T

Tamaricaceae—Tamarix family

Tamarix chinensis Lour.

saltcedar or five-stamen tamarisk

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Synonym. *T. pentrandra* Pall.

Growth habit, occurrence, and use. Saltcedar (*Tamarix chinensis* (Lour.)) and smallflower tamarisk (*T. parviflora* DC.) hybridize in the Southwest (Baum 1967; Horton and Campbell 1974) and are deciduous, pentamerous tamarisks that are both commonly referred to as saltcedar. Saltcedar is a native of Eurasia that has naturalized in the southwestern United States within the last century. It was introduced into the eastern United States in the 1820s (Horton 1964) and was once widely cultivated as an ornamental, chiefly because of its showy flowers and fine, graceful foliage. However, saltcedar has been an aggressive invader of riparian ecosystems in the Southwest (Reynolds and Alexander 1974) and is the subject of aggressive eradication campaigns. It achieves heights of 12 m and trunk diameters of 0.5 m in southern New Mexico and trans-Pecos Texas (Everitt 1980). Although considered a threat to native vegetation, saltcedar has been utilized for browse, firewood, and lumber and also to produce premium honey (Everitt 1980). Saltcedar is halophytic and tolerates an extreme range of environments from below sea level to above 2,100 m (Everitt 1980). Though a riparian plant, it is also drought tolerant and can survive indefinitely in non-saturated soils, making it a "facultative phreatophyte" (Turner 1947). In some areas, saltcedar thickets are valued nesting habitat for white-winged doves (Reynolds and Alexander 1974). Saltcedar can naturally reproduce vegetatively from roots and can layer when foliage is buried by sediment (Everitt 1980). These prodigious reproductive capabilities are well suited to colonizing riverbanks and disturbed areas (Horton and others 1960). Because saltcedar is a heavy water user, its spreads rapidly along drainages and flood plains—for example, the infested area increased from 4,000 to 364,000 ha in 41 years (1920 to 1961), (Robinson 1965)—and has required extensive eradication or control efforts.

Flowering and fruiting. The pink to white flowers, borne in terminal panicles, bloom from March through September. A succession of small capsular fruits ripen and split open during the period from late April through October in Arizona (Horton and others 1960). Seeds are minute and have an apical tuft of hairs (figures 1 and 2) that facilitates dissemination by wind. Large numbers of small short-lived seeds are produced that can germinate while floating on water, or within 24 hours after wetting (Everitt 1980).

Collection, extraction, and storage. Fruits can be collected by hand in the spring, summer, or early fall. It is not practical to extract the seeds from the small fruits. At least half of the seeds in a lot still retained their viability after 95 weeks in storage at 4.4 °C, but seeds stored at room temperature retained their viability for only a short time (Horton and others 1960).

Figure 1—*Tamarix chinensis*, saltcedar: longitudinal section through a seed.

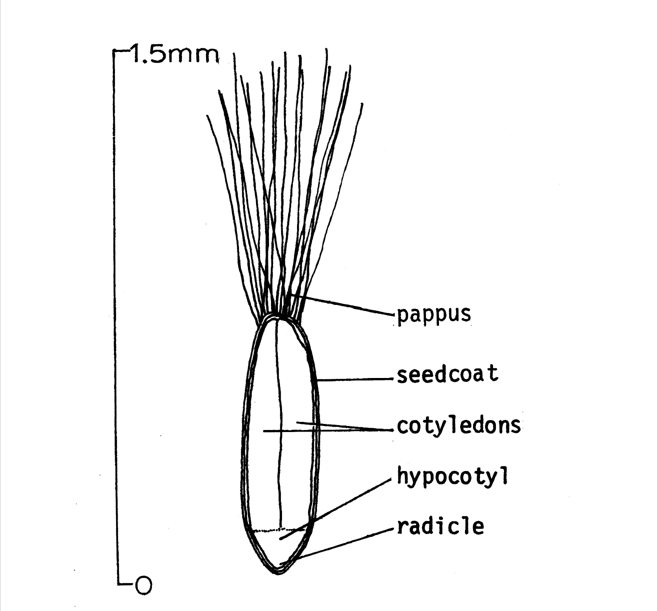
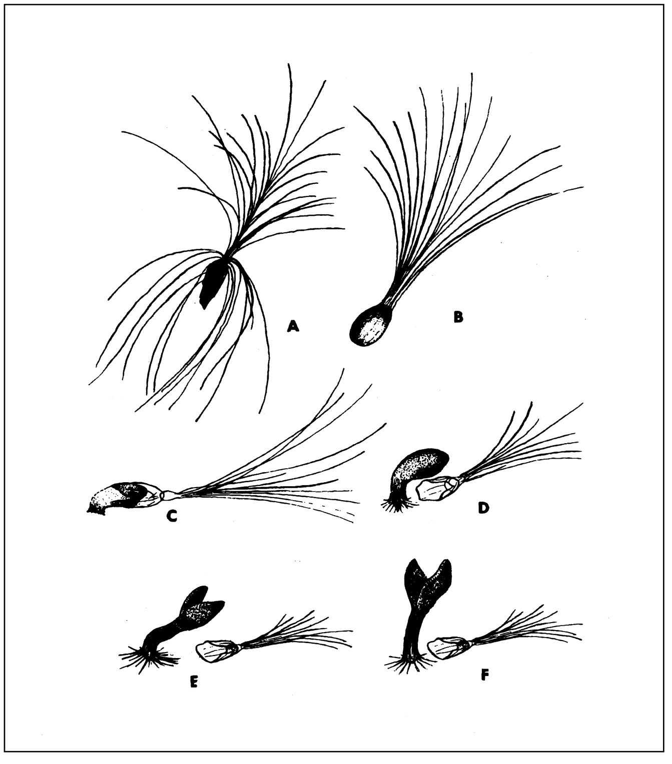


Figure 2—*Tamarix chinensis*, saltcedar: dry seed (**A**) and seedling development at the following intervals after moistening the seed—several hours (**B**), 8 hours (**C**), 24 hours (**D**), 40 hours (**E**), 48 hours (**F**) (drawings by Dennis C. Jackson, from Horton and others 1960).



Germination tests. Fresh seeds usually germinate within 24 hours after imbibing water (figure 2). No pretreatment is necessary. Germination tests have been run in moist soil in covered petri dishes at room temperature. The germination rate after 24 hours averaged 78% and the percentage germination after 6 days was 88% (Horton and others 1960). Seed can survive up to a year in cold storage (Merkel and Hopkins 1957).

Nursery practice. Germination and survival is favored by fine-grain sediment. Bare, sunny, saturated soil is ideal for the first 2 to 4 weeks of life, but survival is limited because of slow early seedling growth (Everitt 1980). Top height averages about 2.5 cm (1.0 in) 30 days after emergence, and seedlings average only 10 cm (4 in) tall after 60 days. At this time, roots are about 15 cm (6 in) long. Soil must be kept continuously moist during this establishment period; 1 day of drought can kill most seedlings (Reynolds and Alexander 1974).

Saltcedar is also readily propagated from cuttings. Cuttings will root during any season, if planted in moist soil at 16 °C (Gary and Horton 1965). Hardwood cuttings should be at least 2 cm ($^{3}/_{4}$ in) thick. A peat and perlite medium under mist works well with softwood cuttings, but root systems may be sparse and difficult to handle (Dirr and Heuser 1987). Seedlings are hearty after they become established and can withstand severe drought (Horton and others 1960). Softwood cuttings should be weaned from mist as soon as rooting begins to avoid decline from excessive moisture (Dirr and Heuser 1987).

References

Baum BR. 1967. Introduced and naturalized tamarisks in the United States and Canada. Quarterly Journal of Horticulture Taxonomy 15(1): 19–25.

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

Everitt BL. 1980. Ecology of saltcedar: a plea for research. Environmental Geology 3(2): 77–84.

Gary HL, Horton JS. 1965. Some sprouting characteristics of five-stamen tamarisk. Res. Note RM-39. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 7 p.

Horton HL. 1964. Notes on the introduction of deciduous tamarisks. Res. Note RM-16. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 7 p.

Horton JS, Campbell CJ. 1974. Management of phreatophyte and riparian vegetation for maximum multiple use values. Res. Pap. RM-117. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 23 p.

Horton JS, Mounts FC, Kraft JM. 1960. Seed germination and seedling establishment of phreatophyte species. Stn. Pap. 48. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station. 26 p.

Merkel DL, Hopkins HH. 1957. Life history of saltcedar. Transactions of the Kansas Academy of Science 60(4): 360–369.

Reynolds HG, Alexander RR. 1974. *Tamarix pentandra* Pall., five-stamen tamarisk. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 794–795.

Robinson TW. 1965. Introduction, spread, and areal extent of salt-cedar (*Tamarix*) in the western states. Prof. Pap. 491-A. Washington DC: USDI Geological Survey. 11 p.

Turner RM. 1974. Quantitative and historical evidence of vegetation changes along the upper Gila River, Arizona. Prof. Pap. 655-H. Washington DC: USDI Geologic Survey: 1–20.

T

Taxodiaceae—Redwood family

Taxodium L.C. Rich.

baldcypress

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Growth habit, occurrence, and use. Baldcypresses are large deciduous conifers that occur naturally in wetlands of the Southeastern and Gulf Coastal Plains. Two species, once classified as varieties of a single species, are now recognized (table 1). The ranges of these species overlap in the Southeast and Gulf South; baldcypress extends much further north and west, however. They are often difficult to identify where mixed (Wilhite and Toliver 1990). Baldcypress may be encountered in almost all temperate regions of the world, as it has been planted extensively as an ornamental. It was introduced in Europe as early as 1640 (Bonner 1974). Baldcypress wood is well-known for its use in boat construction, pilings, interior trim, flooring, paneling, and many other items. It is an important source of wildlife food and habitat and a valuable component of wetland hydrology (Wilhite and Toliver 1990).

Flowering and fruiting. The monoecious flowers of baldcypress appear in March to April, before the leaves. The male catkins are about 2 mm in diameter and are borne at the end of the previous year's growth in slender, purplish, tassel-like clusters 7 to 13 cm long. Female conelets are found singly or in clusters of 2 or 3 in leaf axils near the ends of the branchlets (Vines 1960; Wilhite and Toliver 1990). The globose cones turn from green to brownish purple as they mature in October to December. Flowering and fruiting of pondcypress is essentially the same as for baldcypress (Wilhite and Toliver 1990). Baldcypress cones are 13 to 36 mm in diameter (figure 1), and consist of a few 4-sided scales that break away irregularly after maturity. Each scale bears 2 irregularly shaped seeds that have thick, horny, warty

Figure 1—*Taxodium, baldcypress*: cones of *T. distichum*, baldcypress (**top**) and *T. ascendens*, pondcypress (**bottom**).

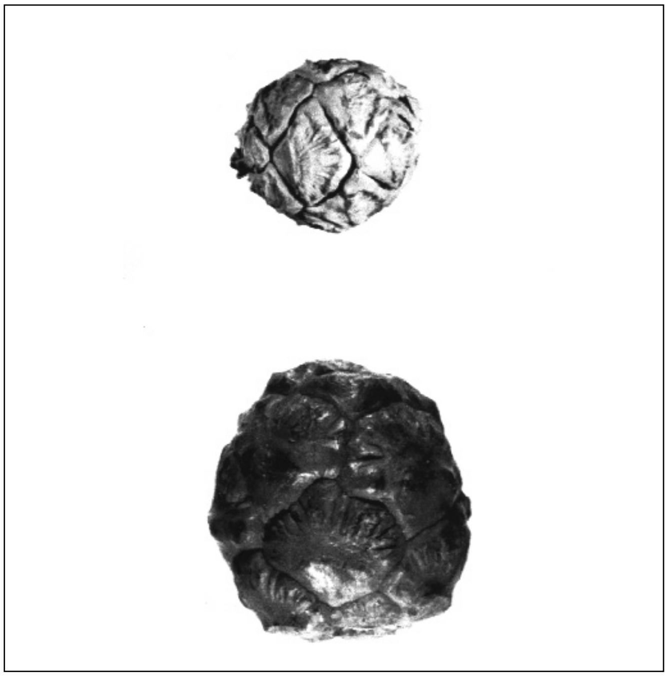


Table 1—*Taxodium,* baldcypress: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***T. ascendens* Brongn.** *T. distichum* var. *imbricarium* (Nutt.) Croom *T. distichum* var. *nutans* (Ait.) Sweet	**pondcypress**, pond baldcypress, cypress	Coastal plain from Virginia to Florida & Louisiana
***T. distichum* (L.) Rich.**	**baldcypress,** common bald cypress, gulf cypress, red cypress, tidewater red cypress, white cypress, yellow cypress, cypress	Coastal plain from Delaware & Florida W to Texas & N to Illinois in Mississippi River Valley; planted from Michigan to Massachusetts

Sources: Little (1979), Wilhite and Toliver (1990).

coats and projecting flanges (figures 2 and 3). Collections from 45 families of baldcypress from Mississippi to Texas found that cones contained anywhere from 2 to 34 seeds, with an average of 16 (Faulkner and Toliver 1983). The proportion of seeds with embryos is frequently less than 50%, however. Some seeds are borne every year, and good crops occur at 3- to 5-year intervals.

