Rosaceae—Rose family

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

osoberry

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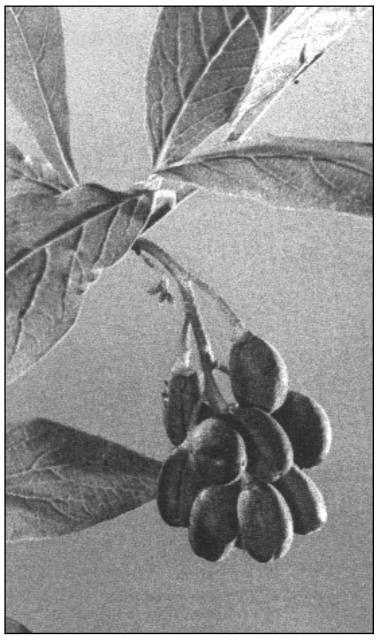
Other common names. Indian plum, squaw-plum, Indian peach.

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

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

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

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



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

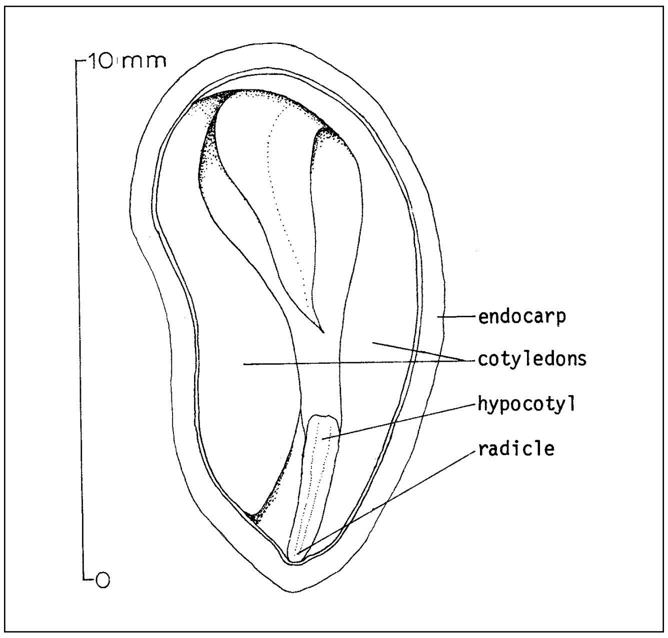
Pistillate flowers may yield up to 5 thin-fleshed, single-seeded drupes per flower, but generally fewer than 60% of pistils on a plant bear fruit; production from 10 to 20 of pistils has been reported (Antos and Allen 1994, 1999). Higher light levels favorably influence fruit set; exposure to light is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

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

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

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

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



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

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

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

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

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

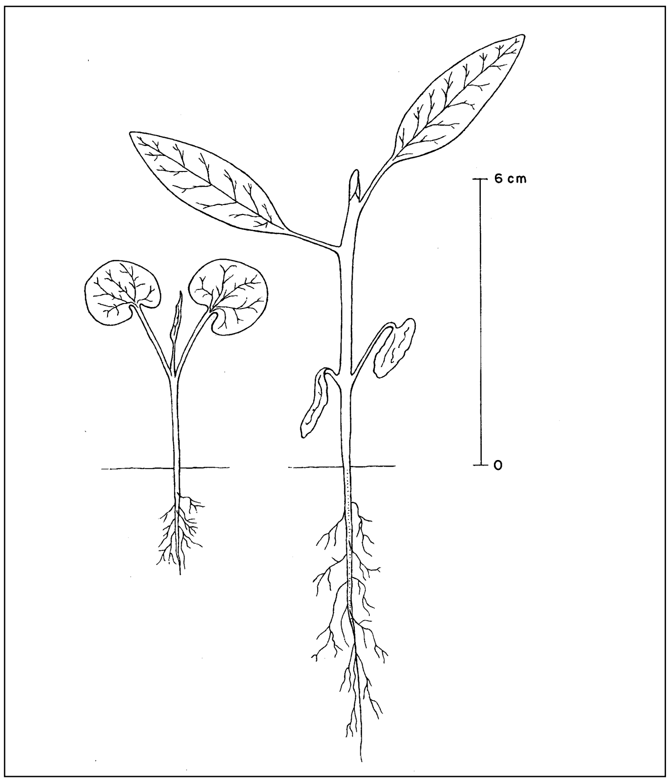


Table 1—*Oemleria cerasiformis,* osoberry: effect of stratification on germination

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

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Oleaceae—Olive family

Olea europaea L.

olive

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

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

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

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

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

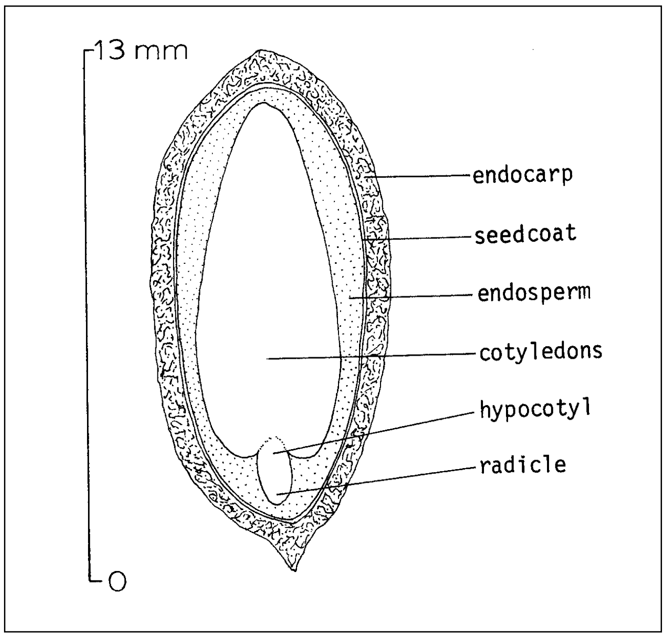
The perfect flower is evidenced by its large pistil, which nearly fills the space within the floral tube. The pistil is green when immature and deep green when open at full bloom. Staminate flower pistils are tiny, barely rising above the floral tube base. The style is small and brown, greenish white,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

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

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

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

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



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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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Fabaceae—Pea family

Olneya tesota Gray

olneya

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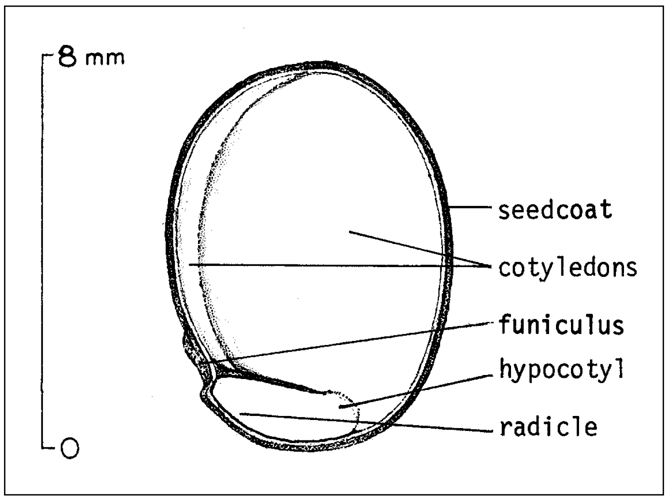
Other common names. ironwood, desert ironwood, *palo fierro, tesota*.

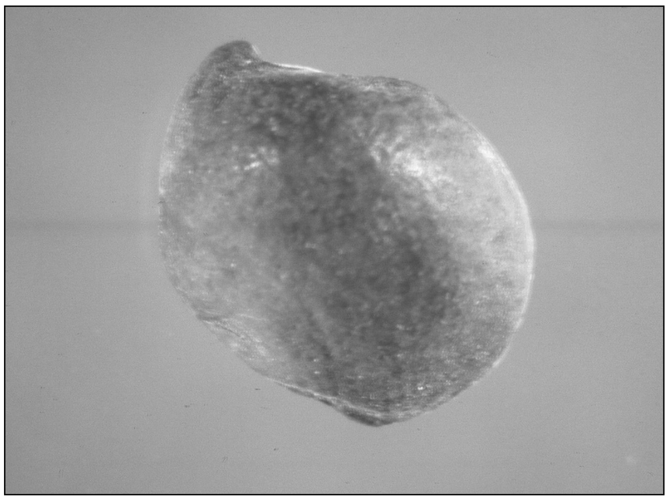
Growth habit, occurrence, and uses. Olneya is a long-lived, multi-trunked, broad-crowned, deciduous tree, 5 to 10 m high, that is commonly found at elevations below 600 m in desert washes and valleys of the Sonora Desert in California, Arizona, Baja California, Baja California Sur, and Sonora (Munz 1974;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

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

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

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





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

Germination and nursery practice. Fresh seeds germinate readily when soaked for 12 to 24 hours in water; stored seeds may require longer soaking. Mild scarification before soaking is often helpful (Emery 1964; Krugman 1974). Seeds can be broadcast sown in the spring and covered with 6 mm ($^1/_2$ in) of soil or sand. Small seedlots can be germinated in planting flats or small containers and then transplanted. Seeds will rot easily, so extra care must be taken in watering (Everett 1957; Krugman 1974). Initial germination is prompt when soaked or watered, often occurring within 18 to 24 hours of sowing (Everett 1957; Krugman 1974). Seedlings appear within 6 days after sowing (Krugman 1974).

