- Stephens HA. 1973. Woody plants of the north central plains. Lawrence: University of Kansas Press. 530 p.
- Stubbendieck J, Hatch SL, Butterfield CH. 1994. North American range plants. Lincoln: University of Nebraska Press. 493 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.
- Welsh SL, Atwood ND, Higgins LC, Goodrich S. 1987. A Utah flora. *Great Basin Naturalist Memoirs* 9: 1–894.

Sassafras albidum (Nutt.) Nees

sassafras

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Synonyms. *Sassafras albidum* var. *molle* (Raf.) Fern., *S. sassafras* (L.) Karst., *S. officinale* Nees & Eberm.

Other common name. white sassafras.

Growth habit, occurrence, and use. Sassafras—*Sassafras albidum* (Nutt.) Nees—is a short to medium-tall, deciduous tree that is native from southwestern Maine to central Michigan and southeastern Iowa, and south to east Texas and central Florida. It is little more than a shrub at the northern portion of its range, but on more fertile sites, trees may reach heights of 30 m at maturity. Sassafras is valuable for timber and wildlife. The light brown wood is soft, lightweight, and very durable. Bark from the roots has been used for making tea, sassafras oil, and perfume for soap and other articles. There is some evidence that extracts of the roots have some insecticidal properties (Jacobson and others 1975). The species has been cultivated since 1630 (Griggs 1990; Little 1979).

Flowering and fruiting. The dioecious, greenish yellow flowers, 12 mm in length, are borne in 5-cm-long axillary racemes in March and April as the leaves appear. The drupaceous fruits are borne on thick red pedicels in clusters (Vines 1960). The single-seeded drupes are ovoid, dark blue, and about 8 to 13 mm long (figure 1). The pulpy flesh covers a hard, thin endocarp that encloses the seed (figure 2). The fruits mature from June to September, depending on latitude, and are dispersed within a month. Primary dispersal is by birds, which often eat the fruits before they fall (Little and Delisle 1962). Minimum seed-bearing age is 4 years for open-grown trees (Halls 1973), and good crops are produced every 1 or 2 years (Bonner and Maisenhelder 1974).

Collection, extraction, and storage. Fruits may be picked from the trees or knocked onto sheets of plastic or canvas by flailing the branches. The fruits are green before maturity, and the change to dark blue indicates that they are ready for collection (Bonner and Maisenhelder 1974). The pulpy flesh is usually removed before storage or sowing by

rubbing the fruits over hardware cloth by hand or by breaking them up with mechanical macerators and washing the debris away with water. In the South, there are about 6,200 fruits/kg (2,800/lb) (Halls 1973). In the North, seeds collected and cleaned averaged 13,000/kg (5,900/lb). In Pennsylvania, 45 kg (100 lb) of fruit yielded about 14 kg (31 lb) of cleaned seeds (Bonner and Maisenhelder 1974).

There are no known storage tests for sassafras, but the seeds can apparently be stored successfully for a few years at 2 to 4 °C and low moisture contents (Bonner and Maisenhelder 1974). This behavior should place sassafras in the orthodox seed storage grouping, although the very high lipid content (47%) of the seeds (Bonner 1971) suggests that long-term storage would be difficult. Soil seedbank studies have demonstrated that seeds buried in litter retained viability for 4 years in Louisiana (Haywood 1994) and for 6 years in West Virginia (Wendel 1977).

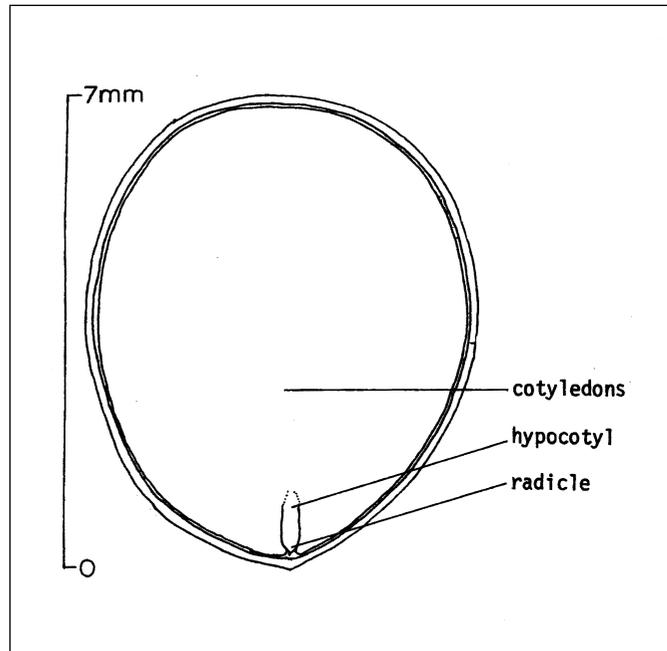
Figure 1—*Sassafras albidum*, sassafras: fruits and seed (lower right).



Germination. Sassafras seeds exhibit strong embryo dormancy, which can be overcome with moist stratification at 2 to 4 °C for 120 days. Germination can be tested in moist sand or other media at temperatures of 22 to 30 °C for up to 120 days. The common laboratory test regime of alternating 20/30 °C will probably produce good results also.

Nursery practice. Although sowing has been done with both cleaned and uncleaned seeds and dried fruits, better results were obtained with cleaned seeds. Because seeds sown early in the fall often germinate before cold weather, unstratified seeds should be sown as late in the fall as possible. It may be necessary to store the seeds for a short period between collection and fall-seeding. Stratification is recommended for seeds to be sown in the spring. The seeds should be drilled in rows 20 to 30 cm (8 to 12 in) apart and covered with 6 to 12 mm ($1/4$ to $1/2$ in) of firmed soil. Beds should be mulched with burlap, straw, or leaf mulch held in place by bird or shade screens until after spring frosts (Bonner and Maisenhelder 1974). Sassafras can also be propagated by layering and by root cuttings (Dirr and Heuser 1987).

Figure 2—*Sassafras albidum*, sassafras: longitudinal section through a seed.



References

- Bonner FT. 1971. Chemical contents of southern hardwood fruits and seeds. Res. Note SO-136. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 3 p.
- Bonner FT, Maisenhelder LC. 1974. *Sassafras albidum* (Nutt.) Nees, sassafras. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 761–762.
- Dirr MA, Heuser CW Jr. 1987. The reference manual of woody plant propagation: from seed to tissue culture. Athens, GA: Varsity Press. 239 p.
- Griggs MM. 1990. *Sassafras albidum* (Nutt.) Nees, sassafras. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 2, Hardwoods. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 773–777.
- 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.
- Haywood JD. 1994. Seed viability of selected tree, shrub, and vine species stored in the field. New Forests 8: 143–154.
- Jacobson M, Redfern RE, Mills GD Jr. 1975. Naturally occurring insect growth regulators. 2. Screening of insect and plant extracts as insect juvenile hormone mimics. Lloydia 38: 455–472.
- Little EL Jr. 1979. Checklist of United States trees (native and naturalized). Agric. Handbk. 541. Washington, DC: USDA Forest Service. 375 p.
- Little EL Jr, Delisle AL. 1962. Time periods in development: forest trees, North American. In: Altman PL, Dittmer DS, eds. Biological handbook on growth. Washington, DC: Federation of American Societies for Experimental Biology: table 104
- Vines RA. 1960. Trees, shrubs, and woody vines of the Southwest. Austin: University of Texas Press. 1104 p.
- Wendel GW. 1977. Longevity of black cherry, wild grape and sassafras seed in the forest floor. Res. Pap. NE-375. Parsons, WV: USDA Forest Service, Northeastern Forest Experiment Station. 6 p.

Anacardiaceae—Sumac family

Schinus L.

peppertree

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Growth habit, occurrence, and use. There are 3 species of the genus *Schinus* that have been introduced into the United States (table 1). They are members of the Anacardiaceae family and closely related to poison ivy—*Toxicodendron radicans* ssp. *radicans* (L.) Kuntze. Peruvian peppertree is native to South America and is grown in Mediterranean climates in Europe and in USDA Hardiness Zone 9 in North America. It has been naturalized in southern California for 100 to 200 years (Nilsen and Muller 1980b). This species is grown as an ornamental and is popular for its gnarled trunk and branches, with droopy, weeping branchlets and cascades of red berries. The trees reach a height and equal spread of 35 to 40 feet in 20 years (Johnson 1973).

Although early reports (Nilsen and Muller 1980a&b) stated that Christmasberry tree had not become naturalized, it has since widely naturalized in peninsular Florida and Hawaii. Its common name is derived from its use in making Christmas wreaths. The plant was first introduced in the United States in 1898 (Morton 1978). Unfortunately, many landowners who planted it as an ornamental have found that in a few years the tree outgrows its allotted space and is difficult to prune or cut down because of its tangle of branches. Mockingbirds (*Mimus polyglottis*), cedar waxwings (*Bombys cedrorum*), and robins (*Turdus migratorius*) feed on the berries and then drop the seeds in harvested fields, pastures, roadsides, canal banks, pinewoods, and hammocks (Morton 1978). Christmasberry tree now covers thousands of acres in south and central Florida and the Florida Keys

(Ewel 1979, 1986; Ewel and others 1989; Lemke 1992; Workman 1979). The plant has been designated a noxious weed throughout the Hawaiian Islands (Morton 1978). In California, it is recommended for planting in substitution for Peruvian peppertree, which is a host of black scale (*Saissetia olea* Oliver), an enemy of the citrus industry (Morton 1978).

The leaves, wood, and berries of Christmasberry tree are toxic to humans, animals, and birds. In Florida, a fine, itching body rash, with swelling of the face and eyelids, is commonly experienced by anyone who cuts down the tree or cuts off even a single branch while the tree is in bloom (Morton 1978). Children who ingest the berries experience digestive upsets and vomiting, along with a rash and swelling of the hands, arm, and face. Calves that have eaten the leaves develop enteritis, a swollen head, and hemorrhages in the eyes. Goats are immune to the tree's effects. Birds that feed excessively on the berries become intoxicated and unable to fly.

Most widespread are the respiratory difficulties that occur when the tree is in bloom. The airborne chemical from the blooms causes sinus and nasal congestion, rhinitis, headache, sneezing, eye irritation, tightness in the chest, and labored breathing (Morton 1978). Physicians are sometimes successful in relieving their patients' symptoms by administering desensitization injections of extracts made from the inflorescences.

Table 1—*Schinus*, peppertree: nomenclature and occurrence

Scientific name	Common name(s)	Occurrence
<i>S. molle</i> L.	Peruvian peppertree, <i>molle</i> , <i>pirul</i> , California peppertree, Peruvian mastic tree	Andes of Peru; naturalized in S California
<i>S. polygamus</i> (Cav.) Cabrera	peppertree, <i>huigen</i>	W South America
<i>S. terebinthifolius</i> Raddi	Christmasberry tree	Brazil; naturalized in S Florida & Hawaii

Source: LHBH (1976), Wasson (2001).

The eradication of the larger trees by harvesting for pulpwood has been explored. The strength properties of the pulp are low: 40 burst factor, 70 tear factor, 8,500 tensile strength (Morton 1978). The fibers are about 0.8 mm long. The strength characteristics of Christmasberry tree would rank it with the poorest of native hardwoods and the extractives could pose a serious processing problem.

Flowering and fruiting. The leaves have 3 to 13 sessile, finely toothed leaflets 2.5 to 5 cm long that are dark green above and paler underneath (Morton 1978). The ivory white flowers are borne profusely in racemes or panicles up to 15 cm long along the outer branches and at the branch tips. The flowers have 5 petals about 3 mm wide and 10 stamens situated on a 5-parted calyx (LHBH 1976). *Schinus* species are dioecious. Peruvian peppertree flowers yield a small amount of nectar for bees, but the species is important because it has a long flowering period (mainly of the male flowers) (Eisikowitch and Masad 1980).

The fruit is a 1-seeded drupe borne in compact masses. At first the berry is green and juicy, then it turns bright red on ripening and dries and remains on the tree for weeks (Johnson 1973).

Extraction and storage. Fruits of Christmasberry tree are collected by hand in the winter before Christmas, then dried and sold in the United States as a spice called "pink peppercorn" (Jones and Doren 1997). Seeds can be collected anytime between January and February by cutting the branches and stripping the berries from the branch (Perekins 2002). Fruits may persist on the shrub until May. A macerator is used to remove the sticky pulp. The seeds are surface-dried naturally by the sun until dry to the touch (Anderson 2002).

Christmasberry tree produces 54,400 cleaned seeds/kg (24,675/lb); Peruvian peppertree and peppertree yield 22,000 cleaned seeds/kg (9,980/lb). Viability of seeds may be maintained by storage at 3 °C or lower and 30% humidity (Eizenbrand 2002). In California, Christmasberry tree seeds can be stored for up to 60 to 90 days in cold storage (Anderson 2002). After 6 months of storage, the germination drops off 50% or more. At room temperature, the seeds grow mold, so cloth or polypropylene bags are used for seed storage to allow air to circulate (Anderson 2002).

Germination tests. The seed germination characteristics that differentiate Peruvian peppertree and Christmasberry tree may be the factors inhibiting the naturalization of Christmasberry tree in southern California (Nilsen and Muller 1980). The latter species may be excluded from the California vegetation because of its slow germination rate, which could preclude its establishment during the periods of brief rainfall and intermittent drought (Nilsen and Muller 1980).

Germination treatments carried out in the dark at 24 °C were performed on the seeds of both species. Peruvian peppertree seeds germinate best after soaking for 5 minutes in a 10% solution of sulfuric acid (H₂SO₄) (Nilsen and Muller 1980); imbibition for 24 hours and stratification (30 days at 2 °C) did not break dormancy in seeds of this species.

Seeds of Christmasberry tree germinate equally well with imbibition or acid treatment, and a significant amount of germination occurred after 30 days of 2 °C stratification (Nilsen and Muller 1980). Seeds of Peruvian peppertree are more inhibited by cold conditions than are those of Christmasberry tree. Seeds of neither species germinated when incubated to 70 °C for 1 hour. Laboratory germination of Peruvian peppertree began on the 17th day and that of Christmasberry tree began on day 28.

Germination tests performed in native soil delayed germination of Peruvian peppertree and inhibited that of Christmasberry tree. In both greenhouse soil mix or field soil, seeds of Peruvian peppertree germinated better than those of Christmasberry tree, except when seeds were germinated in a winter-regimen growth chamber (15/2 °C) (Nilsen and Muller 1980a).

Nursery practices. *Schinus* seeds are usually grown in pots filled with sandy clay loam. In southern California, the seeds germinate in the winter at about 50% relative humidity and 18/10 °C temperatures (Nilsen and Muller 1980a). Christmasberry tree has a higher root net accumulation ratio, which gives it a greater drought tolerance than Peruvian peppertree. Both *Schinus* species show positive relative growth rates within and below the common irradiances under canopies of southern California coastal communities (Nilsen and Muller 1980a).

References

- Anderson E. 2002. Personal communication. Escondido, CA: Anderson Seed Co.
- Correll DS, Johnston MC. 1970. Manual of vascular plants of Texas. Renner: Texas Research Foundation: 1881.
- Eisikowitch D, Masad Y. 1980. Nectar-yielding plants during the dearth season in Israel. *Bee World* 61: 11–18.
- Eizenbrand A. 2002. Personal communication. Bet Nehemia, Israel: Keren Kayemet Lelsrael.
- Ewel JJ. 1979. The ecology of *Schinus*. In: Workman RW, ed. *Schinus—A Technical Proceedings of Techniques for Control of Schinus in South Florida: A Workshop for Natural Area Managers*. Sanibel, FL: Sanibel-Captiva Conservation Foundation: 7–21.
- Ewel JJ. 1986. Invasibility: lessons from south Florida. *Ecological Studies: Analysis and Synthesis* 58: 214–230.
- Ewel JJ, Ojima DS, Karl DA, DeBusk WF. 1982. *Schinus* in successional ecosystems of Everglades National Park. Rep. T-676. Homestead: South Florida Research Center: 141 p.
- Habeck DH, Bennett FD, Grissell EE. 1989. First record of a phytophagous seed chalcid from Brazilian peppertree in Florida. *Florida Entomologist* 72(2): 378–379.
- Johnson H. 1973. *The International book of trees*. New York: Simon and Schuster: 288 p.
- Jones DT, Doren RF. 1997. The distribution, biology and control of *Schinus terebinthifolius* in southern Florida with special reference to Everglades National Park. In: Brock JH, Pysek P, eds. *Green plant invasions: studies from North America and Europe*. Leiden, The Netherlands: D. Backhuys, Publishers: 81–93.
- Lemke DE. 1992. *Schinus terebinthifolius* (Anacardiaceae) in Texas. *Phytologia* 72(1): 42–44.
- 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.
- Little EL, Woodbury RO, Wadsworth FH. 1974. *Trees of Puerto Rico and the Virgin Islands: second volume*. Agric. Handbk. 449. Washington, DC: USDA Forest Service. 1024p.
- Morton JF. 1978. Brazilian pepper: its impact on people, animals and the environment. *Economic Botany* 32(4): 353–359.
- Muñoz MR, Fuentes ER. 1989. Does fire induce shrub germination in the Chilean matorral? *Oikos* 56: 177–181.
- Nilsen ET, Muller WH. 1980a. A comparison of the relative naturalization ability of two *Schinus* species in southern California: 1. Seed germination. *Bulletin of the Torrey Botanical Club* 107(1): 51–56.
- Nilsen ET, Muller WH. 1980b. A comparison of the relative naturalization ability of two *Schinus* species (Anacardiaceae) in southern California: 2. Seedling establishment. *Bulletin of the Torrey Botanical Club* 107(2): 232–237.
- Perkins D. 2002. Personal communication. LaBelle, FL: Perkins Nursery.
- Wasson E. 2001. *Trees and shrubs: illustrated A–Z of over 8500 plants*. Willoughby, NSW, Australia: Global Book Publishing: 704–705.
- Workman RW. 1979. History of *Schinus* in Florida. In: Workman RW, ed. *Schinus—A Technical Proceedings of Techniques for Control of Schinus in South Florida: Workshop for Natural Area Managers*. Sanibel, FL: Sanibel-Captiva Conservation Foundation: 3–6.

Taxodiaceae—Redwood family

Sciadopitys verticillata (Thunb.) Sieb. & Zucc.

umbrella-pine

Paul O. Rudolf and Peyton W. Owston

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Dr. Owston retired from the USDA Forest Service's Pacific Northwest Research Station

Growth habit, occurrence, and use. Native to the mountains of central and southern Japan at elevations of 200 to 1,500 m, the umbrella-pine (also known as Japanese umbrella-pine or parasol-pine)—*Sciadopitys verticillata* (Thunb.) Sieb. & Zucc.—is a pyramidal conifer from 20 to 40 m tall. It is most commonly grown in the United States for ornamental purposes, but it is also planted for erosion control. In Japan, the decay-resistant wood is used for lumber and the bark provides oakum for calking boats (Bailey 1939; Dallimore and Jackson 1967; McClintock 1992; Rehder 1940). Umbrella-pine is the only species in its genus.

Flowering and fruiting. Flowers of both sexes occur at the ends of branchlets in the spring. The male flowers are in clusters and the female flowers, which develop into ovoid cones, are solitary. When the cones ripen in the fall of the second season, they become gray-brown and are about 76 to 127 mm long and 38 to 51 mm wide. Each cone scale bears 5 to 9 ovoid, compressed, narrowly winged seeds (figure 1) about 13 mm long (Dallimore and Jackson 1967; McClintock 1992; Rehder 1940).

Collection of fruits; extraction and storage of seeds. Ripe cones may be picked in the fall from the trees and placed in a warm, dry place to open; seeds are removed by shaking and then de-winged. Numbers of cleaned seeds per weight ranged from 32,600 to 42,800/kg (14,800 to 19,400/lb) and averaged about 38,150/kg (17,300/lb) in more than 30 samples. Purity averaged 96% in 10 samples (Rafn and Son nd; Swingle 1939). Seeds stored at moisture contents of 10% or less in sealed containers at temperatures of 5 °C or lower will probably retain good viability for at least 2 years. Long-term storage data are not available, but the seeds appear to be orthodox in storage behavior.

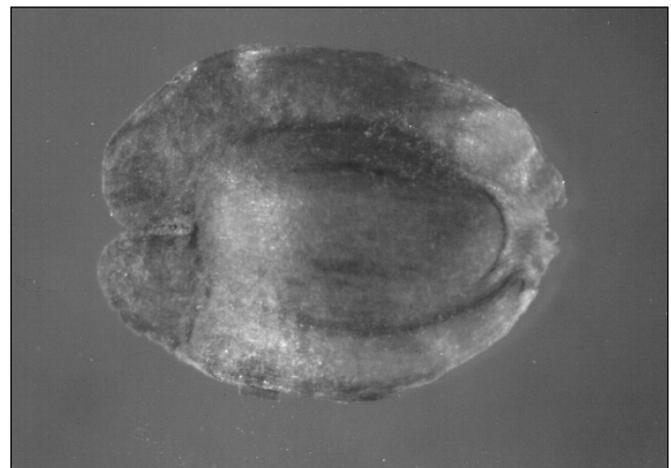
Pregermination treatments. The existing literature is somewhat contradictory. Some authors report reasonable success with 100 days of stratification in moist sand at 17 to

21 °C (Swingle 1939); 90 days of stratification in moist, acid peat at 0 to 10 °C (Barton 1930); and 1 month of stratification at 25 °C followed by 4 to 5 months at 2 °C or a constant 2 °C for 5 to 6 months (Asakawa 1973). Asakawa (1973) also obtained germination rates between 56 and 70% of filled seeds without prechilling. He concluded that their dormancy is not deep.

On the other hand, Hatano (1972) states that it is “well known” that the seeds are deeply dormant and that the dormancy is difficult to break with stratification. He tried a number of pretreatments, including pre-chilling and seed-coat treatments. The only success he had was with 24 hours of pretreatment with 0.02 to 0.10% silver nitrate before stratification, and that success was partial and varied (from 1 to 65% germination).

Germination tests. Germination of umbrella-pine seeds seems to require 2 months or more, even after pretreatment (Asakawa 1973). Germination of pretreated seeds can be tested in germinators or sand flats at a temperature of about 20 °C (night) to 30 °C (day) for 60 to 75 days. Average germination in 14 early tests was 45% (Barton

Figure 1—*Sciadopitys verticillata*, umbrella-pine: seed



1930; Rehder 1940; Waxman 1957). Waxman (1957) obtained best results (76% in 77 days) when seeds were germinated on a sand surface under mist with 9 hours of light daily. In a later test, Asakawa (1973) obtained up to 76% germination on agar with 8 hours of light. Germination is poor in continuous light (Asakawa 1973; Hatano 1972).

Nursery practice. The seeds should be sown in the fall or stratified for sowing in the spring. Umbrella-pine is

not easy to grow and is extremely slow-growing when propagated from seeds (Halladin 1991). It has a tendency to form several leaders. Field planting has been done with 3+2 and 4+2 stock (Dallimore and Jackson 1967). Umbrella-pine can also be propagated by layers or by cuttings of half-ripened wood in summer (Bailey 1939). A nursery in Oregon propagates solely by cuttings because of faster results; Halladin (1991) describes the technique in detail.

References

- Asakawa S. 1973. Germination behavior of *Sciadopitys verticillata* seeds. In: Proceedings, International Symposium on Seed Processing—Seed Problems; 1973; Bergen, Norway. IUFRO. 8 p.
- Bailey LH. 1939. The standard cyclopedia of horticulture. New York: Macmillan. 3639 p.
- Barton LV. 1930. Hastening the germination of some coniferous seeds. American Journal of Botany 17: 88–115.
- Dallimore W, Jackson AB. 1967. A handbook of Coniferae and Ginkgoaceae. 4th ed. 4, Harrison SG, rev. New York: St. Martin's Press. 729 p.
- Halladin P. 1991. *Sciadopitys verticillata*. American Nurseryman 174(8): 73.
- Hatano K. 1972. Dormancy of *Sciadopitys verticillata* seed. Journal of the Japanese Forestry Society 54(8): 264–268.
- McClintock E. 1992. Trees of Golden Gate Park. Pacific Horticulture 53(3): 3–8.
- Rafn J and Son. [nd]. Skovfrøkontoret's Frøanalyser gennem 40 Aar; 1887–1927. Udført paa Statsfrøkontrollen i København. 5 p.
- Rehder A. 1940. Manual of cultivated trees and shrubs. New York: Macmillan. 2996 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.
- Waxman S. 1957. Effects of daylength on the germination of *Sciadopitys verticillata*. Plant Propagators' Society Proceedings 7: 71–72.

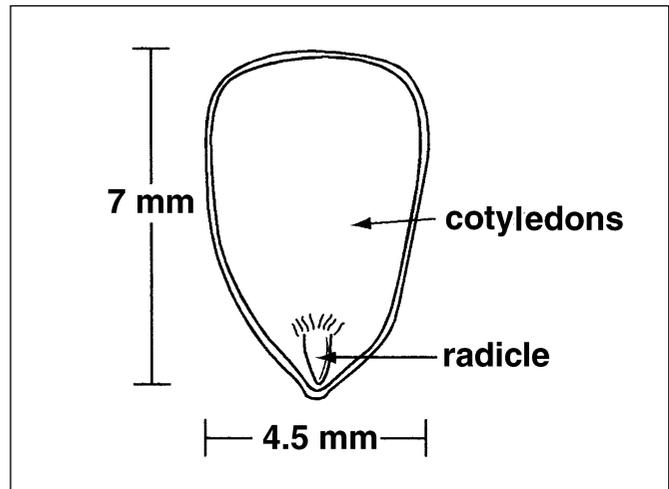
Fabaceae—Pea family

***Senna armata* (S. Watson) Irwin & Barneby**

senna

Jane E. Rodgers

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Synonyms. *Cassia armata* S. Watson**Other common names.** spiny senna, armed senna, bladder senna, partridge pea.**Growth habit, occurrence and use.** The genus *Senna* can be found in herb, shrub, or tree form with even-pinnate leaves; although generally unarmed, it may have weak spines. This large genus is found in the American tropics, temperate zones, and occasionally, the desert (Jepson 1993). This discussion will focus on the Mojave and Colorado species of senna—*Senna armata* (S. Wats.) Irwin & Barneby—which has grooved prominent branches with inconspicuous leaves (Benson and Darrow 1954). The inflated tubular hairs that cover the stem slow air movement, providing some protection against the hot drying air (Bainbridge and Virginia 1989). Senna is common on road berms and edges, preferring a well-drained, gravelly soil (CALR 1995). Senna is an attractive shrub that should be given greater attention in landscaping (Perry 1987).**Flowering and fruiting.** Flowers are yellow to salmon in color with a pleasant fragrance, occurring solitary or several in the axils of the upper leaves (Kay and others 1977). Blooms appear in May to July. The linear, light tan legumes (pods) are 2.5 to 4 cm long and may be somewhat constricted between seeds (Kay and others 1977). Seeds (figures 1 and 2) have a thick, grayish membrane covering a brown surface and are irregularly obovoid, 7 to 9 mm long (Kay and others 1977).**Collection, extraction, and storage.** Seeds may be hand-picked, usually beginning in June and July when they ripen. They should be collected from the bushes, not the ground, to avoid insect infestations. Seed collection must be timed to gather the ripe seeds before they attract small rodents and are eaten by them. Seeds should be dried, then cleaned; freezing may be used to kill pests (Bainbridge and Virginia 1989). Kay (1975) used a belt harvester and fanning mill with a 5.6-mm (#14) top and 7.1-mm (#18) bottom**Figure 1**—*Senna armata*, senna: mature seed.**Figure 2**—*Senna armata*, senna: longitudinal section through a seed.

seed-cleaning screens to extract and clean seeds. Yields were 38,800 seeds/kg (17,600 seeds/lb), 94% undamaged.

The seeds are orthodox in storage behavior. In long-term storage trials by Kay (1988), seeds were stored at room tem-

perature, 4 °C, -15 °C, and in warehouse conditions, with germination rates tested annually over 14 years. The results indicated that, as is common with many legumes stored under low moisture conditions, the already high percentage of hard seeds can increase in cooler temperatures. Bainbridge and Virginia (1989) observed that storage was best in mesh bags stored in a warehouse. In Kay's experiments, decreases in germination rates in sealed containers may reflect some need for after-ripening.

Pregermination treatments. According to Stark (1966), no seed treatment is required for senna, and planting done under optimal conditions produces germination in 2 to 5 days. At the U.S. Department of the Interior, National Park Service's Joshua Tree National Park (JTNP), seeds have been germinated using a 1-hour soak in water or a 1:1 bleach-water solution, followed by leaching for 12 to 24 hours. This method has produced an average germination rate of 50%.

Germination tests. Germination tests at JTNP include direct-sowing to blotter paper, soaking overnight in cold water, and soaking initially in cold water followed by overnight leaching. All 3 methods had moderate success, indicating that no treatment is necessary when seeds are placed directly onto moist toweling; average germination 50% (CALR 1995). Other trials by Kay and others (1988) refer to initial germination of seeds using 4 replications of

100 seeds in damp paper toweling placed in a growth chamber at 15 °C. Test conditions were maintained for 28 days, with germination percentages recorded every 7 days; initial germination rate for senna was 75%. Germination tests, conducted annually to test the effects of storage, were then averaged to a "best germination" of 92%. These annual tests consisted of 4 replications of 50 seeds using the same initial testing methods. The effects of temperature on germination rates were also tested, with the following results (Kay and others 1988):

Temperature (°C)	2	5	10	15	20	25	30	40
Germination (%)	0	0	19	41	46	20	28	0

Nursery practice and seedling care. In direct-seeding trials, germination in Nevada seedlots was best at 15 to 20 °C, but seeds collected at lower elevations may need higher temperatures; no germination was observed at 5 or 40 °C (Bainbridge and Virginia 1989). Nursery stock has been outplanted at JTNP using 3.8-liter (1-gal) and 6.8-liter (1.8-gal) containers that were 35 to 37 cm (14 to 15 in) deep. The plants monitored after 10 months (before late winter precipitation) had respective survival rates of 7 and 14% (CALR 1995). Monitoring continues at the site, and figures may be different after the winter and spring rains. Senna seedlings were noted to be susceptible to rot and should be planted into a well-drained soil with conservative watering (CALR 1995).

References

- Bainbridge DA, Virginia RA. 1989. Restoration in the Colorado Desert: Species notes [unpublished manuscript prepared for the California Department of Transportation].
- Benson L, Darrow RA. 1954. The trees and shrubs of the southwestern deserts. Tucson: University of Arizona Press. 437 p.
- CALR [Center for Arid Lands Management]. 1989-1995. Twentynine Palms, CA: National Park Service, Joshua Tree National Park.
- Jepson WL. 1993. The Jepson manual: higher plants of California. Hickman JC, ed. Berkeley: University of California Press. 1400 p.
- Kay BL. 1975. Tests of seeds of Mojave Desert shrubs [unpublished manuscript prepared for the California Department of Transportation]. Prog. Rep. BLM Contract 53500 CT4-2(N). 24 p.
- Kay BL, Graves WL, Young JA. 1988. Long-term storage of desert shrub seed. Mojave Reveg. Notes 23. Davis: University of California Department of Agronomy and Range Science.
- Kay BL, Ross CM, Graves WL. 1977. Armed senna. Mojave Reveg. Notes 2. Davis: University of California Department of Agronomy and Range Science.
- Perry B. 1987. Trees and shrubs for dry California landscapes. San Dimas, CA: Land Design Publishing. 184 p.
- Stark N. 1966. Review of highway planting information appropriate to Nevada. Bull. B-7. Reno: University of Nevada, College of Agriculture, Desert Research Institute. 71 p.

Sequoia sempervirens (Lamb. ex D. Don) Endl.

redwood

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Other common names. coast redwood, California redwood.