Figure 2—*Taxodium*, baldcypress: seeds of *T. distichum*, baldcypress (**top**) and *T. ascendens*, pondcypress (**bottom**).

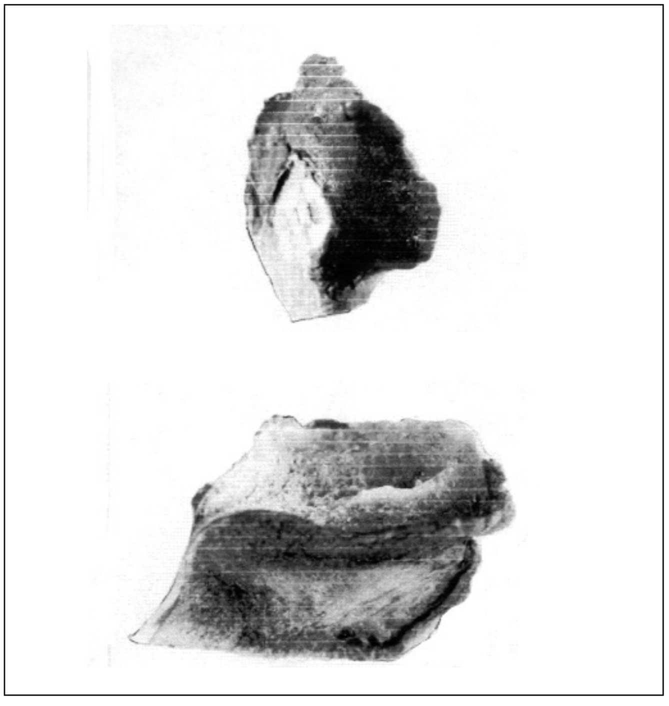
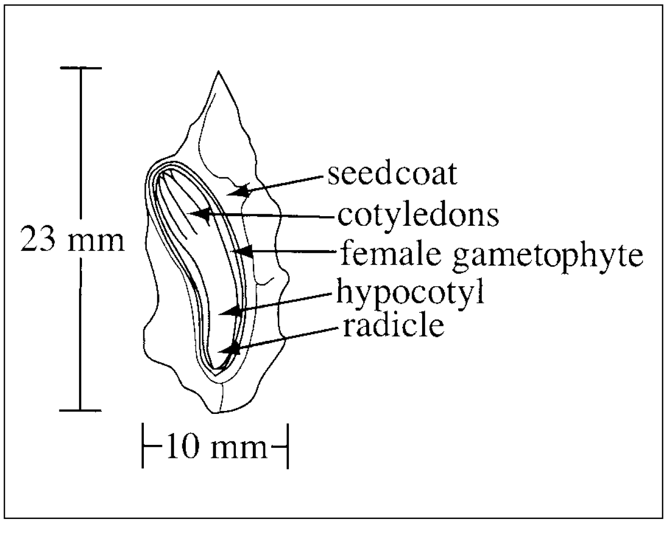


Figure 3—*Taxodium distichum*, baldcypress: longitudinal section through a seed.



Two insect pests destroy significant amounts of baldcypress and pondcypress seeds—southern pine coneworm (*Dioryctria amatella* (Hulst)) and baldcypress coneworm (*D. pygmaeella* Ragonot). The baldcypress seed midge (*Taxodiomyia cupressi* Schweinitz) forms small round galls inside the cones of baldcypress (Hedlin and others 1980; Merkel 1984). The seed midge apparently does little damage to seeds, but the galls are difficult to separate from the seeds and become a quarantine problem for seed exporters.

Collection, extraction, and storage. Mature, dry cones can be picked by hand from standing or felled trees and spread in a thin layer for air-drying. The dried cones should be broken apart by flailing or dry maceration. The resin in the cones presents a major problem in separation and cleaning because it causes seeds and cone fragments to stick together. The resin also gums up mechanical macerators. One possible solution is to place the dried seeds and cone fragments in a freezer to harden the resin, then run them through a macerator again while the resin is still in a solid state. Resin can be cleaned from equipment with alcohol or other organic solvents.

The number of seeds per cone volume for baldcypress averages about 58 kg/hl (45 lb/bu) of fresh cones. About 50 kg of seeds can be obtained from 100 kg (110 lb/220 lb) of fresh cones, and there are 7,300 to 10,000 cones/hl (2,600 to 3,550 cones/bu) (Bonner 1974). For baldcypress, the average number of cleaned seeds per weight determined from 26 samples was 11,500/kg (5,200/lb) with a range of 5,600 to 18,500/kb (2,540 to 8,400/lb). One sample of pondcypress from Florida contained about 9,000 seeds/kg 4,100 seeds/lb) (Bonner 1974). Baldcypress seeds keep well in dry storage at 2 to 5 °C for at least 3 years. Because they appear to be orthodox in storage behavior, longer storage under the same conditions will probably succeed.

Germination. Baldcypress seeds exhibit a moderate amount of dormancy that can be overcome by cold stratification (table 2). For germination testing, moist stratification for 30 days at 3 to 5 °C is recommended, followed by 28 days of testing at alternating temperatures of 20 °C for 16 hours (dark) and 30 °C for 8 hours (light) (ISTA 1993). Studies with collections from the Gulf Coast region suggested that dormancy in both species is regulated by the seedcoat, and any treatment that softens or weakens the coats will increase rate of germination. Soaking for 4 hours in concentrated sulfuric acid was recommended as the easiest treatment (Murphy and Stanley 1975). An alternative method for nursery use has been to soak the seeds in water at 4 °C for 90 days or until ready to plant in the spring. Pondcypress seeds respond well to 60 to 90 days of stratification at 4 °C in peat moss, preceded by a 24- to 48-hour soak in 0.01% citric acid (Bonner 1974). In addition to the test conditions recommended in table 2, tetrazolium staining can be used to determine viability (ISTA 1993).

Nursery practice. Spring-sowing of pretreated seeds and fall-sowing (December) of untreated seeds are both practiced. The latter method has proved successful in northern nurseries. Seeds and cone scales can be broadcast or drilled together and should be covered 6 to 12 mm ($^1/_2$ to $^3/_4$ in) deep with sand, soil, or peat moss. Beds should then be mulched with leaves or other material, especially when fall sowing is used. Shade may be needed in the South from June to September, and beds must always be well watered. The resinous seeds are not eaten to any extent by rodents or birds (Bonner 1974). Germination is epigeal (figure 4). Rooting of cuttings is difficult but possible, as is grafting (Dirr and Heuser 1987).

Figure 4—*Taxodium distichum*, baldcypress: seedling development at 3 and 8 days after germination.

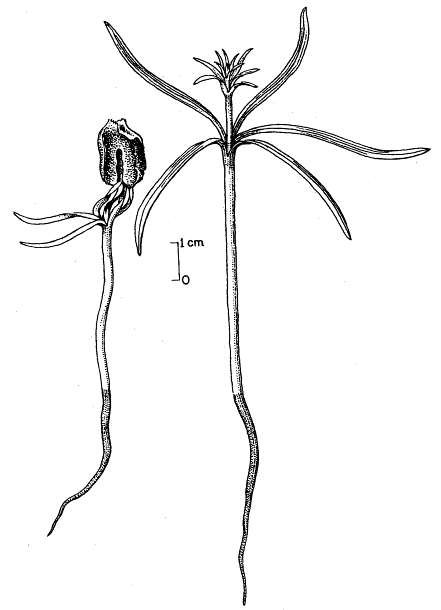


Table 2—*Taxodium,* baldcypress: germination test conditions and results on stratified seedlots

	Germination test conditions				Germinative energy		Germinitive capacity		
	Daily		Temp (°C)						
Species	light (hr)	Medium	Day	Night	Days	(%)	Days	(%)	Samples
T. ascendens	8	Kimpak	30	20	30	76	8	93	4
T. distichum	8	Kimpak	30	20	30	67	17	74	7

Sources: Bonner (1974), ISTA (1996).
Germ = germinitive; percentages are based on full seeds only.

References

Bonner FT. 1974. *Taxodium distichum* (L.) Rich., baldcypress. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 796–798.

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

Faulkner S, Toliver J. 1983. Genetic variation of cones, seed, and nursery-grown seedlings of baldcypress (*Taxodium distichum* (L.) Rich.) provenances. In: Proceedings, 17th Southern Forest Tree Improvement Conference; 1983 June 7–9; Athens, GA. Spons. Pub. 39. Southern Forest Tree Improvement Committee: 281–288.

Hedlin AF, Yates HO III, Tovar DC, Ebel BH, Koerber T, Merkel EP. 1980. Cone and seed insects of North American conifers; North American Forestry Commission, Study Group on Forest Insects and Diseases. Ottawa: Canadian Forestry Service. 122 p.

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

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

Merkel EP. 1984. The baldcypress coneworm, *Dioryctria pygmaeella* Ragonot (Lepidoptera: Pyralidae). In: Yates HO III, ed. Proceedings, Cone and Seed Insects Working Party Conference; Working Party S2-07.01; 1983 July 31–August 6; Athens, GA. Asheville, NC: USDA Forest Service, Southeastern Forest Experiment Station: 85–90.

Murphy JB, Stanley RG. 1975. Increased germination rates of baldcypress and pondcypress seed following treatments affecting the seed coat. Physiologia Plantarum 35: 135–139.

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

Wilhite LP, Toliver JR. 1990. *Taxodium distichum* (L.) Rich., baldcypress. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 563–572.

T

Taxaceae—Yew family

Taxus L.

yew

Nan C. Vance and Paul O. Rudolf

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Growth habit. The yews—members of the genus *Taxus* of the family Taxaceae—are non-resinous evergreen gymnosperms that are widely distributed throughout the moderate zone of the Northern Hemisphere (table 1). They grow primarily in the understory of moist, forested habitats in cool, temperate to subtropical climates (Price 1990). The growth form may be a tree or a shrub. In the understory, the yew's sprawling branchiness and spreading crown enable it to capture light gaps in the canopy. The tree may convert to shrub form if the main shoot is injured or declines and is replaced by lateral branches or new growth. Shrubbiness may also be sustained by frequent browsing. Crowns of these shrubby forms may attain as much as 24 m in diameter (Bugala 1978). The main stem of the yew tree can become quite stout in proportion to its height. Often the large diameter is attained by multiple stems that have fused over time. English yew has reached great age (1,000+ years) and girth, especially those planted in country churchyards (Lewington and Parker 1999).

Cultivated for centuries, the many English yew cultivars show distinct morphological differences in growth form and habit and in needle form and color (Krüssmann 1983). Since the 1920s, cultivars of *T.* × *media* Rehder (a hybrid of English and Japanese yews) have increased the number and variety of these commercially important ornamental shrubs (Chadwick and Keen 1976). The height of most yew species ranges from 6 to 12 m, although open-grown English yew may reach heights of 12 to 25 m and grow extremely thick trunks up to 17 m in girth (Krüssmann 1983; Lewington and Parker 1999). Florida yew is a small, broad tree, about 1 to 5 m in height at maturity (Redmond 1984). Pacific yew trees growing in the wild may reach diameters as large as 6 m and heights up to 18 m under favorable conditions (Bolsinger and Jaramillo 1990). A shrubby form of the

Table 1—*Taxus,* yew: nomenclature and occurrence

Scientific name & synonym(s)	Common name	Occurrence
***T. baccata* L.** *T. baccata* ssp. *eubaccata* Pilger.	**English yew,** common yew	Throughout Europe & Algeria, N Iran & the Himalayas
***T. brevifolia* Nutt.** *T. baccata* ssp. *brevifolia* Pilger.	**Pacific yew**	From SE Alaska S to N California & central Nevada; E to coastal Oregon & Washington to W Montana
***T. canadensis* Marsh.** *T. baccata* ssp. *canadensis* Pilger.	**Canada yew,** eastern yew, ground hemlock	E from Ontario into E Canada, S to Virginia & Tennessee
***T. chinensis* (Pilger.) Rehder** *T. celebica* (Warburg) Li. *T. mairei* S.Y. Hu ex Liu. *T. yunnanensis* Cheng & L.K.Fu.	**Chinese yew,** Maire yew, Yunnan yew	Central & W China from Yunnan to Guangxi
***T. cuspidata* Sieb. & Zucc.** *T. baccata* ssp. *cuspidata* Pilger.	**Japanese yew**	Throughout Japan & in E China
***T. floridana* Nutt. ex Chapman** *T. baccata* ssp. *floridana* Pilger.	**Florida yew**	Along Appalachicola River bluffs in N Florida
***T. globosa* Schltdl.** *T. baccata* ssp. *globosa* Pilger.	**Honduran yew,** Guatemalan yew, Mexican yew	From NE Mexico to Guatemala & El Salvador
***T. wallichiana* Zucc.** *T. baccata* ssp. *wallichiana* Pilger.	**Himalayan yew**	Himalayan Mtns from E Afghanistan & N India, E to Tibet, Burma & the Philippines

Sources: Krüssmann (1983), Rehder (1971), Rudolf (1974), Voliotis (1986).