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O

Betulaceae—Birch family

Ostrya virginiana (P. Mill.) K. Koch

eastern hophornbeam

William B. Leak and Franklin T. Bonner

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

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

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

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

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

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

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

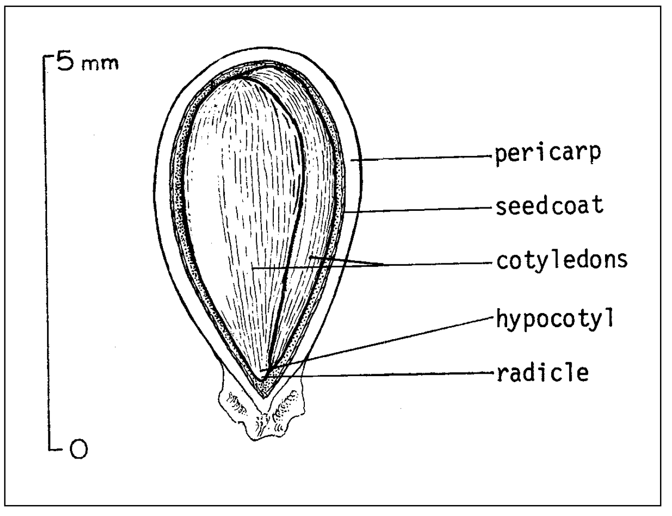
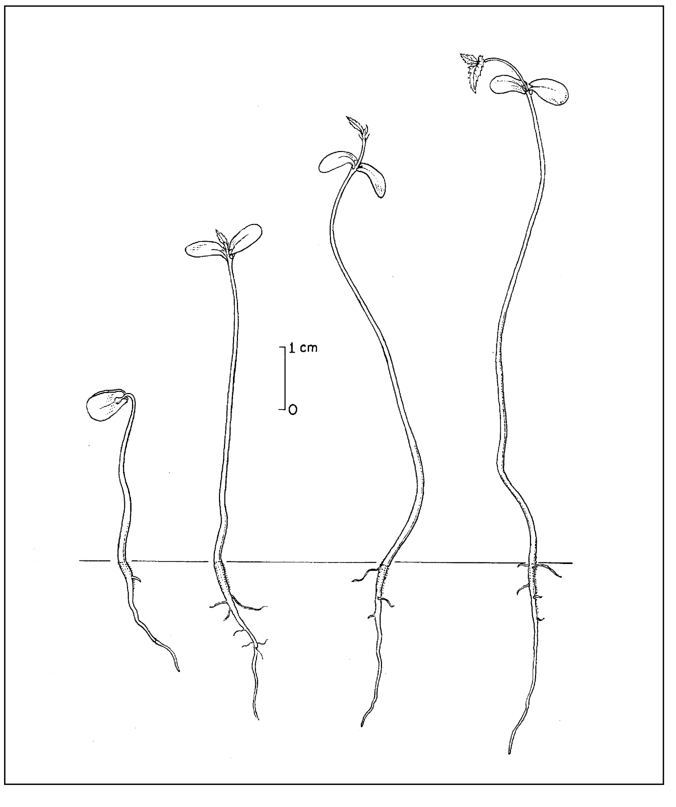


Figure 3—*Ostrya virginiana*, eastern hophornbeam: seedling development at 2, 4, 23, and 27 days after germination.



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

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

Nursery practice. Either fall- or spring-sowing is feasible, but fall-sowing should take place soon after seeds are collected. In Iowa, seeds collected when they were slightly immature (August) and sown immediately germinated 100% the following spring (Titus 1940). Seeds should be covered with 6 mm ($^1/_4$ in) of firmed soil. Fall-sown beds should be covered with burlap, straw, or other suitable mulch, and uncovered when germination begins. Stratified seeds may be sown in the spring as soon as the soil can be worked, and the beds should be mulched or watered to keep them moist until germination starts (Schopmeyer and Leak 1974).

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O

Ericaceae—Heath family

Oxydendrum arboreum (L.) DC.

sourwood

Frank A. Blazich and Mark C. Starrett

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Synonym. *Andromeda arboreum* L.

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

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

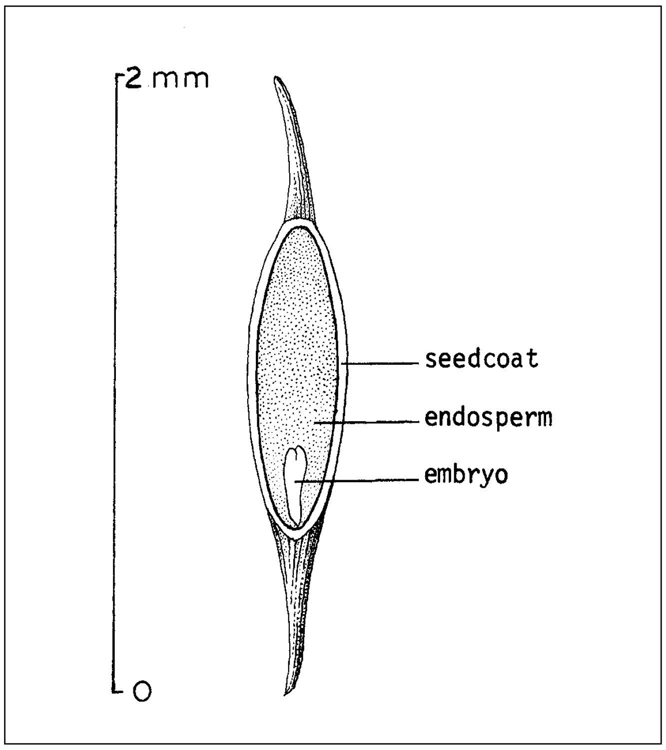
Geographic races and hybrids. Sourwood is monotypic, that is, the only species of its genus. No hybrids are described in the literature.

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

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

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

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



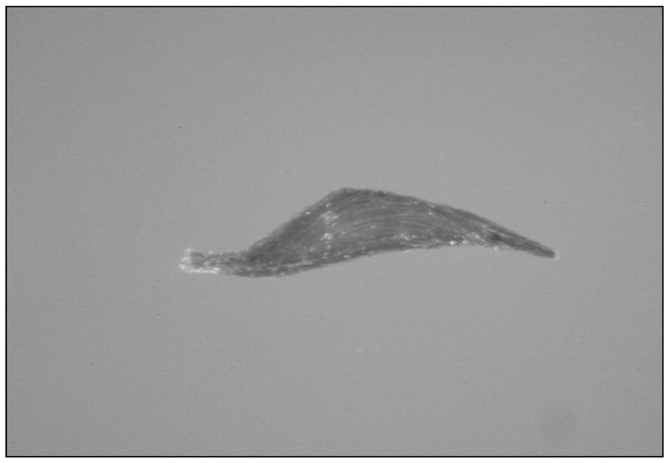
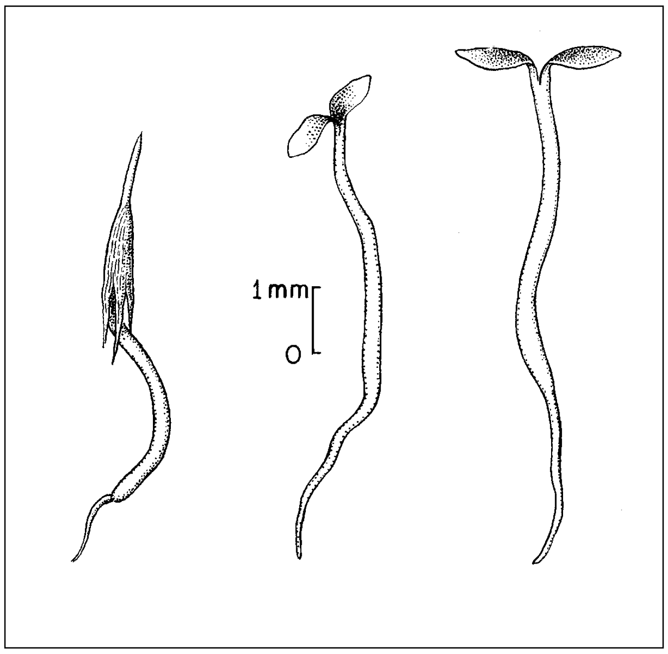


Figure 2—*Oxydendron arboreum*, sourwood: seedlings of sourwood at 2, 6, and 8 days after germination.



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

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

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P

Fabaceae—Pea family

Paraserianthes falcataria (L.) I. Nielsen

peacock-plume

John A. Parrotta and Franklin T. Bonner

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Synonyms. *Albizia falcataria* (L.) Fosberg

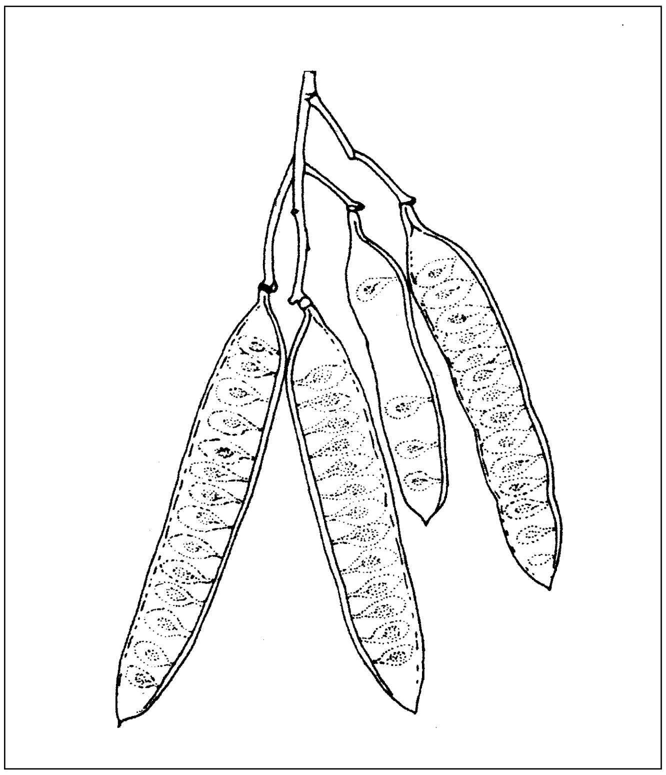
Other common names. Molucca-albizia, *batai, sau,* peacock's plume.