Growth habit, occurrence, and use. Redwood is one of the largest trees in the world. It commonly grows to 60 to 84 m in height and 2.4 to 3.6 m in diameter, with the current champion reaching 101 m in height (Van Pelt 2001). Its relatively shallow but wide-spreading root system rises into a buttressed and somewhat tapering trunk that supports a short, narrowly conical crown (Harlow and Harrar 1969). Individual trees can live 2,000 years or longer. It grows naturally in the summer fog belt of the coastal range from Little Redwood Creek on the Chetco River in southwestern Oregon to Salmon Creek in the Santa Lucia Mountains of southern Monterey County, California. This redwood belt is an irregular coastal strip about 725 km long and 8 to 56 km wide (Roy 1966). Elevation ranges from sea level to 915 m and averages from 635 to 3,100 mm annual precipitation, most of it falling as winter rain (Olson and others 1990).

Redwoods reach their maximum development in the northern part of their range, where the climate is cool and moist and sedimentation from successive floods has created deep fertile alluvial flats. They are smaller and give way to other species as altitude, dryness, and slope increase (Olson and others 1990). Since 1843, redwood has been cultivated outside its natural range, in parts of Europe and New Zealand (Boe 1974; Olson and others 1990).

The wood is used where decay resistance is important. It is made into lumber, plywood, pulpwood, grape stakes, fencing, roof shakes, and other specialized products. Bark is used for insulation and garden mulch (Boe 1974; Harlow and Harrar 1969; Olson and others 1990).

Flowering and fruiting. The tiny male and female flowers grow separately on different branches of the same tree. Ovulate conelets lead to broadly oblong cones with thick scales that are closely packed, woody, and persistent. Each cone scale bears a crescent-shaped row of ovules (Buchholz 1939). Flowering may occur over several months from November to March (Metcalfe 1924), but ovules are

usually fertilized in May (Buchholz 1939). Dry weather during pollination permits better pollen dispersal and improves seed viability (Olson and others 1990). Cone ripening time can range from late September to mid-January, depending on latitude, elevation, and weather (Lippitt 1996).

Trees begin to bear seeds at 5 to 15 years of age (Boe 1974). Good seedcrops occur every 5 to 7 years (Lippitt 1996), with light crops intervening. Fair to abundant crops occurred for 5 consecutive years in north-coastal California (Boe 1968); however, this is unusual (Lippitt 1996). Further south in the redwood type, some stands produce seed poorly and irregularly, whereas others frequently have fair to abundant crops (Muelder and Hansen 1961). A mature seed has a brown wing and a slightly darker seedcoat. The wing, which is part of the seedcoat, is about equal in width to the seed (figure 1). Embryos have 2 cotyledons (figure 2). Opened cones often persist through the next growing season (Boe 1974). Cones have the following quantitative characteristics (Lott 1923; Munz 1959; Olson 1990; Roy 1965):

Seeds per cone scale	2–5
Average seeds per cone	60
Cone length	1.3–2.8 cm
Cone diameter	1.3–2.5 cm
Average fresh cones per weight	500/kg (227/lb)

Because of the polyploid chromosomal make-up of redwood, care should be taken to avoid in-breeding in seed orchards. Seedlings from self-crossed seeds had lower nursery survival under stress and grew slower in the field than those from out-crossed seeds (Libby and others 1981).

A technique for making controlled pollinations on detached redwood cuttings has become practical. Pollination was most effective when dry pollen was brushed between the open scales of the female strobili. In subsequent years, cuttings that have rooted successfully can be pollinated and will produce viable seeds (Libby and McCutchan 1978; Libby and others 1972).

Figure 1—*Sequoia sempervirens*, redwood: seed.

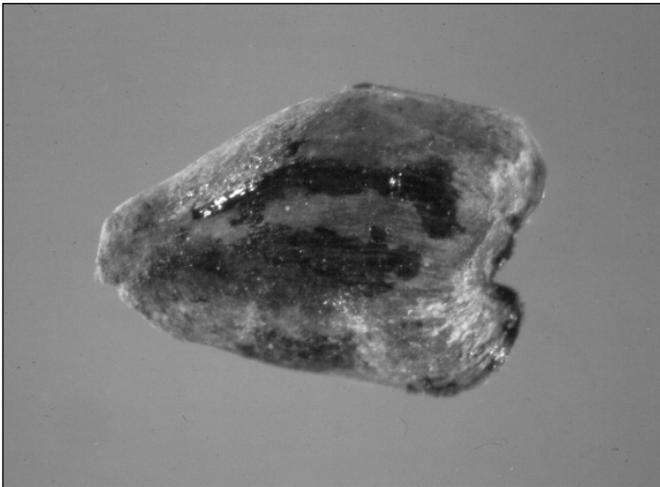
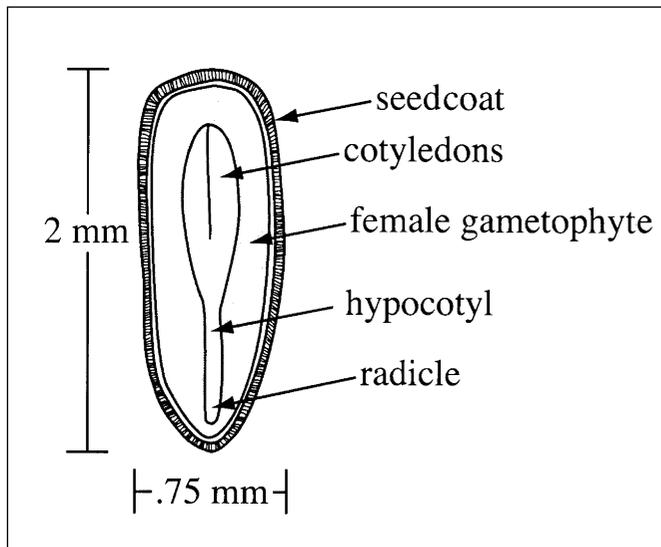


Figure 2—*Sequoia sempervirens*, redwood: longitudinal section through a seed.



Collection of cones and extraction of seeds. Seeds are mature when cone color changes from green to greenish yellow or when cone scales slightly separate (Roy 1965). In the northern part of the redwood's range, cone collections should begin in October (Lippitt 1996). Natural seed dispersal proceeds rapidly after October, reaching a peak from November to February (Boe 1968).

Cones can air-dry in 5 to 8 days at 21 to 24 °C with good air circulation (Lippitt 1996). Large nurseries use a kiln set at 38 to 43 °C to open cones in 24 hours (Lippitt 1996). Seeds are extracted with a screen tumbler. At the L.A. Moran Reforestation Center, Davis, California, the seedlots are repeatedly passed through a 4-way air separator to obtain a high percentage of filled seeds with high germination rate.

Experience with a magnified x-ray makes it possible to distinguish tannin-filled seeds and filled but less viable seeds from seeds that will produce vigorous germinants.

The following seed data have been noted by Lippitt (1996) for cleaned seedlots:

Cleaned seeds per weight		
Low	167,372/kg	(75,920/lb)
High	259,297/kg	(117,617/lb)
Average (N = 37)	194,000/kg	(88,000/lb)
Purity	98%	
Germination	60%	

Storage of seeds. Redwood seeds are orthodox in nature and store well for long periods of time. The L.A. Moran Reforestation Center of the California Department of Forestry and Fire Protection has stored seeds with 5 to 9% water content at -17.8 °C for over 10 years with no loss in viability (Lippitt 1996). Storage of seedlots above freezing has not been successful (Boe 1974; Metcalf 1924; Olson and others 1990; Schubert 1952).

Germination. A 5-year record of seed dispersal in old-growth redwood showed that, of the total seeds dispersed, only 2.5 to 12.4% were sound (Boe 1968). In seeds collected from branch cuttings, Libby and others (1972) measured percentage germination at 5 to 21%. Identification of unsound seeds is often difficult because many seeds that appear to be good are actually filled with tannin (Olson and others 1990). Germination is readily tested in covered petri or plastic dishes on filter paper, vermiculite, or Sponge Rok®. Satisfactory germination has been obtained at a constant temperature of 21 °C as well as at temperatures alternating diurnally from 30 to 20 °C. The International Seed Testing Association (ISTA 1993) prescribes the alternating temperatures on the top of moist paper for 21 days; no pretreatment is needed. Germination speed can be increased by soaking the seeds overnight in aerated water (Olson and others 1990). Germination is epigeal.

Germination capacity has typically been low in the past, but this can be corrected by thorough seed processing. Redwood seed germination can be improved by 24 hours of water soaking followed by 4 weeks of stratification (Lippitt 1996).

Nursery practice and seedling care. Redwood seeds may be sown from March to May. Seeds are sown by drilling to a depth of 3 mm (1/8 in) and at a rate calculated to give a density of 323 seedlings/m² (30/ft²) for either 1+0

or 2+0 planting stock. All seedbeds are fumigated as standard practice. Mineral soil provides the best seedbed, but seeds will germinate in duff, on logs, and on most moist surfaces. Seeds can germinate in either shade or sunlight (Olson and others 1990), but frost protection is important (Lippitt 1996). Redwood seedlings need a greater supply of soil water than most associated species (Fritz 1966). The roots lack root hairs and, therefore, are not efficient in

extracting water from the soil (Olson and others 1990). If the seeds are sown in fumigated beds, the beds should be inoculated with endomycorrhizae (Lippitt 1996). From 10 to 20% of the seedlings may be culled at the time of lifting (Boe 1974). Redwood seedlings are especially susceptible to damping-off, which is caused by gray mold (*Botrytis cinerea* Pers.:Fr.) and a blight caused by *Cercospora sequoiae* Ellis & Everh. (Sinclair and others 1987).

References

- Boe KN. 1968. Cone production, seed dispersal, germination in old-growth redwood cut and uncut stands. Res. Note PSW-184, Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. 7 p.
- Boe KN. 1974. *Sequoia sempervirens* (D. Don) Endl., redwood. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington DC: USDA Forest Service: 764–766.
- Buchholz JT. 1939. The embryogeny of *Sequoia sempervirens* with a comparison of sequoias. American Journal of Botany 26(4): 248–257.
- Fritz E, Rydelius JA. 1966. Redwood reforestation problems: an experimental approach to their solution. San Francisco: Foundation for American Resource Management: 130 p.
- Harlow WM, Harrar ES. 1969. Textbook of dendrology. New York: McGraw-Hill: 171–176.
- ISTA [International Seed Testing Association]. 1993. Rules for testing seeds: rules 1993. Seed Science and Technology 21 (Suppl.): 1–259.
- Libby WJ, McCutchan BG. 1978. "Taming" the redwood. American Forests. 84(8): 37–39.
- Libby WJ, Kiang YT, Yinhardt YB. 1972. Control pollination seeds from cutting of coast redwood. Silvae Genetica 21 (1/2): 17–20.
- Libby WJ, McCutchan BG, Miller CI. 1981. Inbreeding depression in selfs of redwood. Silvae Genetica 30(1): 15–25.
- Lippitt L. 1996. Unpublished data. Davis: California Department of Forestry and Fire Protection, Lewis A. Moran Reforestation Center.
- Lott H C. 1923. The production and viability of redwood (*Sequoia sempervirens*) seed [master's thesis]. Berkeley: University of California. 32 p.
- Metcalf W. 1924. Artificial reproduction of redwood (*Sequoia sempervirens*). Journal of Forestry 22: 873–893.
- Muelder DW, Hansen JW. 1961. Observations on cone bearing of *Sequoia sempervirens*. Calif. For. & Forest Prod. 26. Berkeley: University of California School of Forestry: 6 p.
- Munz PA. 1959. A California flora. Berkeley: University of California Press: 1681 p.
- Olson Jr DF, Roy DF, Walters GA. 1990. *Sequoia sempervirens* (D. Don) Endl., redwood. In: Burns RM, Honkala BH eds. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington DC: USDA Forest Service: 541–551.
- Roy DF. 1965. Redwood (*Sequoia sempervirens* (D. Don) Endl.). In: Fowells HA, comp. Silvics of forest trees of the United States. Agric. Handbk. 271. Washington DC: USDA Forest Service: 663–670.
- Roy DF. 1966. Silvical characteristics of redwood (*Sequoia sempervirens* [D. Don] Endl.). Res. Pap. PSW-28. Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. 20 p.
- Schubert GH. 1952. Germination of various coniferous seeds after cold storage. Res. Note PSW-83. Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station: 7 p.
- Sinclair WA, Lyon HH, Johnson WT. 1987. Diseases of trees and shrubs. Ithaca, NY: Cornell University Press: 574 p.
- Van Pelt R. 2001. Forest giants of the Pacific Coast. Vancouver, BC: Global Forest Society: 16–29.

Taxodiaceae—Redwood family

Sequoiadendron giganteum (Lindl.) Buchholz

giant sequoia

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Synonyms. *Sequoia gigantea* (Lindl.) Decne., *Sequoia washingtoniana* (Winslow) Sudw.

Other common names. bigtree, Sierra redwood.

Growth habit, occurrence, and use. This species grows to heights exceeding 76 m in central California on the western slopes of the Sierra Nevada in more or less isolated groves at 1,400 to 2,300 m of elevation. Its north-south range is about 420 km (Schubert and Beetham 1965; Weatherspoon 1990). It has been cultivated rather widely since 1853 for landscaping, watershed planting, and lumber (Boe 1974).

Geographic race. On the basis of differences of cotyledon number, isoenzyme allele frequencies, variation in germination percentage, and observed heterozygosity in 35 natural populations, a level of genetic variation was detected. Relatively higher levels of heterozygosity were found in the southern parts of the range, suggesting different local selection pressures. Low heterozygosity among embryo samples suggests that inbreeding and/or population structuring has taken place (Fins and Libby 1982). Field studies in Germany further support the concept that there are provenance differences in this species. Best growth was found in seedlings grown from seed sources from the central and southern portions of the natural range (Dekker-Robertson and Svolba 1993).

Flowering and fruiting. Flowering is monoecious. The small, enclosed terminal buds differentiate in late summer, and flowering and pollination occur the following spring between mid-April to mid-May, when conelets are quite small. Conelets are about half size in July and reach full size in August, when fertilization takes place. At the start of winter the embryos have only a few cells, and they remain this way overwinter. Embryos develop rapidly the following summer and by late August, the second year after pollination, they are morphologically mature (Buchholz 1938). Young trees start to bear cones about age 20 (Stark 1968).

Cones may remain attached to the tree for many years, and most seeds are retained. During late summer, however,

when cone scales shrink, some seeds are shed. As soon as cones become detached, they dry out, and the seeds are liberated within a few days (Buchholz 1938). This fruiting characteristic provides seeds every year in the groves. Cones show the following quantitative characteristics (Munz 1959; Schubert and Beetham 1965):

Scales per cone	25–40
Seeds per scale	3–9
Seeds per cone (average)	230
Cone length	5–9 cm

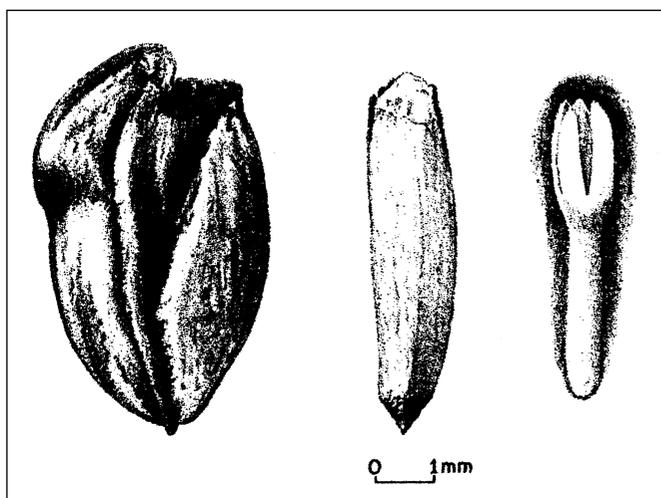
Seeds measure 3 to 6 mm long and are compressed and surrounded by laterally united wings that are broader than the body of the seed (figure 1). Embryos have 3 to 5 cotyledons (Boe 1974).

Collection, extraction, and storage. The old, persistent cones can be collected at any time; but for fresh cones, collections should be made in September and later. Squirrels cut and cache cones that furnish considerable quantity for collection (Boe 1974). Cones should be air-dried at 30 °C for about 7 days, or heated in a cone kiln at 38 to 40 °C for 24 hours. Seeds can be then extracted in a tumbler and screened to remove cones and other debris. Underdeveloped and resin-filled seeds can be removed with pneumatic cleaners. Multiple passes through a cleaner should yield seedlots with > 99% purity (Lippitt 1996). Yield and size of cleaned seeds are as follows (Lippitt 1996):

Average weight of seeds per volume of cones	402 g/hl	5 oz/bu
Cleaned seeds per weight		
Low	113,625/kg	51,530/lb
High	199,810/kg	90,620/lb
Average (29 samples)	173,100/kg	78,500/lb

Giant sequoia seeds are orthodox in storage behavior. They can be stored for 10 years or more at –18 °C with

Figure 1—*Sequoiadendron giganteum*, giant sequoia: seed with wings (**left**), seed with outer coat removed (**center**), and excised embryo (**right**).



seed moisture of 5 to 9% (Lippitt 1996).

Germination. Germination values of giant sequoia seedlots has been reported from 30 to 73%. Optimum constant temperature for germination seems to be between 15 and 21 °C, but diurnally alternating temperatures of 30 to 20 °C are also satisfactory (table 1). A temperature of 6 °C was too cool and continuous 30 °C was too warm. Continuous light (day and night) or alternating light and dark periods produced about the same results. There is some dormancy in these seeds and stratification is needed for prompt germination. Good results (55% average germination) have been obtained by leaching seeds in running water for 24 hours, surface-drying them, and stratifying them in plastic bags without medium for 6 weeks at 2 °C (Lippitt 1996). Average germination values of 41 and 35% were obtained following overnight soaking and stratification at 2.2 to 2.8 °C for 91 days with or without a fungicide. The rate of germination is reduced in the presence of the fungicide (Fins 1981).

Nursery practice. For bareroot production, stratified

seeds should be sown between mid-March and mid-April on the surface of the bed and covered with about 6 mm ($1/4$ in) of aged sawdust. In the absence of fumigation, seeds should be sown in soil that has been used recently to grow an endomycorrhizal species—for example, giant sequoia, coast redwood (*Sequoia sempervirens* (D. Don) Endl., or incense-cedar (*Calo cedrus decurrens* Torr.)—or that has been inoculated with soil from such beds. The target bed density should be 245 seedlings/m² (23/ft²) (Lippitt 1996).

For container production, stratified seeds should be sown in May. Seeds should be covered very lightly, about 3 mm ($1/8$ in). Damping-off and other fungi can be serious problems with this species. Infection can be reduced by minimizing water on the foliage by irrigating early in the day, “wandering” the foliage after irrigation, and using fans to maintain good air circulation (Lippitt 1996).

References

- Boe KN. 1974. *Sequoiadendron giganteum* (Lindl.) Buchholz, giant sequoia. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 767–768.
- Buchholz JT. 1938. Cone formation in *Sequoia gigantea*: 1. The relation of stem size and tissue development to cone formation. 2. The history of the seed cone. American Journal of Botany 25: 296–305.
- CDF [California Division of Forestry]. 1968. Correspondence. Davis, CA: CDF Davis Headquarters Nursery.
- Dekker-Robertson DL, Svolba J. 1993. Results of *Sequoiadendron giganteum* (Lindl.) Buch. provenance experiment in Germany. Silvae Genetica 42(4-5): 199–206.
- Fins L. 1981. Seed germination of giant sequoia. Tree Planters' Notes 32(3): 39.
- Fins L, Libby WJ. 1982. Population variation in *Sequoiadendron*: seed and seedling studies, vegetative propagation, and isozyme variation. Silvae Genetica 31(4): 102–110.
- Lippitt L. 1996. Unpublished data. Davis: California Department of Forestry and Fire Protection, L.A. Moran Reforestation Center.
- Munz PA. 1959. A California flora. Berkeley: University of California Press. 1681 p.
- Schubert GH, Beetham NM. 1965. Giant sequoia (*Sequoia gigantea* [Lindl.] Decne.). In: Silvics of forest trees of the United States. Agric. Handbk. 276. Washington, DC: USDA Forest Service: 658–662.
- Stark N. 1968. Seed ecology of *Sequoiadendron giganteum*. Madroño 19(4): 267–277.
- Weatherspoon CP. 1990. *Sequoiadendron giganteum* (Lindl.) Buchholz, giant sequoia. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA

Table 1—*Sequoiadendron*, giant sequoia: pregermination treatments, germination test conditions, and results

Cold stratification period (days)	Germination test conditions*					Avg % germination	Samples
	Daily light (hr)	Temp (°C)		Days			
		Day	Night				
0	<16	15	15	32		43.1	10
0	24	5	5	32		4.1	10
0	24	20	20	32		40.9	10
0	24	30	30	32		5.6	10
28	—	30	20	28		38.5	2
0	—	30	20	28		30.3	3

Sources: CDF (1968), Stark (1968).

* Tests were made on filter paper in petri dishes (Stark 1968) or on vermiculite (CDF 1968).

Arecaceae—Palm family

Serenoa repens (Bartr.) Small saw-palmetto

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Synonym. *Serenoa serrulata* (Michx.) Nichols.

Growth habit, occurrence, and use. Saw-palmetto usually is an evergreen shrub, 0.6 to 2.1 m tall, with creeping, horizontal stems. Occasionally, the species attains the size of a small tree, reaching a height of 1.8 to 2.3 m, with an erect or oblique stem (Bailey 1976; Vines 1960). The common name, saw-palmetto, derives from the ascending, palmate leaves, which are rather stiff and have long petioles heavily armed with sharp, rigid, recurved teeth. These armed petioles are capable of severely scratching the skin and ripping clothing and shoes.

Saw-palmetto occurs from coastal South Carolina southward to Florida and westward to eastern Louisiana (Bailey 1939). It reaches its most extensive development in the pine flatwoods of the lower coastal plain of Georgia and Florida. Along Florida's eastern seaboard ridge grows a silver leaf variety that is highly prized for ornamental use. Saw-palmetto occurs in highest densities in flatwoods that have been burned annually or biannually (Abrahamson 1984). Saw-palmetto provides wildlife habitat for over 100 animal species (Carrington and others 2000; Hilmon 1986). Fatty acid extracts from the partially dried, ripe fruits (called "serenoa") are used as a phytotherapeutic agent in treating certain irritations of the bladder, prostate gland, and urethra (Ganzer 1999; Vines 1960). In some places, the large fan-shaped leaves (fronds) are used to thatch roofs on temporary structures, and larger stems are occasionally used for crude logs.

Large quantities of saw-palmetto leaves are shipped north for Christmas decorations; the flowers are a significant source of honey; and the stems are a source of tannic acid extract (Vines 1960). Saw-palmetto is increasingly used as a landscape plant to provide a naturalistic effect.

Flowering and fruiting. The numerous, small, white flowers are borne in panicles that emerge in February and March in southern Florida and in April in southern Georgia (Carrington and others 2000; Hilmon 1968; Vines 1960). The panicles appear on branches that are shorter than the leaves. The inflorescences and vegetative branches arise

from buds identical in their position in the leaf axil and indistinguishable in their early development. In an adult plant, as much as half of the axillary buds abort; of those remaining, most (~80%) become inflorescences and the others (~20%) become vegetative suckers (Fisher and Tomlinson 1973). The inflorescence bud's first leaf is called a prophyll and its mouth splits as younger bracts grow through it; subsequent bracts are distichously arranged and encircle the main axis of the inflorescence (Fisher and Tomlinson 1973).

The flowers are perfect with 6 stamens and 1 stigma within 1 style (Radford and others 1964). Several thousand flowers per inflorescence are produced from buds at the bases of the previous year's leaves. Saw-palmetto plants must be at least 60 cm high to flower in the wild (Carrington and others 2000). The number of leaves produced per year after a disturbance is a good indicator of flowering.

Fire stimulates the initiation of inflorescences in sexually mature saw-palmettos by reducing the canopy and thus increasing light availability. Although a burn at any time of year stimulates flowering within 1 year of the fire, frequent burning reduces flower and fruit production. Two sites of 40 saw-palmetto plants were studied in a 6-year period and burned every 2 years. The plants flowered 36 times, with approximately 40% flowering occurring within 1 year of burning (Hilmon 1968). Saw-palmetto plants flowered 65% of the time following a burn on flatwood sites, and 85 to 90% bloomed after 2 or 3 burns (Abrahamson 1999). On scrub stand sites, saw-palmetto flowered 56% after a prescribed burn, 62% after the second-season burn, then returned to preburn levels ($\geq 12\%$) by the third season after burning (Abrahamson 1999). The saw-palmettos produced more inflorescences per plant following the second and third fires. To maximize flower and fruit production, a site should be burned no more than every 4 years (Abrahamson 1999; Hilmon 1968). Stands of saw-palmetto on scrub and sandhills that had not been burned in a long time had relatively closed canopies and low reproductive frequencies ($\geq 16\%$).

Cultural treatments have been used to stimulate flowering. Fertilizer (10% N, 5% P₂O₅, 5% K₂O) and dolomite lime (49% CaCO₃, 36% MgCO₃, and 10% Mg) applied at a rate of 155 g per plant around the plant's drip line, did not influence flowering. But when crowns were clipped and plants fertilized, there was a significant elevation in flowering during the second growing season: 18% flowering in treated plants compared to 4% flowering in control plants (Abrahamson 1999). Saw-palmettos that were only clipped had a 22% flowering response.

The fruit is a drupe measuring about 1.5 to 3 cm long and 15 to 20 mm in diameter, that is ovoid-oblong, green or yellow before ripening, and bluish to black when ripe (Hilmon 1968; McCurrach 1960; Vines 1960) (figure 1). Immature green fruits are present from May through July, turn orange by August, and ripen to bluish-black in September and October (Carrington and others 2001). Each drupe contains a single globose seed (figures 1 and 2), and the embryo is laterally oriented (Bailey 1976).

Each inflorescence typically produces 4 to 5 kg (9 to 11 lb) of fruits (Vines 1960) and can produce up to 12 kg (27 lb) in a good year (Carrington and others 2000). The average fruit yield for a site is 200 kg/ha; yields can vary from 150 kg/ha to over 1,500 kg/ha (Carrington and others 1997).

In Florida, anthracnose infection—by *Colletotrichum gloeosporioides* (Penz.) Penz. & Sacc.—has been identified as a major factor (90%) in fruit loss. The remaining 10% of the loss is caused by a caterpillar (*Atheloca* sp.) (Carrington and others 2001).

Collection of fruits. In south Florida, fruit harvesting begins in August, when fruits turn orange. In south Georgia, harvesting begins in early September, when fruits begin to turn black. The fruits are collected by snapping the panicles by hand, cutting them with pruning shears, or shaking the attached fruits into burlap bags, plastic sheets, or the bed of a truck. Seeds are available commercially within the natural range of the species.

Extraction and storage of seeds. Palmetto fruits can be dried in the sun or in indoors in bins or tobacco barns. The fruits are piled about 0.6 to 1.0 m high (Carrington and others 2000). Fruits are dried at 54 °C (not to exceed 60 °C) for about 3 days; fruits in bins are turned every 12 hours (Carrington and others 2000). The initial moisture content is about 66% fresh weight; the fruits are then dried to a maximum of 10% for storage.

Large suppliers store the freshly harvested fruits in wet tanks holding 100,000 kg (250,000 lb). The berries are conveyed to a stainless steel dryer with a capacity of drying 300,000 kg (750,000 lb) per day. The dryer takes an hour to dry a batch of fruits, thus preserving more of the fatty acids

used for phytopharmaceuticals. After drying, a blower is used to remove leaves, stems, and other trash (SPHC 2002).

Seeds must be extracted from the fruits or germination will not occur, even after 222 days (Hilmon 1968). If high temperatures (35 °C) are maintained throughout the germination period, dried fruits will germinate in a greenhouse (Perkins 2002). Seed may be extracted by running the fruits through a macerator or other suitable device for separating the seeds from the pulp. Dried saw-palmetto fruits average 720/kg (326/lb); the dry seeds average 2,380/kg (1,081/lb) (Hilmon 1968).

Steel silos holding 100,000 kg (250,000 lb) are used for storing dried fruits. In a “low-tech” method, the dried fruits are stored in burlap bags and housed where they will not freeze. Seeds stored dry at room temperature for 3 months retained their viability (Hilmon 1968). After 1 year of storage, viability drops slightly; after the second year, viability drops about 50% (Perkins 2002). No tests of seed storage under a variety of conditions or different time periods have been reported.

Pregermination tests. Pregermination treatments of saw-palmetto seeds indicate that they require high temperatures throughout the germination period. Pretreatment temperatures (25, 35, and 45 °C) were significantly different for maximum germination and days to 50% final germination. Average germination for all treatments at 25 °C was 52.3% and 72 days to 50% final germination; germination at 35 °C was 60.8% and 47 days to 50% final germination; and germination at 45 °C was 41.9% and 61 days to 50% final germination (Carpenter 1986).

Non-imbibed seeds required significantly more time to achieve 50% final germination than did imbibed seeds at 25, 35, and 45 °C. Seed weights increased from 34 to 39% for imbibed seeds (Carpenter 1987). Seedlots that were soaked for 7 days in water or wet peat moss reached 50% final germination in 39.8 and 33.7 days at 35 °C, with maximum germination values of 75 and 80%, compared to lots of un-imbibed seeds, which took 53 days to 50% final germination with 46% germination (Carpenter 1987). Soaking seeds in water for 7 days at 35 °C resulted in 10% higher germination and 27 days earlier germination when compared with soaking seeds in water at 25 °C (Carpenter 1986). There was also a 20% higher germination at 35 °C and 15 days earlier germination when compared with 45 °C soaking temperature (Carpenter 1986). There was no significant difference in germination and days to 50% final germination between seeds soaked for 7 days in water were compared to seeds stored in damp peat moss for 7 days at 25, 35, and 45 °C (Carpenter 1986). There was no interaction in germination response between temperature and seed soaking treatments.

Figure 1—*Serenoa repens*, saw-palmetto: fruit (**top**) and seed (**bottom**).

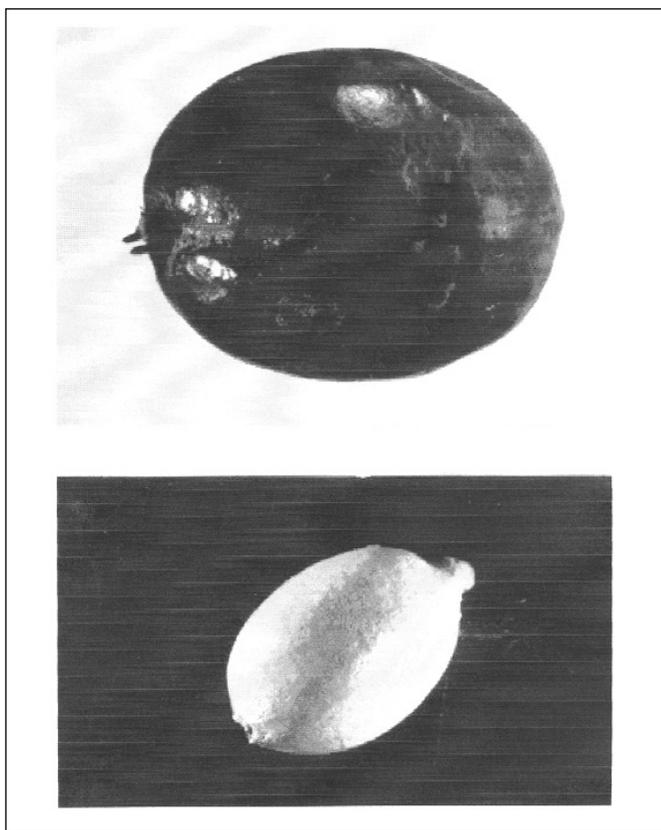
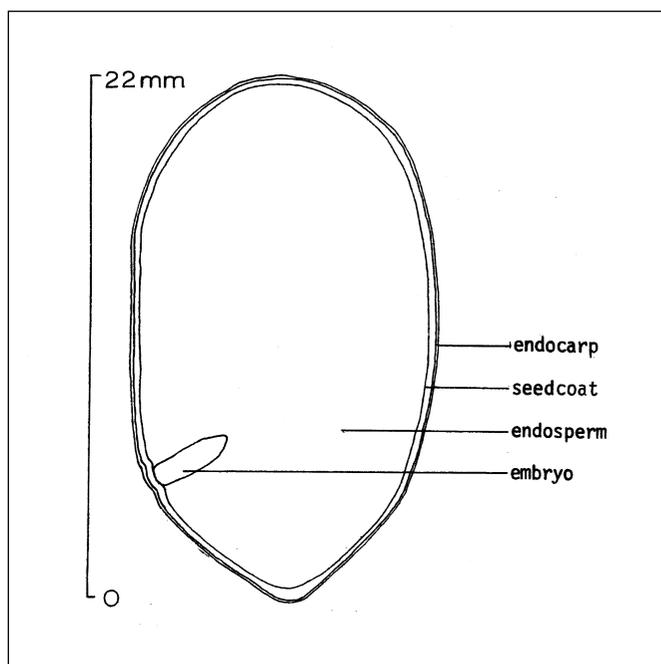


Figure 2—*Serenoa repens*, saw-palmetto: longitudinal section through a seed.