Pacific yew is common east of the Cascade Divide (Arno and Hammerly 1977).

Occurrence. Eight of the recognized species of yews grow in the United States (Krüssmann 1983; Rehder 1951) (table1). English, Japanese, and Himalayan yews occur in Europe and Asia (Bugala 1978; Voliotis 1986) and Honduran, Florida, Canada, and Pacific yews occur in North America (Little 1971) (table 1). Chinese yew, considered a separate species in Chinese flora, is found in the mountainous regions of China up to about 3,000 m (Lee 1973; Zhang and Jia 1991). *Taxus mairei* (Lemee et Level.) S.Y. Hu & Liu; *T. yunnanensis* Cheng and L.K. Fu; and *T. celebica* (Warburg) Li may also be identified as sub-species or varieties of *T. chinensis* (Krüssmann 1983). Species classification within the genus is disputed and its phylogeny is not well understood (Bugala 1978; Voliotis 1986).

Of the 4 species native to the North American continent, 3 of them—Pacific, Canada, and Florida yews—occur in the United States. Honduran yew ranges from Honduras to southern Mexico. Of the species growing in the United States, Pacific yew has the most widespread range (table 1), and Florida yew, which is confined to the Appalachicola River bluffs in northwest Florida, the most restricted. Although distinct geographic races have not been fully established, allozyme evaluation of 54 Pacific yew populations from 174 geographic areas indicate that Sierra Nevada populations were genetically distinct from Idaho, Montana, and northeast Oregon populations (Doede and others 1993). Six geographic seed zones established by the Oregon State Department of Forestry divide Oregon into north coast, south coast, Willamette valley, south valley, north Cascades, south Cascades; and an elevation band in the Cascades separated at 762 m (Randall 1996).

Use. *Taxus* is the only genus of the yew family of economic importance (Price 1990). For centuries, indigenous people have used yew species in traditional utensils and medicines (Hartzell 1991). North American indigenous people used yew for implements, including bows and dip-net and drum frames, as well as for medicines (Alaback and others 1994). In Europe and Asia, the wood of the tree was once prized for making bows and is still valued for its quality in making fine musical instruments, cabinets, and utensils (Ambasta 1986; Hartzell 1991). Yew has gained additional importance in recent years for a unique class of diterpenoid alkaloids, or taxanes, contained in its needles, bark and seeds (Miller 1980). These taxanes are the source of a chemotherapeutic drug (taxol) used to treat cancer (Rowinsky and others 1990). The fruit-like arils are eaten by birds, and birds and small mammals eat the seeds. Although rabbits (*Sylvilagus* spp.), deer (*Odocoileus* spp.), and elk (*Cervus elaphus*) feed on foliage, leaves, and shoots of the Pacific yew, the European yew is reportedly toxic to horses and cattle but apparently not to white-tailed deer (*O. virginianus*) (Nisley 2002; Smith 1989; Veatch and others 1988).

Flowering and fruiting. Almost all yew species are dioecious; however, Canada yew is monoecious. Nevertheless, a small percentage of unisexual plants have been observed in this species (Allison 1991). Co-sexuality has been reported in Pacific yew—fruits and seeds have been observed on branches of male trees (DiFazio and others 1996; Owens and Simpson 1986). Co-sexuality and sex reversion have also been reported in other taxa (Chadwick and Keen 1976).

Yew flowers are small and solitary and arise from axillary buds. Female buds consist of single ovules surrounded by bracts. Anthesis is indicated by the appearance of the micropylar opening in the exposed ovule, which eventually develops into a seed. Male buds usually cluster along the underside of the previous season's branches. The male flower at anthesis is a stalked, globose head on which are 14 stamens, each with 5 to 9 microsporangia or pollen sacs. The pollen is shed between February and May (table 2). Dry pollen grains are yellow, indented spheroids, lacking sacci; diameters range from 19 to 26 μm (Owens and Simpson 1986).

The fruit, which ripens from late summer through autumn, consists of a scarlet fleshy, cup-like aril (figure 1)

Figure 1—*Taxus canadensis*, Canada yew: fruits.

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bearing a single, hard, ovate seed up to 6 mm long (figures 2 and 3). The mature seed has a greenish brown to brown seedcoat and is filled with white megagametaphyte tissue (rich in lipids) that surrounds a small embryo 1 to 2 mm long. Times of flowering, fruit ripening, and seed dispersal for each species are listed in table 2.

Little information is available on the frequency of good seedcrops among the yews, but most species produce some seeds almost every year (Chadwick and Keen 1976; Harlow and Harrar 1958). Flowering and seed production was found for Pacific yew in western Oregon to be related to overstory openness and tree vigor (DiFazio and others 1997; Pilz 1996a). However, predation of fruit on trees in the open was higher, limiting seed production (DiFazio and others 1998). For Japanese yew, good crops are reported every 6 to 7 years (Rudolf 1974). English yew begins to produce seeds at about 30 years of age (Dallimore and Jackson 1967).

Figure 2—*Taxus*, yew: seeds of *T. baccata*, English yew (**left**); *T. brevifolia*, Pacific yew (**middle**); *T. canadensis*, Canada yew (**right**).

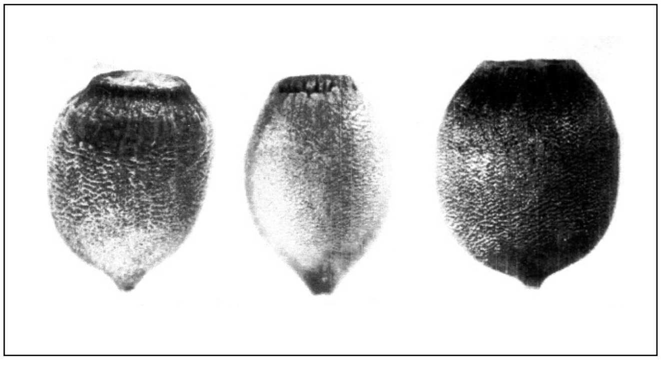
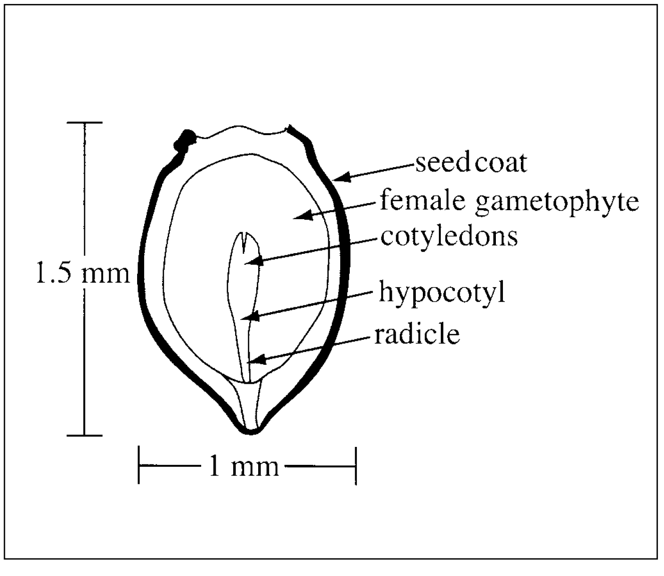


Figure 3—*Taxus canadensis*, Canada yew: longitudinal section through a seed.



Comparable information for the other species is lacking. For dioecious species, good seedcrops are produced where there is a good intermixture of male and female trees. Pollen may limit seed production in some populations of Canada yew where deer browsing has created widely spaced plants that produce little pollen (Allison 1990). Although pollination was found to be limiting, it was not the primary factor limiting seed production in Pacific yew trees examined in western Oregon (DiFazio and others 1998). Yew seeds have been found to survive in a soil seedbank for several years (Minore and others 1996). Although seeds will germinate under mature overstories in canopy gaps, seedlings may be abundant following disturbance such as burning and overstory removal. However, Crawford (1983) noted that, in Idaho, most abundant yew seedlings were found growing in forest litter and decaying wood.

Collection of fruits. The maturation of seeds and ripening of arils (full expansion and orange-red coloration) may occur over a span of months. Over this time, losses to birds and small mammals such as chipmunks (*Eutamia*s spp.) can be considerable (DiFazio 1995). To prevent losses to predation, yew fruits should be picked frequently from the branches, beginning when individual fruits first ripen. To ensure that adequate amounts of seeds are collected in specific seed collection areas, bagging branches of desirable trees well before fruit ripens is recommended so that fruits are not lost or destroyed by squirrels (*Citellus* spp.) and other predators (DiFazio and others 1998). If returning repeatedly to individual trees is impractical, harvesters can bag branches in July with light-weight mesh bags and then collect the fruits in late fall.

Randall (1996), when collecting seeds in Oregon and Washington, noted differences in phenology in nursery-grown yews from seeds collected in the coastal range and the Cascades. Seed zones that have been identified should be used for collecting; ideally seeds should be collected from the approximate area where the yew trees will be grown.

Extraction and cleaning. Seeds should be extracted from the fruit shortly after harvest (storage with fruit promotes mold) by macerating the fleshy arils in water. A blender with the blades covered by rubber tubing (Munson 1986) and set at low speed will efficiently and quickly separate seeds from arils without damaging seeds. Light, unfilled seeds float to the top and can be easily removed. In some species, the membranous outer seedcoat is partially destroyed during extraction; in others, it remains tightly fixed to the bony inner coat. After extraction, excess moisture should be dried from seeds. Seeds can then be weighed, sown, cold-stored, or stratified as soon as possible. The number of cleaned seeds per weight is listed in table 3. Purity of seedlots generally ranges from 96 to 100%, and soundness, from 78 to 99% (Rudolf 1974).

Storage. Yew seeds are orthodox in storage characteristics and, if kept at low moisture content, may be successfully stored frozen for years without losing viability. The viability of yew seeds can be maintained for 5 or 6 years if they are dried just after extraction at room temperature for 1 or 2 weeks and then stored in sealed containers at 1 to 2 °C (Heit 1967). If seeds are dried to 15 to 25% relative humidity (moisture content of 2 to 3%), seedlot viability of greater than 90% can be maintained for weeks at 25 °C. Pacific yew seeds have a high lipid content (mega gametophyte lipid content is about 71% of the dry mass); therefore, long-term storage conditions should maintain seeds at 14% relative humidity and subzero temperatures (Walters-Vertucci and others 1996). Analysis of seeds for cryopreservation indicates that they can be stored at –18 to –20 °C without losing viability, provided that they have reached sufficient maturity, and that they probably will remain viable for decades under these conditions (Walters-Vertucci and others 1996). Yew seeds can be held for several months in cold stratification without losing viability. Reasonably good viability of English yew seeds was maintained for up to 4 years by storing them in moist sand or acid peat at low temperatures (Rudolf 1974).

Pregermination treatments. Yew seeds are slow to germinate; natural germination usually does not take place until the second spring after seedfall (Suszka 1978). Viable seeds of Pacific yew have been found in soil seedbanks for several years (Minore 1994). Although a variety of birds and small mammals eat, digest, and disperse yew seeds (Bartkowiak 1978), germination does not appear to be hastened by their passing through the alimentary canal of birds. Yew seeds have a strong but variable dormancy that can be broken by warm-plus-cold stratification (Suszka 1978). One recommendation is to hold the seeds for 150 to 210 days at 16 to 18 °C, then for 60 to 120 days at 2 to 5 °C (Heit 1967, 1969). The ISTA rules specify prechilling yew seeds for 270 days at 3 to 5 °C. Steinfeld (1993a) reported on 2 groups of seeds collected in the fall in Oregon that were stratified during the fall and winter. One group was chilled for 1 month and the other was kept at warm temperatures for 5 months and then chilled for 2 months. The seeds were sown in bareroot beds covered with mulch the following spring.