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

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

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

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



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

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

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P

Fabaceae—Pea family

Parkinsonia L.

palo verde

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

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

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

Table 1—Parkinsonia, palo verde: nomenclature and occurrence

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

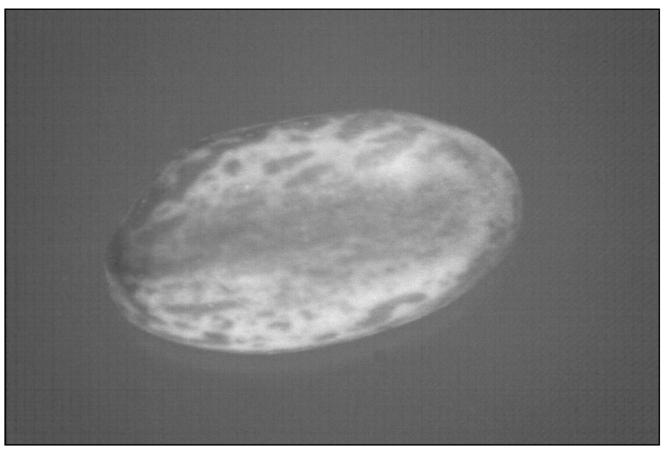
Sources: Bainbridge and Virginia (1989), Little (1979), Little and Wadsworth (1964).

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

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

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

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



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

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

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

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

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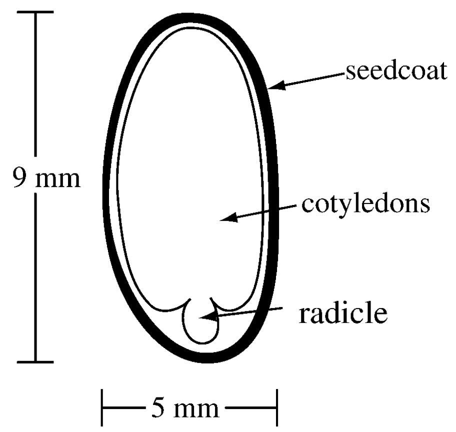
Figure 2—*Parkinsonia aculeata*, palo verde: longitudinal section of a seed.



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

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P

Vitaceae—Grape family

Parthenocissus Planch.

creeper

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

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

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

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

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

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

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

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

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

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

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

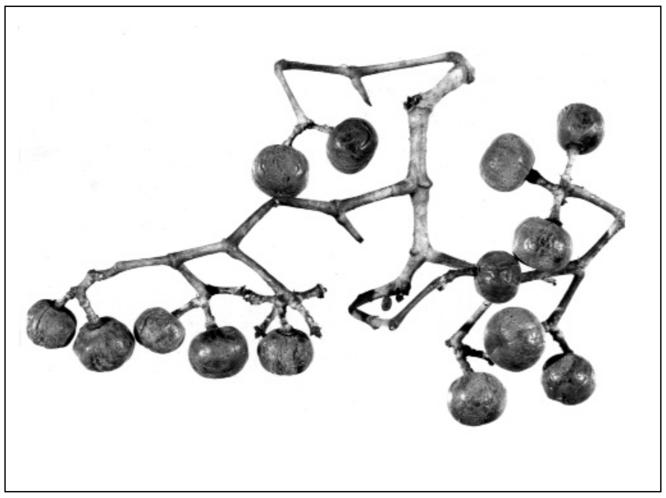


Figure 2—*Parthenocissus*, creeper: seeds of *P. quinquefolia*, Virginia creeper (**left**) and *P. tricuspidata*, Japanese creeper (**right**).

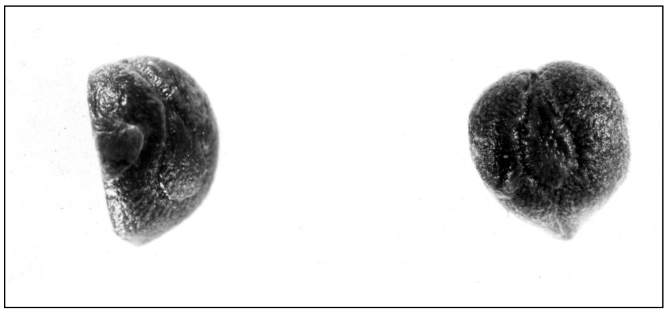
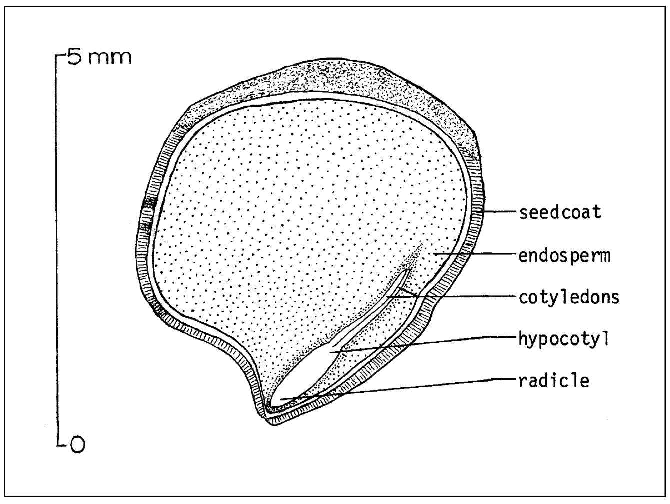


Figure 3—*Parthenocissus quinquefolia*, Virginia creeper: longitudinal section through a seed.



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

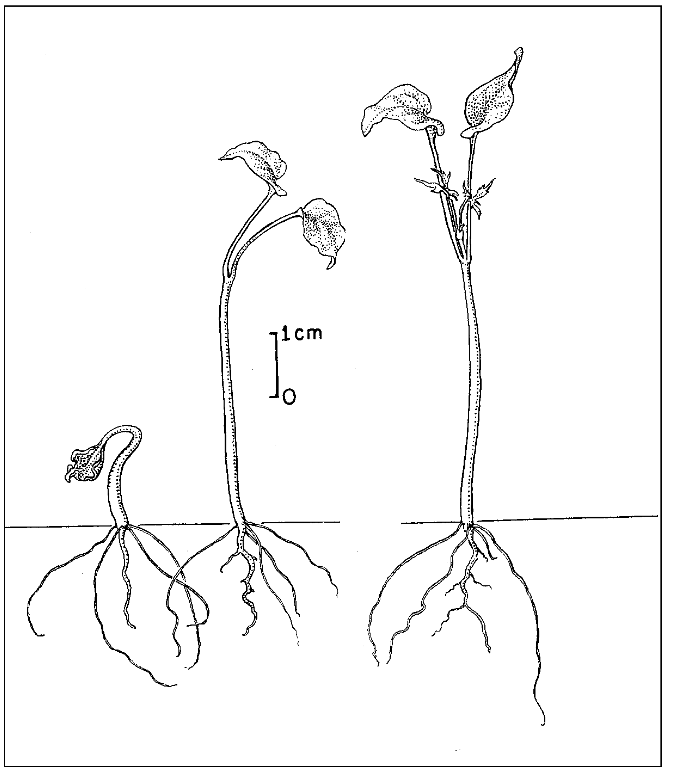
Cleaned Virginia creeper seeds range from 21,600 to 57,800/kg (9,800 to 26,200/lb) and average 36,500/kg (16,560/lb). No seed yield data on Japanese creeper are available, but they are probably similar to those for Virginia creeper.

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

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

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

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



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P

Scrophulariaceae—Figwort family

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

royal paulownia

Franklin T. Bonner

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

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

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

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

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

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

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

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

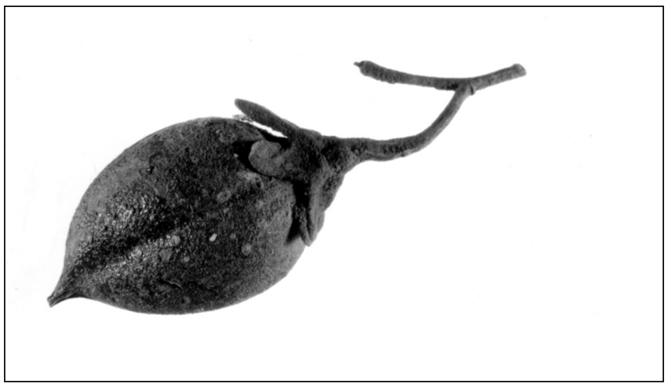


Figure 2—*Paulownia tomentosa*, royal paulownia: winged seed.

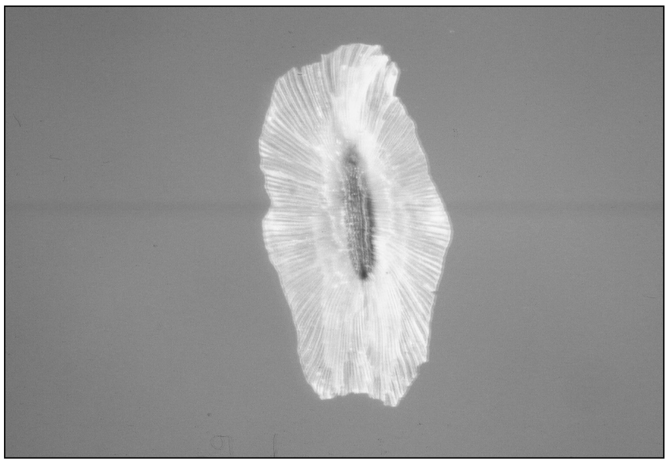
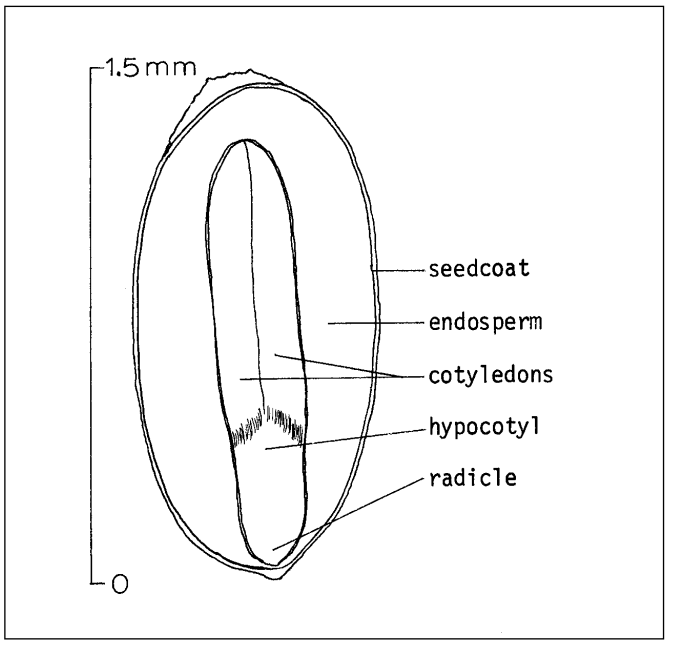


Figure 3—*Paulownia tomentosa,* royal paulownia: longitudinal section through a seed.