All seed treatments resulted in lower germination values than those of controls at each temperature. The germination over all temperatures dropped from 76% for no treatment to 13% for a 15-minute soak in sulfuric acid (H_2SO_4). Seed embryos were injured and killed by soaking in the acid for 15 minutes and to a lesser degree for 5 minutes (Carpenter 1986). Gibberillic acid and mechanical scarification treatments did not increase the total germination or reduce the days to 50% of final germination. Seed germination was reduced and delayed by 15 minutes of scarification (Carpenter 1986). The germination temperatures used in experiments Carpenter (1986 and 1987) were 34 and 21 °C with bottom heat at 30 °C provided to the propagation medium in the greenhouse. Seeds were planted 6 cm deep in clean builders' sand.

Germination tests. Germination tests were made with fresh seedlots treated in several ways—with and without pulp, endocarp intact and crushed, or with embryo and endosperm exposed (Hilmon 1968). Only extracted seeds germinated. The tests were made on moist filter paper with daytime temperatures of 26 to 28 °C and nighttime temperatures of 13 to 22 °C. Seeds with the micropyle cap removed and the embryo exposed began to germinate in 11 days; it took seeds with the cap intact 45 to 66 days to germinate. After 222 days, however, the germinative capacity of all extracted seeds was similar and ranged from 50 to 60%.

In another test, 5 replications of 20 seeds each from 3 different seed sources were tested under conditions nearly identical to those just described (Hilmon 1968). First germination occurred between 45 and 66 days. A period of slow germination was followed by a period of rapid germination (optimum period), during which approximately half of the seeds germinated. Optimum germination began 4½ to 6 months after planting. Germinative capacity after 231 days ranged from 65 to 85%, and all ungerminated seeds appeared viable. The germination temperatures used in the experiments cited above (Carpenter 1986, 1987) were 34 and 21 °C, with bottom heat at 30 °C provided to the propagation medium in the greenhouse. Seeds were planted 6 cm deep in clean builders' sand.

Nursery practices. Freshly cleaned seeds are placed in large vats for a week to ferment. Without rinsing, the seeds are sown 1.25 to 2.5 cm (½ to 1 in) deep in a seedbed in the greenhouse. Dried seeds are soaked in water for 5 to 7 days at 32 to 38 °C before they are sown in the seedbed.

Seeds should not be sown until the nighttime temperature is constantly above 21 °C. Germination of fresh seeds averaged from 50 to 70%, compared to that of dried seeds, which averaged 30 to 50%. The first leaf of the seedling emerges above the soil 1 to 2 months after germination (Fisher and Tomlinson 1973). It takes 90 days to reach peak germination in the greenhouse (Perkins 2002).

After peak germination, the seedlings are transplanted to liners in a well-drained medium and grown with liquid fertilizer for 6 months. They are then transferred to 3.8-liter (1-gal) containers to grow for 12 to 16 months. The final step is transplanting the saw-palmetto into 11.4-liter (3-gal) containers to grow 12 to 16 months before they are finally ready to sell (Perkins 2002). Slow-release fertilizers are used for both sizes of containers.

References

- Abrahamson WG. 1984. Species responses to fire on the Florida Lake Wales Ridge. *American Journal of Botany* 71(1): 35–43.
- Abrahamson WG. 1999. Episodic reproduction in two fire-prone palms, *Serenoa repens* and *Sabal etonia* (Palmae). *Ecology* 80(1): 100–115.
- Bailey LH. 1939. *The standard cyclopedia of horticulture*. New York: Macmillan. 3639 p.
- 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.
- Carpenter WJ. 1986. Temperature and imbibition effects on seed germination of *Sabal palmetto* and *Serenoa repens*. *Horticultural Science* [1987 August] 22(4): 660.
- Carpenter WJ. 1987. Seed germination of *Serenoa repens*. *Proceedings of the Annual Meeting of the Florida State Horticultural Society* [1986] 99: 158–159.
- Carrington ME, Mullah JJ, Roma F. 1997. Saw palmetto: a fountain of youth. *Proceedings of the American Forage and Grassland Council* [1997] 6: 233–237.
- Carrington ME, Mullahey JJ, Krewer G, Boland B, Affolter J. 2000. Saw palmetto (*Serenoa repens*): an emerging forest resource in the southeastern United States. *Southern Journal of Applied Forestry* 24(3): 129–134.
- Carrington ME, Roberts PD, Urs RR, McGovern RJ, Seijo TE, Mullahey JJ. 2001. Premature fruit drop in saw palmettos caused by *Colletotrichum gloeosporioides*. *Plant Disease* 85(2): 122–125.
- Fisher JB, Tomlinson PB. 1973. Branch and inflorescence production in saw palmetto (*Serenoa repens*). *Principes* 17: 10–19.
- Ganzera M, Croom EM, Khan IA. 1999. Determination of the fatty acid content of pumpkin seed, pygeum, and saw palmetto. *Journal of Medicinal Food* [1999 November 1] (1): 21–27.
- Hilmon JB. 1964. *Plants of the Caloosa Experimental Range*. Res. Pap. SE-12. Asheville, NC: USDA Forest Service, Southeastern Forest Experiment Station. 24 p.
- Hilmon JB. 1968. *Autecology of saw-palmetto (Serenoa repens) (Bartr.) Small* [unpublished PhD dissertation]. Durham, NC: Duke University.
- McCurrach JC. 1960. *Palms of the world*. 290 p. Harper Bros., New York.
- Perkins D. 2002. Personal communication. LaBelle, FL: Perkins Nursery.
- Radford AE, Ahles HE, Bell CR. 1964. *Manual of the vascular flora of the Carolinas*. Chapel Hill: University of North Carolina Press. 1183 p.
- SPHC [Saw Palmetto Harvesting Company]. 2002. International supplier of saw palmetto (*Serenoa repens*) raw materials... [website: www.sawpalmetto.com/]. Frostproof, FL.
- Vines RA. 1960. *Trees, shrubs, and woody vines of the Southwest*. Austin: University of Texas Press. 1104 p.

Elaeagnaceae—Oleaster family

Shepherdia Nutt.

buffaloberry

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Growth habit, occurrence, and use. The genus *Shepherdia*—commonly called buffaloberry—is found wholly in the north and west of North America. It includes 3 species with varying distributions and uses (table 1). All are capable of fixing nitrogen in root nodules that contain bacteria (Mozingo 1987; Thilenius and others 1974).

Silver buffaloberry is a shaggy-barked, thorny, deciduous, large shrub to small tree up to 6 m tall, that often forms thickets. Plants spread by underground stems and readily sucker. Leaves are silvery and scurfy; both surfaces are covered with small star-shaped scales that reflect the light and account for the shrub's rusty silver aspect. These scales undoubtedly help reduce water loss during the summer (Knudson and others 1990; Lackschewitz 1991; Mozingo 1987; Wasser 1982; Welsh and others 1987).

Habitat includes moderate-textured soils at 1,100 to 2,300 m, along moist stream banks, terraces, and hillsides to open dry regions of the plains, and frequently on valley bottoms where the soil is not too saline (Knudson and others 1990; Smith 1987; Wasser 1982; Welsh and others 1987).

Silver buffaloberry with its strong grazing resistance, aided by thorny branches and root sprouting, has considerable potential for shelterbelts and for game food and cover plantings. It often forms single-clone patches and nearly impenetrable clumps. It is an important source of cover and

food for small and large game animals (Knudson and others 1990). This species is regarded as poor to fair forage for sheep, deer (*Odocoileus* spp.), and elk (*Cervus elaphus*), and generally considered worthless for cattle. The fruits provide abundant and nutritious food and are highly sought after by birds (Mozingo 1987; Wasser 1982). The berries are edible and were used by Native Americans and are still commonly used as they make excellent jelly (Borland 1994; Knudson and others 1990; Lackschewitz 1991).

Russet buffaloberry is a thornless, deciduous, small to medium shrub with a characteristically spreading growth form, 1 to 3 m tall at maturity (Lackschewitz 1991; Mozingo 1987; Stubbendieck and others 1986). Twigs are slender, round, and densely scurfy with rusty, bran-like scales. Leaves, which are paired, have a bright green upper surface and paler lower surface with conspicuous brown scales (Lackschewitz 1991; Welsh and others 1987). This species is very cold and drought hardy and it can grow in a variety of habitat types. It is typically found along the banks of streams, and on moist open wooded slopes at 1,000 to 3,400 m. It can also be found on sandy or rocky, often sterile, soils. At its southern extremity, it is confined to the higher vegetation zones in the mountains (Link 1993; Mozingo 1987; Thilenius and others 1974).

Table 1—*Shepherdia*, buffaloberry: nomenclature and occurrence

Scientific name & synonym(s)	Common name	Occurrence
<i>S. argentea</i> (Pursh) Nutt. <i>Lepargyrea argentea</i> (Pursh) Greene <i>Elaeagnus utilis</i> A. Nels.	silver buffaloberry , buffaloberry, redberry, silverberry, bullberry, wild-oleaster	Manitoba to Alberta, to Oregon & California, through the Great Basin to New Mexico, Kansas & the Dakotas
<i>S. canadensis</i> (L.) Nutt. <i>Lepargyrea canadensis</i> (L.) Greene <i>Elaeagnus canadensis</i> (L.) A. Nels.	russet buffaloberry , Canadian buffaloberry, thornless buffaloberry, wild-oleaster, wild-olive, nannyberry, soaplallie, soapberry	Newfoundland to Alaska, from central Maine, to Washington, through Oregon, Utah, & New Mexico
<i>S. rotundifolia</i> Parry <i>Lepargyrea rotundifolia</i> (Parry) Green	roundleaf buffaloberry	S Utah, N Arizona

Source: Thilenius and others (1974).

Russet buffaloberry has little or no browse value for cattle and is only fair for sheep before frost. The berries are bitter and though not highly palatable to humans are eaten by birds and other wildlife (Lackschewitz 1991; Stubbendieck and others 1986).

Roundleaf buffaloberry has a low sprawling habit and is mainly 1 to 2 m tall, and 1 to 4 m wide. The thornless brachlets are covered with small white to yellowish hairs often appearing silver. The thick, persistent, somewhat evergreen leaves are silvery green above, and pale densely scurfy beneath, and as the name implies, circular or oval in outline (Welsh and others 1987). This species inhabits warm, dry, sandy or rocky slopes and occurs from southern Utah into the Grand Canyon region of Arizona throughout the saltbrush, sagebrush, and piñon zones. Welsh and others (1987) describe roundleaf buffaloberry thusly: "This is a beautiful shrub. It festoons slopes with silvery clumps." It is reported to have some value as a winter browse in southeastern Utah.

Flowering and fruiting. Buffaloberries are dioecious. The small, petal-less, yellow to yellowish green flowers are borne single or clustered at the nodes. Plants resume growth in very early spring, usually soon after snowmelt. Flowering occurs quite early in the season (March to April), before or soon after the leaves appear. Fruits mature in late summer and fall (late June to September), varying with environment and source of planting stock (Borland 1994; Mozingo 1987; Thilenius and others 1974; Vories 1981; Wasser 1982).

Fruits are 3.2 to 8.5 mm in diameter and drupe-like, with a solitary smooth achene or small nutlet enveloped in a fleshy perianth. Color of mature fruits vary from orange-red (silver buffaloberry), red-yellow (russet buffaloberry), to silvery (roundleaf buffaloberry) (McTavish 1986; Mozingo 1987; Smith 1987; Wasser 1982; Welsh and others 1987). Cleaned achenes are used as seeds (figures 1 and 2). Minimum seed-bearing age is 4 to 6 years (Thilenius and others 1974).

Seedcrop quality and quantity can vary from year to year. McTavish (1986) reports that one of the major propagating problems with russet buffaloberry is poor seed quality. Researchers have obtained widely varying germination percentages from year to year under identical treatments. This seems to be due to poor embryo development. Therefore, it is suggested that seed collectors check the seeds before collection to ensure that proper embryo development has taken place (McTavish 1986).

Collection of fruits. The fruits may be harvested by stripping or flailing them from the bushes onto canvas; they may also be picked by hand or collected from the ground. The use of mechanical shakers has shown to be effective in harvesting the seed of silver buffaloberry (Halderson 1986). Heavy gloves should be used when collecting this species to avoid injury from the thorns. Care should be taken when

Figure 1—*Shepherdia argenta*, silver buffaloberry: exterior view of cleaned achenes.

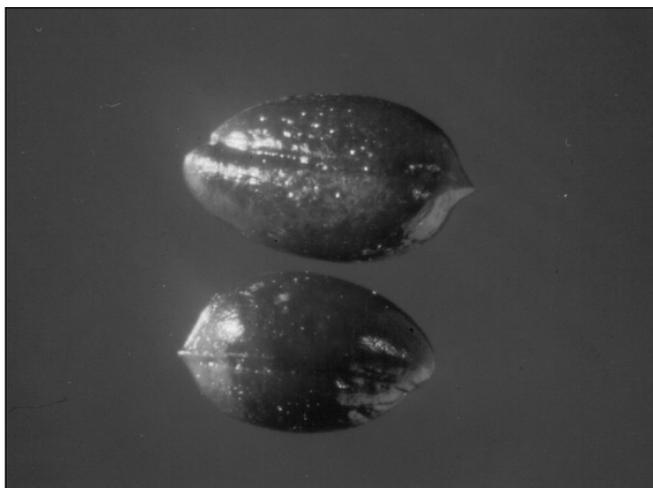
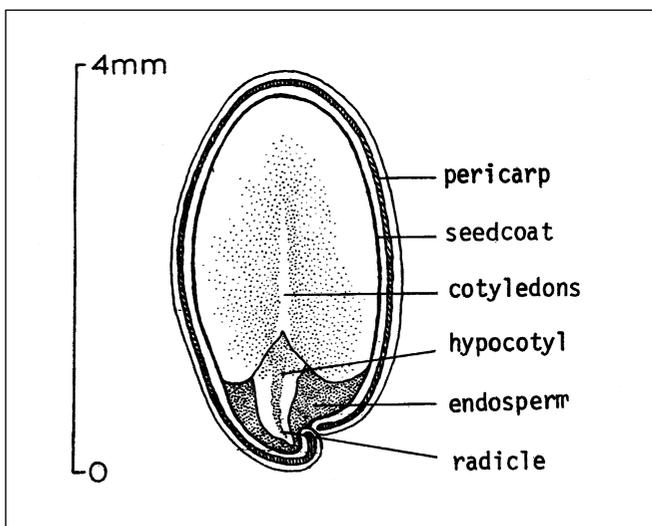


Figure 2—*Shepherdia argenta*, silver buffaloberry: longitudinal section through the embryo of an achenes.



collecting seeds of roundleaf buffaloberry as the silvery hairs that cover the fruit, branches, and leaves can be very irritating to the eyes and skin.

Cleaned seeds can range from 28,600 to 147,700 seeds/kg (13,000 to 67,000/lb), varying with ripening, environmental conditions, and seed source (Jorgensen 1995; Link 1993; Smith 1987; Thilenius and others 1974; Vories 1981; Wasser 1982).

Extraction and storage of seeds. Twigs, leaves, and other debris are removed by running material over an air-screen cleaner. Fruit is then put through a macerator with water, and dried. The dried pulp and seeds can be hand-rubbed or lightly chopped, and again run over the cleaner to separate out the seeds (Link 1993; Thilenius and others 1974; Vories 1981; Wasser 1982).

The seeds are orthodox and should be stored dry, in cool conditions, optimally at 5 °C. Seed can be stored for 4 to 5 years while maintaining good viability (Thilenius and others 1974; Vories 1981). For short-term storage, seed extraction is not necessary. The fruits may be spread out in a thin layer and dried. For short-term storage of fruits, place them in open plastic bags under cool-dry conditions. Care should be taken to prevent heating of the collected fruits (Link 1993; Thilenius and others 1974). Seed quality has not been standardized. Minimum standards established by the USDI Fish and Wildlife Service (Wasser 1982) are 90% purity and about 60% germination.

Germination. A physiologically dormant embryo, and physical dormancy due to impenetrable seedcoats, are the major problems affecting germination (McTavish 1986; Thilenius and others 1974). Two generally accepted methods of breaking dormancy are scarification with sulfuric acid and moist cold stratification (table 2). After pretreatment, the majority of viable seeds of silver buffaloberry germinate in 20 days. Some seeds do delay germination up to 60 days (Wasser 1982). Germination is epigeal (figure 3).

Nursery practice and seeding. In nursery practice, seeds are planted 6 mm ($\frac{1}{4}$ in) deep and covered with up to 2.5 cm (1 in) of mulch. This suggests that seeds could be planted, perhaps to advantage, at depths up to 2 cm ($\frac{3}{4}$ in) in coarse, dry, and loose soil or in fall under wildland conditions. About half of the viable seeds sown produce usable 1+0 seedlings in nurseries, whereas only 5 to 15% establishment would be good survival from seeding under dryland field conditions (Thilenius and others 1974; Vories 1981; Wasser 1982).

The recommended seeding rate for wildland seedings is 1.1 to 2.2 kg/ha (1 to 2 lb/ac) in seeding mixtures totaling 11 to 34 kg/ha (10 to 30 lb/ac) (Wasser 1982). In nursery row plantings, seeds can be sown in rows at a rate of 100 to 160 viable seeds/m (30 to 50/ft). Seeds should be sown in

the fall, but seeds that are prechilled for 3 months can be sown in spring, or probably later where late summer moisture is more reliable, or with irrigation (Thilenius and others 1974).

Silver buffaloberry can be propagated by cuttings, and wildlings can be transplanted successfully. Success of propagating russet buffaloberry from cuttings can vary. Vories (1981) reports that it roots well from cuttings, whereas McTavish (1986) reports that attempts at propagation by cuttings were largely unsuccessful. Roundleaf buffaloberry is generally grown from seeds because cuttings do not do well (Borland 1994; Vories 1981; Wasser 1982).

Figure 3—*Shepherdia argenta*, silver buffaloberry: seedling development at 1, 9, and 38 days after germination.

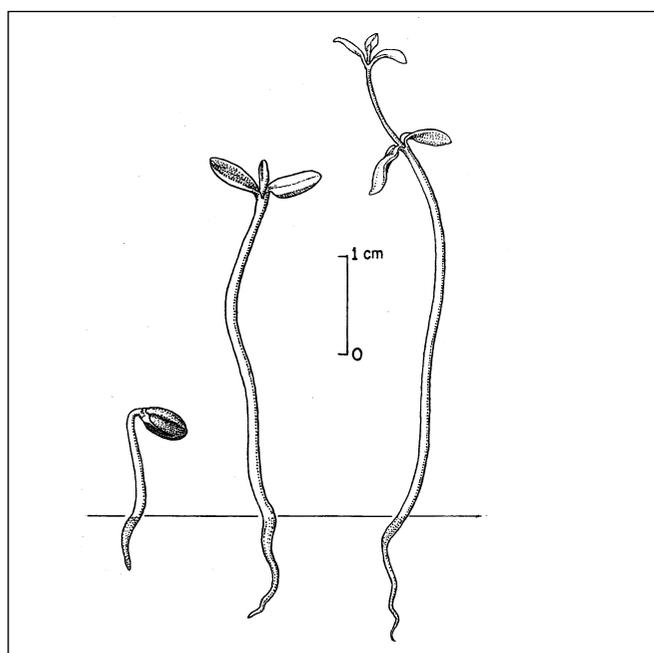


Table 2—*Shepherdia*, buffaloberry: germination treatment conditions and results

Species	Pretreatment	Germination treatment	Percent germination
<i>S. argentea</i>	Moist chill (3 °C for 90 days)	20–30 °C (18 days)	93
	Acid soak (20–30 min)	20–30 °C (21 days)	71–86
	None	Moist chill (3 °C for 170 days)	94
<i>S. canadensis</i>	Acid soak (15 min)	Moist chill (3 °C for 30 days)	89
	Acid soak (20–30 min)	20–30 °C (21 days)	80
	None	Moist chill (3 °C for 170 days)	80
<i>S. rotundifolia</i>	Acid soak (15–30 min)	20–30 °C	80–90
	Moist chill (3 °C for 30–60 days)	20–30 °C	80–90
	None	Moist chill (3 °C for 170 days)	86

Sources: Borland (1994, 1996), Jorgensen (1995), McTavish (1986), Thilenius and others (1974), Vories (1981).

- Borland J. 1994. *Shepherdia rotundifolia*. American Nurseryman 179(7): 106.
- Borland J. 1996. Personal communication. Denver, CO: Genesee Open Space.
- Halderson JL, Howard CG. 1986. Seed harvester development for rangeland shrubs. Pap. 86-1092. American Society of Agricultural Engineers.
- Jorgensen K. 1995. Personal communication. Ephraim UT: Utah Division of Wildlife Resources.
- Knudson MJ, Haas RJ, Tober DA, Darris DC, Jacobson ET. 1990. Improvement of chokecherry, silver buffaloberry, and hawthorn for conservation use in the northern plains. In: McArthur ED, Romney EM, Smith SD, Tueller PT, comps. Proceedings, Symposium on Cheatgrass Invasion, Shrub Die-off, and Other Aspects of Shrub Biology and Management; 1989 April 5-7; Las Vegas, NV. Gen. Tech. Rep. INT-276. Ogden, UT: USDA Forest Service, Intermountain Research Station: 291-299.
- Lackschewitz K. 1991. Vascular plants of west-central Montana: identification guidebook. Gen. Tech. Rep. INT-277. Ogden, UT: USDA Forest Service, Intermountain Research Station. 224 p.
- Link E, ed. 1993. Native plant propagation techniques for national parks. East Lansing, MI: USDA NRCS, Rose Lake Plant Materials Center. 197 p.
- McTavish B. 1986. Seed propagation of some native plants is surprisingly successful. American Nurseryman. 164(4): 55-56, 60.
- Mozingo, H. 1987. Shrubs of the Great Basin. Reno: University of Nevada Press: 195-197.
- Smith RC. 1987. *Shepherdia argentea*. American Nurseryman 166(10): 134.
- Stubbendieck J, Hatch SL, Hirsch J. 1986. North American range plants. Lincoln: University of Nebraska Press. 318-319.
- Thilenius JF, Evans KE, Garrett EC. 1974. *Shepherdia*, buffaloberry. In: Schopmeyer CS, tech coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 771-773.
- Vories KC. 1981. Growing Colorado plants from seed: a state of the art. Volume 1, Shrubs. Gen. Tech. Rep. INT-103. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 47-48.
- Wasser CH. 1982. Ecology and culture of selected species useful in revegetating disturbed lands in the West. FWS/OBS-82/56. Washington, DC: USDI Fish and Wildlife Service: 269-270.
- Welsh SL, Atwood ND, Higgins LC, Goodrich S. 1987. A Utah flora. Great Basin Naturalist Memoirs 9: 1-295.

Sapotaceae—Sapodilla family

Sideroxylon lanuginosum (Michx.)

gum bumelia

Franklin T. Bonner and R. C. Schmidtling

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Synonyms: *Bumelia lanuginosa* (Michx.) Pers.,
B. rufa Raf.

Other common names. Woolly buckthorn, buckthorn, gum elastic, chittamwood.

Growth habit, occurrence, and use. Gum bumelia is a spiny shrub or small tree found from southern Georgia to southern Illinois and west to southern Kansas, southern Arizona, and northern Mexico. Reaching heights of up to 18 m, it is deciduous in its northern range and evergreen in its southern range. Gum bumelia has some value as wildlife food. It has been planted as an ornamental and to some extent for shelterbelts. It has a deep taproot and is extremely resistant to drought (Bonner and Schmidtling 1974).

Flowering and fruiting. The perfect, white flowers are borne on small fascicles 6 to 38 mm across and open during June and July (Bonner and Schmidtling 1974; Vines 1960). The fruit is a single-seeded drupe 8 to 25 mm long. It turns purplish black as it ripens in September and October and persists on the tree into winter (Bonner and Schmidtling 1974; Vines 1960). The single seed is 6 to 13 mm long and is rounded, brownish, and shiny (figures 1 and 2) (Vines 1960).

Collection, extraction, and storage. Fruits should be picked as soon as they turn purplish black. The fleshy outer coat may be removed by careful maceration in water. The following data were obtained on 4 samples from Texas and Oklahoma (Bonner and Schmidtling 1974):

Cleaned seeds per weight of fresh fruit	10–12 kg/50 kg (10–12 lb/50 lb)
No. of cleaned seeds	12,500/kg (5,700/lb)
Purity	94%
Sound seeds	88%

Figure 1—*Sideroxylon lanuginosum*, gum bumelia: seed

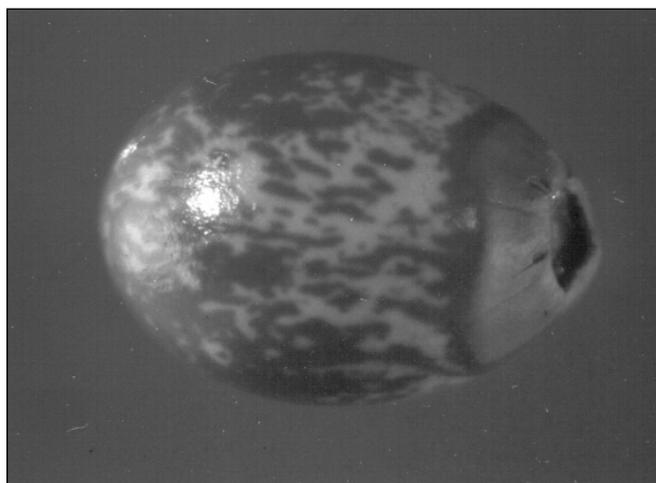
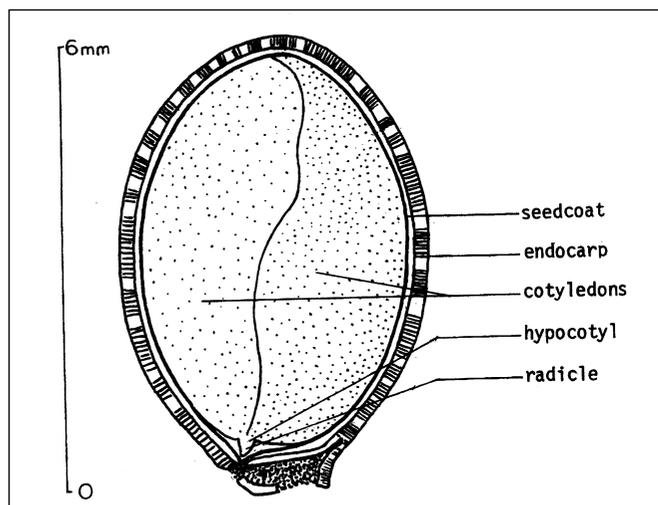


Figure 2—*Sideroxylon lanuginosum*, gum bumelia: longitudinal section through a seed.



Longevity of seeds in storage is not known.

Germination. Gum bumelia seeds germinate slowly and may be influenced by the seedcoat and internal conditions. Stratification for 60 days at 5 °C has been successful in promotion of germination (Bonner and Schmidtling 1974). Scarification by soaking in concentrated sulfuric acid for 20 minutes, followed by 4 to 5 months of stratification at 2 to 7 °C, has also been recommended (Afanasiev 1942).

Preliminary trials on samples of each seedlot are desirable to determine whether the acid treatment is necessary.

Germination may be tested in flats of sand or sand and peat at temperatures of about 20 °C at night and 30 °C during the day. Test periods of 60 to 90 days are needed for complete germination of stratified seeds. Percentage germination of 21 to 44% was reported for 13 samples from Texas and Oklahoma (Afanasiev 1942). Untreated seed from Missouri had a percentage germination of 51% after 150 days (Clark 1940).

Nursery practice. Eighty-two viable seeds should be sown per linear meter (25/ft) and covered lightly with soil. Outplanting at the age of 2 years is suggested (Clark 1940).

References

- Afanasiev M. 1942. Propagation of trees and shrubs by seed. Circ. #106. Stillwater: Oklahoma Agricultural Experiment Station.
- Bonner FT, Schmidtling RC. 1974. *Bumelia lanuginosa* (Michx.) Pers., gum bumelia. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 258–259.
- Clark R. 1940. A hardy woody plant new to horticulture. Bull. 28. St. Louis: Missouri Botanical Garden: 216–220.
- Vines RA. 1960. Trees, shrubs, and woody vines of the Southwest. Austin: University of Texas Press. 1104 p.

Simmondsiaceae—Jojoba family

Simmondsia chinensis (Link) Schneid.

jojoba

Susan E. Meyer

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Other common names. goatnut.

Growth habit, occurrence, and use. The Simmondsiaceae (jojoba family), has only 1 genus, *Simmondsia*, which consists of only 1 species, jojoba—*S. chinensis* (Link) Schneid. Once considered an isolated member of the box family (Buxaceae), jojoba is now regarded as sufficiently distinct to be placed in its own family. Jojoba is found from coastal and cis-montane southern California east to central Arizona and south to Sonora and Baja California (Munz 1974; Yermanos 1974). It is a characteristic plant of upland shrub communities in the Sonoran and Colorado Deserts and is also quite common as a component of chaparral.

Jojoba is a sparsely branched, decumbent to erect shrub that grows to 2 or rarely 3 m in height. Its large (2- to 4-cm-long), opposite, entire leaves are evergreen, leathery, and dull gray. Plants are extremely tolerant of drought (Al-Ani and others 1972) and their foliage is a source of nutritious forage for sheep, goats, and cattle, as well as for wild ungulates and smaller browsers such as rabbits. The large seeds have been used locally as a food source by indigenous people (Brooks 1978).