Table 2—*Taxus*, yew: phenology of flowering and fruiting

Species	Location	Flowering	Fruit & seed ripening	Seed dispersal
T. baccata	W Europe	Mar–May	Aug–Oct	Aug–Oct
T. brevifolia	Washington & Oregon	Mar–May	July–Oct	July–Oct
T. canadensis	Minnesota & Wisconsin	Apr	Aug–Sept	Aug–Sept
T. cuspidata	Japan	Apr–June	Sept–Oct	Oct
T. floridana	NW Florida	Jan–Mar	Aug–Oct	Aug–Oct

Sources: Allison (1990), Chadwick and Keen (1976), Redmond (1984).

Table 3—*Taxus*, yew: seed yield data

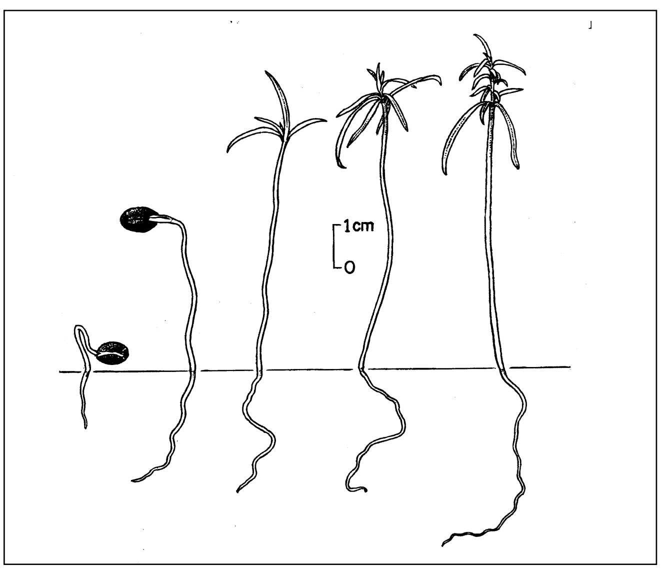
		Cleaned seeds/weight				
		Range		Average		
Species	Place collected	/kg	/lb	/kg	/lb	Samples
T. baccata	Western Europe	13,900–18,000	6,300–8,200	17,000	7,700	14
	NE US	13,200–15,000	6,000–6,800	14,100	6,400	3
T. brevifolia	Carson & Skamania Cos., Washington	32,400–36,200	14,700–16,500	33,100	15,000	2
	S Cascades, Oregon	23,800–25,900	10,800–11,800	24,950	11,300	10
	Central Cascades, Oregon	26,330–39,950	12,000–18,200	31,077	14,100	4
T. canadensis	Upper mid-West	33,000–62,400	15,000–28,400	46,300	21,000	4
	Minnesota & Wisconsin	35,700–38,460	16,200–17,500	37,000	16,800	
T. cuspidata	Japan	24,700–43,000	11,200–19,500	31,300	14,200	7
	NE US	14,840–19,300	6,700–8,800	16,300	7,400	3

Sources: Allison (1995), Heit (1969), Rudolf (1974), Vance (1993), Yatoh (1957).

Germination was negligible for the cold-treated seeds and about 5% for the warm/cold-treated seeds; however, in the following spring, the germination rate of the remaining seeds combined with that of the previous spring exceeded 95%. No difference in total germination between the 2 treatment groups was detected by the second year.

Germination and seed viability tests. Germination of yew seeds is epigeal (figure 4). Because of the deep dormancy of the seeds, germination will be sporadic over the course of several years. Germination percentages after the first year do not indicate the potential of the seeds to germinate, for germination will continue in the following year (Heit 1969; Pilz 1996b). Official testing rules recommend tetrazolium staining as the first choice in testing, followed by germination in sand at 30 °C for 28 days after 270 days of stratification (ISTA 1993). Cutting tests are also recommended for rapid viability checks. After a seed is carefully split in half with sharp knife or scalpel, the embryo and megagametophyte tissue can be examined. If an embryo is opaque and developed, with visible cotyledon buds, and gametophyte tissue is white and fills the seed cavity, the seed should be considered mature and viable. A tetrazolium test for viability requires cutting seeds to expose tissue, staining for about 24 to 48 hours, then cutting out the embryos. A seed is considered viable if all of the embryo and endosperm is stained (Edwards 1987). Removing embryos from Pacific yew seeds and culturing them on nutrient medium with an energy source such as 2% sucrose has resulted in germination of 70 to 100%. Cleaned, mature seeds showed high germination whether seeds were fresh, cold stored, or stratified (Vance 1995). Embryo germination was shown to improve with a 14-hour photoperiod and up to 50 days of cold treatment in *in vitro* germination tests of embryos from English and Japanese yews (Flores and others 1993). Test results for 3 species are given in table 4.

Figure 4—*Taxus baccata*, English yew: seedling development 1, 8, 12, 22, and 39 days after germination.



Nursery practices. Freshly collected yew seeds can be sown in late summer or early fall of the year of collection, whereas stratified seeds can be sown in the spring of the year following collection. The seeds should be covered with about 1 to 2 cm (.4 to .8 in) of soil, and mulching the seedbed is beneficial (Steinfeld 1993a). Beds should be shaded during the summer. Even with these treatments many seeds often will not germinate until the second spring (Heit 1969; Steinfeld 1993a). Seedlings should be shaded after they emerge the first spring and summer. Rabbits have been observed feeding on Pacific yew seedlings in the bareroot beds at the USDA Forest Service's J. Herbert Stone Nursery at Central Point, Oregon (Steinfeld 1993b). Birds eat seeds, and germinants may be susceptible to damping-off fungi (*Fusarium* spp.). Although most ornamental yews are propagated by cuttings, seedlings of the Japanese yew cultivar 'Capitata' are germinated from seeds after 3 months of warm stratification (20 °C) followed by 4 months at 5 °C (Hartmann and others 1990). Seedlings are grown 2 to 3 years in seedbeds in a poly house, followed by 2 to 3 more years in liner beds, then 3 or 4 years in a nursery field

Table 4—*Taxus*, yew: stratification periods, germination test conditions, and results

	Germination test conditions					Germinative capacity		
	Stratification (days)		Temp (°C)			Avg	Range	
Species	Warm	Cold	Day	Night	Days	(%)	(%)	Samples
T. baccata	—	—	16	10	—	67	47–70	12
	120	365	10–16	10–16	60	47	—	1
T. brevifolia	—	—	30	20	60	55	50–99	3
T. cuspidata	120	365	10–16	10–16	60	68	—	1

Source: Rudolf (1974).

before they are of salable size (Hartmann and others 1990; Shugert 1994). In the first 3 years, 55% shade is used from mid-June until November to reduce stress (Shugert 1994). Young yew plants are susceptible to root weevils. Commercial preparation of nematodes that are effective against weevil larvae can be applied in early spring when soil temperatures reach 7 °C.

All yew species can be successfully propagated by rooting cuttings, and most commercial cultivars are produced this way. Successful stecklings from Pacific, Canada, Florida, and Honduran yews were obtained by rooting cuttings in a greenhouse under shaded conditions, on benches that had bottom heat of about 21 °C, an overhead mist system to maintain high humidity, and cool air temperatures (Hartmann and others 1990; Suszka 1978). On 1- to 2-year-old stems, from healthy branch tips, cuttings should be clipped at an angle and needles removed from the clipped end. Cutting length varies depending on the branch but may range from 10 to 20 cm (Chadwick and Keen 1976). The clipped tip should be dipped in a solution containing a root-promoting compound such as indole B-indolebutyric acid (IBA) or a-naphthalenacetic acid (NAA) and a fungicide, then stuck to a depth of about 3 cm (1.2 in) in rooting medium. Using 5,000 to 10,000 ppm of IBA dissolved in 50% ethanol and dipping cuttings quickly achieves satisfactory rooting (Hartmann and others 1990). The medium should hold the cuttings, maintain a high moisture content, and be well drained. A mixture of sphagnum peat moss, coarse vermiculite, and perlite or sand will enhance rootability and promote a desirable root system (Copes 1977). If Pacific yew cuttings are stuck in the winter, rooting may begin to occur within 4 to 6 weeks, depending upon species and cultivar but may also take up to 3 or more months. Rooting ability varies widely by clone or cultivar and by the time of year that yews are propagated. Clonally propagated plants should only be used where genetic selection for desired traits is needed in a cultivated setting. Seedlings are preferred over rooted cuttings for reforestation because they have genetic variation that more nearly approximates that of wild populations.

References

Alaback P, Antos J, Goward T, Lertzman K, MacKinnon A, Pojar J, Pojar R, Reed A, Turner N, Vitt D. 1994. Plants of the Pacific Northwest Coast. Redmond, WA: Lone Pine Publishing. 527 p.

Allison TD. 1990. Pollen production and plant density affect pollination and seed production in *Taxus canadensis*. Ecology 7(2): 516–522.

Allison TD. 1991. Variation in sex expression in Canada yew (*Taxus canadensis*). American Journal of Botany 78(4): 569–578.

Allison TD. 1995. Personal communication. Bethesda, MD: National Science Foundation.

Ambasta SP. 1986. The useful plants of India. New Delhi: Council of Scientific and Industrial Research, Publications and Information Directorate. 622 p.

Arno SF, Hammerly RP. 1977. Northwest trees. Seattle, WA: The Mountaineers. 222 p.

Bolsinger CL, Jaramillo AE. 1990. *Taxus brevifolia* Nutt., Pacific yew In: Burns RM, Honkala BH, tech. coord. Silvics of North America. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 573–579.

Bugala W. 1978. Systematics and variability. In: Bialobok S, ed. The yew: *Taxus baccata* L. [Markiewicz H, trans.]. Nasze Lesne, Warsaw: National Center for Scientific, Technical and Economic Information Service. 149 p.

Chadwick LC, Keen RA. 1976. A study of the genus *Taxus*. Res. Bull. 1086. Wooster, OH: Ohio Agricultural Research and Development Center. 56 p.

Copes DL. 1977. Influence of rooting media on root structure and rooting percentage of Douglas-fir cuttings. Silvae Genetica 26: 102–106.

Crawford, R. 1983. Pacific yew community ecology in north-central Idaho with implications to forest land management [PhD thesis]. Moscow, ID: University of Idaho. 109 p.

Dallimore W, Jackson AB. 1967. A handbook of Coniferae and Ginkgoaceae. 4th ed. 4 [rev. by SG Harrison]. New York: St. Martin's Press. 729 p.

DiFazio, SP, Wilson MV, Vance, NC. 1996. Variation in sex expression of *Taxus brevifolia* in western Oregon. Canadian Journal of Botany 74: 1943–1946.

DiFazio SP, Vance NC, Wilson MV. 1997. Strobilius production and growth of Pacific yew under a range of overstory conditions in western Oregon. Canadian Journal of Forest Research 27: 986–993.

DiFazio SP, Wilson MV, Vance NC. 1998. Factors limiting seed production in *Taxus brevifolia* (Taxaceae) in western Oregon. American Journal of Botany 85: 910–918.

Doede DL, Carroll E, Westfall R, Miller R, Kitzmiller JH, Snader KM. 1993. Geographic variation in allozymes and taxol, and propagation by rooted cuttings in Pacific yew. In: Temple CR, ed. International Yew Resources Conference Extended Abstracts; 1993 March 12–13. Berkeley, CA: University of California: 10–11.

Edwards DGW. 1987. Methods and procedures for testing tree seeds in Canada. For. Tech. Rep. 36. Ottawa: Canadian Forestry Service. 31 p.

Flores T, Wagner LJ, Flores HE. 1993. Embryo culture and taxane production in *Taxus* spp. In Vitro Cellular and Developmental Biology Plant 29: 160–165.

Harlow WM, Harrar ES. 1958. Textbook of dendrology. 4th ed. New York: McGraw-Hill. 561 p.

Harmann HT, Kester DE, Davies FT, Jr. 1990. Plant propagation principles and practices. 5th ed. Englewood Cliffs, NJ: Regents/Prentice-Hall. 647 p.

Hartzell H. 1991. The yew tree. Eugene, OR: Hulogosi Press. 319 p.

Heit CE. 1967. Propagation from seed, part 10: storage methods for conifer seeds. American Nurseryman 126(8): 14–15, 38–54.