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

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

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

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Scrophulariaceae—Figwort family

Penstemon Schmidel

penstemon, beardtongue

Susan E. Meyer

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

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

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

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

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

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

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

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

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

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

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

Source: Meyer (2002).

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

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

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

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

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

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

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

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

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Rosaceae—Rose family

Peraphyllum ramosissimum Nutt.

squaw-apple

Janene Auger and Justin G. Smith

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

Uses. Wildlife known to eat squaw-apple fruits and seeds or both in Utah include grouse and wild turkeys (family Phasianidae), deer mice (*Peromyscus maniculatus*), chipmunks (*Eutamias* spp.), ground squirrels (*Spermophilus* spp.), and American black bears (*Ursus americanus*) (Auger and others 1995). Deer (*Odocoileus* spp.) browse squaw-apple lightly during the fall and winter (Shaw and others 2004; Smith 1974), and small birds use the intricately branched shrubs as cover even when leaves are not present (Shaw and Monsen 2004). Livestock also browse squaw-apple, and opinions vary widely on its forage value. In central Utah, squaw-apple is said to be almost worthless; in western Colorado, it is considered poor to fair; in eastern Oregon and northeastern California, it is commonly considered fair to moderately good sheep and cattle browse in the spring; and finally, in southwestern Utah, squaw-apple ranks as a valuable browse (Dayton 1931; Plummer and others 1968; Smith 1974). On ranges grazed by cattle during late winter and very early spring, individual plants may be severely hedged (Smith 1974). Even though squaw-apple grows slowly, Monsen and Davies (1985) suggest that it can persist in native plant landscaping for arid environments.

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

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

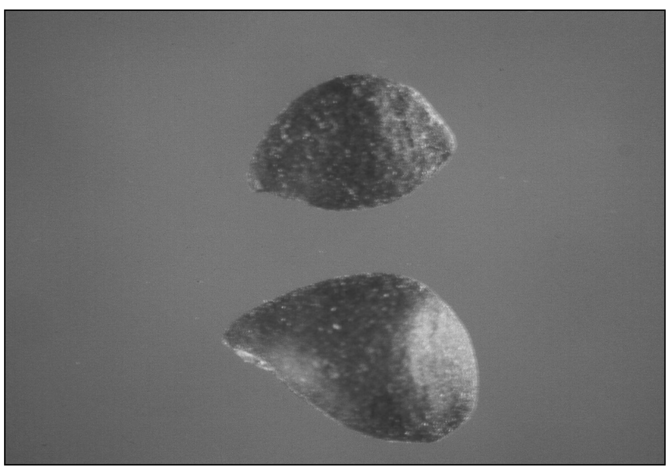


Figure 2—*Peraphyllum ramosissimum*, squaw-apple: longitudinal sections through a seed.

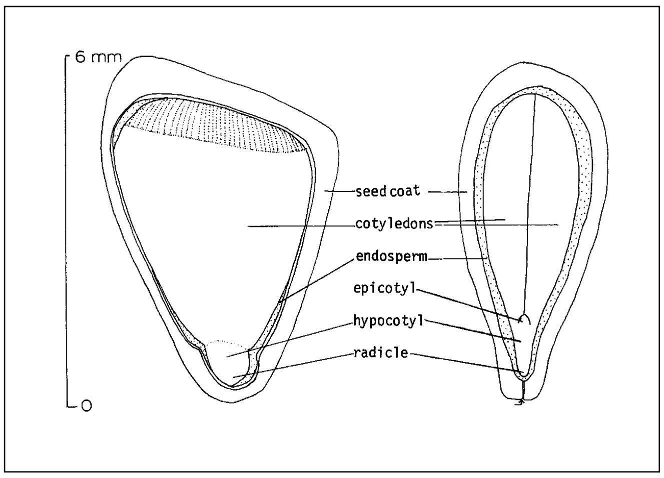
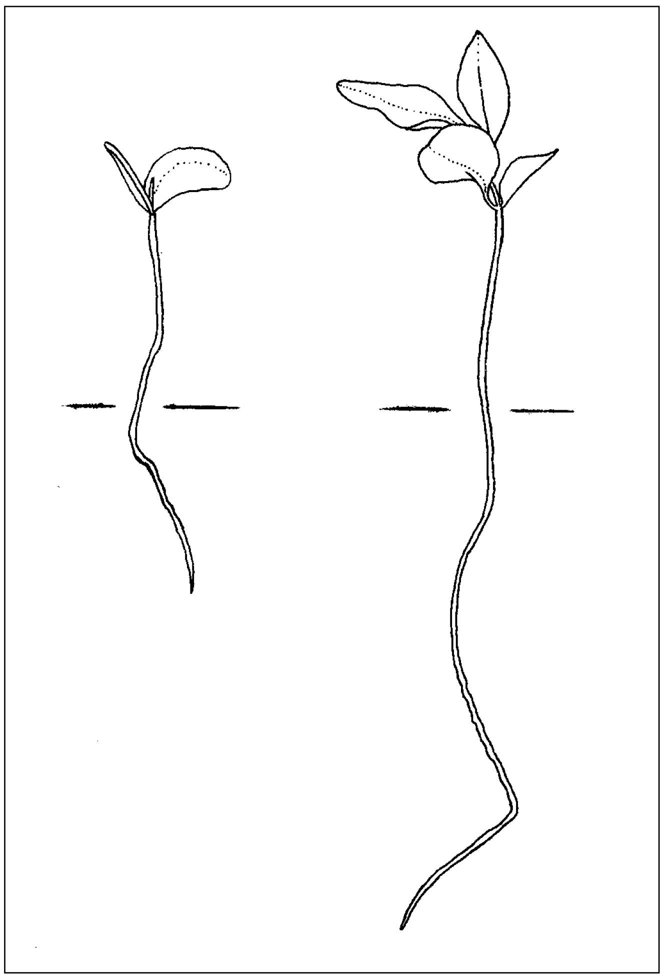


Figure 3—*Peraphyllum ramosissimum*, squaw-apple: germinating seedlings.



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

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

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

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

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Lauraceae—Laurel family

Persea borbonia (L.) Spreng.

redbay

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Other common names. shorebay, swampbay, swampbay persea.

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

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

Collection, extraction, and storage. Redbay fruits can be easily collected by hand from the branches when the exteriors of the fruits turn dark blue or purple. Even though the fruits persist for a short while on the trees, early collection may be necessary to prevent predation by birds. Removal of the fleshy exocarp should not be necessary if seeds are to be planted immediately. If they are to be stored temporarily, removal of this tissue may help avoid damage from pathogens. There are about 3,680 seeds/kg (1,670/lb) (the sample came from Mississippi). Storage data are not available for redbay, so viability retention under typical storage conditions is unknown. Avocado, however, is considered to be recalcitrant in nature and difficult to store (King and

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

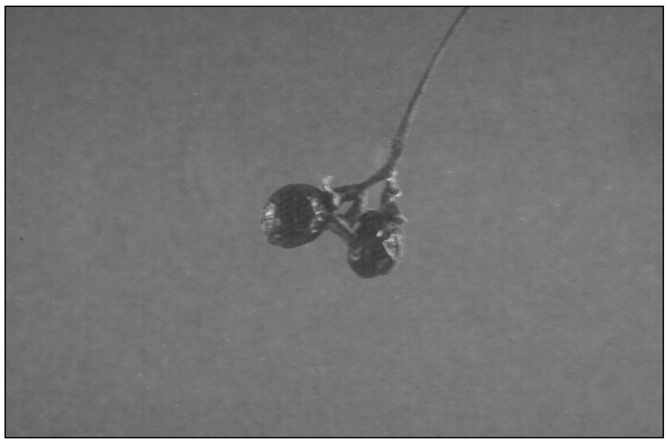

Figure 2—*Persea borbonia*, redbay: cleaned seed.

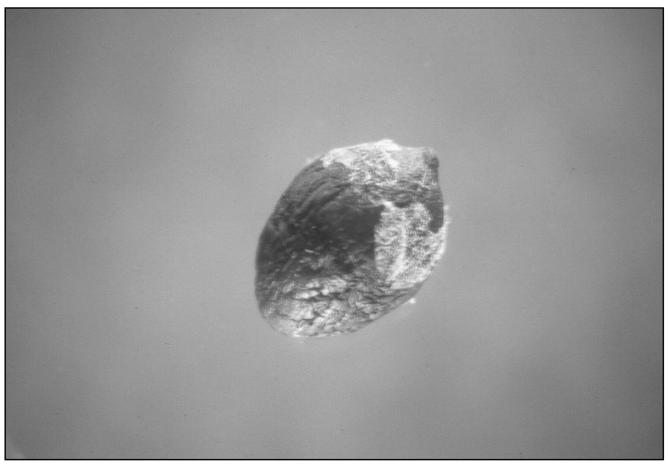

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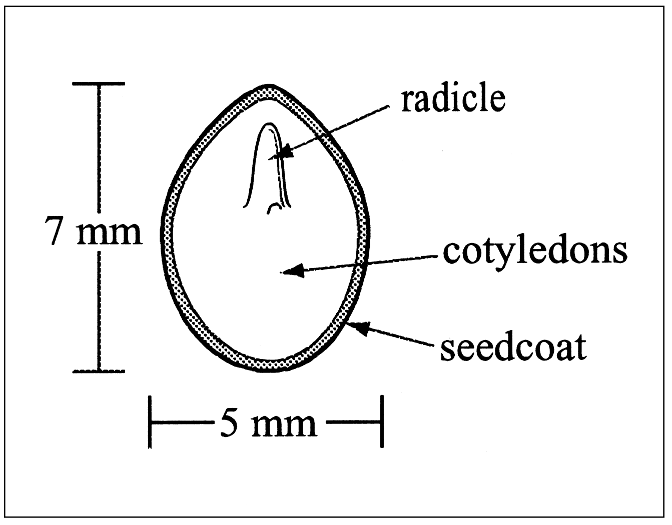
Figure 3—*Persea borbonia*, redbay: longitudinal section through a seed.