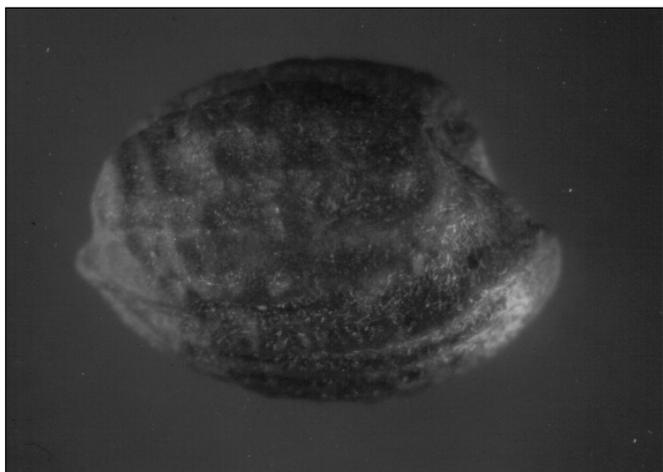
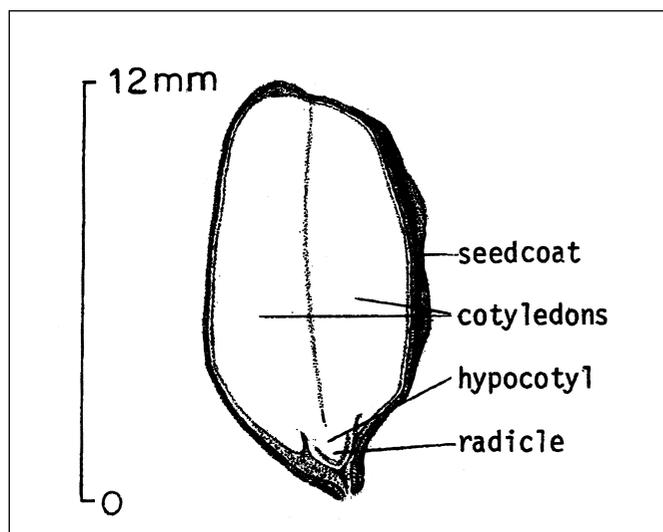
The most noteworthy feature of jojoba from a human perspective is the unusual liquid wax that makes up the storage reserve of its seeds. This substance, a fatty acid ester of a long-chain alcohol, is unique in the plant kingdom. It has chemical and rheological properties similar to those of sperm whale oil, which make it useful in a host of applications (Brooks 1978). Interest in commercial production of jojoba seed was greatly increased in the mid-1970s, when import of sperm whale oil into the United States was banned. First efforts were focused on harvesting seeds from wildland stands, but it was soon realized that for cost-effective production, cultivation in an agronomic setting would be necessary (Foster 1980; Yermanos 1979). Since that time, jojoba has been successfully cultivated in many semi-arid regions of the world (Ismail 1988; Kumari and others 1991;

Milthorpe 1989; Muthana 1981; Nimir and Ali-Dinar 1991), where it has the advantage of low water requirements and the ability to grow on agriculturally marginal land. Selection on natural variability and breeding have given rise to improved cultivars (Dunstone 1990, 1991; Palzkill and others 1989).

Flowering and fruiting. Jojoba is dioecious and relies on wind for successful pollination (Niklas and Buchmann 1985). The flowers, which are greenish yellow, inconspicuous, and without petals, are borne in the axils of the leaves. The male flowers are clustered at the nodes, and the female flowers are usually borne singly. Flowering occurs in March through May in response to winter rains. Plants of most populations appear to have a short (2-week) vernalization requirement for induction of flowering (Nord and Kadish 1974). Under plantation conditions, jojoba usually begins producing seeds the second or third year after planting (Nord and Kadish 1974; Yermanos 1974). Seeds ripen during the summer. The endosperm is absent (figure 1), and the cotyledons (which function as the storage organs) contain about half of their weight as wax (Brooks 1978). Good seedcrops are produced at intervals of 2 to several years (Brooks 1978; Castellanos and Molina 1990). Some individuals appear to be genetically predisposed to be more productive than others, making selection for higher yield possible (Nord and Kadish 1974; Yermanos 1974).

The 1 to 3 large seeds are borne in a capsule that superficially resembles an acorn. This splits open apically and down the sides to release the seeds. As is the case with many large-seeded North American desert species, jojoba seeds are dispersed by scatter-hoarding rodents that are also their principal consumers (Castellanos and Molina 1990). Sherbrooke (1976) reported that only 1 heteromyid species in southern Arizona—Bailey's pocket mouse (*Perognathus baileyi*)—was able to utilize jojoba seeds. The seeds contain a unique toxic cyanogenic glucoside (simmondsin). He concluded that Bailey's pocket mouse had evolved a detoxifica-

Figure 1—*Simmondsia chinensis*, jojoba: longitudinal section through a seed (**top**) and exterior view of a seed (**bottom**).



tion mechanism, enabling it to eat the seeds without harm. The seeds are, however, not particularly toxic to humans.

Jojoba seedlings emerge in response to autumn, winter, or spring rains (Castellanos and Molina 1990; Sherbrooke 1977). Germination is hypogeal. Wildland stands are often strongly male-biased—sometimes as many as 4 males to 1 female—but in cultivation the sex ratio is more equal (Brooks 1978). Male plants are thought to be more stress-tolerant as seedlings and thus to have higher survival rates under natural conditions. Seedling survival depends principally on weather patterns (Castellanos and Molina 1990) but may be higher in the protection of nurse plants or other sheltering objects (Sherbrooke 1977).

Seed collection, cleaning, and storage. Seeds of jojoba are most readily collected by raking or vacuuming after they have fallen to the ground, but where rodents are active, seeds do not remain on the ground for long (Castellanos and Molina 1990). Also, the growth form may or may not be

conducive to this activity, a problem that is solved in cultivation by bottom-pruning (Yermanos 1974). For small lots, seeds can be collected by beating the branches over a hopper or by hand-stripping them when still slightly green, the “hard-dough” stage (Nord and Kadish 1974). Seeds picked green should be allowed to dry in a shady, well-ventilated area. A pneumatic device has been developed for commercial harvest (Coates and Yacizi 1991). If collected intact, the capsules may be broken up using a barley de-bearder or hammermill. The seeds can then be cleaned of debris and unfilled seeds in a conventional fanning mill or air-screen cleaner. The purity and viability of cleaned seedlots are usually high (Nord and Kadish 1974).

Jojoba seeds are quite variable in size, both within and among seedlots (Yermanos 1979). Nord and Kadish (1974) report an among-lot mean seed weight range of 660 to 3,300/kg (300 to 1,500/lb). Ismail (1988) sorted seeds of a single lot into 3 size classes with the following mean values:

	Seeds/weight		Length	
	/kg	/lb	cm	in
small	2,300	1,045	0.93	1/3
medium	1,300	590	1.38	1/2
large	1,060	480	1.84	3/4

Castellanos and Molina (1990) reported an even wider spread in the size of viable seeds, 670 to 20,000/kg (305 to 900/lb). Jojoba seeds lose viability relatively rapidly in laboratory storage at room temperature (from 100% to <60% after 2 years), but they are apparently still orthodox in storage behavior. When stored at low moisture content and temperature (3 °C), seedlots have retained high viability for 10 to 12 years (Nord and Kadish 1974). Under natural conditions, jojoba seeds do not form a persistent seedbank; all seeds either germinate, lose viability, or are consumed within a year of production (Castellanos and Molina 1990).

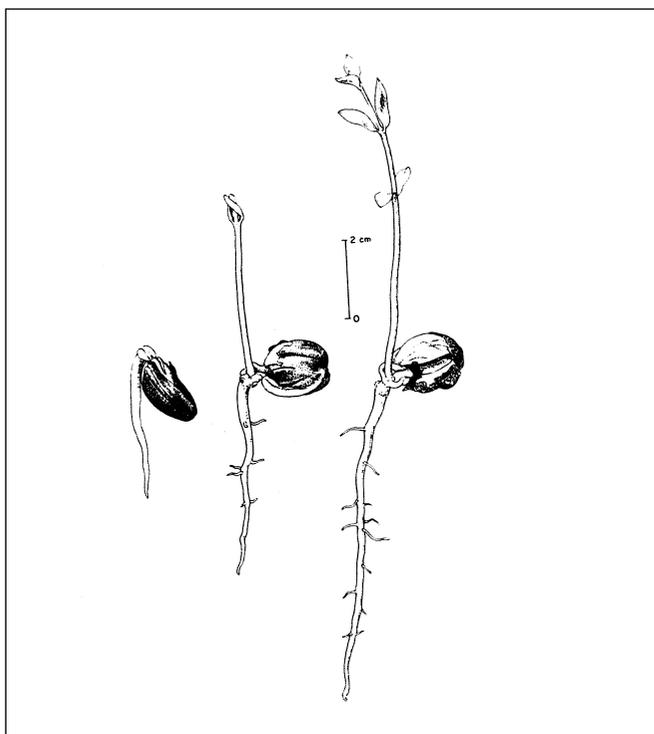
Germination. Jojoba seeds require no pretreatment and are usually readily germinable immediately after harvest (Nord and Kadish 1974; Rao and Iyengar 1982). They are protected from premature summer germination by a requirement for relatively cool temperatures—an optimum 15 to 23 °C (Nord and Kadish 1974), with no germination at 30/40 °C (Ismail 1988)—and slow germination rates. It takes 3 days for the first emergence of the radicle at 20/30 °C and 7 days at 10/20 °C (Ismail 1988). Seedlots of large seeds germinated more quickly and to higher percentages than did lots of small seeds, suggesting that seed size is associated with germination polymorphism (Ismail 1988). This may function to reduce germination risk under field conditions by spreading out germination across rain events

(Castellanos and Molina 1990). Dormancy could be removed in most seeds by breaking the testa at the radicular end. Nord and Kadish (1974) reported that jojoba seeds could germinate at 5 to 10 °C but only after an 8-hour pre-treatment at 20 °C. Germination is hypogeal (figure 2).

Nursery practice and field seeding. Jojoba may be direct-seeded if the plots are protected from seed predation and seedling grazing by rodents. The seeds should be planted in spring, when daytime soil temperatures are above 60 °C, at a depth of 2.5 to 5 cm (1 to 2 in) (Nord and Kadish 1974). Although mature plants can tolerate some freezing, the seedlings do not, perishing at temperatures below -2 °C.

Seedlings may also be readily be produced as container stock (Yermanos 1974). Seedlings emerge in 7 to 12 days at 60 to 75 °C. The plants may be held in 3.8-liter (1-gal) pots outdoors for 8 to 24 months. With the longer period, flowering takes place in the pots, making it possible to optimize sex ratios in plantation plantings. Another alternative is to establish plants from cuttings of known sex. Jojoba can be propagated from softwood stem cuttings taken in the spring or summer (Nord and Kadish 1974).

Figure 2—*Simmondsia chinensis*, jojoba: seedling development at 3, 7, and 14 days after germination.



References

- Al-Ani HA, Strain BR, Mooney HA. 1972. The physiological ecology of diverse populations of the desert shrub *Simmondsia chinensis*. *Journal of Ecology* 60: 41–57.
- Brooks WH. 1978. Jojoba—a North American desert shrub: its ecology, possible commercialization, and potential as an introduction into other arid regions. *Journal of Arid Environments* 1: 227–236.
- Castellanos AE, Molina FE. 1990. Differential survivorship and establishment in *Simmondsia chinensis* (jojoba). *Journal of Arid Environments* 19: 65–76.
- Coates W, Yazici E. 1991. Pneumatic device for harvesting jojoba seeds. *Transactions of the ASAE* 34: 2304–2308.
- Dunstone R. 1990. Jojoba (*Simmondsia chinensis*). *Plant Varieties Journal* 3: 14–16.
- Dunstone R. 1991. Jojoba (*Simmondsia chinensis*) variety: 'Wadi wadi'. *Plant Varieties Journal* 4: 19–20.
- Foster KE. 1980. Environmental consequences of an industry based on harvesting the wild desert shrub jojoba. *Bioscience* 30: 255–258.
- Ismail AMA. 1988. The ecological and agronomic role of seed polymorphism in *Simmondsia chinensis*. *Journal of Arid Environments* 14: 35–42.
- Kumari A, Chikara J, Iyengar ERR. 1991. Variability in *Simmondsia chinensis* under semiarid conditions. *Indian Journal of Genetics and Plant Breeding* 51: 85–88.
- Milthorpe PL. 1989. The potential of jojoba (*Simmondsia chinensis*) in New South Wales: 2. Some factors affecting yield. *Australian Journal of Experimental Agriculture* 29: 389–395.
- Munz PA. 1974. *A flora of southern California*. Berkeley: University of California Press. 1086 p.
- Muthana KD. 1981. Jojoba: an oil-yielding desert shrub. *Indian Farming* 31: 28–31.
- Niklas KJ, Buchmann SL. 1985. Aerodynamics of wind pollination in *Simmondsia chinensis* (Link) Scheider. *American Journal of Botany* 72: 530–539.
- Nimir MN, Ali-Dinar HM. 1991. Jojoba, a new cash crop in marginal lands. *Acta Horticulturae* 270: 369–372.
- Nord EC, Kadish A. 1974. *Simmondsia chinensis* (Link.) C. K. Schneid., jojoba. In: Schopmeyer CS, tech. coord. *Seeds of woody plants in the United States*. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 774–776.
- Palzkill DA, Younes MH, Hogan L. 1989. AT-1310, AT-1487, and AT-3365: clonal jojoba germplasm for horticultural use. *HortScience* 24: 526–527.
- Rao PHV, Iyengar ERR. 1982. Studies in seed morphology and germination in jojoba (*Simmondsia chinensis* Link). *Current Science* 51: 516–518.
- Sherbrooke WC. 1976. Differential acceptance of toxic jojoba seed (*Simmondsia chinensis*) by four Sonoran Desert heteromyid rodents. *Ecology* 57: 596–602.
- Sherbrooke WC. 1977. First year seedling survival of jojoba (*Simmondsia chinensis*) in the Tucson Mountains, Arizona. *Southwestern Naturalist* 22: 225–234.
- Yermanos DM. 1974. Agronomic survey of jojoba in California. *Economic Botany* 28: 161–174.
- Yermanos DM. 1979. Jojoba: a crop whose time has come. *California Agriculture* 33: 4–11.

Solanaceae—Nightshade family

Solanum dulcamara L. bitter nightshade

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Growth habit, occurrence, and use. Bitter nightshade—*Solanum dulcamara* L., also known as European bittersweet—is a climbing perennial vine, somewhat woody at the base. It grows to a height of 1.8 to 3.6 m. It is native in Europe, northern Africa, and eastern Asia. In its natural range in Europe, it occurs on sites ranging from wet and shaded to dry and exposed. Its presence indicates a habitat in which the moisture regime may fluctuate from moist to waterlogged. It occurs on mineral to peat soils characterized by a high nitrogen supply and with a pH range of 4.8 to 7.9 (Pegtel 1985). Pegtel (1985) has briefly summarized many aspects of the species biology within its natural range.

Naturalized in North America, it is often found in moist thickets, from Nova Scotia to Minnesota, south to North Carolina and Missouri (Curtis 1959; Gleason 1958) and from Idaho to Washington and California (Crossley 1974). Bitter nightshade has been cultivated since 1561, chiefly for ornamental purposes, but is now often considered invasive. The fresh berries are poisonous to most humans and fatal to rabbits, but some birds and other wildlife eat them with impunity. Gunn and Gaffney (1974) state that any medicinal values are offset by the poisonous properties of the fruits and berries. Recommendations for medicinal use are only for external application; it has been used as an ingredient in ointments.

Leaves of the typical variety are minutely pubescent or nearly glabrous. Many plants from Nova Scotia to Ontario, however, have distinctly hairy leaves and branches. These plants have been segregated as the variety *villosissimum* Desv. (Gleason 1958). Mathe and Mathe (1973) found that plants from western and eastern European sources differ in their alkaloid chemistry, suggesting the presence of chemical taxa within the species.

Bitter nightshade is 1 of 1,200 species in the genus, most of which occur in the tropical and subtropical regions of both hemispheres (Crossley 1974). The genus contains economically important agricultural species—such as potato (*S. tuberosum* L.) and eggplant (*S. melongena* L.)—that have been domesticated through plant breeding and for which

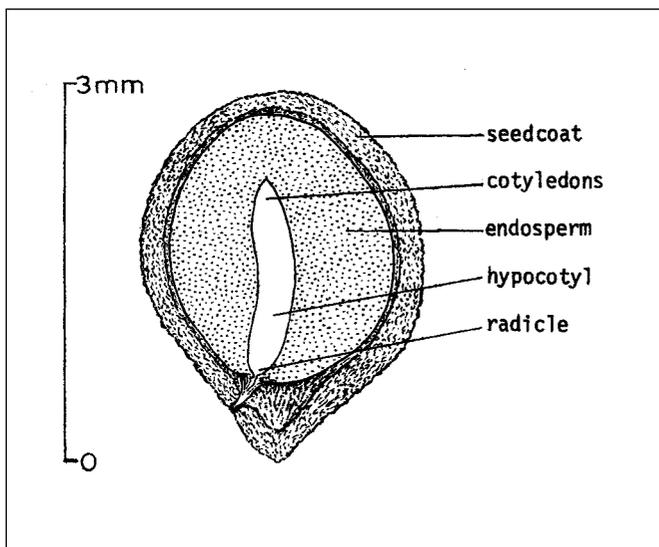
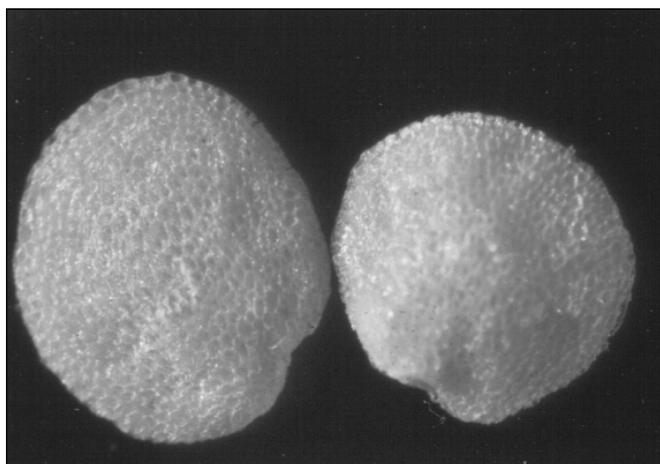
there is a large amount of information available. (The tomato genus—*Lycopersicon*—is also a member of the Solanaceae.) The nightshade genus also contains a number of agricultural weed species that affect the production of crops such as sorghum, soybeans, and cotton, and for which there is a significant amount of information available on various aspects of seed biology (for example, Rogers and Ogg 1981). Some of the information may be useful for understanding the seed biology of bitter nightshade, but we did not review this information in detail. Seed characteristics of 42 economically important *Solanum* spp., including bitter nightshade, have been described (Gunn and Gaffney 1974).

Flowering and fruiting. The violet flowers, which occur in long peduncled cymes, bloom from July to August. Bumble bee species—*Bombus* spp.—are important pollinators (Liu and others 1975). The ovoid to ellipsoid scarlet berries ripen from August to October.

The fruit is a juicy berry 8 to 11 mm in diameter that contains from 40 to 60 seeds. The seeds are 2 to 3 mm by 1.7 to 2.5 mm by 0.7 to 1 mm, strongly flattened, tannish pink, irregular disks, and dully glistening as if coated with fine sugar. The embryo is coiled within the seed (figure 1) (Gleason 1958; Gunn and Gaffney 1974). In cross-section, the embryo is seen as 4 small round structures within the endosperm; the presence of 2 or 3 sections of embryo in a cross-section of the seed is common in the genus (Gunn and Gaffney 1974). Good seedcrops are borne almost annually.

Collection of fruits; extraction and storage of seeds. Seeds may be collected from July to September by hand-picking the ripe berries (Crossley 1974). The fruits may be rubbed through a 10-mesh (2-mm) soil screen, and the pulp and empty seeds floated off with water. Large-scale extraction can be done in a macerator. Parts of the fruit may adhere to the seed (Gunn and Gaffney 1974). Crossley (1974) found in 1 collection that there were about 700,000 seeds/kg (350,000/lb) and that, after careful cleaning, purity should be 99 to 100% and soundness from 92 to 99%. Seeds from genetically transformed plants had seed weights that

Figure 1—*Solanum dulcamara*, bitter nightshade: exterior view of seeds (**top**); longitudinal section through seed (**bottom**). A cross-section of the seed would intersect the coiled embryo 4 times. Longitudinal section based on Crossley (1974) and Gunn and Gaffney (1974).



were 40 to 70% of those of normal plants (Lee and Davey 1988).

Seeds have maintained high viability when stored in airtight containers for 1 year at either 2 to 3 °C or room temperature (20 °C). A moisture content of 6% has been satisfactory for storage periods of less than 1 year (Crossley 1974; Roberts and Lockett 1977). Information is lacking on viability after longer periods, but these seeds appear to be orthodox in storage behavior and should keep well as described above.

Germination. Freshly collected seeds have a high germination capacity with no pretreatment. Seeds germinate at constant temperatures of 30 to 35 °C, but the best germination occurs at alternating temperatures (Crossley 1974; Pegtel 1985; Roberts and Lockett 1977) (table 1). There are no official test prescriptions for bitter nightshade, but other species of nightshade tested at alternating temperatures of 20 and 30 °C (AOSA 1993). Stratification (4 to 5 °C) increases germination at constant temperatures but not at alternating temperatures. Germination of fresh and 1-year-old unstratified seeds at constant temperatures of 20 to 30 °C was greater than 95%; treatment with potassium nitrate improved germination at 30 °C but not at lower temperatures (Roberts and Lockett 1977). Pegtel (1985) found no effect of potassium nitrate on germination. Stratification did not significantly widen the range of constant temperatures at which seeds would germinate (Crossley 1974; Roberts and Lockett 1977; Pegtel 1985). Seeds appear to germinate well without light, however light requirements have not been studied in detail. Seeds will germinate completely in 5 to 6 months under field conditions when covered by 5 cm (2 in) of soil (Roberts and Lockett 1977). Seeds collected from plants growing in a variety of microclimatic conditions did not differ in their response to constant and alternating temperature conditions (Pegtel 1985). Germination is epigeal (figure 2).

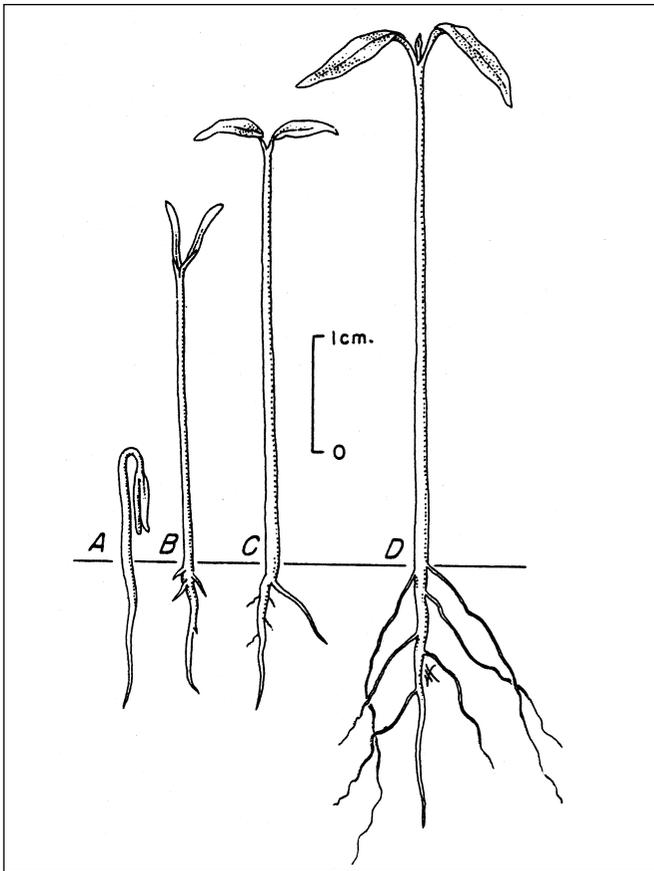
Table 1—*Solanum dulcamara*, bitter nightshade: pregermination treatments and germination

Storage (months)	Stratification (days)	Germination conditions*		Total germination (%)
		Days	Temp (°C)	
0	0	ND	20/30	95
3	0	ND	20/30	95
6	0	ND	20/30	95
0	0	ND	25	5
1	1	ND	25	80
3	3	ND	25	85
6	6	ND	25	75
0	0	ND	15	0
1	1	ND	15	5
3	3	ND	15	30
6	6	ND	15	65

Source: Roberts and Lockett (1977).

* ND = exposed to natural daylight for short periods but no light in germination incubators; 20/30 = 16 hours at low temp and 8 hours at high temp (10/25 °C and 10/30 °C were also used but they made little difference).

Figure 2—*Solanum dulcamara*, bitter nightshade: seedling development at 1, 2, 6, and 12 days after germination.



Nursery practice. It is suggested that seeds be sown in the fall if untreated or if stratified, sown in the spring and covered with about 0.3 cm (0.1 in) of soil. Seeds mixed thoroughly in the surface 7.5 cm (3 in) of soil in September–October and kept under field conditions (in Great Britain) began to emerge in late March; 6, 41, and 2% of seedlings appeared in March, April, and May, respectively. Forty-nine percent of the seeds planted produced germinants; 95% of seeds germinated in laboratory tests (Roberts and Lockett 1977). In other nightshade species, maximum seedling emergence occurred when seeds were covered by 1 to 2.5 cm (0.4 to 1.0 in) of soil (Boyd 1981). Root or stem cuttings can be used for vegetative propagation (Crossley 1974).

References

- AOSA [Association of Official Seed Analysts]. 1993. Rules for testing seeds. *Journal of Seed Technology* 16(3): 1–113.
- Boyd JW. 1981. Effects of certain environmental factors on the growth and development of silverleaf nightshade (*Solanum eleagnifolium*). *Dissertation Abstracts International* [B] 42(9): 3513–3514.
- Crossley JA. 1974. *Solanum dulcamara* L., bitter nightshade. In: Schopmeyer CS, tech. coord. *Seeds of woody plants in the United States*. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 777–778.
- Curtis JT. 1959. *The vegetation of Wisconsin*. Madison: University of Wisconsin. 657 p.
- Gleason HA. 1958. *The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada*. New York: New York Botanical Garden.
- Gunn CR, Gaffney FB. 1974. Seed characteristics of 42 economically important species of Solanaceae in the United States. *Tech. Bull.* 1471. Washington, DC: USDA. 34 p.
- Lee JY, Davey MR. 1988. Morphological variation of *Solanum dulcamara* plants transformed with Ri plastids [abstract]. *Research Report of the Office of Rural Development (Korea)* [Biotechnology] 30(3): 21–27.
- Liu HJ, Macfarlane RP, Pengelly DH. 1975. Relationships between flowering plants and four species of *Bombus* (Hymenoptera: Apidae) in southern Ontario [abstract]. *Canadian Entomologist* 107: 577–588.
- Mathe I, Mathe I Jr. 1973. Data to the European area of the chemical taxa of *Solanum dulcamara* L. [abstract]. *Acta Botanica Academiae Scientiarum Hungaricae* 19(1/4): 441–451.
- Pegtel DM. 1985. Germination in populations of *Solanum dulcamara* L. from contrasting habitats. *New Phytologist* 100(4): 671–679.
- Roberts HA, Lockett PM. 1977. Temperature requirements for germination of dry-stored, cold-stored and buried seeds of *Solanum dulcamara* L. *New Phytologist* 79(3): 505–510.
- Rogers BS, Ogg AG Jr. 1981. Biology of weeds in the *Solanum nigrum* complex (*Solanum* section *Solanum*) in North America [abstract]. *Agric. Rev. Manual (West. Ser.) ARM-W-23*. Washington, DC: USDA Science and Education Administration. 30 p.

Fabaceae—Pea family

Sophora L.

sophora

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Growth habit, occurrence and use. There are 50 to 70 woody and herbaceous species of the sophora genus found in the warm temperate and tropical regions of the world (Little 1979). Of the species found in the United States, 2 are discussed in detail here.

Mescalbean (also known as *frijolito* and Texas mountain-laurel)—*Sophora secundiflora* (Ortega) Lag. ex DC.—is a small tree of western Texas, New Mexico, and northern Mexico (Little 1976; Ruter and Ingram 1990). *Mamane*—*Sophora chrysophylla* (Salisb.) Seem.—is found in the forests of Hawaii. Mescalbean is a favored tree for landscaping in areas with alkaline soils and moderate drought (Ruter and Ingram 1990). Its seeds reportedly have hallucinogenic properties (Murakoshi and others 1986) and contain many alkaloids (Hatfield and others 1977; Izaddoost 1975; Keller 1975; Keller and others 1976). Vines (1960) lists 2 other southwestern species: silverbush (*Sophora tomentosa* L.), an evergreen shrub, and Texas sophora (*Sophora affinis* Torr. & Gray), a small tree. The Japanese pagoda tree (or Chinese scholar tree) (*S. japonica* L.) is planted in the United States as an ornamental (LHBH 1976; Wasson 2001).

Flowering and fruiting. The fragrant violet flowers of mescalbean appear in terminal clusters 5 to 12 cm in length during March and April. Fruits mature in September as brown pubescent legumes (pods) 2.5 to 13 cm long, usually containing 3 or 4 red globose seeds that are about 12 mm long (figures 1 and 2) (Vines 1960). Mamane racemes are 5 cm in length and golden yellow in color. The legumes are 10 to 15 cm long, and contain 4 to 8 flattened, yellow seeds that are about 8 mm long (Little and Skolmen 1989). Wagner and others (1989) describes the seeds as brown to grayish black.

Storage and germination. There are no long-term storage data on sophora seeds, but they are probably orthodox in storage behavior. Fresh mescalbeans and seeds stored for 1 year at 20 °C successfully germinated when given an acid pretreatment (Ruter and Ingram 1990). Germination rate was best in seeds soaked for 120 minutes in concentrated sulfuric acid. Pretreatment in hot water was unsuccessful. Wang (1991) reported that germination of red, untreated fresh and untreated 1-year-stored seeds was 50 and 8%, respectively. Treating fresh seeds with undiluted (93%) sul-

Figure 1—*Sophora secundiflora*, mescalbean: seed.

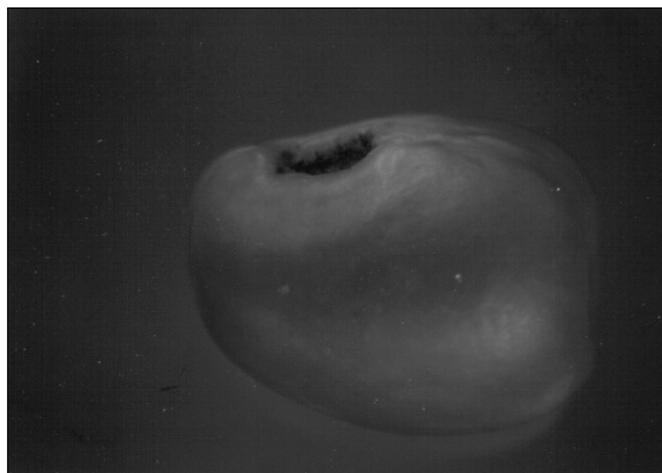
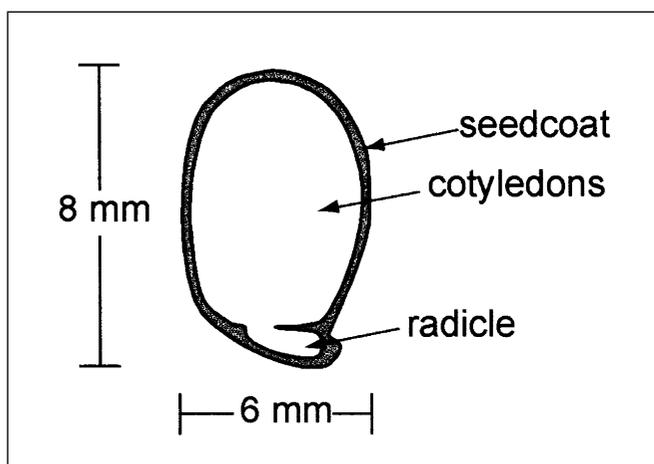


Figure 2—*Sophora*, sophora: longitudinal section through a seed.



furic acid for 10 minutes and stored seeds for 60 minutes increased germination to 80 and 70%, respectively, and reduced germination time to within 14 days. Highest germination values were obtained by drilling a small hole in the seedcoat (>83%). There were also differences in germination between the red seeds and those with a light yellow seedcoat which were harvested 10 days earlier. Untreated red seeds reached maximum germination (99%) within 24 days of sowing, whereas untreated yellow seeds reached maximum germination (93%) within 14 days.

Nursery practice. Field tests of mamane seeds showed that seeds that were pretreated either by sanding or by soaking in sulfuric acid and then were sown in the spring at a depth of 3.8 or 6.4 cm (1 1/2 to 2 1/2 in) had the highest percentage emergence and 1-year survival rates (Scowcroft 1981). Of the 2 treatments, spring survival was significantly lower for acid pretreated seeds than for untreated seeds, but sowing depth had no effect. However, mortality was thought to be due to low rainfall and extreme soil surface temperatures.