Heit CE. 1969. Propagation from seed: 18. Testing and growing seeds of popular *Taxus* forms. American Nurseryman 179(2): 10–11, 118–128.

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

Krüssmann G. 1983. Manual of cultivated conifers. 2nd rev. ed. Berlin: Verlag Paul Parey. 361 p.

Lee S. 1973. Forest botany of China, supplement. November 30, 1973: 1–2.

Lewington A, Parker E. 1999. Ancient trees: trees that live for 1000 years. London: Collins and Brown: 66–76.

Little EL Jr. 1971. Atlas of United States trees. Volume 1, Conifers and important hardwoods. Misc. Pub. 1146. Washington, DC: USDA Forest Service. 9 p. + 200 maps.

Miller RW 1980. A brief survey of *Taxus* alkaloids and other taxane derivatives. Journal of Natural Products 43: 425–437.

Minore D, Weatherly HG, Cartmill M. 1996. Seeds, seedlings, and growth of Pacific yew (*Taxus brevifolia*). Northwest Science 70: 223–229.

Nisley RG. 2002. Personal observation. Avon, CT: USDA Forest Service, Northeastern Research Station.

Owens JN, Simpson S. 1986. Pollen from conifers native to British Columbia. Canadian Journal of Forest Research 16: 955–967.

Pilz D. 1996a. Propagation of Pacific yews from seed: Part 1. American Conifer Society Bulletin 13(1): 13–19.

Pilz D. 1996b. Propagation of Pacific yews from seed: Part 2. American Conifer Society Bulletin 13(2): 80–83.
Price RA. 1990. The genera of Taxaceae in the southeastern United States. Journal of the Arnold Arboretum 71: 69–91.
Randall WK. 1996. Forest tree seed zones for western Oregon. Salem: Oregon Department of Forestry. 82 p.
Redmond AM. 1984. Population ecology of *Taxus floridana* (Nutt.), a dioecious, understory tree [MS thesis]. Gainsville: Florida State University. 61 p.
Rehder A. 1951. Manual of cultivated trees and shrubs. New York: Macmillan.
Rowinsy EK, Cazenave LA, Donehower RC. 1990. Taxol: a novel investigational antimicrotubule agent: review. Journal of the National Cancer Institute 82: 1247–1259.
Rudolf PO. 1974. *Taxus* L., yew. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 799–802.
Shugert R. 1994. Sexual propagation of *Taxus cuspidata* 'Capitata'. Grand Haven, MI: Comb. Proceedings of the International Plant Propagation Society; 1990; 43: 467–468.
Smith RA. 1989. Comments on diagnosis of intoxication due to *Taxus*. Veterinary and Human Toxicology 31: 177.
Steinfeld D. 1993a. Early lessons from propagating Pacific yew. In: Proceedings, Western Forest Nursery Association Meeting; 1992 September 14–18; Fallen Lake, CA. Gen. Tech. Rep. RM-221. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: 92–94.
Steinfeld D. 1993b. Personal communication. Central Point, OR: USDA Forest Service, JH Stone Nursery.
Suszka B. 1978. Generative and vegetative reproduction In: Bialobok LS, ed.; Markiewicz H, trans. The yew: *Taxus baccata*. Washington, DC: USDC National Technical Information Service, PB-280 758-T: 87–102.
Vance NC. 1993. Unpublished observations. Corvallis, OR: USDA Forest Service, Pacific Northwest Research Station.
Veatch JK, Reid FM, Kennedy GA. 1988. Differentiating yew poisoning from other toxicoses. Veterinary Medicine 83: 298–300.
Voliotis D. 1986. Historical and environmental significance of the yew (*Taxus baccata* L.). Israel Journal of Botany 35: 47–52.
Walters-Vertucci C, Crane J, Vance NC. 1996. Physiological aspects of *Taxus brevifolia* (Nutt.) seeds in relation to seed storage characteristics. Physiologia Plantarum. 98: 1–12.
Yatoh KI. 1957. Conifers of the Kii Peninsula (IV). Mie University Fac[ulty] Agric[ulture] B(TSu) 14:111-120.
Zhang Z, Jia Z. 1991. Taxanes from *Taxus chinensis*. Phytochemistry 30: 2345–2348.

Verbenaceae—Verbena family

Tectona grandis L. f.

teak

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Growth habit, occurrence, and use. Native to Southeast Asia in India, Myamar (Burma), Thailand, and Indochina, teak is the only important species of the 3 in the genus *Tectona* (Schubert 1974). It is a large deciduous tree that reaches maximum heights of 30 to 40 m. It grows best in warm, moist tropical climates with 1,250 to 3,000 mm of mean annual precipitation and a marked dry season of 3 to 6 months (Webb and others 1984). Teak has probably been cultivated for centuries in Asia and has been planted for timber production in India and Burma since at least 1840 (Troup 1921). In the Western Hemisphere, teak has been planted since about 1900, beginning in the Caribbean region (Marshall 1929; Moldenke 1935). Because it is a tropical species, in the continental United States, it grows successfully only in southern Florida. Adaptability trials have been successful in Hawaii (Whitesell and Walters 1976). About 130 ha of teak plantations have been established in Puerto Rico and the U.S. Virgin Islands (Weaver 1993). Teak wood is famous the world over for its strength, durability, dimensional stability, working qualities, and the fact that it does not cause corrosion when in contact with metal (Kukachka 1970; Troup 1921). It is currently used for shipbuilding, fine furniture, trim, decorative objects, veneer for decorative plywood, posts, poles, and fuel (Kukachka 1970; Webb and others 1984).

Geographical races of teak have been distinguished by differences in stem form and rate of growth (Champion 1933). These are not recognized botanically even as varieties, but it is most important when establishing plantations to use seeds from a race that will grow well under local conditions (Beard 1943; Champion 1933; Laurie 1938). In Trinidad, trees grown from seeds of Burmese origin have been more satisfactory than those grown from seeds of Indian origin (Beard 1943).

Flowering and fruiting. The small white, perfect flowers of teak are borne on short pedicels, in large erect terminal panicles, about 2 months after the dry season has ended and the large obovate leaves have emerged. The dates vary somewhat depending on the climatic regime, but flowering generally takes place for several months between June and September, and the fruits ripen 2 $^1/_2$ to 3 months later (Chable 1969; Mahapol 1954; Troup 1921; White and Cameron nd). The fruits gradually fall to the ground during the following dry season. The fruit consists of a subglobose, 4-lobed, hard bony stone about 1.2 cm in diameter, surrounded by a thick felty, light brown covering (figure 1), the whole enclosed in an inflated bladder-like papery involucre. The stone (often called a nut) contains 1 to 3, rarely 4, seeds (figure 2) and has a central cavity, giving the appearance of a fifth cell. Schubert (1974) found that the average number of seeds per stone was 1.7. In a survey of the fruits from 23 provenances in India, an average of 51% of the fruits were found to have no seeds, 35% had 1 seed, 12% had 2 seeds, 2% had 3 seeds, and 0.4% had 4 seeds per fruit (Gupta and Kumar 1976).

Figure 1—*Tectona grandis*, teak: (**top**) and side (**bottom**) views of fruits with their bladder-like involucres removed.

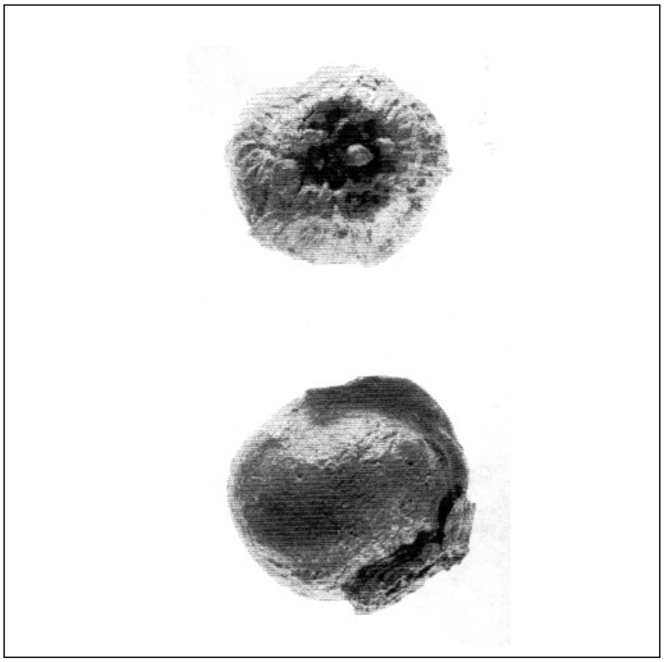

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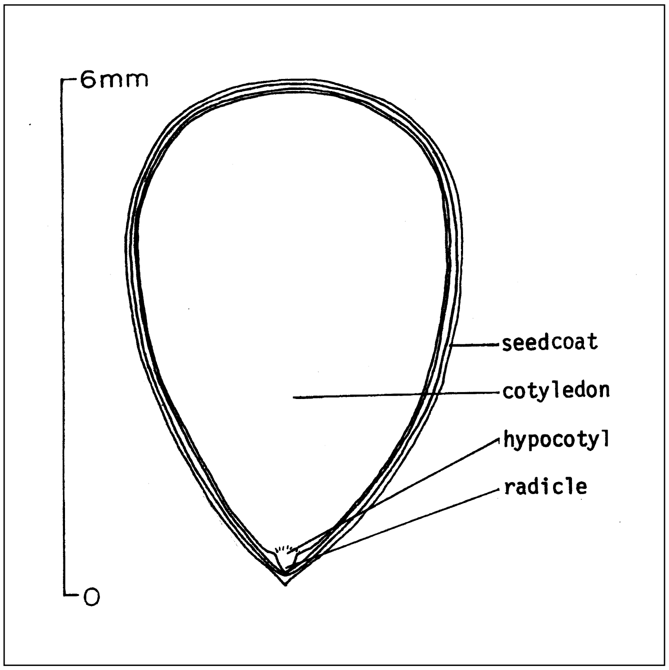
Figure 2—*Tectona grandis*, teak: longitudinal section through a seed.



Collection, extraction, and storage. Teak has borne viable seeds when only 3 years old (Schubert 1974), and good seedcrops are produced by plantations less than 20 years old (Troup 1921). The bladder-like involucre turns from green to brown when the seeds are ripe. The fruits can be swept up from the ground beneath the trees as they fall or else clipped with pruning poles or shaken from the branches. Drying can be completed by spreading the fruits on racks in the sun. For convenience in handling and storage, the involucre can be removed in a mechanical dehusker or by working a cloth bag half-filled with dried fruits against the ground with a foot and then winnowing to separate the fruits from the chaff. Teak fruits in Honduras average 705/kg (320/lb) with the involucres intact and 880/kg (400/lb) with the involucres removed (Chable 1969). In other parts of the world, the number of clean fruits per weight varies from a low of 880 to a high of 3,070/kg (400 to 1,400/lb) (Champion and Brasnett 1958; Parry 1956). The seeds make up about 3% of the weight of the cleaned fruits (Dabral 1976). Teak seeds are true orthodox in storage behavior and keep best at low temperatures and moisture contents. Keiding (1985) reported that seeds stored at 0 to 4 °C and about 12% moisture for 7 years lost no viability. Seeds from fruits stored in sacks in dry warehouses retained their viability for about 2 years (Kushalappa 1977). Longer periods of storage have not been needed in most areas because teak produces good seedcrops almost every year (Mahapol 1954; Troup 1921).