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

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

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

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Rutaceae—Rue family

Phellodendron amurense Rupr.

Amur corktree

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Dr. Zasada retired from the North Central Research Station

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

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

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

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

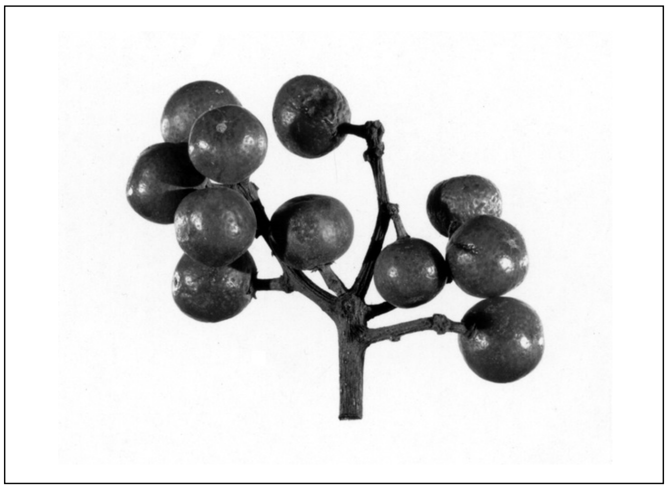
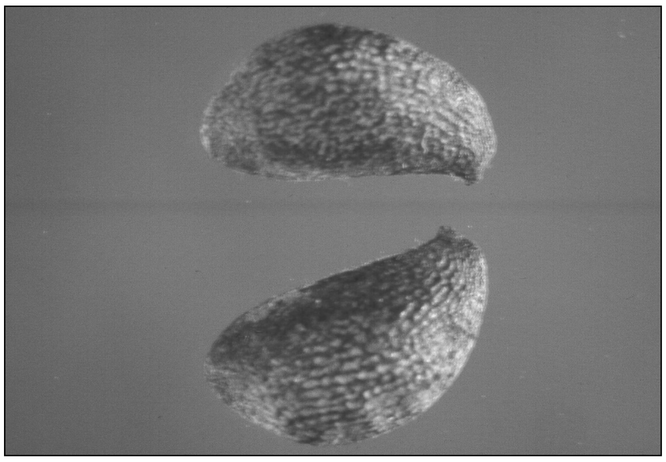


Figure 2—*Phellodendron amurense*, Amur corktree:



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

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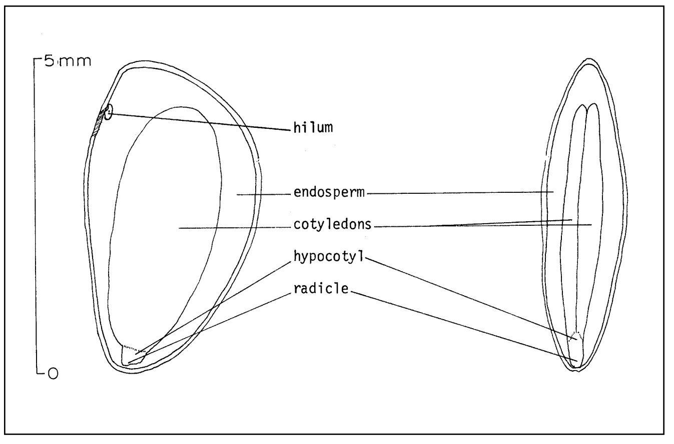
Figure 3—*Phellodendron amurense*, Amur corktree: longitudinal section through 2 planes of a seed.



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

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

Germination. Fresh seeds germinate well without pretreatment (Dirr 1990; Read 1974). However, there are a number of reports of greatly improved germination following stratification. Stratification is recommended for seeds stored any length of time (Dirr and Heuser 1987). Germination for a seedlot (for which the handling and storage history was not described) was best following cold moist, underground stratification for 166 days (Timm 1989). In another study, seeds stratified for 8 weeks had a higher germination rate and the same germination percentage as seeds stratified 4 weeks; germination of unstratified seeds was less than half that of stratified seeds (Mukai and Yokoyama 1985). Based on the information available, it is recommended that seeds be stratified if the history of collection, handling, and storage is not documented. Seeds of other *Phellodendron* spp. vary in their requirements for stratification (Dirr and Heuser 1987; Lin and others 1994).

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

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

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

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Hydrangeaceae—Hydrangea family

Philadelphus L.

mock orange

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

Lewis mock orange, the state flower of Idaho, was named for Captain Meriwether Lewis, who collected the plant in 1806. It is an extremely variable plant, growing from 1.5 to 3 m tall and producing leaf blades that are 25 to 75 mm long. The species is distributed from British Columbia to California and eastward into Montana (table 1). It exhibits wide ecological amplitude, growing in riparian areas and on cliffs, talus slopes, and rocky hillsides from the big sagebrush (*Artemisia tridentata* Nutt.) zone to ponderosa pine (*Pinus ponderosa* Dougl.) and lodgepole pine (*Pinus contorta* Dougl.) forests at elevations from sea level to 2,440 m (Hitchcock and others 1961; Hopkins and Kovalchik 1983).

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

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

Table 1—*Philadelphus,* mockorange: nomenclature and occurrence

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

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

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

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

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

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

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

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

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

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

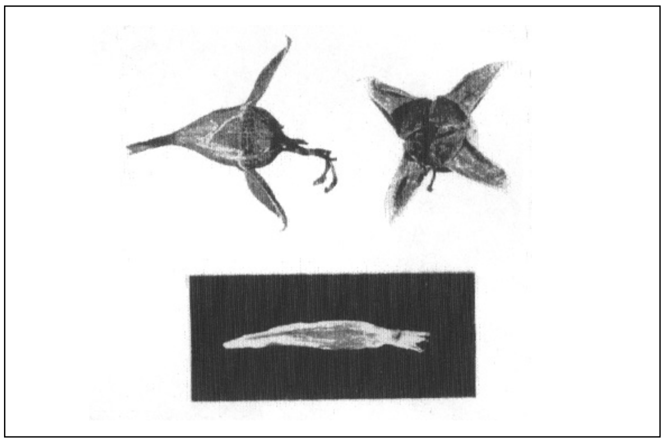
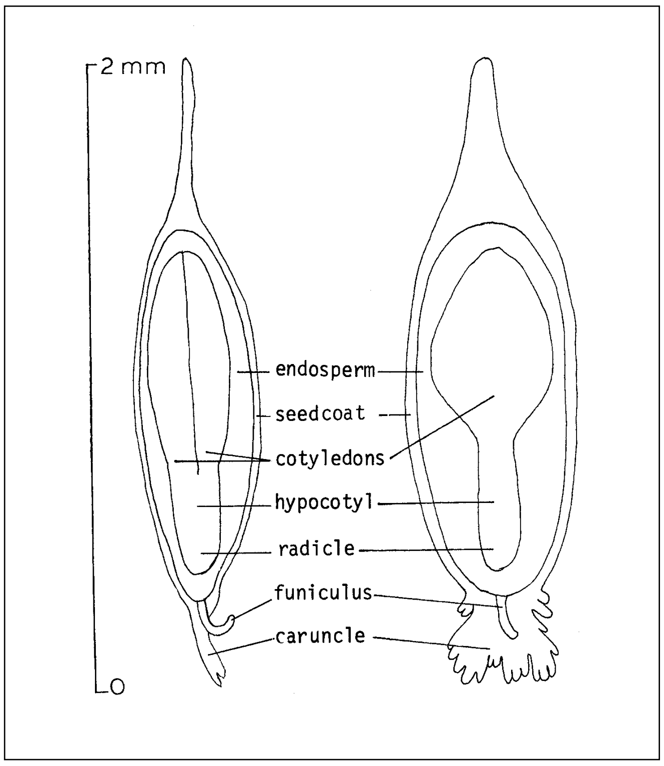


Figure 2—*Philadelphus lewisii*, Lewis mock orange: longitudinal sections of a seed.



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

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

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

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

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

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

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

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

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

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

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

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

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P

Rosaceae—Rose family

Physocarpus (Camb.) Raf.

ninebark

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

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

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

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

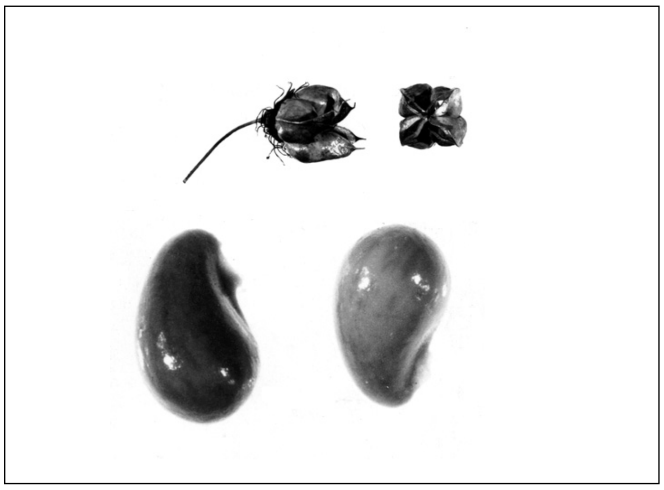
Table 1—*Physocarpus,* ninebark: nomenclature, occurrence, and first cultivation

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

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

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

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



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

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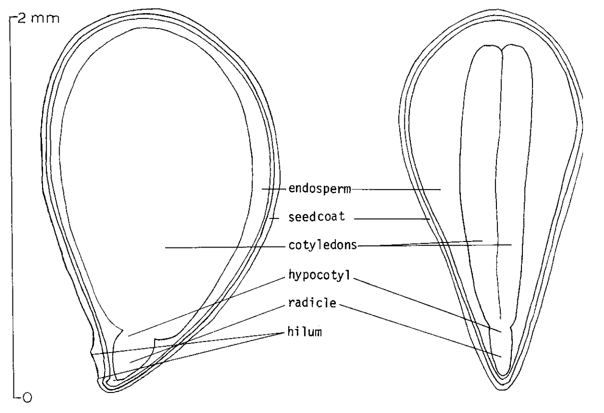
Figure 2—*Physocarpus malvaceus*, mallow ninebark: longitudinal sections through a seed.