References

- Hatfield GM, Valdes LJ, Keller WJ, Merrill WL, Jones VH. 1977. An investigation of *Sophora secundiflora* seeds (mescalbeans). *Lloydia* 40(4): 374–383 [Horticultural Abstracts 1973+].
- Izaddoost M. 1975. Alkaloid chemotaxonomy of the genus *Sophora*. *Phytochemistry* 14(1): 203–204 [Horticultural Abstracts 1973+].
- Keller WJ. 1975. Alkaloids from *Sophora secundiflora*. *Phytochemistry* 14(10): 2305–2306 [Herbage Abstracts 1973+].
- Keller WJ, Hatfield GM, Valdes LJ. 1976. Isolation of lupinine and DELTA 5-dehydrolupanine from *Sophora secundiflora*. *Lloydia* 39(6): 472 [Horticultural Abstracts 1973+].
- LHBH [Liberty Hyde Bailey Hortorium]. 1975. *Hortus third: a concise dictionary of plants cultivated in the United States*. New York: Macmillan. 1290 p.
- Little EL Jr. 1979. Checklist of United States trees (native and naturalized). *Agric. Handbk*. 541. Washington, DC: USDA Forest Service. 375 p.
- Little EL Jr., Skolmen RG. 1989. Common forest trees of Hawaii (native and introduced). *Agric. Handbk*. 679. Washington, DC: USDA Forest Service. 321 p.
- Murakoshi I, Kubo H, Ikram M, Israr M, Shafi N, Ohmiya S, Otomasu H. 1986. (+)-11-oxocytisine, a lupin alkaloid from leaves of *Sophora secundiflora*. *Phytochemistry* 25(8): 2000–2002 [Horticultural Abstracts 56: 9115; 1986].
- Ruter JM, Ingram DL. 1990. Effect of scarification on germination of *Sophora secundiflora* seeds. *Combined Proceedings of the International Plant Propagators' Society* 40: 423–426 [Horticultural Abstracts 62: 7585; 1992].
- Scowcroft PG. 1981. Regeneration of mamane: effects of seedcoat treatment and sowing depth. *Forest Science* 27(4): 771–779.
- Vines RA. 1960. *Trees, shrubs and woody vines of the Southwest*. Austin: University of Texas Press. 1104 p.
- Wagner WL, Herbst DR, Sohmer SH. 1990. *The manual of flowering plants of Hawaii*. Honolulu: University of Hawaii Press and Bishop Museum Press. 1853 p.
- Wang YT. 1991. Enhanced germination of *Sophora secundiflora* seeds. *Subtropical Plant Science* 44: 37–39 [Seed Abstracts 15: 3304; 1992].
- Young JA, Young CG. 1992. *Seeds of woody plants in North America*. Portland, OR: Dioscorides Press. 407 p.

Rosaceae—Rose family

***Sorbaria sorbifolia* (L.) A. Braun**

false spirea

Paul O. Rudolf and Peyton Owston

Dr. Rudolf (deceased) retired from the USDA Forest Service's North Central Forest and Range Experimental Station; Dr. Owston retired from the USDA Forest Service's Pacific Northwest Research Station

Synonyms. *Spiraea sorbifolia* L., *Schizonotus sorbifolius* (L.) Lindl.

Other common names. Ural false spirea.

Growth habit, occurrence, and use. False spirea—*Sorbaria sorbifolia* (L.) A. Braun—is native to northern Asia from the Urals to Kamchatka, Sakhalin, and Japan. It is a deciduous shrub from 1 to 3 m tall, usually grown as an ornamental for its bright-green foliage and conspicuous panicles of white flowers (Krüssmann 1960; LHBH 1976; Rehder 1940; Schnelle 1990); the species has been planted for watershed protection and wildlife habitat. It is 1 of about 8 species native to northern and eastern Asia (Rehder 1940; Rosendahl 1955). False spirea often escapes from cultivation in the eastern United States.

Flowering and fruiting. The shiny, white, bisexual flowers bloom in May, June, and July in the northern United States (Rehder 1940; Rosendahl 1955). The fruits are small shiny follicles that ripen in August in Minnesota (Rehder 1940; Rosendahl 1955; Rudolf 1974). Good seedcrops are borne almost every year (Rudolf 1974). Seeds are small and fusiform (figures 1 and 2).

Collection, cleaning, and storage. The ripe fruits should be picked from the bushes by hand and separated from the panicles. The fruits may be kneaded in a bag or rubbed to break them up and then fanned carefully to separate the seeds from the debris. Rudolf (1974) reported that there were about 416,750 dried follicles/kg (189,000/lb) and about 1,667,000 seeds/kg (756,000/lb). No data on seed purity or soundness are available. Seeds may be stored dry in sealed containers at 1 to 5 °C if they are to be held longer than overwinter. Duration of viability under these conditions is not known, but the seeds appear to be orthodox in storage behavior, making a long duration probable.

Figure 1—*Sorbaria sorbifolia*, false spirea: seeds.

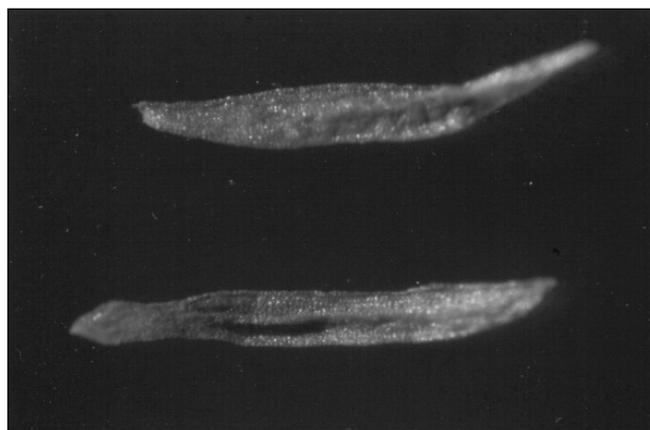
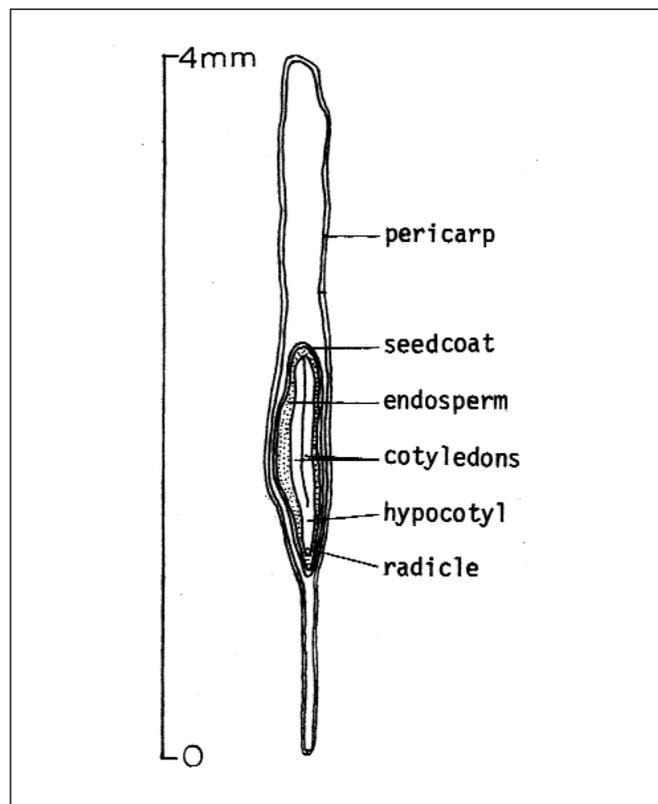


Figure 2—*Sorbaria sorbifolia*, false spirea: longitudinal section through a seed.



Germination. Apparently, some of the seeds have internal dormancy and it is suggested that they be stratified in a moist medium for 30 to 60 days at 1 to 5 °C. Germination test data are unavailable, but it is suggested that tests be made in germinators or sand flats, using pretreated seeds at a temperature of about 20 °C (night) to 30 (day) °C for 40 days. Seeds should be sown immediately after collection in the late summer or stratified seeds used in the spring (Swingle 1939). The seeds should be covered only lightly with soil (LHBH 1976).

References

- Krüssmann G. 1960. Handbuch der Laubgehölze [in German]. 2 vols. Berlin: Parey. 495 and 608 p.
- 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.
- Rehder A. 1940. Manual of cultivated trees and shrubs hardy in North America. 2nd ed. New York: Macmillan. 996 p.
- Rosendahl CO. 1955. Trees and shrubs of the upper Midwest. Minneapolis: University of Minnesota Press. 411 p.
- Rudolf PO. 1974. *Sorbaria sorbifolia*, Ural false spirea. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 779.
- Schnelle MA. 1990. *Sorbaria sorbifolia*, Ural false spirea. American Nurseryman 171 (June 1): 122.
- 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.

Rosaceae—Rose family

Sorbus L.
mountain-ash

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Growth habit, occurrence, and uses. The mountain-ash genus—*Sorbus*—includes 80 to 100 species of deciduous trees and shrubs that are distributed in the Northern Hemisphere (Chalupa 1992; Little 1979). Mountain-ash, like other genera in the Rosaceae, is a plastic genus comprised of poorly defined taxa that show extensive introgression where their ranges meet or overlap (Calder and Taylor 1968; McAllister 1985). Geographic races probably have developed, especially in European mountain-ash, as evidenced by its wide range and its several forms and varieties. Hybrids are common among species of mountain-ash, yet the seeds of several species are produced asexually and the resulting progeny are always true to the parent (McAllister 1985; Wright 1981). Hybrids between species of mountain-ash and chokeberry (*Aronia*) or serviceberry (*Amelanchier*) also occur (Rehder 1940).

In growth form, the various species of mountain-ash range from low shrubs to medium-sized trees. Many tend to be multiple-stemmed. Four tree and 3 shrub species are native to North America. A species native to Eurasia, European mountain-ash, has been most widely planted and has become naturalized in parts of the United States and Canada (Calder and Taylor 1968; Little 1979; Viereck and Little 1972). The 5 species listed in table 1 are widely distributed and may be found from low to alpine elevations and ecosystems.

Graceful foliage, showy flowers, brightly colored fruits, hardiness, and a choice of sizes make mountain-ash species especially desirable for ornamental plantings (Wright 1981). The fruits are an important food for birds and rodents (Englund 1993; Van Dersal 1938) and those of some species are consumed by humans, either directly or in preserves and

Table 1—*Sorbus*, mountain-ash: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
<i>S. americana</i> Marsh. <i>Pyrus americana</i> DC.	American mountain-ash, mountain-ash, small-fruited mountain-ash	Newfoundland W to Manitoba, S to E Tennessee, N Georgia, & N South Carolina
<i>S. aucuparia</i> L. <i>Pyrus aucuparia</i> (L.) Gaertn.	European mountain-ash, rowan-tree, rowan	Native of Eurasia; widely cultivated & naturalized across S Canada & N US, including California & SE Alaska
<i>S. decora</i> (Sarg.) Schneid. <i>Pyrus americana</i> DC. var. <i>decora</i> Sarg. <i>S. americana</i> var. <i>decora</i> (Sarg.) Sarg <i>Pyrus decora</i> (Sarg.) Hyland	showy mountain-ash, mountain-ash, large-fruited mountain-ash	S Greenland to W Ontario, S to NE Iowa, & E to New York
<i>S. scopulina</i> Greene <i>S. cascadenis</i> G.N. Jones <i>Pyrus scopulina</i> (Greene) Longyear <i>S. andersonii</i> G.N. Jones	Greene mountain-ash, western mountain-ash	NW Alaska S & E to Saskatchewan, South Dakota, & New Mexico to central California
<i>S. sitchensis</i> M. Roemer <i>S. californica</i> Greene <i>Pyrus sitchensis</i> (Roem.) Piper <i>S. cascadenis</i> G.N. Jones	Sitka mountain-ash, Pacific mountain-ash, western mountain-ash, California mountain-ash	Yukon to S Alaska S to central California & W Nevada; N to Idaho, W Montana, & Alberta

Sources: Chalupa (1992), Little (1979), Rosendahl (1955), Viereck and Little (1972).

alcoholic beverages (Chalupa 1992; Pojar and Mackinnon 1994). The foliage and twigs are important browse for deer (*Odocoileus* spp.) and moose (*Alces americana*) and to a lesser extent, for domestic livestock (Van Dersal 1938). The wood of European mountain-ash is hard and tough and is used for production of household utensils and tool handles (Chalupa 1992); this species tolerates atmospheric pollution and is used to reforest areas where such conditions exist (Chalupa 1992).

Flowering and fruiting. The creamy white, complete flowers of mountain-ash are borne in large flattened clusters. Flowering occurs during mid-spring to mid-summer, depending on species and location (table 2). Kronenberg (1994) determined that European mountain-ash flowers in Europe after first fulfilling a 750-hour cold requirement under 7 °C and then a sum of 160 degree-days (with 6 °C as the base temperature) in a period when mean day temperatures are above 6 °C.

Fruits ripen from July to November (table 2). The showy fruits are scarlet to bright red when ripe (table 3). Fruits are fleshy, 2- to 5-celled, berrylike pomes (figure 1) with each cell containing 1 or 2 small, brown seeds (figures 2 and 3). Fruits may remain attached until late winter and are thus available for birds during critical forage periods. Seeds are chiefly dispersed by birds.

European mountain ash begins bearing seeds at about 15

years of age, and good seedcrops occur almost annually (Harris and Stein 1974). Mountain-ash seeds are subject to attack by several species of chalcidid flies (Chalcididae) (Rohwer 1913), and the fruits are damaged by a fungus and a bacterium (Chalupa 1992).

Collection, extraction, and storage. Fruits should be picked, shaken, or raked from the trees or shrubs as soon as

Figure 1—*Sorbus decora*, showy mountain-ash: a cluster of fruits, which are vermillion red when ripe.

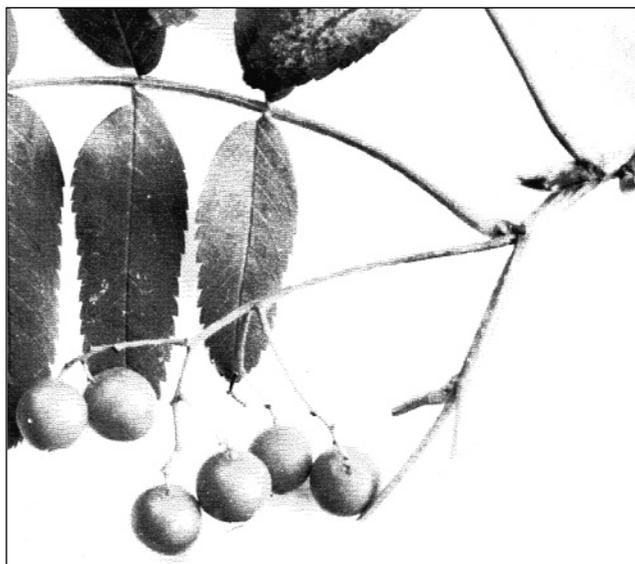


Table 2—*Sorbus*, mountain-ash: phenology of flowering and fruiting

Species	Flowering	Fruit ripening	Seed dispersal
<i>S. americana</i>	May–July	Aug–Oct	Aug–Mar
<i>S. aucuparia</i>	May–July	Aug–Oct	Aug– winter
<i>S. decora</i>	May–July	Aug–Nov	Aug–Mar
<i>S. scopulina</i>	May–July	July	July–Dec
<i>S. sitchensis</i>	June–Aug	Aug–Oct	Aug–late winter

Sources: Fernald (1950), Harris and Stein (1974), Hitchcock and others (1961), Miller and others (1948), Rehder (1940), Rosendahl (1955), Van Dersal (1938), Viereck and Little (1972).

Table 3—*Sorbus*, mountain-ash: growth habit, height, fruit diameter, and color of ripe fruit

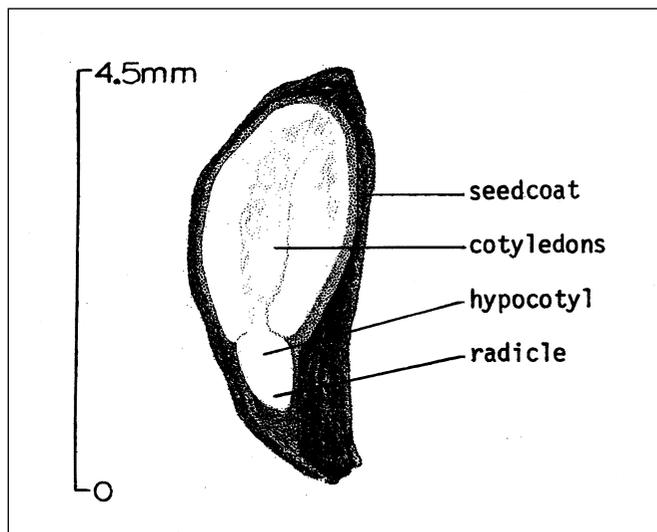
Species	Growth habit	Height at maturity (m)	Fruit diameter (mm)	Color of ripe fruit
<i>S. americana</i>	Shrub or tree	4–10	4–6	Bright red
<i>S. aucuparia</i>	Tree	5–20	8–10	Scarlet–bright red
<i>S. decora</i>	Shrub or tree	6–12	8–12	Vermillion red
<i>S. scopulina</i>	Shrub or tree	1–6	8–10	Orange–bright red
<i>S. sitchensis</i>	Shrub or tree	1–6	10–12	Red with bluish cast

Sources: Fernald (1950), Hitchcock and others (1961), Rehder (1940), Rosendahl (1955), Viereck and Little (1972).

Figure 2—*Sorbus*, mountain-ash: two seeds of *S. americana*, American mountain-ash (**left**) and one of *S. sitchensis*, Sitka mountain-ash (**right**).



Figure 3—*Sorbus aucuparia*, European mountain-ash: longitudinal section through a seed, showing large cotyledons.



they are ripe to prevent losses to birds and other foragers. They may be picked slightly immature (Shoemaker and Hargrave 1936) but they then require after-ripening. One suggested method is to pile immature fruits in heaps and allow them to decompose for about 2 months before seeds are removed (NBV 1946). Collected fruits should be transported and stored in cool, aerated conditions to minimize molding and fermentation.

Prompt extraction of seeds from ripe mountain-ash fruits is recommended for best results (Flemion 1931; Heit 1967a); however, extended storage of fruits at low temperature before cleaning resulted in good germination of seeds in comparison tests of European mountain-ash (Flemion 1931) or white mountain-ash (*S. glabrescens* Cardot.) (Taylor and Gerrie 1987). The fruits can be macerated by hand or by mechanical methods available for fleshy fruits (Stein and

others 1974), taking care not to cause physical damage. Seeds can be separated from wet pulp by flotation, skimming, or screening; dried; and then fanned to remove debris and empty seeds. In an alternate process, the fruits can be pressed, the matted pulp broken up, and dried pulp and seeds sown together, or the seeds can be separated out by a blower. The weight of cleaned seeds varies less among species in North America than among lots within the same species (table 4.)

Cleaned seeds of mountain-ash retain viability for an extended period if dried to a low moisture content and stored dry in cold, cool, or moderate temperatures. The length of time that seeds remain viable under different storage conditions has not been adequately determined. Seeds of American mountain-ash stored in a tightly closed metal container at -1 to 10 °C lost no viability in 8 years (USDA FS 1948). Seeds or intact fruits of European mountain-ash stored at temperatures ranging from -8 °C to room temperature in sealed or unsealed storage retained high viability for 1 to 2 years, but viability was much reduced at humidity levels above 25% or temperatures of 25 °C (Flemion 1931). Seeds can be stored over-winter under stratification conditions in outdoor pits or flats (Flemion 1931; Shoemaker and Hargrave 1936). Seeds of European mountain-ash retained some viability for 5 years when fruits were buried in the mor layer (acid humus in cold, wet soils) in northern Sweden (Granstrom 1987).

Low-temperature storage of cleaned mountain-ash seeds in sealed containers at 6 to 8% moisture content has been recommended (Heit 1967b). Considering their performance after storage under various conditions, seeds of this genus are likely to store well for extended periods under conditions best for many tree species—at low moisture content in closed containers at subfreezing temperatures.

Pregermination treatments and germination tests.

Fresh mountain-ash seeds will not germinate readily; they require lengthy after-ripening, including cold stratification (Barclay and Crawford 1984; Flemion 1931; Taylor and Gerrie 1987; Zentsch 1970). The stratification requirements for European mountain-ash seeds vary somewhat by tree and year (Zentsch 1970). Seeds of this species require less cold stratification at 1 °C if they are first stored dry at room temperature for 6 months (Flemion 1931). They will enter into secondary dormancy if subjected to warm germination conditions when incompletely stratified or if stored dry after cold, moist stratification (Flemion 1931). To shorten the stratification period, Zentsch (1970) tested warm stratification at 20 °C for 1 to 6 months before cold stratification and germination at 3 °C; warm stratification generally prolonged

Table 4—*Sorbus*, mountain-ash: fruit weight and seed yield data

Species	Fruit wt/ fruit vol		Seed yield/ fruit vol		Cleaned seeds				Samples
	kg/ha	lb/bu	kg/ha	lb/bu	Range		Average		
					/kg	/lb	/kg	/lb	
<i>S. americana</i>	—	—	1.3–2.6	1–2	183,000–521,000	83,000–236,300	319,400	144,900	9
<i>S. aucuparia</i> *	—	—	—	—	229,300–374,800	104,000–170,000	286,200	129,800	10
<i>S. decora</i>	—	—	—	—	—	—	280,400	127,200	1
<i>S. sitchensis</i> †	52	40	1.3	1	146,400–385,000	66,400–174,600	290,800	131,900	8

Sources: Harris and Stein (1974), King (1947), McKeever (1938), Mirov and Kraebel (1939), Swingle (1939), Van Dersal (1938).

* Data represent seeds only from North American sources.

† The number of dry fruits in one sample was 13,690/kg (6,210/lb) (Mirov and Kraebel 1939).

the total time required, but did not improve the high total germination. Lenartowicz (1988) reached a similar conclusion but recommended that European mountain-ash seeds be stratified at 20 °C for 6 weeks and then germinated at 3 °C to gain the benefits of a shortened period during which most germination occurs. Mechanical or chemical scarification of the seeds has not shortened the stratification or germination period (Flemion 1931; Harris and Hilton and others 1965; Stein 1974) but sulfuric acid treatment increased total germination in one instance (Hilton and others 1965).

The standard germination test procedure for mountain-ash species requires pre-chilling the seeds for 4 months at 3 to 5 °C followed by germination for 28 days at alternating temperatures of 20 and 30 °C (ISTA 1996). It is noteworthy that the highest germination (90% or higher) for mountain-ash seeds was obtained in various lengthy comparison tests at markedly lower germination temperatures than those prescribed in the standard test—at 1 to 3 °C (table 5). In fact, the same substrate and temperature were used during many tests for both stratification and germination. Given enough time, seeds of American and European mountain-ashes completed germination under moist low-temperature conditions (Flemion 1931; Harris and Stein 1974; Lenartowicz 1988; Zentsch 1970), a capability also demonstrated by other species of mountain-ash (Nikolaeva 1967).

Review of the methods employed and results obtained in comparison studies leads to the conclusion that the standard germination test for mountain-ash needs a firmer foundation. Hints among published results point to 2 aspects that deserve further investigation—after-ripening and germination temperature. After-ripening requirements may vary, depending on when and where fruits are collected, as indicated by collections made over an altitudinal gradient (Barclay and Crawford 1984). As early as 1931, Flemion reported that dry storage at room temperature shortened the time needed for cold stratification and that germination tem-

peratures above 20 °C caused secondary dormancy. Warm stratification at 20 °C (Lenartowicz 1988; Zentsch 1970) may be too high and moist conditions may not be necessary. Likewise, germination at alternating 20 and 30 °C may approach or cause secondary dormancy; lower germination temperatures may prove more satisfactory as indicated by Taylor and Gerrie (1987) for white mountain-ash.

Viability of mountain-ash seeds is most easily and rapidly determined by a tetrazolium (TZ) test on excised embryos. It is the first choice among methods recognized by the International Seed Testing Association (ISTA 1996). Preparation and evaluation procedures to use are listed in the TZ testing handbook (AOSA 2000). Test procedures include soaking the seeds in water for 6 hours or more at 20 °C, exposing or excising the embryos, then soaking them in a 1% TZ solution for 18 to 24 hours at 30 to 35 °C, and evaluating the resulting staining. A fully viable embryo is uniformly stained red to pink, with even borders and shape. Growing excised embryos is a slightly longer yet also a quick means of determining seed viability. The excised embryos are incubated at 20 °C for about 6 days and their development evaluated. Those that retain their freshly excised appearance or whose cotyledons have enlarged and become deep green are viable; those that deteriorate or turn pale yellow-green are not (Flemion 1938; Heit 1955). Comparable estimates of the viability of mountain-ash seeds have been obtained by these 2 quick tests (Hilton and others 1965), but viability values determined by such tests are often higher than that obtained by germination test (Flemion 1938).

Nursery practice. Mountain-ash species can be propagated from seeds, cuttings, suckers, grafts, and small plant parts. Reproduction from seeds is most common but other methods also serve production objectives.

Untreated mountain-ash seeds can be sown in late summer and early fall or pretreated seeds can be sown in the fol-

Table 5—*Sorbus*, mountain-ash: stratification and germination test conditions and results*

Species	Stratification†			Germination test				Total germination	
	Days	Temp (°C)	Moist medium	Temp (°C)	Days	Germination (%)	Days	(%)	Samples
<i>S. americana</i>	60	5	Sand	20–30	14	13	8	13	4
	90	5	Sand	10	60	11	22	12	4
	CSG	5	—	5	150	15	132	16‡	4
<i>S. aucuparia</i>	CSG	1	Peat moss	1	127	70	99	94	1
	CSG	1	Peat moss	1	82	69	61	96	1
	CSG	1	Peat moss	1	120	58	90	93	6
	CSG	1	Peat moss	1	120	57	90	90	4
	120	2	Paper	20	—	68	90	76	1
	CSG	3	Sand	3	150–210	—	—	95+	26
	30–180	20	Sand	3	150–210	—	—	90+	52
	CSG	3	Peat & sand	3	560	60	420	88	1
	70	20	Peat & sand	3	350	86	300	93	1
	126	2	Peat	20	42	—	—	30	3
<i>S. decora</i>	—	—	—	20–30	60	—	—	10	4
<i>S. scopulina</i>	115	3–5	Peat–verm	20	38	61	17	61	1
<i>S. sitchensis</i>	90§	3	Paper	20–30	53	30	10	30	1
	120	0	—	—	50	—	—	21	1
	140	5	Sand	21	17	15	11	15	1

Sources: Barclay and Crawford (1984), Flemion (1931), Harris and Stein (1974), Hilton and others (1965), Lenartowicz (1988), McKeever (1938), Mirov and Kraebel (1939), Trindle (1996), Zentsch (1970).

CSG = stratification and germination as a continuum under the same conditions; verm = vermiculite.

* Only the better test results for each species are listed.

† Stratification in moist sand, peat moss, soil, or petri dish.

‡ Reached 33% germination in 330 days (USDA FS 1948).

§ Ten-minute soak in H₂SO₄ before stratification.

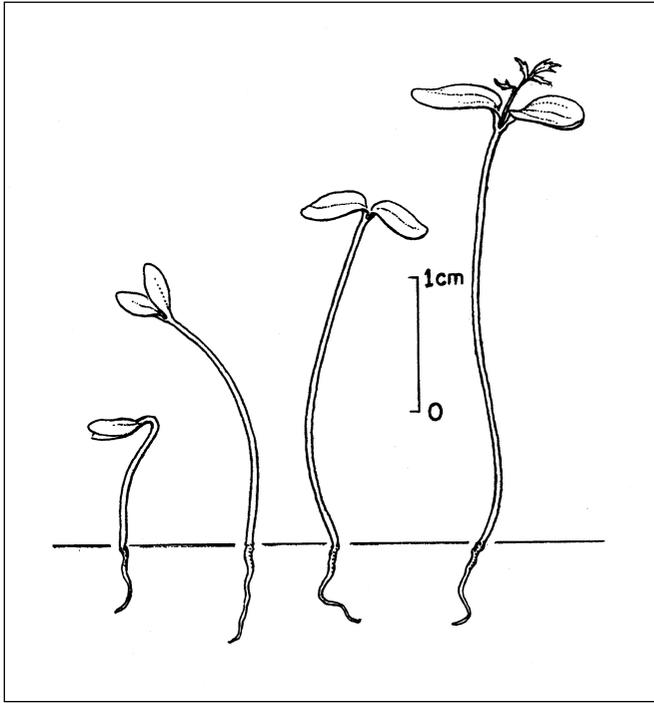
lowing spring for production of seedlings in the same growing season. Fall-sowing involves the following considerations: (1) sowing should perhaps be done as early as mid-summer, because some seedlots or species benefit from moist warm conditioning prior to the moist chilling that is supplied by winter weather (Heit 1968); (2) the seeds are subject to predation by rodents, insects, and birds for a long time and may need protection; and (3) stored seeds must be available because time for after-ripening may not be sufficient for freshly collected seeds. Sowing outdoors in late winter or spring requires use of cold-stratified seeds or sowing early enough that natural cold stratification can still occur. Cold stratification at or near 1 °C for 60 to 120 days is needed for best results (Barclay and Crawford 1984; Flemion 1931; Hilton and others 1965; Taylor and Gerrie 1987). If seeds are sown late or are not sufficiently preconditioned, or conditions are too warm, germination will be delayed until the second or even third year (Fabricius 1931; Flemion 1931; Harris and Stein 1974). Mountain-ash seedlings can also be container-grown in greenhouses where good germination and growth conditions are readily maintained (McDonald 1989).

Cleaned seeds can be sown in drills; berries or dried macerated pulp with seeds must necessarily be broadcast. When seeds are sown without removal from berries or pulp, germination is slower and generally not as satisfactory (Fabricius 1931; Flemion 1931; Heit 1967a). Seeds should be lightly covered with sand, sawdust, sandy soil, or peat moss and the beds mulched heavily with pine needles, peat moss, wood chips, straw, or hardwood leaves to protect them from exposure and freezing (Heit 1967a). Late fall- or winter-sowing of untreated seeds in board-covered but unmulched coldframes and on snow has also produced satisfactory results (Fabricius 1931; Flemion 1931). Germination is epigeal (figure 4).

Cuttings of several mountain-ash species taken in early summer rooted readily and quickly developed into sturdy plants (McAllister 1985). Micropropagation of European mountain-ash has been successful by grafting, softwood cuttings, and in vitro culture (Chalupa 1992). Trees produced by shoot tip and axillary bud culture have been planted, survived well, and grew at about the same rate as trees grown from seeds—3.5 to 4 m (11 to 13 ft) in 5 years (Chalupa 1992). Tree production from excised embryos also appears feasible.

Mountain-ash seedlings are hardy and not very susceptible to insects or disease; however, they are subject to nipping by deer and moose (Fabricius 1931; Van Dersal 1938). For field planting, 1+1 transplants are best, but 2+0 seedlings are also suitable (Harris and Stein 1974).