Germination tests. Cut tests of fruits on 56 collections from across the range of teak revealed a potential mean viability of 71% and ranged from 40 to 96% (Danish/FAO Forest Tree Seed Centre 1973). Laboratory germination tests should be carried out in sand at a constant 30 °C for 28 days. Pretreatment to stimulate germination should be 6 repetitions of soaking the fruits in water, followed by 3 days of drying (ISTA 1993). Germination in nursery beds in various parts of the world has varied from 0 to 96% in periods varying from 10 days to 3 months. Seeds extracted from the fruits and treated with fungicide gave a germination of 54% in 12 days (Dabral 1976). Because it is difficult to extract teak seeds from their fruits and untreated teak fruits give protracted, often low and unpredictable germination, some pre-treatment is usually applied to fruits. Various pretreatments to hasten or improve germination have been used. Soaking the fruits in water for several days, or alternate wetting and drying as in laboratory testing, have proven effective (Schubert 1959; Troup 1921; White and Cameron nd). In one test, clean fruits were pretreated by 5 cycles of alternate soaking in water for 24 hours and drying in the sun for 48 hours and then sown. Germination began 18 days after sowing and continued to increase for 15 days, after which it gradually decreased. Germination 68 days after sowing was 61% of the total number of fruits sown (Schubert 1974). Weathering of the epicarp and mesocarp aids germination. Seeds inoculated with *Scytalidium* sp. (a cellulolytic fungus isolated from teak litter), 0 and kept moist for 21 days had 96% germination compared to 20% for uninoculated control (Dadwal and Jamaluddin 1988). Increases in germination of 5 to 12% over controls (21% germination) were obtained with treatments of IAA and GA alone and in combination at various concentrations (Uanikrishnan and Rajeeve 1990). A novel method reported from Thailand is to expose the fruits to ants for 1 to 2 weeks: they attack and remove the felty covering and thus speed up germination without loss of viability (Bryndum 1966). Soaking fruits from 11 Indian provenances in a nutrient solution resulted in a higher seedling yield (34%) than control (18%), water soak (30%) or scarification (28%). It is felt that nutrient deficiencies in some of the sources resulted in lower germination or early seedling failure (Gupta and Pattanath 1975). A temperature of 30 °C appears to be optimal for germinating teak seeds (Dabral 1976). Some seeds that were stored for several months germinated better than fresh seeds (Champion and Brasnett 1958; Mahapol 1954; Troup 1921), probably because seeds need a period of after-ripening (Coster 1933). Because they tend to have a greater number of seeds per fruit, larger fruits yield a significantly higher number of seedlings per fruit. It is recommended that fruits smaller than 14 mm in diameter be culled (Banik 1977). Seeds from dry regions frequently are more difficult to germinate (Troup 1921). Germination is epigeal (Troup 1921).

Nursery practice. Teak fruits are usually broadcast in nurserybeds and covered with 1.2 to 2.5 cm ($^1/_2$ to 1 in) of sand, soil, or sawdust (Schubert 1956; White and Cameron nd). A seedling yield of about 25% can be expected from good seedlots (White and Cameron nd). The beds should be watered just enough to keep them moist. Once the seedlings have become established, watering should gradually be reduced. Field planting is generally done with "stump" plants (seedlings with the tops removed) or potted plants grown in plastic nursery bags. The stump plants are grown in the nursery until they reach 1.2 to 2.5 cm ($^1/_2$ to 1 in) in diameter at the root collar; then they are top-pruned to about 2.5 cm (1 in) and root-pruned to 18 or 20 cm (7.0 to 7.9 in) in length (Schubert 1956; White and Cameron nd). Ideally, plants of suitable size can be grown in 6 to 9 months. In Thailand (Kushalappa 1977) and India (Gupta and Pattanath 1975) at least some nurseries undercut the beds and remove seedlings large enough for stump plants after 1 year and allow the rest to grow another year when the whole bed is harvested. Sowing of the nurserybeds should be timed so that the proper size is reached in time for planting at the start of the rainy season. Another approach is to harvest in the dry season and store the dormant stumps in beds of dry sand for 3 months before planting at the start of the wet season (Kushalappa 1977). Direct seeding into prepared seed spots is practiced, but early growth is slow and often high mortality results (Weaver 1993). Teak can also be reproduced by coppicing, because cut stumps produce very vigorous sprouts.

References

Banik RL. 1977. Studies on grading of teak fruits: 1. Fruit size is a factor in germination of teak seeds. Bano Biggyan Patrika 6(1): 1–7.

Beard JS. 1943. The importance of race in teak, *Tectona grandis* L. Caribbean Forester 4(3): 135–139.

Bryndum K. 1966. The germination of teak. Bulletin of the Natural History Society of Siam (Thailand) 21: 75–86.

Chable AC. 1969. Reforestation in the Republic of Honduras, Central America. Ceiba 13(2): 1–56.

Champion HG. 1933. The importance of the origin of seed used in forestry. Indian Forest Records 17(5): 1–76.

Champion HG, Brasnett NV. 1958. Choice of tree species. For. Dev. Pap. 13. Rome: FAO. 307 p.

Dabral SL. 1976. Extraction of teak seeds from fruits, their storage and germination. Indian Forester 102(10): 650–658.

Dadwal VS, Jamaluddin. 1988. Role of fungi in weathering of teak fruits. Indian Forester 114(6): 328–330.

Danish/FAO Forest Tree Seed Centre. 1973. Provenance collections of teak. For. Occ. Pap. 1973/2. Rome: FAO: 54–61.

Gupta BN, Kumar A. 1976. Estimation of potential germination of teak (*Tectona grandis* L.f.) fruits from twenty three Indian sources by cutting test. Indian Forester 102(11): 808–813.

Gupta BN, Pattanath PG. 1975. Factors affecting germination behavior of teak seeds of eighteen Indian origins. Indian Forester 101(10): 584–588.

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

Keiding H. 1985. Teak, *Tectona grandis*, Linn. f. Seed Leaflet 4. Humlebaek, Denmark: DANIDA Forest Seed Centre. 21 p.

Kukachka BF. 1970. Properties of imported tropical woods. Res. Pap. FPL-125. Madison, WI: USDA Forest Service, Forest Products Laboratory. 68 p.

Kushalappa KA. 1977. Teak plantations in Thailand. Indian Forester 103(5): 323–328.

Laurie MV. 1938. Branching and seed origin in Coorg teak plantations. Indian Forester 64(10): 596–600.

Mahapol S. 1954. Teak in Thailand. R-16. Bangkok: Ministry of Agricultural Research, Forest Department. 31 p.

Marshall RC. 1929. Growing teak in Trinidad. Tropical Woods 19: 1–3.

Moldenke HN. 1935. A monograph of the genus *Tectona* as it occurs in America and in cultivation. Phytologia 1(4): 154–164.

Parry MS. 1956. Tree planting practices in tropical Africa. For. Dev. Pap. 5. Rome: FAO. 302 p.

Schubert TH. 1974. *Tectona grandis*, teak. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 803–804.

Troup RS. 1921. Silviculture of Indian trees. Volume 2. Oxford, UK: Clarendon Press: 337–783.

Uanikrishnan K, Rajeeve KP. 1990. On germination of Indian teak (*Tectona grandis* L.f.). Indian Forester 102(10): 650–658.

Weaver PL. 1993. *Tectona grandis* L.f., teak. Res. Note SO-ITF-SM-64. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 18 p.

Webb DB, Wood PJ, Smith JP, Henman GS. 1984. A guide to species selection for tropical and sub-tropical plantations. Trop. For. Pap. 15. Oxford, UK: Oxford University, Commonwealth Forestry Institute, Unit of Tropical Silviculture. 256 p.

White KJ, Cameron AL. [no date] Silvicultural techniques in Papua and New Guinea forest plantations. Bull. 1. Port Moresby, Territory of Papua and New Guinea: Division of Silviculture, Department of Forests. 99 p.

Whitesell CD, Walters GA. 1976. Species adaptability trials for man-made forests in Hawaii. Res. Pap. PSW-118. Berkeley, CA: USDA Forest Service, Pacific Southwest Forest and Range Experiment Station. 30 p.

T

Asteraceae—Aster family

Tetradymia DC.

horsebrush

Lee E. Eddleman

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Growth habit, occurrence and use. *Tetradymia* (horsebrush) is a rather low-growing, multi-branched unarmed or spiny shrub, found either as well-scattered individuals or as small colonies mixed in with other vegetation. Some species may reach heights of 2 to 2.5 m but they are more commonly 1 m or less. Reproduction is from wind-dispersed seeds and from sprouting of root crowns and rhizomes in longspine horsebrush, hairy horsebrush, spiny horsebrush, and cotton horsebrush (Hartman 1984; McArthur and others 1979; Mozingo 1987; Strother 1974). Eight species (table 1) are found, primarily in the intermountain region and its fringe areas, and 2 species are found in southern California and Baja California (McArthur and others 1979; Strother 1974). Elevational range is from 800 to 2,400 m, although the southern California species range downward to 300 m. Horsebrush is commonly associated with the sagebrush vegetation type, but the genus has widespread occurrence from barren slopes and alkaline plains upward into the piñyon–juniper and yellow pine types.

Horsebrush provides ground cover and soil stability. It is generally considered of low forage value, although buds and new leaders are consumed by cattle, sheep, goats, antelope (*Antilocapra americana*), and mule deer (*Odocoileus hemionus*) (McArthur and others 1979). Most species are

Table 1—*Tetradymia,* horsebrush: nomenclature and occurrence

Scientific name & synonym(s)	Common name	Occurrence
***T. argyraea* Munz & Roos**	**striped horsebrush,** striped cottonthorn	Mountains of E Riverside & San Bernadino Cos., California
***T. axillaris* A. Nels.** *T.a.* var. *axillaris* *T.a.* var. *longispina* (M. E. Jones) Strother	**longspine horsebrush**	S Nevada into Inyo Co., California; S California
***T. canescens* DC.** *T. inermis* Nutt.; *T. multicaulis* A. Nels. *T. linearis* Rydb.	**gray horsebrush,** spineless horsebrush, common horsebrush	S British Columbia to S California E of Cascades–Sierra Nevada and from S Saskatchewan to N Arizona
***T. comosa* Gray**	**hairy horsebrush**	SW California to N Baja California
***T. filifolia* Greene**	**threadleaf horsebrush**	Central New Mexico
***T. glabrata* Torr. & Gray**	**smooth horsebrush,** littleleaf horsebrush	Great Basin, SE Oregon & SW Idaho, Utah, Nevada, to S California, mostly E of Sierra Nevada
***T. nuttallii* Torr. & Gray** *T. spinosa* Nutt. x *T. permixta* Payson	**Nuttall horsebrush**	SE Wyoming across central & N Utah to NE Nevada
***T. spinosa* Hook. & Arn.** *Lagothamnus ambiguus* Nutt. *L. microphyllus* Nutt.	**spiny horsebrush,** cottonthorn horsebrush, catclaw horsebrush, shortspine horsebrush, thorny horsebrush	SE Oregon, S Idaho, SW Montana S across W Wyoming & and Colorado, NW Arizona, W to Sierra Nevada
***T. stenolepis* Greene**	**Mojave horsebrush**	S California to extreme S tip of Nevada
***T. tetrameres* (Blake) Strother** *T. comosa* Gray ssp. *tetrameres* Blake	**cotton horsebrush,** four-part horsebrush, dune horsebrush	Central N Nevada SW to Mono Co., California

Sources: Cronquest (1994), McArthur and others (1979), Mozingo (1987), Strother (1974).

poisonous to sheep, especially smooth horsebrush (Johnson 1974; Kingsbury 1964). Flowers are used by small moths, bees, flies, and beetles (McArthur and others 1979). Gelechiid moths form galls in leaves and stems (Hartman 1984). Smooth horsebrush is considered ideal for desert landscaping because its leaves develop early and are dropped by mid-summer (Mozingo 1987). Late-season flowering species of horsebrush provide an attractive contrast to the vegetation types of dry areas.

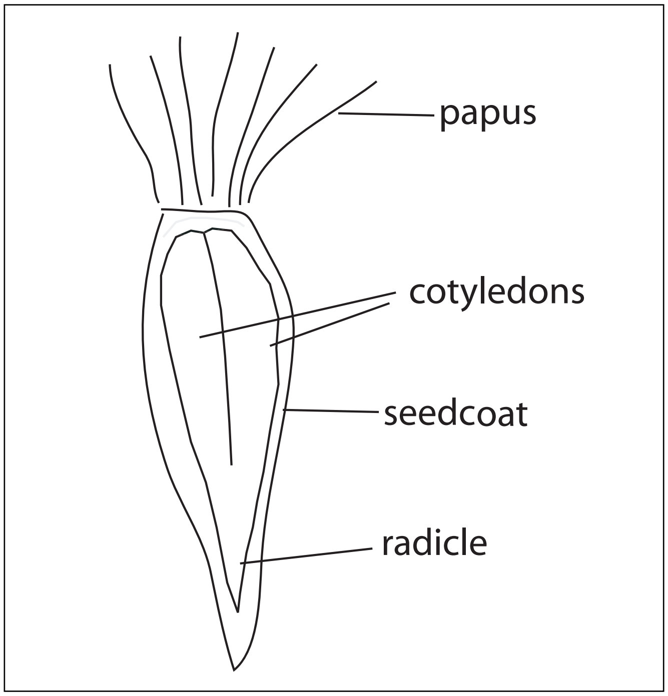
Flowering and fruiting. Horsebrush flowers are borne in heads of 4 to 8 florets each and are located either in the axil of primary leaves or are clustered as dense racemes or corymbs at the tips of branches. Flowering begins as early as April and may last into September. Horsebrush species flower at the following times: striped horsebrush, late June to early August; longspine horsebrush, April and May; gray horsebrush, late May through September; hairy horsebrush, June through mid-August; threadleaf horsebrush, July; smooth horsebrush, May through July; Nuttall horsebrush, late May and June; spiny horsebrush, April through August; Mojave horsebrush, late May through early August; and cotton horsebrush, June and July (Cronquist and others 1994; Mozingo 1987; Strother 1974). Longspine and smooth horsebrushes are the first to flower, where as gray horsebrush flowers from late May through mid-September and has the unique characteristic (among the horsebrush species) of flowering earliest in the north and progressively later southward (McArthur and others 1979; Strother 1974).