Nursery practices. Mallow ninebark seeds may be planted in the fall or planted in the spring after 30 days of prechilling (Link 1993). Seeds of common ninebark and Atlantic ninebarks are sown in raised beds either in the fall or in the spring after 60 days of prechilling (Yoder 1995). Seeds are mixed one part seeds to three parts (by volume) dry, sifted sawdust to provide bulk and facilitate even distribution; sown at a depth of about 3 mm ($^{1}/_{8}$ in); and mulched with a layer of sawdust about 6 mm ($^{1}/_{4}$ in) thick (Yoder 1995). The ninebarks are easily propagated by softwood cuttings planted under mist, or hardwood cuttings planted in the field (Everett 1981; Dirr and Heuser 1987).

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

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Pinaceae—Pine family

Picea A. Dietr.

spruce

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

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

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

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

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

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Table 1—*Picea,* spruce: nomenclature and occurrence of native and cultivated species in North America

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

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

ever, especially when growing on sites with moist soils or high water tables. The conical form and dense, persistent branches of spruce species make them highly desirable for environmental plantings. All 7 North American species and the introduced Norway, Ezo, dragon, and Serbian spruces are planted as ornamentals. Many cultivars featuring variations or extremes in crown height, shape and symmetry, or thickness; rate of height growth; branch angle and degree of twig droop; and needle color exist (Everett 1981, Huxley 1992). In general, spruce species do not tolerate droughty sites but do thrive on slightly acidic and moist but well-drained soils. Of all the species, Serbian spruce may best tolerate industrial air pollution (Dallimore and Jackson 1967).

Geographic races and superior strains. The wide ranges and diverse environments to which the spruce species have adapted provide an array of individual, ecological, and geographic variations. Natural hybridization and introgression commonly occur where ranges of compatible species overlap. Hybridization between white spruce and Sitka spruce (first reported by Little 1953 as *P.* × *lutzii)*, occurs in British Columbia and throughout the Kenai Peninsula in Alaska (Copes and Beckwith 1977). This hybrid has demonstrated a genetically based resistance to attack by the Sitka spruce weevil—*Pissodes strobi* Peck—which causes severe height growth and stem form reduction in Sitka spruce (Mitchell and others 1990). Hybridization between white spruce and Engelmann spruce occurs in northern Montana and British Columbia (Daubenmire 1974). Artificial crosses of Engelmann spruce with Sitka spruce and with blue spruce suggest the close relatedness of these North American species (Fowler and Roche 1977). Electrophoresis has yet to clearly identify hybrids of Engelmann spruce and blue spruce along a 1,200-m elevational transect in the front range of the Colorado Rocky Mountains, where the species grow together. Morphological similarity between the 2 species, such as number of bud scales, number of stomatal rows, and location of resin sacs, however, suggests either convergent evolution or the influence of environmental variation on the morphological characters (Mitton and Andalora 1981). Natural introgression between the maritime Sitka spruce and the more interior complex of white and Engelmann spruces occurs in a portion of British Columbia, and the hybrid fraction was estimated by restriction fragment length polymorphisms of the nuclear ribosomal RNA genes (Sutton and others 1994). Differences in monoterpene composition from black spruce oleoresin (including α–pinene, 3-carene, and terpinolene) vary among geographic origins in an east–west pattern, except for seeds from sources in New England that have close affinity in monoterpene composition to red spruce (Chang and Hanover 1991). Natural introgression of black spruce into red spruce may result in greater height and diameter growth in New Brunswick, yet the hybrid performed unpredictably in managed stands (Fowler and others 1988).

Early crosses within the genus have provided a thorough background in potential crossability of the genus, including specimens from artificial crosses between nonsympatric species (Wright 1955). Analysis of morphological characteristics and monoterpene composition from artificial crosses between white, red, and blue spruces later verified the hybridity of the seedlings, evaluated the utility of spruce hybrids, and clarified the evolutionary relation among members of the genus (Bongarten and Hanover 1982). Height growth of Englemann spruce × Sitka spruce hybrids proved unsuitable for reforestation purposes in the north central interior of British Columbia (Kiss 1989). Hybrids of black spruce and Serbian spruce out-performed the black spruce parents in height and diameter growth and can be produced sexually en masse in seed orchards (Fowler 1980).

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

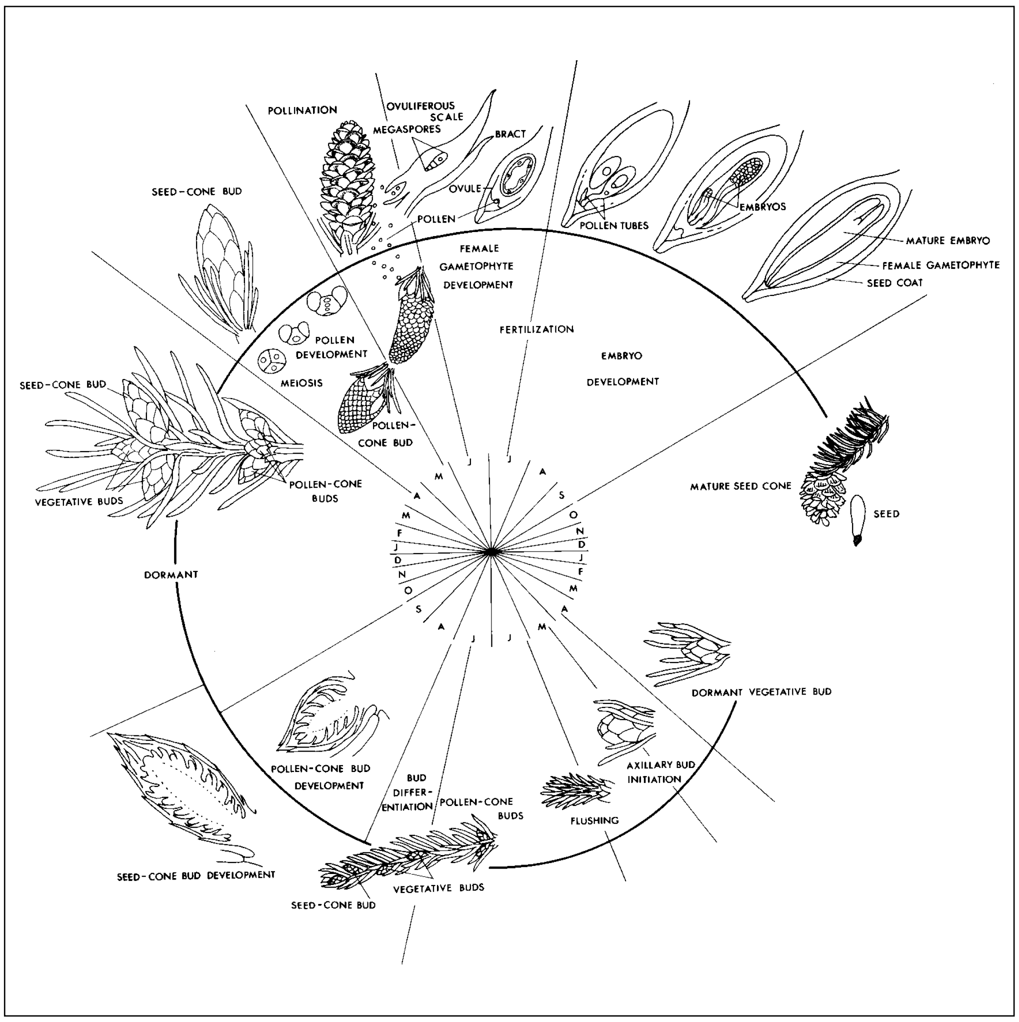
Genetic variation of Engelmann spruce may correlate with latitude and elevation; the species grows at 762 to 1,067 m in British Columbia and as high as 3,658 m in the southern Rocky Mountains (Alexander 1987). After 10 years, seedlings from more northern and lower elevation sources grew better than those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

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

Norway spruce, perhaps the most intensively studied non-native species, shows strong latitudinal and elevational gradients. Seeds from northern latitudes and higher elevations weigh less than seeds from southern latitudes and lower elevations (Heit 1968; Tyszkiewics 1968). Seed source also influences mineral nutrient content of seeds (Youngberg 1951) and early growth of seedlings in nursery beds (Heit 1968). Seed source of Serbian spruce can affect the crown shape and susceptibility to frost (Dirr and Heuser 1987).

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

Figure 1—*Picea glauca*, white spruce: reproductive cycle (from Owens and Molder 1984, used with permission of the author and publisher).



bright purple, or crimson male strobili have ovoid to cylindrical shape and uniform distribution over the crown. Each scale (microsporophyll) bears 2 pollen sacs (microsporangia) and are spirally arranged on a central axis. Male strobili dry out and fall off soon after pollen-shedding.

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

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

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

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

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

Sources: Alden (1955), Alexander (1987), Alexander and Shepperd (1984), Edwards (1980), Fechner (1985), Nikolov and Helmisaari (1992), Safford (1974), Zasada and Viereck (1970).