Figure 4—*Sorbus americana*, American mountain-ash: seedling appearance at 1, 3, 7, and 24 days after germination



References

- AOSA [Association of Official Seed Analysts]. 2000. Tetrazolium testing handbook. Lincoln, NE: Association of Official Seed Analysts. 21+ p.
- Barclay AM, Crawford RMM. 1984. Seedling emergence in the rowan (*Sorbus aucuparia*) from an altitudinal gradient. *Journal of Ecology* 72(2): 627–636.
- Calder JA, Taylor RL. 1968. Flora of the Queen Charlotte Islands: I. Systematics of the vascular plants. Monogr. 4, Pt. 1. Ottawa: Canada Department of Agriculture, Research Branch. 659 p.
- Chalupa V. 1992. Micropropagation of European mountain ash (*Sorbus aucuparia* L.) and wild service tree (*Sorbus torminalis* (L.) Cr.). In: Bajaj YPS, ed. High-tech and micropropagation II. Volume 18, Biotechnology in Agriculture and Forestry. Berlin: Springer-Verlag: 211–226.
- Englund R. 1993. Fruit removal in *Viburnum* species: copious seed predation and sporadic massive seed dispersal in a temperate shrub. *Oikos* 67(3): 503–510.
- Fabricius L. 1931. Die Samenkeimung von *Sorbus aucuparia* L. *Forstwissenschaftliches Zentralblatt* 53: 413–418.
- Fernald ML. 1950. Gray's manual of botany. 8th ed. New York: American Book Co. 1632 p.
- Flemion F. 1931. After-ripening, germination, and vitality of seeds of *Sorbus aucuparia* L. *Contributions from the Boyce Thompson Institute* 3: 413–439.
- Flemion F. 1938. A rapid method for determining the viability of dormant seeds. *Contributions from Boyce Thompson Institute* 9: 339–351.
- Granstrom A. 1987. Seed viability of fourteen species during five years of storage in a forest soil. *Journal of Ecology* 75(2): 321–331.
- Harris AS, Stein WI. 1974. *Sorbus* L., mountain-ash. In: Schopmeyer CS, tech. coord. *Seeds of woody plants in the United States*. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 780–784.
- Heit CE. 1955. The excised embryo method for testing germination quality of dormant seed. *Proceedings of the Association of Official Seed Analysts* 45: 108–117.
- Heit CE. 1967a. Propagation from seed: 8. Fall planting of fruit and hardwood seeds. *American Nurseryman* 126(4): 12–13, 85–90.
- Heit CE. 1967b. Propagation from seed: 11. Storage of deciduous tree and shrub seeds. *American Nurseryman* 126(10): 12–13, 86–94.
- Heit CE. 1968. Propagation from seed: 15. Fall planting of shrub seeds for successful seedling production. *American Nurseryman* 128(4): 8–10, 70–80.
- Hilton RJ, Jaswal AS, Teskey BJE, Barabas B. 1965. Rest period studies on seeds of *Amelanchier*, *Prunus*, and *Sorbus*. *Canadian Journal of Plant Science* 45: 79–85.
- Hitchcock CL, Cronquist A, Ownbey M, Thompson JW. 1961. *Vascular plants of the Pacific Northwest*. Part 3. Seattle: University of Washington Press. 614 p.
- ISTA [International Seed Testing Association]. 1996. *International Rules for Seed Testing: rules 1996*. *Seed Science and Technology* 24 (Suppl.): 1–335.
- King JE. 1947. The effect of various treatments to induce germination of seeds of some plants valuable for soil conservation and wildlife [MS thesis]. Moscow, ID: University of Idaho. 97 p.
- Kronenberg HG. 1994. Temperature influences on the flowering dates of *Syringa vulgaris* L. and *Sorbus aucuparia* L. *Scientia Horticulturae* 57: 59–71.
- Lenartowicz A. 1988. Warm-followed-by-cold stratification of mountain-ash (*Sorbus aucuparia* L.) seeds. *Acta Horticulturae* 226: 231–238.
- Little EL Jr. 1979. Checklist of United States trees, native and naturalized. Agric. Handbk 541. Washington, DC: USDA Forest Service. 375 p.
- MacDonald B. 1989. Introducing new and recommended plants—the British Columbia way. *International Plant Propagators' Society Combined Proceedings* 38: 413–416.
- McAllister H. 1985. The Aucuparia section of *Sorbus*. *Plantsman* 6(4): 248–255.
- McKeever DG. 1938. The effect of various methods of treatment on the germination of seeds of some plants valuable for game and erosion purposes [MS thesis]. Moscow, ID: University of Idaho. 132 p.
- Miller HW, Ball CC, Knott NP. 1948. The comparative value of woody plants as food for upland game birds. *Biol. Bull.* 8. Olympia: Washington State Game Department. 39 p.
- Mirov NT, Kraebel CJ. 1939. Collecting and handling seeds of wild plants. For. Pub. 5. Washington, DC: USDA Civilian Conservation Corps. 42 p.
- NBV [Nederlandsche Boschbouw Vereniging]. 1946. Boomzaden: handleiding inzake het oogsten, behandelen, bewaren en uitzaaien van boomzaden. Wageningen, The Netherlands: Ponsen and Looijen. 171 p.
- Nikolaeva MG. 1967. Fiziologiya glubokogo pokoya semyan. *Akademiya Nauk SSSR, Botanicheskii Institut IM.V.L. Komarova. Leningrad: Izdatel'stvo "Nauka"* [Physiology of deep dormancy in seeds [Translation TT 68-50463. 1969. Springfield, VA: USDC CFSTI. 220 p.].
- Pojar J, MacKinnon A, eds. 1994. *Plants of the Pacific Northwest Coast*. Redmond, WA: Lone Pine Publishing. 527 p.
- Rehder A. 1940. *Manual of cultivated trees and shrubs hardy in North America*. 2nd ed. New York: Macmillan. 996 p.
- Rohwer SA. 1913. Technical papers on miscellaneous forest insects: 6. Chalcidids injurious to forest-tree seeds. Tech. Ser. 20, Part VI. Washington, DC: USDA Bureau of Entomology: 157–163.
- Rosendahl CO. 1955. *Trees and shrubs of the upper Midwest*. Minneapolis: University of Minnesota Press. 411 p.
- Shoemaker JS, Hargrave PD. 1936. Propagating trees and shrubs from seed. Circ. 21. Edmonton: University of Alberta, College of Agriculture. 22 p.
- Stein WI, Slabaugh PE, Plummer AP. 1974. Harvesting, processing, and storage of fruits and seeds. In: Schopmeyer CS, tech. coord. *Seeds of woody plants in the United States*. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 98–125.
- 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 CW, Gerrie WA. 1987. Effects of temperature on seed germination and seed dormancy in *Sorbus glabrescens* Cardot. *Acta Horticulturae* 215: 185–192.
- Trindle JDC. 1996. Personal communication. Corvallis, OR: USDA Natural Resources Conservation Service, Plant Materials Center.
- USDA FS [USDA Forest Service]. 1948. *Woody-plant seed manual*. Misc. Pub. 654. Washington, DC: USDA Forest Service. 416 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.
- Viereck LA, Little EL Jr. 1972. *Alaska trees and shrubs*. Agric. Handbk. 410. Washington, DC: USDA Forest Service. 265 p.
- Wright D. 1981. *Sorbus: a gardener's evaluation*. *Plantsman* 3(2): 65–98.
- Zentsch W. 1970. Stratification of *Sorbus aucuparia* L. seeds. In: Bialobok S, Suszka B, eds. *Proceedings, International Symposium on Seed Physiology of Woody Plants; 1968 September 3–8; Kornik, Poland*. Kornik, Poland: Institute of Dendrology and Kornik Arboretum: 127–132.

Bignoniaceae—Trumpet-creeper family

Spathodea campanulata Beauv.

African tuliptree

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Other common names. fountain tree, *tulipan Africano*

Growth habit, occurrence, and use. The African tuliptree—*Spathodea campanulata* Beauv.—is a medium-sized tree that commonly reaches a height of 21 m (Neal 1948) but may reach 30 m in some parts of West Africa (Unwin 1920). In Puerto Rico, the largest African tuliptree measures 35 m tall and 1.75 m in dbh (Francis 1990); heart and butt rots are common in trees older than 20 to 25 years that have suffered mechanical or fire damage.

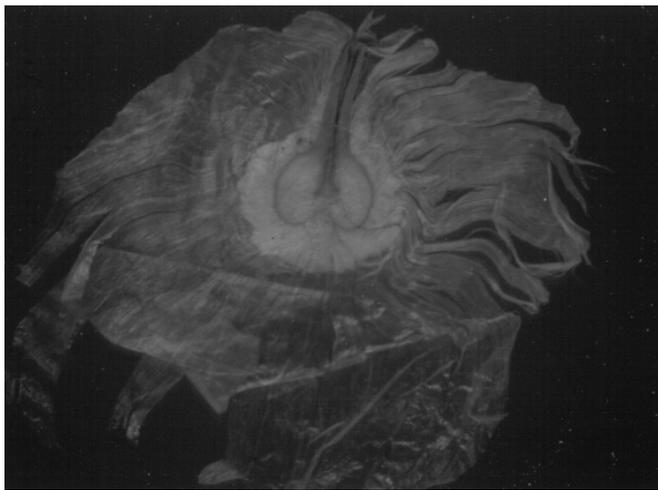
African tuliptree grows naturally in the secondary forests in the high forest zone and in the deciduous, transition, and savanna forests of equatorial Africa. Its native range extends along the western coast of Africa from Ghana to Angola and inland across the humid center of the continent to southern Sudan and Uganda (Irvine 1961). It develops best in fertile, deep, well-drained loams but will also colonize heavily eroded sites (Francis 1990). The African tuliptree has been successfully planted outside its natural range (Little and Wadsworth 1964; Mahecha Vega and Echeverri Restrepo 1983). Throughout the humid tropics, its large brilliant flame-orange flowers have made it one of the most popular flowering ornamentals. The species has naturalized in at least Colombia (Mahecha Vega and Echeverri Restrepo 1983), Costa Rica (Holdridge 1942), Puerto Rico (Liogier and Martorell 1982), Cuba (White 1951), Jamaica (Streets 1962), Sri Lanka (Worthington 1959), and Guam (McConnell and Muniappan 1991). The wood of this fast-growing species is light and little used.

Flowering and fruiting. The 10-cm-long, bright red-orange flowers occur in terminal racemes on trees as young as 3 to 4 years of age (Francis 1990). Yellow-flowering trees have also been reported (Francis 1990; Menninger and others 1976). Flowering time varies, depending on location. Nalawadi and others (1980) report flowering of African tuliptree in India from early January until early March, with

peak flowering in mid-February. However, in southern Africa, flowers occur in fall and winter and, in the Caribbean, trees bloom from late winter to early summer (Francis 1990). The 1 to 4 boat-shaped brown pods are 15 to 25 cm long and usually develop from each flower cluster (Eggeling 1947; Little and Wadsworth 1964); seeds mature 5 months after flowering (Francis 1990). The wind-dispersed seeds are lightweight and surrounded by a membranous wing (figure 1) (Vozzo 2002).

Collection, storage, and germination. The seeds should be collected from undehisced, brown pods and air-dried until they split open (Francis 1990). Seeds of most species in this genus are orthodox and should store well. The reported number of seeds per weight varies from 125,000/kg (57,000/lb) (Holdridge 1942) to 290,000/kg (132,000/lb) (Francis and Rodriguez 1993). Francis and Rodriguez (1993) report germination of 38% of the African tuliptree seeds sown on the surface of wet potting soil in a covered tray and kept at ambient (24 to 30 °C) temperatures. Germination is epigeous and may begin in as little as 2 days.

Figure 1—*Spathodea campanulata*, African tuliptree: winged seeds.



Nursery practices. Germinating seeds are fragile and should not be covered by more than a dusting of peat or fine sand. Francis (1990) reports that, under 50% shade, African tuliptree seedlings took 2 months after germination to develop the first true leaves; when transplanted into nurserybeds

at 25% shade, the seedlings attained plantable size—that is, 35 cm (14 in) tall—in 5 months. He concluded that a regimen with more sunlight would probably have reduced the time needed to reach plantable size.

References

- Eggeling WJ. 1947. Working plan for the Budongo and Siba forests. Entebbe: Uganda Protectorate. 66 p.
- Francis JK. 1990. African tulip tree (*Spathodea campanulata* Beauv.). Res. Note SO-ITF-SM-32. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 5 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.
- Holridge LR. 1942. Trees of Puerto Rico. Occ. Pap. 2. Río Piedras, PR: USDA Forest Service, Tropical Forest Experiment Station. 105 p.
- Irvine FR. 1961. Woody plants of Ghana. London: Oxford University Press. 868 p.
- Liogier HA, Martorell LF. 1982. Flora of Puerto Rico and adjacent islands: a systematic synopsis. Río Piedras, PR: Editorial de la Universidad de Puerto Rico. 342 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.
- Mahecha Vega GE, Echeverri Restrepo R. 1983. Aborales del Valle del Cauca. Bogota: Litografía Arco. 208 p.
- McConnell J, Muniappan R. 1991. Introduced ornamental plants that have become weeds on Guam, Micronesia 3 (Suppl.): 47–49.
- Menninger EA, Soderholm PK, Greensmith P, MacKenzie G. 1976. Propagating the yellow African tulip tree. Proceedings of the Florida State Horticultural Society 88: 443–444; 1975 [Horticultural Abstracts 1973+].
- Nalawadi UG, Gowda JVN, Sulladmath UV. 1980. Varied season of flowering of *Spathodea campanulata* (Beauv.) under Bangalore conditions. Current Research 9(4): 58–59 [Horticultural Abstracts 1973+].
- Neal MC. 1948. In gardens of Hawaii. Spec. Pub. 40. Honolulu: Bernice P. Bishop Museum Press. 805 p.
- Streets RJ. 1962. Exotic forest trees in the British Commonwealth. Oxford: Clarendon Press. 750 p.
- Unwin AH. 1920. West African forests and forestry. New York: E.P. Dutton. 527 p.
- Vozzo JA. 2002. Tropical tree seed manual. Agric. Handbk. 721. Washington, DC: USDA Forest Service. 891 p.
- White WC. 1951. Flowering trees of the Caribbean. New York: Rineland and Co. 125 p.
- Worthington TB. 1959. Ceylon trees. Colombo, Sri Lanka: Colombo Apothecaries' Co., 429 p.

Rosaceae—Rose family

Spiraea L.

spirea

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Growth habit, occurrence, and uses. There are about 80 species of the genus *Spiraea* throughout the world. The genus is subdivided into subgenera and sections in several ways depending upon the author—all classifications are based primarily on the structure of the inflorescence. In the system followed here (Batta 1977), the genus has 3 sections: Chamaedryon, Calospira, and Spiraria. In the United States and Canada, the taxa listed in table 1 are fairly common (Curtis 1959; Esser 1995; Fernald 1950; Habeck 1991; MacKinnon and others 1992; Ogle 1991b; Viereck and Little 1972). Virginia spirea occurs primarily in the southeastern United States and has been listed as a threatened species (Ogle 1991a).

Spireas are important ornamental shrubs—Dirr (1990) lists 13 species used as ornamentals. Within a species, as many as 15 to 20 cultivars may have been recognized. Most of the important ornamentals have been introduced from

China and Japan; many of the original introductions occurred in the early to mid-1800s (Dirr 1990). Some introduced species, for example, Japanese spirea (*Spiraea japonica* L.f.), have become naturalized and occupy habitats similar to those of native spireas (Batta 1977; Fernald 1950; Ogle 1991a).

A common habitat for the genus in general seems to be in riparian areas, bogs, or other wetland habitats (Curtis 1959; Esser 1995; Klinka and others 1985; MacKinnon and others 1992; Ogle 1991a&b; Viereck and Little 1972). However, the eastern and western forms of birchleaf spirea and the hybrid *S. × pyramidata* Greene (pro sp.) occur on drier upland sites than do other species (Corns and Annas 1986; Stickney 1986). These species can be found at all stages of succession, but they seem to achieve their greatest stature and best growth following disturbances—such as fire or flooding—that remove the overtopping trees and thus

Table 1—*Spiraea*, spirea: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
<i>S. alba</i> Du Roi	meadowsweet	Newfoundland, Quebec to Alberta S to North Carolina, Missouri, & South Dakota
<i>S. alba</i> var. <i>latifolia</i> (Ait.) Dippel <i>S. latifolia</i> (Ait.) Borkh.	meadowsweet	SE Canada & NE US
<i>S. betulifolia</i> var. <i>corymbosum</i> (Raf.) Maxim.	birchleaf spirea	Maryland, Virginia, West Virginia S to Alabama
<i>S. betulifolia</i> var. <i>lucida</i> (Dougl. ex Greene) C.L. Hitchc.	birchleaf spirea	South Dakota, Montana, Idaho, Washington, Oregon, Wyoming, British Columbia, Alberta, & Saskatchewan
<i>S. douglasii</i> Hook.	Douglas spirea	Alaska S to N California, British Columbia, Montana, Oregon
<i>S. stevenii</i> (Schneid.) Rydb. <i>S. beauverdiana</i> (Schneid.)	Beauverd spirea, Alaska spirea	Alaska & NW Canada
<i>S. tomentosa</i> L.	hardhack, steeplebush	Nova Scotia, New Brunswick, & Quebec to Minnesota & S to North Carolina, Tennessee, & Arkansas
<i>S. virginiana</i> Britt.	Virginia spirea, Appalachian spirea	West Virginia, Virginia, Tennessee, North Carolina, & Georgia

Sources: Curtis (1959), Habeck (1991), MacKinnon and others (1992), Ogle (1991a&b), Viereck and Little (1972).

make light and other resources more available (Ogle 1991b; Stickney 1974, 1986, 1989, 1990).

Native spireas are generally 1 to 2 m tall. Plants growing at higher elevations tend to be shorter in stature than those at low elevations. Individual plant form tends to be a multi-stemmed clump arising from basal sprouting. Many species are rhizomatous and capable of forming dense stands (clones). Beauverd spirea does not appear to be rhizomatous. Layering occurs in some species when aerial stems come in contact with a suitable substrate long enough for rooting to occur (Calmes and Zasada 1982; Esser 1995; Fowler and Tiedemann 1980; Habeck 1991; Ogle 1991b; Stickney 1974, 1986, 1990).

Planting as an ornamental seems to be the major use of plants in the genus. Native species occurring in riparian and wetland areas can be used in rehabilitation projects on these sites. Some species were used to a limited extent for medicinal purposes by Native Americans (Dirr 1990; Esser 1995; Habeck 1991; Meeker and others 1993; Ogle 1991b).

Flowering and fruiting. Batta (1977) found that the various species and varieties of spirea growing in a common garden in Norway exhibited marked differences in phenology and the timing of floral bud differentiation. Differences in timing of floral bud initiation are determined in part by the type of shoot on which the buds form. Species in section *Chamaedryon* form buds on the previous year's growth; species in section *Spiraria*, on the current year's growth; and species in *Calospira*, on both types of shoots (Batta 1977). Goi and others (1974, 1975) demonstrated that species differ in their temperature requirements for initiation of flower buds. In the species they studied, one initiated flower bud development at temperatures below 20 °C and the other below 25 °C.

Within a species, microclimate significantly influenced the timing of flowering and fruit maturation. Birchleaf spirea flowered at about 16,000 degree-hours (threshold temperature 0 °C) at elevations of 590, 1,105, and 1,635 m, but the heat sums were attained over a period of 30 to 40 days, with earliest flowering in mid-to late May at the lowest elevation (Fowler and Tiedeman 1980). At elevations around 985 m in the northern Rocky Mountains, flowering may occur from early June to early July (Drew 1967; Stickney 1974). Fruits ripen from mid-July to early September (Drew 1967; Stickney 1974), and seeds disseminate in October (Drew 1967). Flowering in Beauverd spirea in Alaska occurs in June–August and fruit maturation from July–September. Timing, as in birchleaf spirea varies significantly with elevation and between boreal forest and tundra populations (Viereck and Little 1972). In the southern

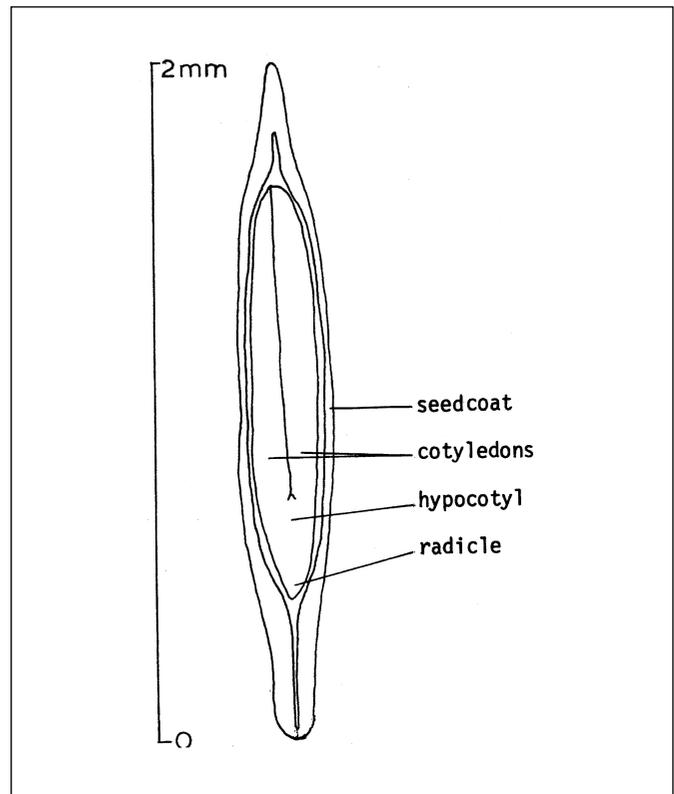
Appalachian Mountains, follicles of Virginia spirea begin to dehisce in late August–September and the process continues through late winter (Ogle 1991a&b).

Individual flowers are very small (1.5 mm) and perfect; they are borne in terminal clusters of various sizes shapes and colors (white and pink–deep rose) (Hitchcock and others 1961; MacKinnon and others 1992; Stickney 1974). Seeds are borne in a follicle and measure 2 to 3 mm in length (figures 1 and 2). Dispersal begins when the fruit

Figure 1—*Spiraea betulifolia* var. *lucida*, birchleaf spirea: seed.



Figure 2—*Spiraea betulifolia* var. *lucida*, birchleaf spirea: longitudinal section through a seed.



becomes straw-colored or light brown and splits down one side. Although there are no estimates of the number of seeds per weight, the number is probably in the millions per kilogram (500,000+ per pound), due to the extremely small size of the seeds, usually 2 mm or less \times 0.05 mm (0.8 \times 0.02 in).

Annual variation in the quantity and quality of the seed-crop will depend on microclimate and its effect on pollination, flowering, seed maturation, time since disturbance, and other variables. Fowler and Tiedemann (1980) reported frost damage to birchleaf spirea flowers in early-flowering lower-elevation populations but not in later-flowering higher-elevation plants. Abortion of flowers and fruits is high in Virginia spirea growing in the southern Appalachian Mountains, particularly in years of low water availability (Ogle 1991b). Factors regulating flower bud differentiation, and thus flowering potential, vary for those species that differentiate flower buds in late summer–fall compared to those that differentiate in the spring shortly before flowering (Batta 1977).

Birchleaf spirea exhibits the phenomena of mass flowering after fire (Stickney 1986, 1989, 1990). In studies of succession following fire over a 20-year period, this species flowered profusely in the first postfire growing season, but only occasionally in scattered individuals during the subsequent 19 years. As tree canopies develop and light intensity declines, flowering is rare and the species maintains itself through vegetative reproduction.

Collection of fruits, seed extraction and storage.

Seeds can be collected when the fruits turn brown. Fruits can be dried at room temperature so that they open fully; seeds are removed by tumbling or shaking the dried fruits. Seeds can be stored for several months to at least a year. In birchleaf spirea, mass flowerings in 1-year-old burns provides the best opportunity for seed collection.

Seeds have been recovered from studies of forest seed-banks in both the eastern and western United States. However, there is no good evidence that buried seeds are a significant source of regeneration after disturbance (Graber and Thompson 1978; Morgan and Neuenschwander 1988). These studies did not provide information on the length of time seeds remain viable in the forest floor or mineral soil.

Germination. Seeds germinate readily with no pretreatment, particularly if sown before there has been any significant drying (Dirr and Haeuser 1987). Birchleaf spirea seeds germinate at 0 to 2 °C when kept under such conditions for more than 120 days (McLean 1967). This suggests that seeds sown in the fall and overwintering under the snow will germinate at about the time of snowmelt to take best advantage of conditions favorable for seedling development. Unstratified seeds of Beauverd spirea germinated only at 25 °C. Germination of stratified seeds (30 days at 2 °C) was greater than 95% between 10 to 25 °C and 40% at 5 °C. Neither stratified nor unstratified seeds germinated to any degree in the dark (Calmes and Zasada 1982). Filled seeds made up 68 and 85% of seedlots of birchleaf and Beauverd spireas, respectively (Calmes and Zasada 1982; McLean 1967).

Nursery practice and natural regeneration. Natural regeneration following disturbance appears to be mostly by basal sprouting or from rhizomes. Only very severe fires or soil disturbances can eliminate vegetative reproduction (Calmes and Zasada 1982; Morgan and Neuenschwander 1988; Ogle 1991; Stickney 1986, 1989).

Seed regeneration of birchleaf spirea occurs 2 to 3 years after fire, when seeds are abundant following the mass flowering in the first post-fire growing season (Stickney 1989). This appears to be the main window for seed regeneration, as seed availability and seedbed conditions are best at this time (Stickney 1986, 1989, 1990). However, recent germinants and 1- to 2-year-old seedlings are not common (Miller 1996; Morgan and Neuenschwander 1988; Stickney 1990).

Plants can be produced from seeds or by vegetative propagation. Seeds should be sown immediately after collection for the most rapid germination. Stored seeds may require some stratification for best germination, but unstratified seeds germinate well. Softwood or hardwood cuttings of horticultural varieties can be rooted and grow fairly rapidly, filling a 3.8-liter (1-gal) container in a single growing season. Softwood cuttings appear to be used most commonly (Dirr and Heuser 1985). Shoot explants and micropropagation can be used to increase desirable clones; performance and vigor of plants produced in this way varies with season of the year and the number of times vegetative material is subcultured (Norton and Norton 1988 a&b).

- Batta J. 1977. Studies of the genus *Spiraea*. Rep. 62. Ås, Norway: Agricultural University of Norway, Department of Dendrology and Nursery Management. 12 p.
- Calmes MA, Zasada JC. 1982. Some reproductive traits of four shrub species in the black spruce forest type of Alaska. *Canadian Field Naturalist* 96(1): 35–40.
- Corns IGW, Annas RM. 1986. Field guide to forest ecosystems of west-central Alberta. Edmonton, AB: Canadian Forest Service, Northern Forestry Centre.
- Curtis JT. 1959. The vegetation of Wisconsin: an ordination of plant communities. Madison: University of Wisconsin Press. 657 p.
- Dirr MA. 1990. Manual of woody landscape plants: their identification, ornamental characteristics, culture, propagation, and uses. Champaign, IL: Stipes Publishing. 1007 p.
- Dirr MA, Heuser CW Jr. 1987. The reference manual of woody plant propagation: from seed to tissue culture. Athens, GA: Varsity Press. 239 p.
- Drew LA. 1967. Comparative phenology of seral shrub communities in the cedar/hemlock zone [unpublished MS thesis]. Moscow, ID: University of Idaho, College of Forestry. 108 p.
- Esser LL. 1995. *Spiraea douglasii*. In: Fischer WC, comp. The Fire Effects Information System [data base]. Missoula, MT: USDA Forest Service, Intermountain Research Station, Fire Science Laboratory.
- Fernald ML. 1950. Gray's manual of botany. 8th ed. New York: American Book Co. 1632 p.
- Fowler WB, Tiedemann AR. 1980. Phenological relationships of *Spiraea betulifolia* Pall. and *Apocynum androsaemifolium* L. *Northwest Science* 54(1): 17–25.
- Goi M, Kawanishi T, Ihara Y. 1975. Studies on the acceleration of flowering in woody ornamentals by low temperature treatments: 5. The flowering behavior of *Spiraea cantonensis* [abstract]. *Kagawa Daigaku Nogakubu Gakujutsu Hokoku* 26: 84–93.
- Goi M, Hasegawa A, Kashiwaga Y. 1974. Studies on the acceleration of flowering in woody ornamentals by low temperature treatments: 4. Flowering behavior of *Spiraea thunbergii*. *Kagawa Daigaku Nogakubu Gakujutsu Hokoku* 25: 35–42.
- Graber RE, Thompson DF. 1978. Seeds in the organic layers and soil of four beech–birch–maple stands. Res. Pap. NE-401. Upper Darby, PA: USDA Forest Service, Northeastern Forest Experiment Station. 8 p.
- Habeck RJ. 1991. *Spiraea betulifolia*. In: Fischer WC, comp. The Fire Effects Information System [data base]. Missoula, MT: USDA Forest Service, Intermountain Research Station, Intermountain Fire Science Laboratory.
- Hitchcock CL, Cronquist A, Ownbey M, Thompson JW. 1961. Vascular plants of the Pacific Northwest. Part 3: Saxifragaceae to Ericaceae. Seattle: University of Washington Press. 614 p.
- Klinka K, Scagel AM, Courtin PJ. 1985. Vegetation relationships among some seral ecosystems in southwestern British Columbia. *Canadian Journal of Forest Research* 15: 561–569.
- MacKinnon A, Pojar J, Coupe R. 1992. Plants of northern British Columbia. Edmonton, AB: Lone Pine Publishing. 345 p.
- McLean A. 1967. Germination of forest range species from southern British Columbia. *Journal of Range Management* 20(5): 321–322.
- Meeker JE, Elias JE, Heim JA. 1993. Plants used by the Great Lakes Ojibway. Odanah, WI: Great Lakes Indian and Fish and Wildlife Commission. 440 p.
- Miller M. 1996. Personal communication. Boise, ID: USDI Bureau of Land Management, Office of Fire and Aviation.
- Morgan P, Neuenschwander LF. 1988. Seed-bank contributions to regeneration of shrub species after clear-cutting and burning. *Canadian Journal of Botany* 66: 169–172.
- Norton ME, Norton CR. 1988a. The role of season in determining explant suitability for *in vitro* culture of *Prunus* and *Spiraea*. *Acta Horticulturae* 227: 450–452.
- Norton CR, Norton ME. 1988b. Manipulation of differentiation in *Spiraea in vitro*. *Acta Horticulturae* 226: 191–194.
- Ogle DW. 1991a. *Spiraea virginiana* Britton: 1. Delineation and distribution. *Castanea* 56(4): 287–296.
- Ogle DW. 1991b. *Spiraea virginiana* Britton: 2. Ecology and species biology. *Castanea* 56(4): 297–303.
- Stickney PF. 1974. *Spiraea betulifolia* var. *lucida* (Dougl.) C.L. Hitchc., birchleaf spiraea. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 785–786.
- Stickney PF. 1986. First decade plant succession following the Sundance forest fire, northern Idaho. Gen. Tech. Rep. INT-197. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station. 26 p.
- Stickney PF. 1989. After forest wildfire, then what? ... masses of flowers. Words on Wilderness [newsletter of the Wilderness Studies and Information Center] April/May: 6.
- Stickney PF. 1990. Personal observation. Missoula, MT: USDA Forest Service.
- Viereck LA, Little EL Jr. 1972. Alaska trees and shrubs. Agric. Handbk. 410. Washington, DC: USDA Forest Service. 265 p.

Styracaceae—Storax family

Styrax L.

snowbell

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Growth habit, occurrence and use. The genus *Styrax*—the snowbells—comprises about 100 species of trees and shrubs in the warm temperate and tropical regions of the Northern Hemisphere (LHBH 1976). The snowbells in the United States are shrubs or small trees planted for their showy flowers (table 1). Southeastern Asian species are the source of the balsamic resin benzoin (LHBH 1976).

American snowbell grows to 5 m and 9 cm dbh, with 9-cm-long pubescent leaves. Even though American snowbell is common, it rarely grows large enough to be considered a tree. It grows under 200 m of elevation in moist to wet places, such as bottomland woods, flood plains, swamps, and stream banks (Duncan and Duncan 1988; LHBH 1976).

Bigleaf snowbell reaches 8 m and 10 cm dbh, with 18-cm-long gray pubescent leaves. It grows to 1,000 m elevation in deciduous or mixed woods, usually in well-drained areas. Bigleaf snowbell rarely reaches tree size (Duncan and Duncan 1988; LHBH 1976). The USDI Fish and Wildlife Service has designated Texas snowbell as an endangered species.