Collection, extraction, and cleaning. Horsebrush achenes (figures 1 and 2) are more or less hairy and sometimes glabrous; they possess a well-developed pappus of bristles. As in similar plant forms (Eddleman 1977), the seeds may be hand-stripped or knocked from the head onto a canvas. Mature achenes from which the hairs have been removed have a light to medium reddish brown cast and a parismatic to fusiform shape. Cleaned seeds per weight are reported at 309/g (140,000/lb) for gray horsebrush (McArthur and others 1979) and may be less for the larger seeded species—Nuttall, spiny, Mojave, and cotton horsebrushes.

Germination. Germination is poor for gray horsebrush (Stark 1966), and only 2% of spiny horsebrush seeds germinated in one test (Swingle 1939). Some germination may occur without pretreatment, but prechilling seeds for 4 to 6 weeks is reported to help germination (Young and Young 1992).

Figure 1—*Tetradymia* horsebrush: seeds. *T. comosa* **(left),** *T. spinosa* **(right)**.

Figure 2—*Tetradymia* horsebrush: *T. comosa* longitudinal section through achene.



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References

Cronquist A, Holmgren AH, Holmgren NH, Reveal JL, Holmgren PK. 1994. Intermountain flora. Volume 5, Asterales. Cronquest A, ed. Bronx, NY: New York Botanical Garden. 496 p.

Eddleman LE. 1977. Indigenous plants of southeastern Montana. 1. Viability and suitability for reclamation in the Fort Union Basin. Spec. Pub. 4. Missoula: University of Montana Montana, Forest and Conservation Experiment Station. 122 p.

Hartman H. 1984. Ecology of gall-forming lepidoptera on *Tetradymia*. 1. Gall size and shape. Hilgardia 52: 1–16.

Johnson AE. 1974. Experimental photosensitization and toxicity in sheep produced by *Tetradymia glabrata*. Canadian Journal of Comparative Medicine 38: 408–410.

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

McArthur ED, Blauer AC, Plummer AP, Stevens R. 1979. Characteristics and hybridization of important intermountain shrubs. 3. Sunflower family. Res. Pap. INT-220. Ogden: USDA Forest Service, Intermountain Forest and Range Experiment Station. 82 p.

Mozingo HN. 1987. Shrubs of the Great Basin: a natural history. Reno: University of Nevada Press. 342 p.

Stark N. 1966. Review of highway planting information appropriate to Nevada. Bull. B-7. Reno: University of Nevada, College of Agriculture, Desert Research Institute. 209 p.

Strother JL. 1974. Taxonomy of *Tetradymia* (Compositae: Senecioneae). Brittonia 26: 177–202.

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

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

T

Malvaceae—Mallow family

Thespesia Soland. ex Correa

thespesia

John K. Francis

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Species, occurrence, and growth habit. There are 17 species of *Thespesia,* all trees or shrubs (Howard 1989). Two are of particular interest. *Thespesia populnea* (L.) Soland. ex Correa—with botanical synonyms *Hibiscus populneus* L. and *T. lampas* (Cav.) Dalz. ex. Dalz. & Gibson—is known locally as portiatree, seaside mahoe, *emajagüilla, milo*, and many other names (Little and Skolmen 1989; Parrotta 1994). Portiatree is native to tropical shores from East Africa to Polynesia. It has naturalized (and is sometimes considered invasive) and is planted in coastal areas throughout the tropics. Portiatree is a small tree in moist habitats, although it is often shrubby on dry or salty coastal soils.

Thespesia grandiflora DC.—known as *maga*—is a small to medium-sized tree with a straight stem that is endemic to Puerto Rico (Francis 1989). This species has been referred to in the literature by the botanical synonyms *Montezuma speciocissima* Sessé & Moc., *M. grandiflora* DC., and *Maga grandiflora* (DC.) Urban (Francis 1989).

Use. Portiatree is planted as an ornamental throughout the tropics, especially in coastal areas. Its manageable size, heart-shaped, yellow-green leaves, and yellow flowers endear it to many. More than for any other reason, portiatree succeeds as an ornamental because it can grow on almost any soil. Maga is planted as an ornamental in Florida, Hawaii, Puerto Rico, and several other locations (Little and Wadsworth 1964; Neal 1965). Although its dark-green foliage is very attractive, its large (15 cm) dark pink flowers are its principal asset. Maga requires fertile soils and does not tolerate compaction. The wood of both species is dark reddish brown to chocolate brown, moderately heavy, and moderately hard, with excellent working properties. The small amounts of portiatree wood available fetch high prices and are used for carving, furniture, and posts. The small amounts of maga harvested are used for making musical instruments, furniture, and craft items. Seeds of portiatree are widely used for medicinal purposes (Little and Skolmen 1989; Parrotta 1994).

Flowering and fruiting. Open-grown maga are reported to begin flowering when 5 to 10 years old (Francis 1989); portiatree flowers even earlier. Except in dry areas and seasons of drought, flowering and fruiting of both species proceeds throughout the year (Francis 1989; Parrotta 1994). The fruits of portiatree are flattened, leathery 5-celled capsules 2.5 to 4.0 cm in diameter and 2 cm long (Rashid 1975). They may remain attached to the tree for some time. A sample of 50 fruits from Puerto Rico contained from 1 to 11 seeds/fruit with an average of 5.7 seeds/fruit (Parrotta 1994). The seeds are hairy, 1 cm long, and 0.6 cm broad (figure 1). Reported weights of air-dried seedlots range from 3,500 to 6,700/kg (1,600 to 3,000/lb) (Francis and Rodríguez 1993; Parrotta 1994; Rashid 1975; Von Carlowitz 1986). The fruit of maga is smooth and green, subglobose, and 3 to 5 cm in diameter. From 1 to 12 brown seeds are embedded within a white, fleshy matrix. Fresh seeds numbered 2,500/kg (1,100/ lb); air-dried seeds, 3,900 seeds/kg (1,800/lb) (Francis 1989). The seeds of portiatree are dispersed by wind and water (Parrotta 1994). Maga depends upon fruit bats and birds for dispersal (Francis 1989).

Collection, cleaning, and storage. Quantities of portiatree fruits can be easily picked off the ground under bear-

Figure 1—*Thespesia*, thespesia: fruits and seeds of *T. grandiflora*, maga (**left**), and *T. populnea*, portiatree (**right**).

ing trees, or they can be picked by hand or clipped with a pruning pole from the branches. The fruits are mature when they have turned black (Rashid 1975). Accumulating quantities of maga seeds is more difficult. Maga fruits can be clipped from the trees when they reach full size (no color change is observed). Fruits that are still hard should be left for 2 or 3 days and will continue to ripen. If not eaten by bats and birds, the fruits fall soon after ripening and can be picked up from the ground. Because bats and birds drop the seeds as they consume the fruits, seeds can be collected from the ground under bearing trees or beneath nearby perch trees. Good seeds have a cinnamon-brown color with a waxy luster and are free of fungal spots. Lighter or darker colors denote immaturity or overmaturity and loss of viability (Marrero 1949). Nursery workers normally clean the seeds by hand, a fairly rapid process. Cleaning with macerators may not be possible due to the fragile nature of the seeds, especially those of maga. Seeds of portiatree are apparently recalcitrant but somewhat resistant to drying and can be stored in sealed containers for weeks to months under refrigeration (4 °C). The seeds of maga are highly recalcitrant. The folded cotyledons (figure 2) are active and turn green within the seed as germination begins. The seeds begin germinating 5 to 7 days after the fruit ripens (Francis 1989). Many of the seeds picked up from the ground, either loose or within rotting fruits, already have the radicle exposed. It is best to place moist paper towels or other moistened material in the collection container and sow the seeds as soon as possible. Viability of maga seeds can be extended to nearly 4 months by drying to 62.5% moisture and storing at 2 to 4 °C (Marrero 1942).

Germination. No pregermination treatments are necessary. Seeds of portiatree should be sown in sandy media and lightly covered (Parrotta 1994). From 65 to 79% of fresh seeds germinate, beginning in 8 days and continuing over a 9-week period (Francis and Rodríguez 1993; Ricardi and others 1977; Parrotta 1994). Maga seeds may be sown and lightly covered in ordinary potting mix. Marrero (1942) reported that, although 70 to 80% of fresh seeds germinated, only 20% of seeds stored at room temperature for 2 weeks germinated. Francis and Rodríguez (1993) reported 80% germination beginning 6 days after sowing. Germination of both species is epigeal (figure 3) (Francis 1989; Parrotta 1994).

Nursery practice. Ordinary nursery practice is to germinate seeds in germination trays or beds and transplant seedlings into containers (pots or plastic nursery bags) after the first true leaves emerge. Portiatree seedlings reach 15 cm (6 in) in height about 3 months after sowing (Parrotta 1994). Moving portiatree seedlings into full sunlight after they are established in the pots is recommended. Rooted cuttings are also used to produce portiatree stock. Maga seedlings develop rapidly in partial shade, reaching 20 cm (8 in) in 3 months and 40 cm (16 in) in 6 months (Francis 1989). Maga seedlings should be moved into full sun a few weeks before outplanting. Seedling stock of either species from 15 to 50 cm (6 to 20 in) can be used to establish plantations. Trees destined to become ornamentals are often grown in pots until they attain 1 to 2 m (39 to 79 in) in height. Wildlings are sometimes collected, potted, and allowed to rebuild their root system before outplanting.

Figure 2—*Thespesia grandiflora*, maga: seed cut in longitudinal section.

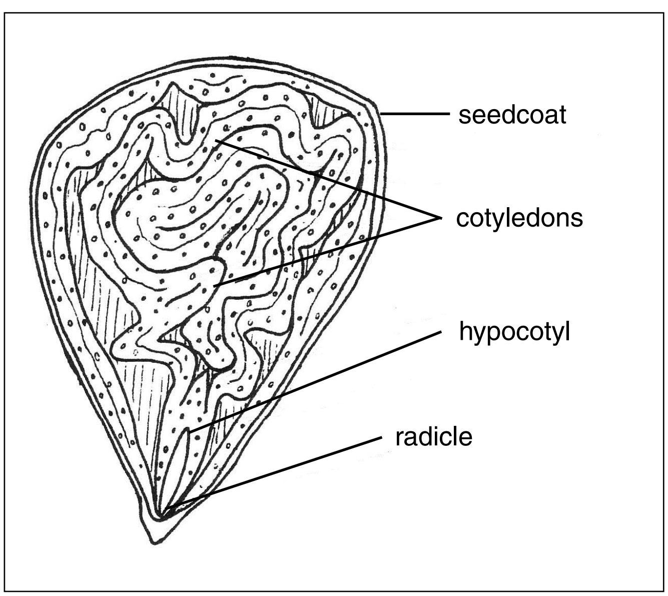
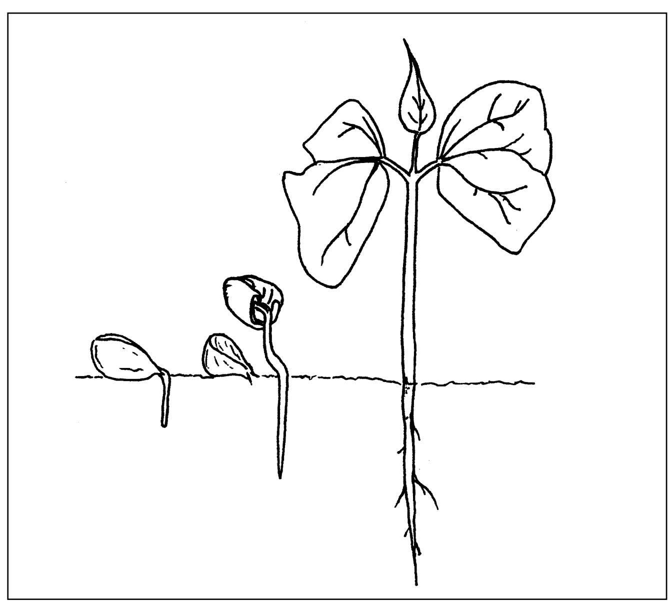


Figure 3—*Thespesia grandiflora*, maga: germination and seedling development.