* Cones of *P. mariana* are semi-serotinous and release seeds throughout the year for several years.

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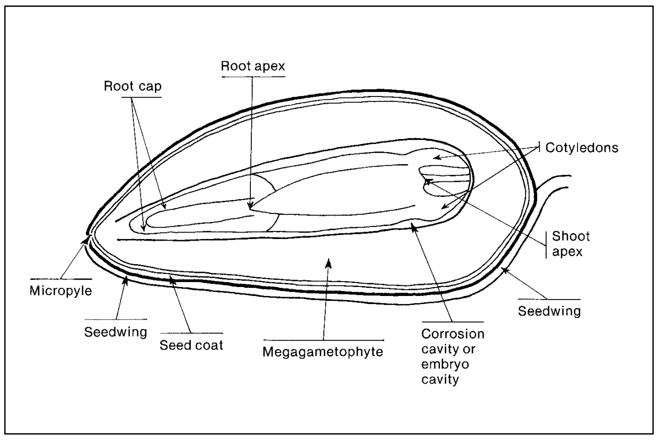
Figure 2—*Picea glauca*, white spruce: diagrammatic longitudinal section of a mature seed at dispersal, showing seedcoat, gametophyte, and fully developed embryo (from Alden 1985, used with permission of the author and publisher).



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

At maturity, the pendent cones open to shed seeds during autumn and winter (table 2). Persistent cone scales on mature cones may have rounded, pointed, irregular, notched, or reflexed ends. Most species shed cones at the end of the season, but some cones may remain on the tree throughout the next growing season. Cones should be harvested before inclement weather reduces workers' productivity or losses to squirrels increase (Curran and others 1987). Cones may be collected before they are fully ripe and, if artificially ripened, release seeds with maximal germination capacity (Edwards 1980). Cones may be collected from standing trees, slash, or animal caches, although cones that have been in contact with the forest floor may acquire seed-killing fungi. Seeds generally reach maturity before cones show their characteristic ripe color (table 2). Time of ripening varies among cones on an individual tree and among trees in a single stand (Fechner 1974; Jensen and others 1967; Zasada 1988). Various measures of estimating seed maturity have emphasized (1) physical attributes such as color and firmness of cones; (2) moisture content and specific gravity of cones; (3) color of testa and brittleness of seeds (Crossley 1953; Edwards 1980); (4) a cone moisture content of 30% or less for Norway spruce; (5) specific gravity between 0.78 and 0.95 (Winston and Haddon 1981; Zasada 1973) and a soft "spongy feel" of cones when squeezed in the fingers for white spruce; or (6) dark brown or black testa and seeds that "snap" when cut with a sharp instrument. All of these indicate that cones are sufficiently ripe for harvest.

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

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

Attempts to enhance seed yields in seed orchard programs have been hampered by the relatively long period of tree growth before flowering begins. Documented minimal seed-bearing age (table 2) for most species ranges from 10 to 60 years, although crops of sufficient quantity to warrant collection may not occur until much later. Efforts to stimulate flowering in younger trees have involved girdling of the bole, nitrogen fertilization, and root pruning. Top-pruning of grafted white spruce in seed orchards, done to maintain the cone-bearing branches at a height within reach of a short ladder, may also increase cone production and decrease the cost of cone collection (Nienstaedt 1981).

Several lines of research have attempted to define the physiological processes and procedures for large-scale stimulation of flowering to either shorten the length of breeding programs or to increase production of cones and seeds. Application of gibberellins A_4, A_7, and A_9 stimulated female cone production in grafted Norway spruce clones, although the response differed by year and clone (Dunberg 1980). Gibberellin $A_{4/7}$ applied in the top 2 branch whorls of mature Sitka spruce grafts increased female flowering and seed production (Tompsett and others 1980); girdling in combination with stem injections of gibberellin $A_{4/7}$ in grafted clones of Sitka spruce may stimulate pollen-cone production (Philipson 1985a); and top-pruning and stem injection of gibberellin $A_{4/7}$ may increase cone production in the lower crown and increase the ease of cone collection (Philipson 1985b). Heat and drought also promote flowering, although by a different induction mechanism. Potted grafts of Engelmann spruce produced high numbers of both male and female cone buds after exposure to high temperature within heated polyethylene-covered houses when the exposure occurred during the late stage of slow shoot elongation, whereas drought during the period of rapid shoot elongation after vegetative bud burst enhanced female cone production (Ross 1985). Optimal daytime temperature is 22 to 25 °C (Ross 1988a). In contrast, polyhouse temperatures that frequently exceed 30 °C during the pollination sequence of Engelmann spruce resulted in accelerated pollen shed, increased underdevelopment of pollen cones, and reduced yields of seed (Ross 1988b). These results suggest a need for a year's rest between treatments to allow time for cone maturation and vegetative replenishment of shoots. Repeated injection of gibberellin $A_{4/7}$ into container-grown grafts of Sitka spruce in a polyhouse during May and June effectively stimulated flowering (Philipson 1992). Application of gibberellin $A_{4/7}$ also stimulated flowering of white spruce (Ho 1988b; Marquard and Hanover 1984), even though white spruce has been classed as recalcitrant because of its sporadic flowering and usually nominal response to gibberellin $A_{4/7}$ alone (Pharis and others 1986). Stem injection of gibberellin $A_{4/7}$ in combination with nondestructive girdling greatly increases flowering in mature white spruce trees (Pharis and others 1986) and grafted clones (Ross 1992). Whole-tree spraying of branches at relatively high concentrations (800 mg/liter gibberellin $_{4/7}$) during May through July promoted cone production the next year (Ho 1988b). In the Great Lakes region, elongating shoots sprayed in May produced more male and female strobili than shoots sprayed in June (Cecich 1985). Flowering of white spruce responded to heat similar to that of Engelmann spruce by enhanced pollen-cone production after subjecting potted grafts to 30 °C for 10 hours, whereas seed-cone production was enhanced after 5 hours at 20 °C (Ross 1991). Seed-cone production of black spruce also has been stimulated by application of gibberellin; the greatest increase occurred with 200 mg/liter of gibberellin $A_{4/7}$ sprayed repeatedly on young grafts during the period of rapid shoot elongation (Ho 1991). Seed-cone production also may be enhanced in field-grown seed orchards by applying a foliar spray of 400 mg/liter gibberellin $A_{4/7}$ during the period before lateral shoot elongation and bud-type differentiation (Ho 1988a), and in seed orchards of seedling origin by applying a foliar spray of 200 to 800 mg/liter gibberellin $A_{4/7}$ (Hall 1988). Attempts with several species to promote male flowering preferentially by the synthetic auxin naphthalene acetic acid (NAA) have been inconclusive (Hall 1988; Ross 1992).

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

Figure 3—*Picea*, spruce: seeds with wings of *P. breweriana*, Brewer spruce; *P. engelmannii*, Engelmann spruce; *P. glauca*, white spruce; *P. mariana*, black spruce; *P. rubens*, red spruce; and *P. sitchensis*, Sitka spruce (**left to right**).

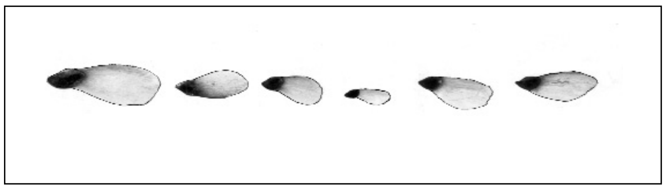


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Table 3—*Picea*, spruce: common cone- and seed-damaging insects

Insect species	Common name	Damage	Affected species*
Choristoneura occidentalis Freeman	western spruce budworm	Larvae feed externally on cones	***P. engelmannii***
Dasineura canadensis Felt	spruce cone gall midge	Larvae form gall on cone scale	***P. glauca***
Dasineura rachiphaga Tripp	spruce cone axis midge	Larvae mine through scales into axis	***P. engelmannii, P. glauca****, P. sitchensis, P. mariana*
Dioryctria abietivorella Grote	fir cone moth	Larvae mine & riddle cone	***P. mariana, P. glauca****, P. engelmannii, P. pungens,*
Henricus fuscodorsanus Kearfott	cone cochylid	Larvae feed on scales & seeds	***P. sitchensis, P. glauca***
Hylemya anthracina Czerny	spruce cone seed maggot	Larvae tunnel around cone axis	***P. mariana, P. glauca, P. engelmannii, P. sitchensis***
Laspeyresia youngana Kerfott	spruce seed moth	Larvae feed on seeds	***P. engelmannii, P. glauca****, P. mariana, P. pungens, P. rubens, P. sitchensis*
Mayetiola carpophaga Tripp	spruce seed midge	Larvae feed on seeds	***P. glauca***
Megastigmus atedius Walker	spruce seed chalcid	Larvae feed on seeds	All native *Picea*
Strobilomyia neanthracina Michelson	spruce cone maggot	—	***P. mariana***

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

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

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

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

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

Many species of birds consume spruce seeds. Several finches (families Fringillidae and Estrildidae) feed almost exclusively on conifer seeds, including the common (red) crossbill (*Loxia curvirostra*), the two-barred (white-winged) crossbill (*L. leucoptera)*, and the pine siskin (*Carduelis pinus*). Spruce seeds often provide an important winter food source for the American goldfinch—*C. tristis*. In addition, the pine siskin and the pine grosbeak—*Pinicola enucleator*—may feed on reproductive buds (Benkman 1987; Clement and others 1993).