Several Asian snowbells are grown in the United States. Japanese snowbell grows to 9 to 10 m with 8-cm-long

glabrous leaves. Fragrant snowbell also reaches 9 to 10 m but has 25-cm-long tomentose or densely pubescent leaves (LHBH 1976).

Flowering and fruiting. Snowbells have bell-shaped, showy white flowers that are deeply lobed (5 to 8 lobes), with 10 to 16 stamens and a superior ovary 3-celled below and 1-celled above (LHBH 1976). The fruit, although often referred to as a drupe, is a berry—or a capsule in dehiscent species such as drug snowbell or keminyan (*Styrax officinalis* L.)—because the stony layer is really the seedcoat instead of endocarp (Ng 1976). The American snowbell berry is about 7 mm across, grayish, with dense, short hairs (Dirr and Heuser 1987; Duncan and Duncan 1988). It matures in August and drops by November (Dirr and Heuser 1987).

Collection of fruit, extraction, and storage. The single, hard, shiny brown seed separates from the fruit at maturity (Dirr and Heuser 1987) and is easily collected. The fruits may also be collected while they are still green in September (in Louisiana) or should be collected at least 14 weeks after flowering for Japanese snowbell, and air-dried in a well-ventilated place until the drupe walls turn brown

Table 1—*Styrax*, snowbell: nomenclature and occurrence

Scientific name & synonyms(s)	Common name(s)	Occurrence
<i>S. americanus</i> Lam. <i>S. americanus</i> var. <i>pulverulentur</i> (Michx.) Perkins ex Rehd. <i>S. pulverulentus</i> Michx.	American snowbell, mock-orange*	Virginia to Florida & Louisiana
<i>S. grandifolius</i> Ait. <i>S. japonicus</i> Sieb. & Zucc.	bigleaf snowbell Japanese snowbell, Japanese snowdrop tree, snowbell tree	Virginia to Florida & Louisiana Japan, Korea, & China
<i>S. obassia</i> Sieb. & Zucc.	fragrant snowbell, bigleaf snowbell	China, Japan, & Korea
<i>S. platanifolius</i> Engelm. ex Torr. ssp. <i>texanus</i> (Cory) P.W. Fritsch	Texas snowbell	Texas

Sources: Duncan and Duncan (1988), LHBH (1976), Wasson (2001).

* Although this common name is in use, it is more correctly applied to members of the genus *Philadelphus*.

and seeds become loose. The dried seeds can be separated from the fruit fragments by running them through a de-bearder or macerator (Delaney (2002). Small amounts may be separated by rubbing the lot between the hands. Seed weight data are listed in table 2.

There have been no storage data reported for the snowbells, but the nature of the seeds suggests that they are orthodox in storage behavior and should store well in cold, dry conditions. Seeds stored dry at room temperature (20 to 21 °C) for a year germinated well after a proper warm and cold stratification treatment.

Seed germination as influenced by seed maturity. In 1999, when Japanese snowbell seeds were harvested on August 25 and September 8, there were 67 and 80% of seeds germinated in 6 and 7 weeks, respectively (table 3) (Roh and others 2003). More than 80% of the seeds germinated in less than 4.5 weeks when seeds were harvested after September 8. Based on the final seed germination rate, seeds were considered to be mature when harvested on or after August 25, which is 12 weeks after flowering. In 2000, more than 73% of seeds germinated in a period of 6 weeks or less when seeds were harvested on or after October 4 (table 3), and seeds were considered to be mature when harvested on September 13, about 14 weeks after flowering. For both years, the mean peak germination, and the mean number of weeks for germination peak were significantly influenced by harvest date, that is, seed maturity.

Pregermination treatments and germination tests.

American snowbell germinates successfully after 3 months of cold stratification. Fall-sowing of fresh, cleaned seeds in Alabama also yielded excellent spring germination (Dirr and Heuser 1987). Bigleaf snowbell, another snowbell from the southeastern United States, is believed to have the same germination requirements as American snowbell (Dirr and Heuser 1987). Japanese snowbell seeds that are sown in the fall without a sequential warm stratification and cold stratification may germinate the second spring (Dirr 1990; Kwon 1995). Kwon (1995) suggested that the radicle might emerge after 3 months of warm stratification and then enter a dormancy. Stratification of seeds using warm and cold temperatures is required to break seed dormancy for many woody

Table 2—*Styrax*, snowbell: seed data (average cleaned seeds per weight)

Species	Seeds/weight		Samples
	/kg	/lb	
<i>S. americanus</i>	11,200	5,090	1
<i>S. japonicus</i>	8,000	3,630	2
<i>S. obassia</i>	2,950	1,340	2

Table 3—*Styrax japonicus*, Japanese snowbell: effect of seed maturity on seed germination

Harvest date	Mean peak germination* (%)	Mean no. of weeks until peak germ.
1999		
23 June	0	—
14 July	0	—
27 July	0	—
10 Aug	7 d	3.0 b
25 Aug	67 c	6.0 a
8 Sept	80 b	7.0 a
22 Sept	83 ab	4.0 b
5 Oct	84 a	4.5 ab
26 Oct	80 b	3.0 b
2000		
19 July	0	—
2 Aug	0	—
16 Aug	5 e	2.3 c
30 Aug	16 d	7.0 a
13 Sept	65 c	8.0 a
4 Oct	73 b	4.7 b
19 Oct	88 a	6.0 ab

Source: Roh and others (2003).

Note: For each year, means within each column followed by the same letters are not significantly different from each other.

* For mean peak germination, 1999: F = 80.20; df = 5, 11; P < 0.0001; and N = 12. For 2000: F = 254.17; df = 4, 14; P < 0.0001; and N = 15.

† For mean number of weeks until peak germination, 1999: F = 4.88; df = 5, 11; P < 0.0398; and N = 12. For 2000: F = 15.61; df = 4, 14; P < 0.003; and N = 15.

plants to improve seed germination (Young and Young 1992). It has been recommended that snowbell seeds should be stored in a moist, warm environment for 3 (Kwon 1995) or 5 (Dirr 1990) months, and then stored at low temperatures for 3 or 4 months (Dirr 1990; Kwon 1995). Seeds that are sown immediately after collection may germinate by the following spring, suggesting that non-fresh seeds may take longer to germinate (Dirr 1990).

Japanese snowbell has been reported to need 3 to 5 months of warm stratification followed by 3 months of cold stratification to germinate (Dirr and Heuser 1987). Seedlots in one study germinated at 64% after 3 months of warm and 3 months of cold stratification and at 76% after 3 months of warm and 4 months of cold stratification. Seeds with 3 or 4 months of cold stratification did not germinate (Dirr and Heuser 1987).

Fragrant snowbell germinated 88% after 3 months of warm stratification and 3 months of cold stratification (Dirr and Heuser 1987). Benzoin tree—*Styrax benzoin* Dryander, a species from Southeast Asia—is one of the few trees in Malaysia with dormant seeds. They germinate when the stony layer cracks open about 7 months after fruit fall. Fresh seeds will germinate if the stony layer is removed (Kiew 1982).

However, recent research results indicate that 3 months of warm stratification is not required for high germination of mature seeds (Roh and Bentz 2003; Roh and others 2003). Japanese snowbell seeds need warm moist stratification for at least 1 month followed by cold stratification for 3 months to improve germination. Without any warm stratification, seeds would not germinate. Control seeds that were kept dry in a 18.5 °C greenhouse did not germinate by the time the completion of the experiment (table 4). Examination of non-germinated seeds revealed that the seedcoat was intact in most of the seeds, but a radicle was visible through the seedcoat in less than 10% of the non-emerged seeds (figure 1). After 1 month of dry warm stratification, more than 70% of the seeds had germinated. For example, seeds that were sown in the fall germinated in the second spring in the field. If seeds were on the ground dry, warm stratification requirements could not be fulfilled, and thus seeds may not be able to respond to cold stratification. When seeds become dried after experiencing the moist conditions, germination percentage will be low (table 5). The low germination of seeds that were harvested in 2000 and stored dried for 4 months could be due to an unknown physiological process in the seeds, because seeds that were harvested in 1999 showed higher than 80.8% germination while seeds harvested in 2000 showed less than 53.5% (table 3).

Nursery practice and seedling care. American snowbell seeds should be planted in the fall or stratified and planted in the spring. Fragrant and Japanese snowbell seeds should be planted in summer or given warm stratification before cold stratification. Seeds should be sown immediately

upon harvest to avoid any possible reduction in the germination percentage by dry storage. At least 1 month of warm stratification is required, followed by 3 months of cold stratification to improve germination. Japanese snowbell seeds harvested 12 to 14 weeks after flowering are mature and respond to germination-promoting treatments. One month of warm stratification at 18.5/18 °C followed by 2 months of cold stratification at 5.5 °C resulted in germination higher than 73%, while the maximum germination percentage was 98% after 2 months of warm stratification, followed by 3 months of cold stratification (figure 2).

Figure 1—*Styrax japonicus*, Japanese snowbell: seeds, with only a few showing an emergent radicle (courtesy of Roh and Bentz 2003).



Table 4—*Styrax japonicus*, Japanese snowbell: effect of seed harvest year and months in moist storage on seed germination

Seed harvest year	Moist storage at 18.5 °C	Germination %
1999	0	0
	1	70.8 ± 2.4 b
	2	85.0 ± 2.4 a
	3	80.8 ± 2.4 a
	4	85.0 ± 2.4 a
2000	0	0
	1	72.5 ± 2.4 b
	2	75.8 ± 2.4 b
	3	52.5 ± 2.4 c
	4	53.3 ± 2.4 c

Sources: Roh and Bentz (2003), Roh and others (2003).

Note: Germination values are means ± standard error of the means; means within each column, followed by the same letters, do not differ significantly from each other.

Figure 2—*Styrax japonicus*, Japanese snowbell: uniform and well-germinated seedlings from seeds that received 2 months of warm stratification followed by 3 months of cold stratification (courtesy of Roh and Bentz 2003).

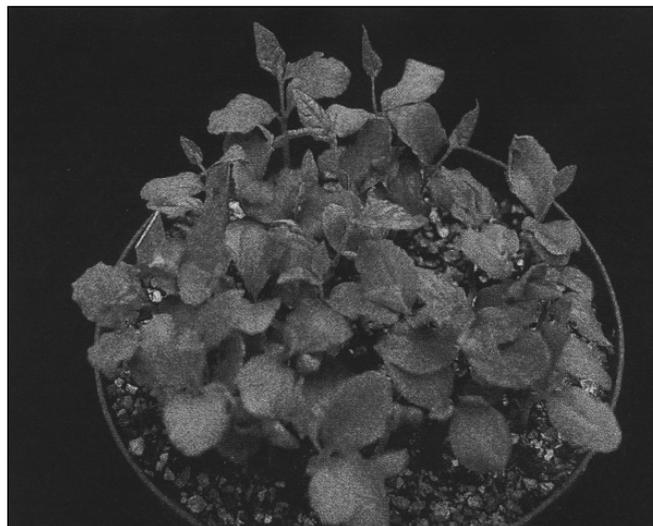


Table 5—*Styrax japonicus*, Japanese snowbell: effect of storage duration and moisture on seed germination, as evidenced by the number of weeks to reach peak germination

Months in storage	Moisture during storage	Germination peak (%)	Weeks to peak germination
0	Dry	0	—
	Moist	0	—
1	Dry	70.8 ± 2.2 a	6.3 ± 0.45
	Moist	53.3 ± 2.2 c	6.3 ± 0.45
2	Dry	59.2 ± 2.2 bc	7.0 ± 0.45
	Moist	65.0 ± 2.2 ab	5.0 ± 0.45
3	Dry	41.7 ± 2.2 d	6.7 ± 0.45
	Moist	61.7 ± 2.2 b	5.3 ± 0.45
4	Dry	28.3 ± 2.2 e	5.3 ± 0.45
	Moist	66.7 ± 2.2 a	5.7 ± 0.45

Sources: Roh and Bentz (2003).

Note: Values are means ± standard error; means within each column followed by the same letters do not differ significantly from each other at P < 0.05.

References

- Delaney J. 2002. Personal communication. Lecompte, LA: Louisiana Forest Seed Co.
- Dirr M, Heuser C Jr. 1987. The reference manual of woody plant propagation: from seed to tissue culture. Athens, GA: Varsity Press. 239 p.
- Dirr M. 1990. Manual of woody landscape plants: their identification, ornamental characteristics, culture, propagation and uses. Champaign, IL: Stipes Publishing. 1007 p.
- Duncan W, Duncan M. 1988. Trees of the southeastern United States. Athens, GA: University of Georgia Press. 322 p.
- Johnson W. 1997. Unpublished data. Dry Branch, GA: USDA Forest Service, National Tree Seed Laboratory.
- Kwon HJ. 1995. Ecological characteristics, propagation method, and new cultivar of Korean *Styrax japonicus* Sieb. et. Zucc. for landscape tree uses [PhD thesis]. Suwon, Korea: Sung Kyun Kwan University.
- Kiew R. 1982. Germination and seedling survival in keminyan, *Styrax benzoin*. Malaysian Forester 45(1): 69–80.
- 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.
- Ng FSP. 1976. The fruits, seeds and seedlings of Malayan trees: XII–XV. Malaysian Forester 39(3): 110–146.
- Roh MS, Bentz JA. 2003. Germination of *Styrax japonicus* seeds as influenced by storage and sowing conditions. Acta Horticulturae 630: 411–416.
- Roh MS, Bentz JA, Wang P, Li E, Koshioka M. 2003. Maturity and temperature stratification affects the germination of *Styrax japonicus* seeds [unpublished data, submitted to Seed Technology].
- Wasson E. 2001. Trees and shrubs: illustrated A–Z of over 8500 plants. Willoughby, NSW, Australia: Global Publishing: 725.

Meliaceae—Mahogany family

Swietenia Jacq.

mahogany

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Growth habit, occurrence and use. There are 3 species of mahogany and 1 important hybrid, all of which grow in dry or moist, tropical or subtropical forests of the New World (table 1). All are large trees capable of reaching to 20 to 40 m of height (depending on site) and more than 2 m in diameter. Mahogany species are medium- to long-lived, mid-successional species. Their wood is used for furniture, trim, cabinets, carving, boat building, timbers, posts, and fuel (Chudnoff 1984; Francis 1991). Mahogany wood is particularly desirable because it is dimensionally stable, easily worked with hand and power tools, and very attractive. The mahoganies are also extensively planted as shade and ornamental trees.

Flowering and fruiting. The small greenish white flowers are borne in panicles attached at leaf axials near the ends of branches. The flowers are pollinated by insects and

usually produce only 1 fruit (a capsule) per inflorescence. Flowering generally takes place during the spring, with fruits ripening 9 months later. Season of fruiting varies between portions of the range and individual trees.

Occasional trees can be found with fruits at any season of the year in Puerto Rico. Fruiting begins when trees are between 10 and 25 years old for open-grown and dominant or codominant trees. A few to more than a hundred capsules may be produced, depending on the size and vigor of the tree. Mahogany species produce good seedcrops nearly every year. Table 2 lists the fruit sizes, seeds per fruit, and seeds per weight for members the genus.

Collection, cleaning, and storage. As the fruits mature, they turn from gray-green to reddish brown. At maturity, the capsule walls split into 5 carpels from the bottom upwards and then fall off. The exposed seeds (samaras)

Table 1—*Swietenia*, mahogany: nomenclature and occurrence

Scientific name & synonym	Common name(s)	Occurrence—native (& planted)
<i>S. humilis</i> Zucc.	Pacific Coast mahogany	Mexico to Costa Rica
<i>S. macrophylla</i> King	bigleaf mahogany,	Mexico to Bolivia (Puerto Rico & Hawaii)
<i>S. candollei</i> Pittier	Honduras mahogany	
<i>S. mahagoni</i> (L.) Jacq.	West Indies mahogany,	Florida, Cuba, Bahamas, Jamaica, & Hispaniola
	littleleaf mahogany	(Puerto Rico, US Virgin Islands, & Hawaii)
<i>S. macrophylla</i> x <i>mahagoni</i>	hybrid mahogany	St. Croix, Puerto Rico*

Sources: Blake (1920), Francis (1991), Lamb (1966), Whitmore and Hinojosa (1977).

* Arose spontaneously from the introduced parent species.

Table 2—*Swietenia*, mahogany: seed yield data

Species	Median fruit dimensions (cm)	Seeds/fruit	Seeds/weight	
			/kg	/lb
<i>S. humilis</i>	17 x 11	50 +	1,500	680
<i>S. macrophylla</i>	15 x 8	50–70	1,400–2,400	640–1,100
<i>S. mahagoni</i>	7 x 4	35–60	5,400–7,800	2,500–3,500
<i>S. macrophylla</i> x <i>mahagoni</i>	12 x 7	45–65	1,900–3,000	860–1,400

Sources: Blake (1920), Francis and Rodriguez (1993), Marraro (1949), Montalvo and others (1991), Whitmore and Hinojosa (1977).

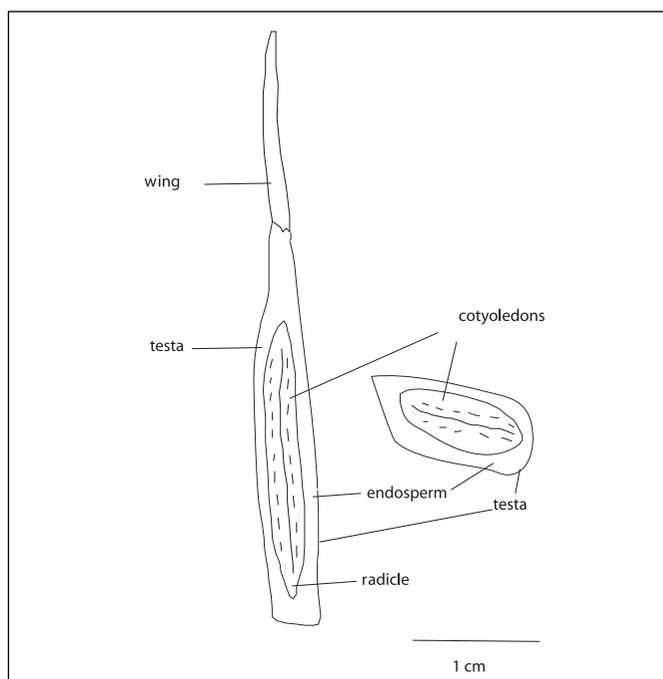
dry quickly and are released a few at a time, usually in the afternoon. Borne on papery wings (figures 1 and 2), they spiral downward and outward and usually land within 1 or 2 tree lengths of the mother tree.

Small quantities of seeds can be picked up from the ground near seed-bearing trees. Seeds can be collected in quantity by clipping the capsules from short-statured trees with pruning poles after the first few capsules on a tree have opened. Large trees must be climbed or collections must be made at logging sites. When spread on trays in ventilated rooms or in the sun, the capsules open in a few days and the seeds can be separated by hand. Two or three days of further

Figure 1—*Swietenia*, mahogany: seeds, showing the papery wings.



Figure 2—*Swietenia macrophylla*, bigleaf mahogany: longitudinal and cross sections of seed.

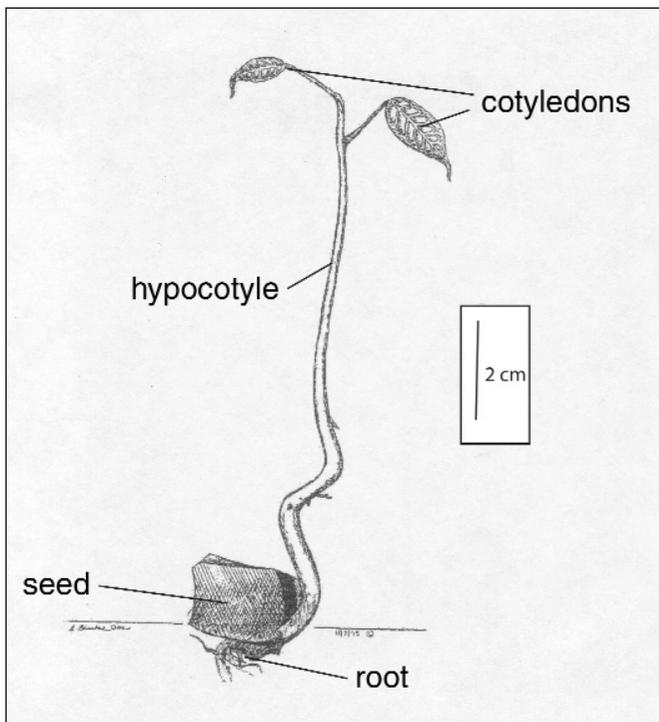


drying at mild temperatures is recommended before storage, but no precise guideline for storage moisture content is available. Considerable volume, but little weight, can be saved by de-winging the seeds. Room temperature is adequate for short-term storage (up to 4 months); for longer periods, 4 °C is recommended. Perhaps because of their high oil content, mahogany seeds lose their ability to germinate during storage. Storage at temperatures ranging from 0 to 30 °C resulted in significant losses in germinative capacity after 3 or 4 months. Reductions in germinative capacity were more severe for seedlots having high initial germination than those with moderate germinative capacity (Vivekanandan 1978). Bigleaf mahogany in Puerto Rico stored at room temperature also began to lose germinative capacity rapidly after 3 to 4 months and finally approached 0% between 1 and 2 years (Marrero 1943). Seeds of bigleaf mahogany from Cuba that were stored at 5 °C with an initial germination percentage of 39% had 13% germination after 2 years and 4% germination after 3 years (Montalvo and others 1991).

Germination. Seeds from 14 provenances of bigleaf mahogany in Cuba were subjected to cutting tests. Ninety-eight percent were sound, 1.2% were empty, and 0.9% were diseased (Montalvo and others 1991). However, sound endosperm is not a reliable indicator of germinative capacity. Seedlots of fresh mahogany seeds normally give 39 to 98% germination (Campbell de Araujo 1971; Francis and Rodriguez 1993; Marrero 1949; Montalvo and others 1991; Ricardi and others 1977). Conditions during the seed year appear to affect the ability of fresh seeds to germinate. Mahogany seeds usually began to germinate (figure 3) 12 to 18 days after sowing, with complete germination within about 30 days of sowing (Campbell de Araujo 1971; Francis and Rodriguez 1993; Marrero 1949; Ricardi and others 1977). No pretreatments are necessary. Germination is hypogeal.

Nursery practice. A common method of sowing mahogany seeds is to insert them edge-wise by hand, leaving half of the seed's width exposed and keeping the medium moist until germination. Orientation of the seeds is for convenience only, as it has no significant effect on germination or growth (Mondala 1977). Seeds may also be sown and covered with about 1 cm (1/2 in) of sand, sawdust, or loose soil. In a test of depth of sowing on bigleaf mahogany seeds, depth did not affect germination, but deep sowing adversely affected early seedling growth (Schmidt 1974). In a Brazilian test of deep sowing at 6 cm (2.4 in), germinants failed to reach the soil surface (Campbell de Araujo 1971). In nurserybeds, seeds are sown 5 to 10 cm (2 to 4 in) apart

Figure 3—*Swietenia*, mahogany: germinating seedling.



in rows spaced 20 to 30 cm (8 to 12 in) apart. Seeds are spaced at about 2.5 cm (1 in) in germination trays and pricked-out after they develop 1 or 2 true leaves. Another approach is to sow directly into nursery containers (usually 2 seeds per container) and thin the plants to 1 seedling per container.

Mahogany species are easy to grow in the nursery and transplant well. They may be grown in full sun or light shade. The most common method today is to grow mahogany seedlings in plastic nursery bags. Bareroot seedlings with the leaves removed (striplings), stump plants (Jacalne and others 1957), and top- and bottom-pruned large seedlings about 1 m (3 ft) tall—all have performed well. Bigleaf and hybrid mahogany seedlings are ready to out-plant in 6 to 9 months and West Indies mahogany seedlings are ready in 1 year. Bigleaf mahogany seedlings in a Brazilian nursery were reported to reach a maximum of 30 cm (12 in) in 3 months and 60 cm (24 in) in 6 months (Campbell de Araujo 1971). Direct seeding, which is best done with prepared seed spots, has been successful on several occasions (Lamb 1966). Bigleaf mahogany can be reproduced with cuttings (Burgos 1954; Zaroni-Mendiburu 1975).

References

- Blake SF. 1920. Revision of mahoganies. *Journal of the Washington Academy of Science* 10(10): 286–297.
- Burgos JA. 1954. Un estudio de la silvicultura de algunas especies forestales de Tingo Maria, Peru. *Caribbean Forester* 15(1/ 2): 14–53.
- Campbell de Araujo U. 1971. Sobre a germinação do mogno (aguano) *Swietenia macrophylla* King. *Acta Amazonica* 1(3): 59–69.
- Chudnoff M. 1984. *Tropical timbers of the world*. Agric. Handbk. 607. Washington, DC: USDA Forest Service. 464 p.
- Francis JK. 1991. *Swietenia mahagoni* Jacq., West Indies mahogany. Res. Note SO-ITF-SM-46. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 7 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.
- Jacalne DV, Heimban JR, Tadle JF. 1957. A study of the stump planting of mahogany (*Swietenia macrophylla* King). *Philippine Journal of Forestry* 13(1/ 2): 63–80.
- Lamb FB. 1966. *Mahogany of tropical America*. Ann Arbor: University of Michigan Press. 220 p.
- Marrero J. 1943. A seed storage study of some tropical hardwoods. *Caribbean Forester* 4(3): 99–106.
- Marrero J. 1949. Tree seed data from Puerto Rico. *Caribbean Forester* 10(1): 11–36.
- Mondala CA. 1977. Depth and position of sowing large-leaf mahogany seeds. *Sylvatrop* 2(2): 131–137.
- Montalvo JM, Pena A, Castillo E, Sordo L. 1991. Características de la calidad intrínseca de las semillas de *Swietenia macrophylla*. *Revista Barroca* 21(2/3): 75–84.
- Ricardi M, Torres F, Hernandez C, Quintero R. 1977. Morfología de plantulas de arboles Venezolanos: I. *Revista Forestal Venezolana* 27: 15–56.
- Schmidt PB. 1974. Sobre a profundidade ideal de sementeira do mogno (Aguano): *Swietenia macrophylla* King. *Brasil Florestal* 5(17): 42–47.
- Vivekanandan K. 1978. Retention of viability of mahogany seed through cold storage. *Sri Lanka Forester* 13(3/4): 67–68.
- Whitmore JL, Hinjosa G. 1977. Mahogany (*Swietenia*) hybrids. Res. Paper ITF-23. Río Piedras, PR: USDA Forest Service, Institute of Tropical Forestry. 8 p.
- Zaroni-Mendiburu CA. 1975. Propagación vegetativa por estacas de ocho especies forestales [MS thesis]. Turrialba, Costa Rica: University of Costa Rica. 100 p.

Caprifoliaceae—Honeysuckle family

***Symphoricarpos* Duham.**
snowberry

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Growth habit, occurrence, and use. Species of the genus *Symphoricarpos* occur in North America from Alaska to Mexico (with 1 additional species native to China). There are over a dozen species and varieties (Evans 1974; SCS 1982); 7 are presented here (table 1). Common names include buckbrush, wolfberry, and other vernacular names. The white-berried species are most commonly known as snowberries and the red-berried species as coralberry (Evans 1974; Grimm 1957; Shiell 1992). Snowberry species are usually 40 to 150 cm tall, erect to spreading, densely opposite-branched, thicket-forming, deciduous shrubs. Leaves are 1 to 8 cm long by 0.3 to 4 cm wide, oval or ovate to roundish, opposite, simple, with entire leaf margins (Welsh and others 1987; Grimm 1957). Snowberry species form distinct colonies by underground rhizomes, except for Parish

snowberry, which layers by rooting at above-ground stem nodes that touch the ground (Mozingo 1987). This dense colony stand pattern results in grazing resistance and fire tolerance, making them suitable for stabilizing disturbed lands. Western snowberry and coralberry have been used to some extent for erosion control (Evans 1974). Snowberry can be quite adaptable to site conditions and can grow on a variety of soil types from sandy to heavy clays and on both alkaline and acidic soils (Plummer 1968; Thames 1977). Most species within the genus are generally quite drought tolerant (Shiell 1992).

The snowberries have considerable value for wildlife, for they produce high-quality forage and good cover for game birds and small animals. The foliage provides considerable forage for big game and livestock, and the berries are

Table 1—*Symphoricarpos*, snowberry: nomenclature and occurrence

Scientific name & synonyms	Common name(s)	Natural occurrence*
<i>S. albus</i> var. <i>albus</i> (L.) Blake <i>S. racemosus</i> Michx.	common snowberry	Hudson Bay to Alaska, S to California, & E to North Carolina
<i>S. albus</i> var. <i>laevigatus</i> (Fern.) Blake <i>S. albus</i> ssp. <i>laevigatus</i> (Fern.) Hulten <i>S. rivularis</i> Suksdorf	garden snowberry, Columbia snowberry	S Alaska, S to California, Montana, & Colorado
<i>S. occidentalis</i> Hook.	western snowberry, buckbrush	Saskatchewan to British Columbia, wolfberry, N Washington, Utah, New Mexico, to Minnesota, Missouri, & Illinois
<i>S. orbiculatus</i> Moench	coralberry, Indian currant, snowberry	New York to North Dakota, S to E Texas & Georgia
<i>S. oreophilus</i> var. <i>oreophilus</i> Gray	mountain snowberry,	Southeast variety, Colorado, Arizona, New Mexico, N Sonora, occasionally in Utah
<i>S. oreophilus</i> var. <i>utahensis</i> (Rydb.) A. Nels. <i>S. utahensis</i> Rydb. <i>S. vaccinooides</i> Rydb.	Utah snowberry	Northern variety, British Columbia to Montana, S to California, central Nevada, Utah, & Colorado
<i>S. rotundifolia</i> var. <i>parishii</i> (Rydb.) Dempster <i>S. parishii</i> Rydb.	Parish snowberry	Southern variety, from S California to Arizona & central Nevada, & barely entering the W edge of Utah

Sources: Conquist and others (1984), Evans (1974).* Distribution of *Symphoricarpos* species used in cultivation can vary.

used by birds and black bear (*Ursus americanus*) (Auger 1994; Banister 1991; Evans 1974; Mozingo 1987). Coralberry, common snowberry, and garden snowberry make desirable ornamental plantings because of their attractive fruits (Evans 1974; Shiell 1992).

Flowering and fruiting. Flowers of coralberry are inconspicuous green and purple, whereas the flowers of other species of snowberry are pinkish to yellowish white. All are bell-shaped with 5 rounded lobes, perfect, and borne in dense axillary or terminal clusters (table 2). The fruit is a 2-seeded berrylike drupe that is 5 to 10 mm long (Mozingo 1987; Shiell 1992; Vories 1981; Welsh and others 1987). Fruit color is white in the snowberry species but dark red, pink, or bluish black in coralberry. Fruits mature mid- to late summer or early fall (mid-June through September) (Evans 1974; Link 1993; Shaw 1984; Shiell 1992; Vories 1981). Each fruit contains 2 nutlets (pyrenes). These are flattened on 1 side and are composed of a tough, bony endocarp, a seedcoat, a fleshy endosperm, and a small embryo (figures 1 and 2). The nutlets are used as seeds. They are dispersed from late fall to the following spring, largely by birds and mammals. Normally, a good seedcrop is produced each year (Evans 1974).

Collection of fruits. Fruits persist on the plants until the following spring, except for those consumed by birds and mammals, making collection of fruit relatively easy (Evans 1974; Link 1993). Collection is done by stripping or flailing the fruit into a hopper or container, or the fruits may

be picked by hand. Those collected in early fall contain considerable moisture and therefore require careful handling to prevent heating (Evans 1974; Vories 1981). Weight of fruits per volume for western snowberry (fresh weight) are 3.6 kg/liter (58 lb/bu) and for coralberry (dry weight) are 0.81 kg/liter (13 lb/bu) (Evans 1974).

Figure 1—*Symphoricarpos*, snowberry: nutlets of *S. albus* var. *laevigatus*, garden snowberry (**top**); *S. occidentalis*, western snowberry (**center**); and *S. orbiculatus*, coralberry (**bottom**).

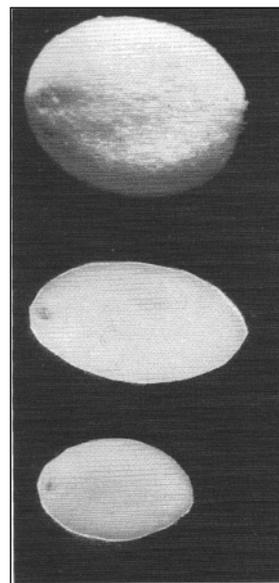


Table 2—*Symphoricarpos*, snowberry: phenology of flowering and fruiting.

Species	Location (& elevation)	Flowering	Fruit ripening
<i>S. albus</i> var. <i>albus</i>	Michigan	June 1–July 31	Sept 1–Oct 31
	Michigan Idaho 700 m	May 1–Sept 30	Aug 1–Oct 31
var. <i>laevigatus</i>	Missoula Co., Montana 1,000 m	June 5–Aug 5	Aug 1–Sept 5
	1,300 m	June 20–Aug 15	Aug 15–Sept 30
	1,650 m	July 1–July 30	Aug 25–Sept 20
	2,000 m	July 15–Aug 30	Sept 10–Oct 5
	2,000 m	July 25–Sept 5	Sept 25–Oct 25
<i>S. occidentalis</i>	Pennington Co., South Dakota 750 m	June 1–July 31	Sept 1–Oct 31
<i>S. orbiculatus</i>	—	July 1–Aug 31	Sept 1–heavy frost
<i>S. oreophilus</i>	Wasatch Plateau, Utah 2,230 m	June 17–June 26	Aug 20–Sept 18
	2,576 m	June 22–June 30	Aug 17–Sept 12
	2,698 m	July 2–July 8	Aug 21–Sept 26
	Northern Utah 2,080 m	June 5–June 10	July 15–Aug 3

Sources: Billington (1943), Costello and others (1939), Evans (1974), Willard (1971).

Extraction and storage of seeds. Twigs, leaves, and other non-fruit debris should first be screened out. Seeds can then be readily extracted by running the fruits through a macerator with water, floating off pulp and empty seeds. Dried fruits should be soaked for several hours before maceration. Remaining seeds and pulp should be dried and then cleaned on an air-screen cleaner (Evans 1974; Link 1993; Shaw 1984; Vories 1981; Wasser 1982). After being dried and cleaned, the seeds are ready for storage. Numbers of cleaned seeds per weight are listed in table 3.

Stored snowberry seeds have been reported to retain good viability when stored dry at low temperature near 5 °C (Vories 1981; Evans 1974). Seeds of coralberry are reported by Vories (1981) to maintain good viability for over 5 years.

Figure 2— *Symphoricarpos albus* var. *albus*, common snowberry: longitudinal section through a nutlet.

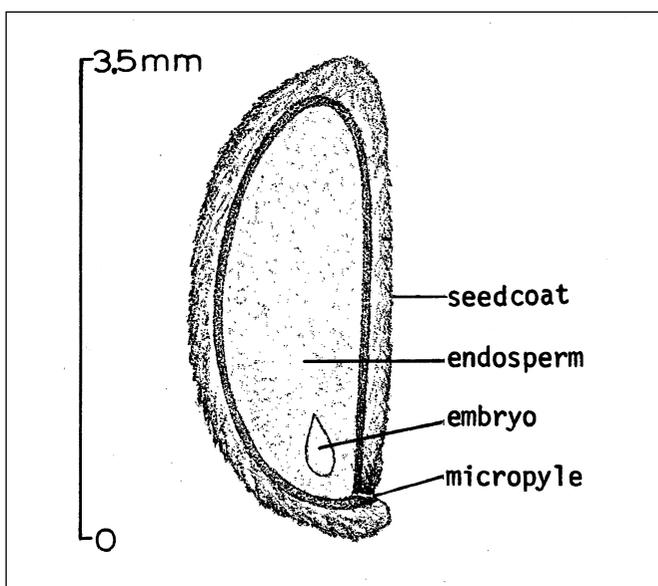
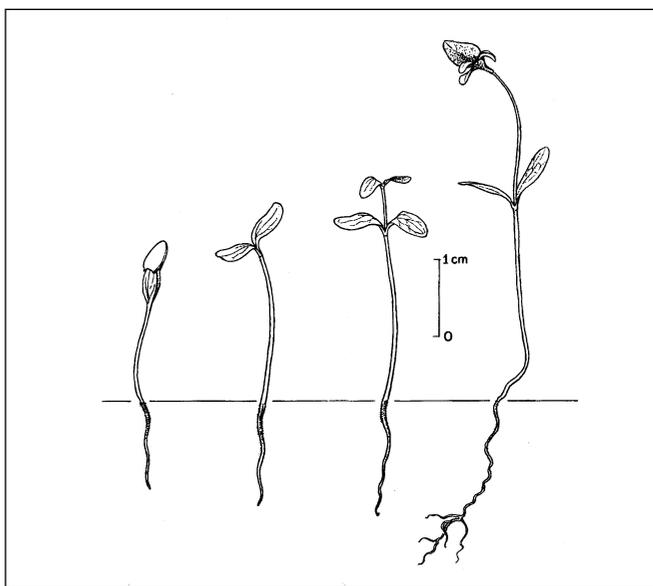


Figure 3— *Symphoricarpos albus* var. *albus*, common snowberry: seedling development at 5, 7, 13, and 20 days after germination.



Mountain snowberry germinated to 80% after 7 years, 44% after 10 years, and 8% after 25 years of dry storage in an open warehouse (Stevens and Jorgensen 1994). Dried seed-lots of common snowberry stored in a sealed container at 5 °C yielded 45% germination after 2 years, with an additional 35% still sound at the conclusion of the test (Evans 1974). Acceptable purity is 95%, with 80% germination (Shaw 1984).

Pregermination treatments. The nutlet-like seeds of snowberries have a hard endocarp and an undeveloped embryo (Evans 1974; Plummer 1968). Hidayati and others (2001) reported that the endocarp and seedcoat of coralberry are permeable to water; thus the seeds do not have physical dormancy. Warm stratification at room temperature between

Table 3— *Symphoricarpos*, snowberry: seed yield data

Species	Seed wt/ fresh fruit wt	Seeds (1,000s)/weight				Samples
		Range		Average		
		/kg	/lb	/kg	/lb	
<i>S. albus</i>						
var. <i>albus</i> *	3	119–250	54–113	167.5	76	10
var. <i>laevigatus</i>	—	86–144	39–65.2	122	55.4	5+
<i>S. occidentalis</i>	5–10	114–217	52–98.7	164	74.4	6+
<i>S. orbiculatus</i> †	7	298–317	135–144	308	140	2
<i>S. oreophilus</i>						
var. <i>oreophilus</i>	—	117–165	53–75	141	53.9	1

Source: Evans (1974).

* Number of dried fruits per weight was 39,600/kg (18,000/lb).

† Seed yield per weight of dried fruit was 18 to 33 kg/100 kg (18 to 33lb/100lb).

22 to 30 °C for 3 to 4 months has been used to soften the endocarp and is reported to be an adequate treatment for fall-planting where cold stratification will occur naturally (Wasser 1982; Evans 1974). For spring-planting or situations where natural stratification will not occur, a subsequent period of cold stratification at 5 °C for 4 to 6 months is necessary to induce full development of the embryo. Sulfuric acid scarification (soaking for 30 to 60 minutes) can be used in place of warm stratification to soften the endocarp. However, warm stratification has been shown to be more effective than the acid treatment (table 4), possibly because it is necessary for embryo maturation (Evans 1974; Shaw 1984).

In seedlots collected from the Book Cliffs of northeastern Utah, 72.5% of viable seeds germinated after 20 weeks of wet chill at 2 °C; 5 weeks of warm stratification at 10/30 °C did not increase germination substantially. Scarification in the form of passage through a black bear's digestive system actually lowered germination to 51.6% (Auger 1994).

Germination. Results of germination tests of non-stratified seedlots showed 0 to 46% germination at 4 °C for over 12 months, and 55% after 24 months. Under moist warehouse storage conditions, germination ranged from 0% after 1 year to 37% after 24 months, for mountain snowberry (GBRC 1985). Once seedlots have been adequately pretreated, they can be germinated at diurnally alternating temperatures of 20 and 30 °C for 30 days in the light (Akagi

1996; Evans 1974). Germination could be expected to be between 40 to 90% in 28 days (Akagi 1996; Evans 1974). Germination is epigeal (figure 3). Weber and Wiesner (1980) showed that, for common snowberry, tetrazolium chloride (TZ) testing did not distinguish between dormant and non-dormant seeds, but was adequate for viability evaluation.

Nursery practice. Effective propagation from seeds is possible if they are properly treated and given sufficient cold stratification. Desired seedling density in nursery beds is about 325/m² (30 seedlings/ft²). Seeds should be covered with about 6 mm (¹/₄ in) of soil and 2 cm (³/₄ in) of mulch. Early shade has been beneficial for seedlings of Indian currant (Evans 1974).

Cuttings and transplanting of pulled-up wildlings and pieces of stem with roots can be especially successful when planted in early spring (Plummer 1968; Vories 1981; Wasser 1982). Expected transplanting establishment success is nearly 90% when proper transplanting techniques are used for both bareroot and container stock (Stevens 1994). Cuttings should be irrigated when set out and as needed afterward until they are well established. Mountain snowberry has been shown to do poorly when planted as 1+0 stock but to perform much better when planted as 2+0 or larger stock (Monsen 1984). Plant competition needs to be reduced to a minimum during the first season. When seeding in rangeland conditions, species should be mixed with other adapted browse and forage plants and preferably planted in rows, strips, or blocks separate from grasses (Wasser 1982).

Table 4—*Symphoricarpos*, snowberry: effect of pregermination treatments on germination percentage

Species	Immersion in H ₂ SO ₄ (min)	Stratification (days)		Germination (%)
		Warm*	Cold†	
<i>S. albus</i>				
var. <i>albus</i>	60	60	180	35
	75	20	180	74
var. <i>laevigatus</i>	20	0	60	1
	0	112	182	45
	60	84	168	69
	0	91	182	87
	60	0	140	32
<i>S. orbiculatus</i>	0	120	120	72
	30	20	120	58
	30	120	180	81

Sources: Evans (1974), Flemion (1934), Flemion and Parker (1942).

* Room temperature.

† 5 to 10 °C.

- Akagi ST. 1996. Personal communication. Salt Lake City: Utah Department of Agriculture and Food.
- Auger J. 1994. Viability and germination of seeds from seven fleshy-fruited shrubs after passage through the American black bear (*Ursus americanus*) [zoology MS thesis]. Provo, UT: Brigham Young University. 48 p.
- Banister R. 1991. Snowberry. *Rangelands* 13(1): 33–34.
- Billington C. 1943. Shrubs of Michigan. *Cranbrook Institute of Science Bulletin* 20: 1–249.
- Costello DF, Price R. 1939. Weather and plant-development data as determinants of grazing periods on mountain range. *Tech. Bull.* 686. Washington, DC: USDA. 31 p.
- Cronquist A, Holmgren AH, Holmgren NH, Reveal JL, Holmgren PK. 1984. Intermountain flora: vascular plants of the Intermountain West. Volume 4. Bronx, NY: New York Botanical Garden. 573 p.
- Evans KE. 1974. *Symphoricarpos*, snowberry. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. *Agric. Handbk.* 450. Washington, DC: USDA Forest Service: 787–790.
- Flemion F. 1934. Physiological and chemical changes preceding and during the after ripening of *Symphoricarpos racemosus* seeds. *Contributions of the Boyce Thompson Institute* 6: 91–102.
- Flemion F, Parker E. 1942. Germination studies of seeds of *Symphoricarpos orbiculatus*. *Contributions of the Boyce Thompson Institute* 12: 301–307.
- GBRC [Great Basin Research Center]. 1985. Unpublished data. Ephraim: Utah Division of Wildlife Resources.
- Grimm WC. 1957. *The book of shrubs*. Harrisburg, PA: Stackpole Books. 533 p.
- Hidayati SN, Baskin JM, Baskin CC. 2001. Dormancy-breaking and germination requirements for seeds of *Symphoricarpos orbiculatus* (Caprifoliaceae). *American Journal of Botany* 88(8): 1444–1445.
- Landis TD, Simonich EJ. 1984. Producing native plants as container seedlings. In: Murphy PM, comp. The challenge of producing native plants for the Intermountain area. *Proceedings, Intermountain Nurseryman's Association*; 1983 August 8–11; Las Vegas, NV: 16–25.
- Link E. 1993. Native plant propagation techniques for national parks: interim guide. East Lansing, MI: USDA NRCS Rose Lake Plant Materials Center. 197 p.
- Monsen SB. 1984. Use of shrubs on mine spoils. In: Murphy PM, comp. The challenge of producing native plants for the Intermountain area. *Proceedings, Intermountain Nurseryman's Association*; 1983 August 8–11; Las Vegas, NV: 26–31.
- Mozingo HN. 1987. Shrubs of the Great Basin: a natural history. Reno: University of Nevada Press: 251–254.
- Plummer AP, Christiansen DR, Monsen SB. 1968. Restoring big game range in Utah. *Pub.* 68-3. Salt Lake City: Utah Division of Fish and Game. 183 p.
- Shaw N. 1984. Producing bareroot seedlings of native shrubs. In: Murphy PM, comp. The challenge of producing native plants for the Intermountain area. *Proceedings, Intermountain Nurseryman's Association*; 1983 August 8–11; Las Vegas, NV: 6–15.
- Shiell R. 1992. *Symphoricarpos orbiculatus*. *American Nurseryman* 176(10): 130.
- SCS [Soil Conservation Service]. 1982. National list of scientific plant names. Volume 1, List of plant names. SCS-TP-159. Washington, DC: USDA Soil Conservation Service. 416 p.
- Stevens R. 1994. Interseeding and transplanting to enhance species composition. In: Monsen SB, Kitchen SG, comps. 1994. *Proceedings, Ecology and Management of Annual Rangelands*; 1992 May 18–21; Boise, ID. *Gen. Tech. Rep INT-GTR-313*. Ogden, UT: USDA Forest Service, Intermountain Research Station. 416 p.
- Stevens R, Jorgensen KR. 1994. Rangeland species: germination through 25 and up to 40 years of warehouse storage. In: Monsen SB, Kitchen SG, comps. 1994. *Proceedings, Ecology and Management of Annual Rangelands*; 1992 May 18–21; Boise, ID. *Gen. Tech. Rep INT-313*. Ogden, UT: USDA Forest Service, Intermountain Research Station. 416 p.
- Thames JL, ed. 1977. *Reclamation and use of disturbed land in the Southwest*. Tucson: University of Arizona Press. 682 p.
- Vories KC. 1981. Growing Colorado plants from seed: a state of the art. Volume 1, Shrubs. *Gen. Tech. Rep INT-103*. Ogden, UT: USDA Forest Service, Intermountain Research Station.
- Wasser CH. 1982. Ecology and culture of selected species useful in revegetating disturbed lands in the West. *FWS/OBS-82/56*. Washington, DC: USDI Fish and Wildlife Service. 347 p.
- Weber GP, Wiesner LE. 1980. Tetrazolium testing procedures for native shrubs and forbs. *Journal of Seed Technology* 5(2): 23–34.
- Welsh SL, Atwood ND, Higgins LC, Goodrich S. 1987. A Utah flora. *Great Basin Naturalist Memoirs* 9: 1–894.
- Willard EE. 1971. Some factors involved in activation of sprouting in little rabbitbrush and snowberry on summer range [dissertation]. Logan: Utah State University. 116 p.

Oleaceae—Olive family

Syringa L.
lilac

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Growth habit, occurrence, and use. The lilac genus comprises about 30 species of deciduous shrubs or small trees with opposite, usually undivided leaves. The genus name—*Syringa*—is derived from the Greek word *syrix*, a “pipe,” and refers to the hollow shoots. Lilacs are native to temperate Asia and southeastern Europe (Everett 1982) and were probably introduced to America before 1700 (Heriteau 1990; Wyman 1986). They are grown primarily as ornamentals because of their large, showy, and often fragrant inflorescences (Rehder 1940). Lilacs are generally hardy and long lived (Everett 1982). At least 3 species are used in shelterbelts and windbreaks. Four species or varieties grown for conservation purposes in the United States are discussed in this chapter (table 1); their heights at maturity and years of first cultivation are also listed (Hoag 1965; Rehder 1940).

Hybrids and cultivars. Numerous lilac hybrids and cultivars have been developed for horticultural use. These selections exhibit variation in such characteristics as flower color, period of flowering, and growth habit. Krüssmann (1986) reported that more than 900 cultivars are grown, including more than 800 developed from common lilac (*S. vulgaris* L.). The largest collections and numbers of varieties

are found in the United States. Persian lilac (*S. × persica* L.), previously considered a separate species, is now thought to be a hybrid of *S. laciniata* Mill. (*S. afghanica* C.K. Schneid.) (Everett 1982; LHBH 1976; Wyman 1986); a fixed juvenile form of *S. laciniata* (Krüssmann 1986); or a backcross between *S. × laciniata* and *S. vulgaris* with *S. × laciniata* = *S. protolaciniata* P.S. Green & M.C. Chang × *S. vulgaris* L. (Griffiths 1994).

Flowering and fruiting. Flowers are borne in panicles that develop on the previous year's shoots. The small, perfect flowers have 4-lobed, funnel-shaped to cylindrical corollas and colors ranging from white to violet, purple, and deep reddish purple. Flowers bloom in spring or early summer after development of the foliage (table 2). Seedcrops are produced annually on cultivated plants. The fruit, a 2-celled capsule, is smooth, brown, woody, oblong, and terete or compressed (figure 1). It ripens in late summer or fall. Each capsule contains 4 shiny, brown, lozenge-shaped seeds that are about 13 mm long, 5 mm wide, and more or less obliquely winged at the base (figure 2). Seeds are covered by a thin, brown seedcoat and a thick layer of living endosperm. Cotyledons are large and well developed.

Table 1—*Syringa*, lilac: nomenclature and original occurrence

Scientific name & synonyms	Common name(s)	Occurrence	Height at maturity (m)	Year first cultivated
<i>S. × persica</i> L.	Persian lilac	Iran to NW China	1.5–3.0	1614
<i>S. reticulata</i> ssp. <i>amurensis</i> (Rupr.) P.S. Greene & M.C. Chang	Amur lilac, Manchurian lilac	SE Siberia in Amur River region		
<i>S. amurensis</i> Rupr. <i>S. reticulata</i> var. <i>mandschuria</i> (Maxim.) Hara				
<i>S. villosa</i> Vahl.	late lilac, villous lilac	N China to Himalayas	3.0–3.9	1882
<i>S. bretschneideri</i> Lemoine				
<i>S. vulgaris</i> L.	common lilac	SE Europe	3.0–7.0	1563

Source: Rudolf and Slabaugh (1974).

Table 2—*Syringa*, lilac: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening
<i>S. × persica</i>	NE US, Kansas	May–June	Late Mar–Apr
<i>S. reticulata</i> var. <i>amurensis</i>	North Dakota Manitoba	Early June June–July	— Sept–Oct
<i>S. vulgaris</i>	NE US & Europe Kansas W US	Apr–June Late Mar–early May Late Mar–mid-May*	Aug–Oct — —

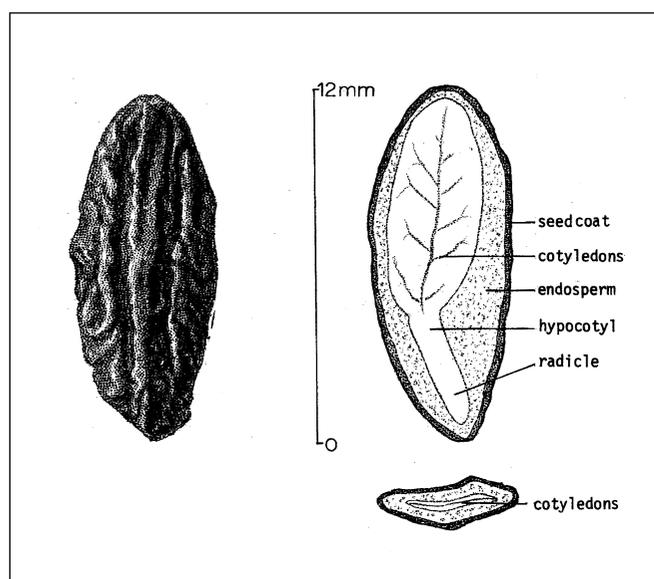
Sources: Caprio and Snyder (1989), Cummings (1963), Hoag (1965), Hulbert (1963), LHBH (1976), NBV (1946), Rehder (1940), Walker (1968).

*First flowering.

Figure 1—*Syringa amurensis*, Amur lilac: fruits (capsules).

Collection of fruits and extraction and storage of seeds. Mature capsules are hand-harvested in fall. A late (October 9) collection of Amur lilac capsules yielded seeds with greater germinability than an early (September 10) collection (Walker 1968). Harvested fruits should be spread to dry in a well-aerated room (NBV 1946). Air-dried fruits may be crushed in a macerator. A fanning mill is used to remove impurities, but fanning must be done carefully or good seeds will be lost (NBV 1946). Air-dried fruits may also be stored over winter in paper bags. By spring, many seeds will have fallen from the capsules and can be separated by fanning or sieving.

Data on seed yields are available for only 2 species. For common lilac, 45 kg (100 lb) of capsules yielded 0.9 to 3.2 kg (2 to 7 lb) of cleaned seeds (Swingle 1939). The number of cleaned seeds per weight in 16 samples ranged from 74,956 to 286,598/kg (34,000 to 130,000/lb), averaging

Figure 2—*Syringa vulgaris*, common lilac: exterior view of seed (**left**), longitudinal section through a seed (**top right**), and transverse section (**bottom right**).

189,630/kg (86,000/lb) (Rafn and Son 1928; Rudolf and Slabaugh 1974; Swingle 1939). Average purity of cleaned lots of common lilac seeds is 60% and sound seeds made up 85% (Rudolf and Slabaugh 1974; Swingle 1939). For late lilac, purity of a cleaned seed sample was 91% and number of seeds per weight was 90,830/kg (41,200/lb).

Lilac seeds will remain viable for up to 2 years if stored in bags or sacks in a dry, well-aerated place (NBV 1946). For longer storage, air-dried seeds should be kept in sealed containers or polyethylene bags at 1 to 3 °C (Heit 1967; Walker 1968).

Pregermination treatments. Dormancy varies among species and seed collections, but is usually not very strong (Junttila 1973a). It may be induced by high temperatures during seed development (Junttila 1971).

In common, nodding (*S. reflexa* C.K. Schneid.), and Hungarian lilacs (*S. josikaea* Jacq. F. ex Reichenb.), the mechanical restraint imposed by the endosperm surrounding the radicle imposes an embryo dormancy at low incubation temperatures (9 to 15 °C). This dormancy is generally relieved by embryo excision, wet prechilling at 1 to 9 °C for periods of 30 to 90 days, or application of gibberellic acid (which increases the growth potential of the embryo) (Junttila 1970a&b, 1971; Walker 1968; Wyman 1986). Mechanical resistance of the endosperm decreases prior to germination. At high incubation temperatures (27 to 30 °C), dormancy is imposed by seedcoat and endosperm restriction of oxygen uptake (Junttila 1970b, 1973a, 1974a).

Embryos are generally nondormant. Some nodding lilac embryos, however, may be dormant at high incubation temperatures during the early stages of maturation, whereas some mature embryos are dormant at low incubation temperatures (Junttila 1973b).

Germination tests. Official rules for testing germination of common lilac seeds prescribe a 21-day incubation at 20 °C (ISTA 1966; Isely and Everson 1965). Junttila (1974b) recommends germinating excised common lilac embryos at 24 °C and seeds at 18 °C. Light is not required (Heit 1968b). Maximum germination of late lilac may be obtained by incubating seeds at 30/20 °C in artificial light with a good supply of water (Heit 1974). Test results for 3 lilac species are shown in table 3. Germination is epigeal.

Nursery practice. Rudolf and Slabaugh (1974) recommend that lilac seeds be sown at a rate adjusted to produce 270 to 430 seedlings/m² (25 to 40/ft²). Macdonald (1993) recommends densities of 150 to 200 seedlings/m²

(14 to 19/ft²) for lining-out stock and 250 to 300/m² (23 to 28/ft²) for rootstocks. For some lots of common lilac seeds, yield of usable 1+0 seedlings has been as low as 12% of viable seeds planted. Seeds may be planted in fall without pretreatment (Cram and others 1960; Heit 1968a), or untreated or wet-prechilled seeds may be planted in spring (LHBH 1976; NBV 1946; Rudolf and Slabaugh 1974). Seeds should be covered with 6 to 9 mm (0.2 to 0.4 in) of soil. A mulch may be helpful on fall-sown beds (Heit 1968a; Walker 1968). Nursery beds should be given half-shade, kept moist, and protected from late spring frosts (NBV 1946). Field plantings can be made using 1+1 stock (LHBH 1976).

Lilac cultivars are generally propagated vegetatively to maintain genetic constancy (Hartmann and others 1990). Plants are commonly obtained by rooting softwood cuttings under mist. The time-frame for making softwood cuttings, however, is limited to the spring flush of active growth, which extends from slightly before to slightly after flowering, usually a 4- to 6-week period (Macdonald 1993; Wyman 1986). Grafting is often used as an alternative to propagating cuttings, because grafting can be done at any time during the winter. Lilac, privet (*Ligustrum* spp.), and green ash (*Fraxinus pennsylvanica* Marsh.) seedlings are used as rootstocks. Scions cut from vigorous 1-year-old wood should be planted deeply to improve the rooting. Understock can be removed later, thus creating “own-root” plants (Fordham 1959; Hartmann and others 1990).

Root cuttings, budding, layers, divisions, hardwood cuttings, t-budding, and micropropagation are also used for propagation if only small numbers of plants are needed (Everett 1982; LHBH 1976; Macdonald 1993). If vegetative material for propagation is harvested from grafted plants not growing on their own rootstocks, shoots produced by the understock must be avoided.

Lilacs grow on a variety of soils having a pH of 6.0 to 7.5 (Fordham 1959). They do best on moderately rich, moist soils with good drainage and aeration and exposure to full sun (LHBH 1976). Though persistent without care, flowering is enhanced by removal of inflorescences after flowering (deadheading), proper pruning, and periodic fertilization (Macdonald 1993; Wyman 1986).

Table 3—*Syringa*, lilac: germination test results

Species	% germination		Tests
	Average	Range	
<i>S. reticulata</i> var. <i>amurensis</i>	72	64–80	5
<i>S. villosa</i>	77	70–84	2
<i>S. vulgaris</i>	61	33–85	13
	44	—	61

Sources: Heit (1968a&b, 1974), Junttila (1974b), Rafn and Son (nd), Rudolf and

- Caprio JM, Snyder RD. 1989. Within-station analysis of hourly thermal and solar thermal phenological models for flowering of *Syringa vulgaris* L. In: Driscoll D, Box EO, eds. Proceedings, 11th International Society of Biometeorology Congress. The Hague: SPB Academic Publishing: 53–65.
- Cram WH, Nagy MH, Lindquist CH. 1960. Propagation research. Forest Nursery Station Summary Report. Indian Head, SK: Canadian Department of Agriculture, Research Branch: 16–18.
- Cumming WA. 1963. Late flowering lilacs for the prairies. *Prairie Gardening* 20: 95.
- Everett TH, ed. 1982. The New York Botanical Garden illustrated encyclopedia of horticulture. Volume 10, STE–ZY. New York: Garland Publishing: 3225–3601.
- Fordham AJ. 1959. Propagation and care of lilacs. *Arnoldia* 19: 36–44.
- Griffiths M. 1994. Index of garden plants. Portland, OR: Timber Press. 1234 p.
- Hartmann HT, Kester DE, Davies FT Jr. 1990. Plant propagation principles and practices. 5th ed. Englewood Cliffs, NJ: Prentice-Hall. 647 p.
- Heit CE. 1967. Propagation from seed: 11. Storage of deciduous tree and shrub seeds. *American Nurseryman* 126: 12–13, 86–94.
- Heit CE. 1968a. Propagation from seed: 15. Fall planting of shrub seeds for successful seedling production. *American Nurseryman* 128: 8–10.
- Heit CE. 1968b. Thirty-five years' testing of tree and shrub seed. *Journal of Forestry* 66: 632–634.
- Heit CE. 1974. Laboratory germination and testing method for *Syringa villosa* (late lilac) seed. *Newsletter of the Association of Official Seed Analysts* 48: 26–28.
- Heriteau J. 1990. The National Arboretum book of outstanding garden plants. New York: Simon and Schuster: 292 p.
- Hoag DG. 1965. Trees and shrubs for the Northern Plains. Minneapolis: Lund Press. 376 p.
- Hulbert LC. 1963. Gates' phenological records of 132 plants at Manhattan, Kansas, 1926–1955. *Transactions of the Kansas Academy of Science* 66: 82–106.
- ISTA [International Seed Testing Association]. 1966. International rules for seed testing. *Proceedings of the International Seed Testing Association* 31: 1–152.
- Isely D, Everson LE, eds. 1965. Rules for testing seeds. *Proceedings of the Association of Official Seed Analysts* 54: 1–112.
- Junttila O. 1970a. Effects of gibberellic acid and temperature on the germination of *Syringa vulgaris* L. and *S. reflexa* Schneid. *Meldinger fra Norges Landbrukshøgskole* 49(36): 1–8.
- Junttila O. 1970b. Effects of stratification, growth substances and temperature on the germination of some *Syringa* species. *Meldinger fra Norges Landbrukshøgskole* 49(35): 1–58.
- Junttila O. 1971. Effects of mother plant temperature on seed development and germination in *Syringa reflexa* Schneid. *Meldinger fra Norges Landbrukshøgskole* 50(10): 1–16.
- Junttila O. 1973a. The mechanism of low temperature dormancy in mature seeds of *Syringa* species. *Physiologia Plantarum* 29: 256–263.
- Junttila O. 1973b. Seed and embryo germination in *Syringa vulgaris* and *S. reflexa* as affected by temperature during seed development. *Physiologia Plantarum* 29: 264–268.
- Junttila O. 1974a. Effects of low oxygen concentrations on the germination of *Syringa* seeds. *Zeitschrift für Pflanzenphysiologie* 74: 168–171.
- Junttila O. 1974b. Seed quality and seed production of woody ornamentals in Scandinavia. *Meldinger fra Norges Landbrukshøgskole* 53: 1–41.
- Krüssmann G. 1986. Manual of cultivated broad-leaved trees and shrubs. Volume 3, PRU–Z. *Handbuch der Laubgehölze*. Portland, OR: Timber Press. 510 p.
- 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.
- Macdonald B. 1993. Practical woody plant propagation for nursery growers. Volume 1. Portland, OR: Timber Press. 669 p.
- NBV [Nederlandsche Bosbouw Vereeniging]. 1946. Boomzaden: Handleiding inzake het oogsten, behandelen, bewaren en witzaaien van boomzaden. Wageningen, The Netherlands: Ponsen and Looijen. 171 p.
- Rafn J and Son. [nd, circa 1928]. Skovfrøkontoret's Frøanalyser gennem 40 Aar, 1887–1927. Udført paa Statsfrøkontrollen i København. 5 p.
- Rehder A. 1940. Manual of cultivated trees and shrubs hardy in North America. 2nd ed. New York: Macmillan. 996 p.
- Rudolf PO, Slabaugh PE. 1974. *Syringa* L., lilac. In: Schopmeyer CS, tech. coord. *Seeds of woody plants in the United States*. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 791–793.
- 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.
- Walker J. 1968. Immature vs. mature seed. *Western Canadian Society of Horticulture Proceedings* 24: 70–72.
- Wyman D. 1986. *Wyman's gardening encyclopedia*. New York: Macmillan. 1221 p.