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

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

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

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

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

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

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

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

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

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

Sources: Dirr and Heuser (1987), Jeglum and Kennington (1993), Nikolov and Helmisaari (1992), Safford (1974), Stein and others (1986), Willan (1985).
Note: TB = top of blotters; P = petri dishes covered with blotters, filter paper, or sand.

for 14 months showed only a slight loss of percentage germination; under these conditions black spruce lost about one-third of its percentage germination and germination of all 3 species declined to about 10% of the original capacity after 27 months (MacGillivary 1955). Prechilling, or cold stratification, may widen the range of temperatures over which seeds can subsequently germinate, increase the maximal percentage germination at some temperatures, and increase the rate of germination at almost any temperature (Gosling and Rigg 1990). Prechilling of white spruce seeds at 2 to 4 °C for 6 weeks results in high percentage germination (Caron and others 1990). Other researchers have prechilled white spruce seeds by soaking them in cold running water for 24 hours, blotting them dry, and then refrigerating them at 4 °C for 3 weeks (Chanway and others 1991). Storage of cones at 5 °C for 4 weeks, however, may eliminate any subsequent need for stratification of white spruce seeds (Winston and Haddon 1981). White spruce seeds from high-latitude sites in Alaska (> 55° latitude) do not undergo dormancy, and stratification is detrimental for mature seeds (Alden 1995). Before nursery sowing, Engelmann spruce seeds need to be primed for 24 hours, then prechilled for 6 to 8 weeks at 2 °C in loosely closed polyethylene bags (Tanaka and others 1986). Unstratified seeds of black spruce incubated for 24 days at 3 or 20 °C germinated completely within18 days with 14:10 (light:dark) hours of fluorescent light, whereas moist seeds prechilled for 24 hours at 3 °C in a polyethylene bag in the dark reached 95% germination within 12 days when incubated at 5 to 30 °C, regardless of lighting regime (Farmer and others 1984). Priming black spruce seeds for 5 to 6 days in water (until the radicles nearly emerge) and surface-drying before sowing accelerated germination by about 1 week (Malek 1992). Seeds of black spruce from high latitudes in Alaska, collected and immediately extracted in the spring, will germinate in 2 to 6 days after becoming fully imbibed with water; no dormancy exists and stratification is not required (Alden 1995). Dormancy of Sitka spruce seeds is broken and 95% germination is possible after priming for 72 hours (until seeds reach 30% moisture content), then chilling for 6 weeks in loosely closed polyethylene bags at 4 °C (Gosling and Rigg 1990).

Treating seedlots with various fumigants, insecticides, fungicides, and rodent repellents in storage or before sowing may reduce germination of seeds. Germination of white spruce seeds treated with a finely ground rodent repellent mixed with graphite declined slightly from that of untreated seeds after more than 5 years of storage (Radvanyi 1980). Aluminum powder, which is used as a lubricant on Sitka and white spruce seeds in bareroot nurseries in Canada, may decrease the percentage germination of treated seeds and reduce first-year survival of seedlings (Sutherland and others 1978). Embedding black spruce seeds in pellets may discourage their consumption by small mammals, depending on the material surrounding the seeds (Martell 1981). As always, pesticide users should closely follow the manufacturer's recommended dosages.

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

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

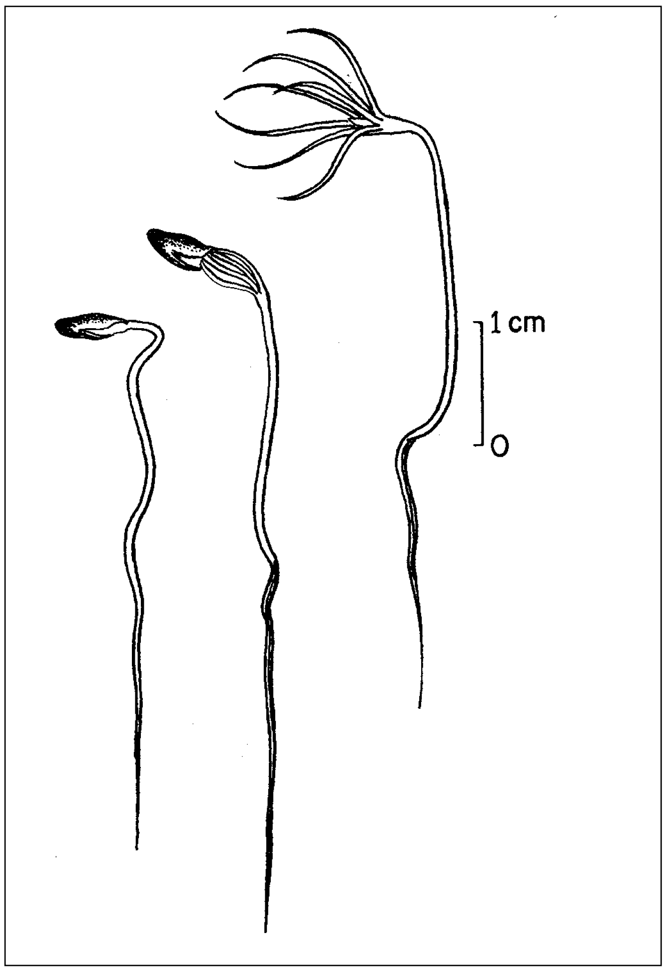
Under natural conditions, most species of spruce germinate on various media, including rotten wood, shallow duff, and mixtures of mineral and organic soil. Mineral soil makes an ideal seedbed because of greater water availability. Commercial growers raise white spruce seedlings with high stem caliper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

Seeds of most species germinate promptly and completely under a wide range of temperatures either with or without light. Once germinated, seedlings in greenhouses require extended daylength to accelerate growth and prevent dormancy. Continuous fluorescent lighting providing about 150 μmol/m^2/sec photosynthetically active radiation at 25 °C allows continuous vigorous growth of blue spruce seedlings (Young and Hanover 1978). White spruce seedlings respond favorably to photoperiodic lighting intensities of about 414 to 4,150 μmol/m^2/sec, although Engelmann spruce has a much narrower response range of about 210 to 520 μmol/m^2/sec (Arnott and Macey 1985). Seedlings of white spruce also have been grown with photosynthetically active radiation at the seedling canopy level of about 300 μmol/m^2/sec in a 16-hour photoperiod at 23 °C and a night temperature of 17 °C (Chanway and others 1991). Failure of the lighting system for only a few days reduced the effectiveness of extended or intermittent photoperiod, leading to increased root rather than shoot growth in white spruce seedlings (Arnott and Simmons 1985). Under laboratory or greenhouse conditions, newly germinated seedlings of red spruce require a light period of at least 16 hours to prevent the onset of dormancy (Safford 1974).

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

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

Figure 4—*Picea pungens*, blue spruce: seedling development at 2, 5, and 7 days after germination.



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

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

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Ericaceae–Heath family

Pieris floribunda (Pursh) Benth. & Hook.

mountain andromeda

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Synonym. *Andromeda floribunda* Pursh.

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

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

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

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

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

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

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

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

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

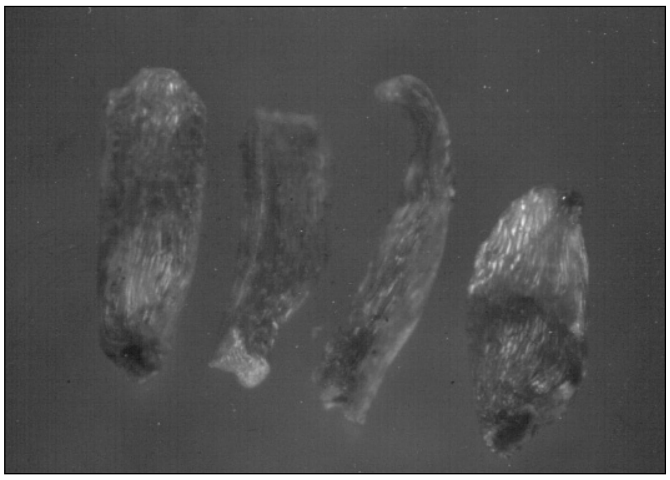
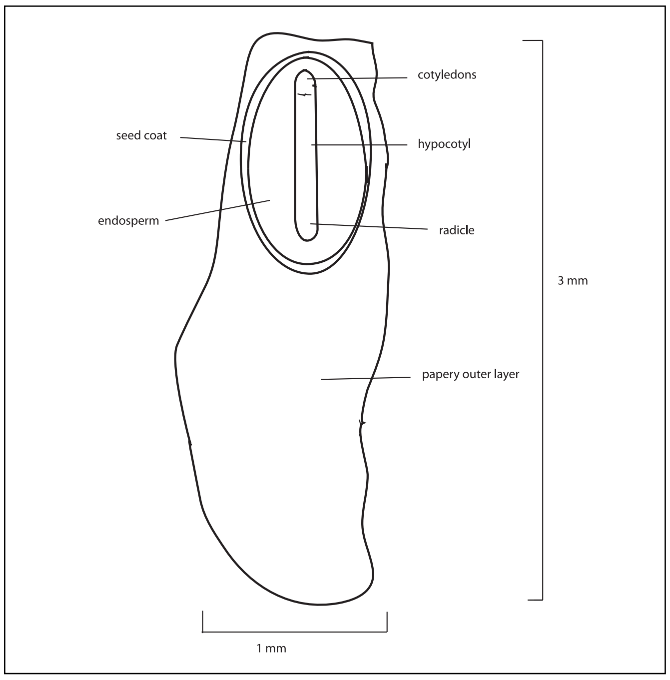


Figure 2—*Pieris floribunda*, mountain andromeda: longitudinal section of a seed.



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

Nursery practice. Typically, a germination medium is warmed to 24 °C via bottom heat (Bir 1987). Seeds are sown on the surface of a steam-pasteurized medium such as pine bark sifted through a 6-mm ($^1/_4$-in)-mesh screen and irrigated slightly. The surface of the germinating medium should never be allowed to dry completely (Bir 1987). Once seeds have germinated, seedlings have very slow initial growth. The authors have observed that seedlings will often produce 1 true leaf above the cotyledons and then fail to exhibit any further growth for several weeks. Current practice is to fertilize seedlings at the first-true-leaf stage with a half-strength solution of a 15-45-5 ($N:P_2O_5:K_2O$) complete fertilizer (Bir 1987). After 2 weeks, nursery workers then shift the seedlings to a full-strength fertilizer with weekly application until they transplant the seedlings into liner flats or pots (Bir 1987).

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

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