References

Francis JK. 1989. *Thespesia grandiflora* (DC.) Urban, maga. Res. Note SO-ITF-SM-21. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 4 p.

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

Howard RA. 1989. Flora of the Lesser Antilles, Leeward and Windward Islands. Volume 5. Jamaica Plain, MA: Harvard University, Arnold Arboretum. 604 p.

Little EL Jr, Skolmen RG. 1989. Common forest trees of Hawaii (native and introduced). Agric. Hdbk. 679. Washington, DC: USDA Forest Service: 194.

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

Marrero J. 1942. A seed storage study of maga. Caribbean Forester 3(4): 173–184.

Marrero J. 1949. Tree seed data from Puerto Rico. Caribbean Forester 10: 11–30.

Neal MC. 1965. In gardens of Hawaii. Spec. Pub. 50. Honolulu: Bernice P. Bishop Press. 924 p.

Parrotta JA. 1994. *Thespesia populnea* (L.) Soland. ex Correa: portiatree, emajagüilla. Res. Note SO-ITF-SM-76. New Orleans: USDA Forest Service, Southern Forest Experiment Station. 5 p.

Rashid MA, ed. 1975. The silviculture of Indian trees. rev. ed. Volume 1. Delhi: Government of India Press. 307 p.

Ricardi M, Torres F, Hernandez C. Quintero R. 1977. Morfología de plantulas de árboles Venezolanos. Revista Forestal Venezolana 27: 15–56.

Von Carlowitz PG. 1986. Multipurpose tree and shrub seed directory. Nairobi: International Council for Research in Agroforestry. 265 p.

T

Cupressaceae—Cypress family

Thuja L.

arborvitae

Gary J. Brand and C. S. Schopmeyer

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Growth habit and occurrence. The arborvitae genus—*Thuja*—includes 2 species native to North America and 3 or 4 (depending on the authority consulted) Asian species (table 1). All individuals in the genus are aromatic, evergreen trees, but some species also have shrubby forms.

Mature northern white-cedars are medium-sized trees, usually 12 to 15 m tall and 60 to 90 cm in dbh (Harlow and others 1991). The rooting habit of mature trees is usually shallow and spreading. In addition to regeneration from seeds, vegetative reproduction by layering is common where there is sufficient moisture (Johnston 1990). Northern white-cedar grows on a wide variety of organic and mineral soils but does not develop as well on extremely wet or extremely dry sites (Johnston 1990). However, most commercial stands of northern white-cedar are in swamps. Geographical range for the species extends from Nova Scotia to Maine and westward to Manitoba and Minnesota. Isolated stands occur in west-central Manitoba, northern Ontario, southern Wisconsin, northern Illinois, Ohio, Massachusetts, Connecticut, and the Appalachian Mountains as far south as Tennessee (Little 1971).

Western redcedar can grow into large trees, especially in stream bottoms, moist flats, and gentle, north-facing slopes at low elevations (Curran and Dunsworth 1988; Schopmeyer 1974). It will grow to 45 to 60 m tall and 120 to 240 cm in dbh (Harlow and others 1991). Western redcedar develops extensive roots with a dense network of fine roots (Minore 1990). As in northern white-cedar, vegetative reproduction in western redcedar is common and provides the dominant means of regeneration in some stands. Branch layering, rooting of fallen branches, and rooting of branches attached to fallen trees have all been reported (Minore 1990). Western redcedar grows on many different soils and at a wide range of elevations. Its native range includes the Pacific Coast from northern California to southeastern Alaska; the Cascade Mountains in Oregon and Washington; and the Rocky Mountains in southeastern British Columbia, northeastern Washington, northern Idaho, and western Montana (Little 1971).

Table 1—*Thuja,* arborvitae: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***T. occidentalis* L.** *T. obtusa* Moench *T. odorata* Marshall	**northern white-cedar,** white-cedar, eastern arborvitae, swamp-cedar, arborvitae, eastern white-cedar	Nova Scotia to Maine & W to Minnesota & Manitoba; S in Illinois, Ohio, & New York; locally in Appalachian Mtns.
***T. plicata* Donn ex D. Don** *T. plicata* D. Don; *T. plicata* Donn *T. plicata* Donn ex D. Don in Lamb. *T. gigantea* Nutt. *T. menziesii* Dougl. ex Endl. *T. lobbii* Hort. ex Gord.	**western redcedar,** Pacific redcedar, giant-cedar, arborvitae, giant arborvitae, canoe-cedar, shinglewood	Pacific Coast region, from SE Alaska to N California, Cascade Mtns. in Washington & Oregon, Rocky Mtns in British Columbia, N Idaho, & W Montana
***T. standishii* (Gord.) Carr.** *T. japonica* Maxim. *Thujopsis standishii* Gord.	**Japanese thuja,** Japanese arborvitae	Japan
***T. koraiensis* Nakai** *T. kongoënsis* Nakai	**Korean thuja,** Korean arborvitae	Korea
***T. sutchuensis* Frachet**	**Sichuan thuja**	China

Sources: Cope (1986), Kartesz (1994a&b), Little (1979), Rushforth (1987), Vidakovic (1991).

The 3 Asian species listed (table 1) are only planted for ornamental purposes in the Untied States. Korean thuja reaches a height of 11 m, and Japanese thuja may grow as tall as 15 m (LHBH 1976).

Use. Both native species are valuable timber trees because their heartwood is light in weight and resists decay. The wood is used extensively for shingles, shakes, siding, and poles. Young northern white-cedar and the crowns of felled trees are browsed extensively by deer (Schopmeyer 1974). Many horticultural varieties of arborvitae with distinctive growth forms and foliage colors are propagated vegetatively for ornamental use (Cope 1986; Dirr 1990; Rushforth 1987; Vidakovic 1991). Northern white-cedar is commonly used as a root stock for horticultural grafts of *Thuja* spp. (LHBH 1976). Extractives from western redcedar inhibit the growth of numerous bacterial and fungal species (Minore 1983).

Geographic races and hybrids. Although no naturally occurring races or hybrids of northern white-cedar or western redcedar have been reported (Kartesz 1994a; Vidakovic 1991), a hybrid between western redcedar and Japanese thuja has been produced (Minore 1990; Vidakovic 1991).

The many horticultural varieties of northern white-cedar and western redcedar suggest that these 2 species have considerable genetic variability. However, variation in growth and survival has not been demonstrated by all provenance tests. Northern white-cedar provenance tests demonstrated some differences in height growth rates but not consistent differences in survival rates (Jeffers 1976; Jokela and Cyr 1979). Based on their provenance work, Bower and Dunsworth (1988) concluded that western redcedar has little genetic variability. In contrast, Sakai and Weiser reported differences in frost-tolerance for western redcedar (1973).

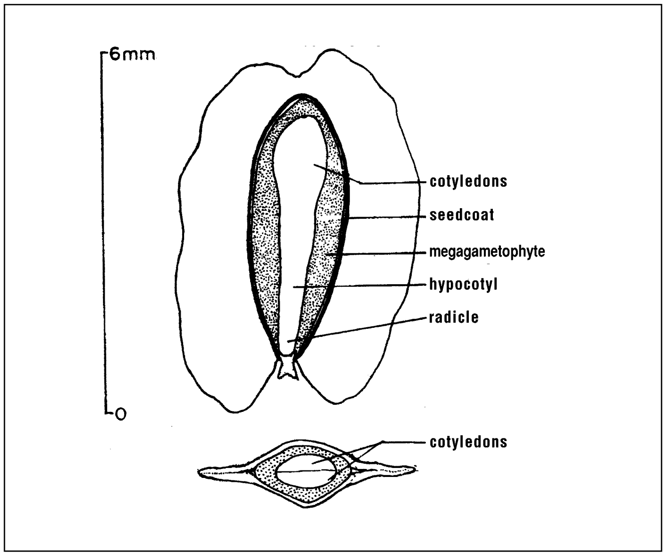
Flowering and fruiting. Male and female flowers are borne on the same tree but usually on separate twigs or branchlets (Schopmeyer 1974). Flower initiation begins in spring to early summer, development ceases in the fall, pollen is shed in late winter to early spring, and fertilized cones are mature by fall (Owens and Molder 1984). Female flowers form near the tips of vigorous lateral branches (figure 1) and are usually higher on the tree than the male flowers. The presence of low numbers of cone buds in the dormant season indicates that a poor cone crop will follow in the fall (Owens and Molder 1984). Cones of both native and Asian species are about 8 to 12 mm long (Little 1976; Schopmeyer 1974). Western redcedar cones have 5 to 6 pairs of scales. The 3 middle pairs are fertile and contain 2 to 3 seeds (Owens and Molder 1984). Cones of northern white-cedar have 4 to 5 pairs of scales with the middle 2 or 3 pairs fertile (Briand and others 1992). Each fertile scale contains 2 seeds. During the ripening period, cones change in color from green to yellow and finally to a pale cinnamon brown. Depending on location, cones are ripe in August or September (Schopmeyer 1974). Their light chestnut-brown seeds are 3 to 5 mm long and have lateral wings about as wide as the body (figures 2 and 3). Embryos of both species have 2 cotyledons.

Collection of cones. Trees as young as 10 years old have produced cones (Curtis 1946; Edwards and Leadem 1988), but heavy cone production usually occurs only on older trees. Cones may be picked by hand from standing or recently felled trees, or the cones maybe flailed or stripped onto a sheet of canvas, burlap, or plastic. Cones of western

Figure 1—*Thuja*, arborvitae: mature cones of *T. occidentalis*, northern white-cedar, with female cone buds on branch tips above the brown mature cones.

Figure 2—*Thuja*, arborvitae: mature cones and seeds of *T. occidentalis*, northern white-cedar.

Figure 3—*Thuja occidentalis*, northern white-cedar: longitudinal section **(top)**, and transverse section showing 2 cotyledons **(bottom)**.



redcedar have been harvested with aerial rakes attached to helicopters (Edwards 1986; Wallinger 1986). A good time for collection is when seeds have become firm and most of the cones have turned from yellow to brown. For northern white-cedar, the period between cone ripening and start of cone opening is only 7 to 10 days (Schopmeyer 1974). Cones of western redcedar also start to open soon after they ripen. Owens and Molder (1984) recommend collecting cones in late August to early September. Peak rate of seed-fall from both species occurs about 4 to 6 weeks after the first cones have opened (Schopmeyer 1974). Mature trees of both species produce cones prolifically every 3 to 5 years, but all cones do not open at the same time. Seed release therefore progresses slowly. Substantial seed yields probably can be obtained from cones collected as late as 1 month after the first cones have opened.

Extraction, cleaning, and storage of seeds. Seeds can be extracted from cones by air-drying for 1 to 3 weeks (VanSickle 1994) or cones may also be spread out to sun-dry. Kiln-drying is more efficient for large quantities of cones. Cones of northern white-cedar have been opened by exposing them for 4 hours in an internal-fan-type kiln at a temperature of 54 °C and a relative humidity of 38% (Schopmeyer 1974). Kiln temperatures below 43 °C are preferred, however, to prevent damage to the seeds (Schopmeyer 1974). Western redcedar cones were opened in 24 to 36 hours at a temperature of 33 °C (Edwards 1986), 18 to 20 hours at 41 °C (Owens and Molder 1984), or 27 °C for 12 hours (Henchell 1994). Higher temperatures increase the probability that seeds will be damaged. After cones have opened, seeds are extracted in a mechanical cone shaker or tumbler and separated from the cone scales by fanning or gravity separation. Seeds should not be de-winged (Edwards and Leadem 1988; Gordon and others 1991).

The number of fully developed seeds in each cone can vary dramatically. As few as 2 to as many as 12 (average 7.7) fully developed seeds were counted in northern white-cedar cones (Briand and others 1992). For western redcedar, cones from natural stands contained an average of 2.6 filled seeds/cone, whereas cones from seed orchards contained an average of 6 fully developed seeds per cone (Colangeli and Owens 1990). One kilogram of cleaned northern white-cedar seeds contains an average of 763,000 seeds (346,000/lb) (Schopmeyer 1974). The average number of cleaned western redcedar seeds reported is 913,000/kg (414,000/lb) (Schopmeyer 1974). Empty seeds can be readily separated from full seeds in a seed aspirator or blower.

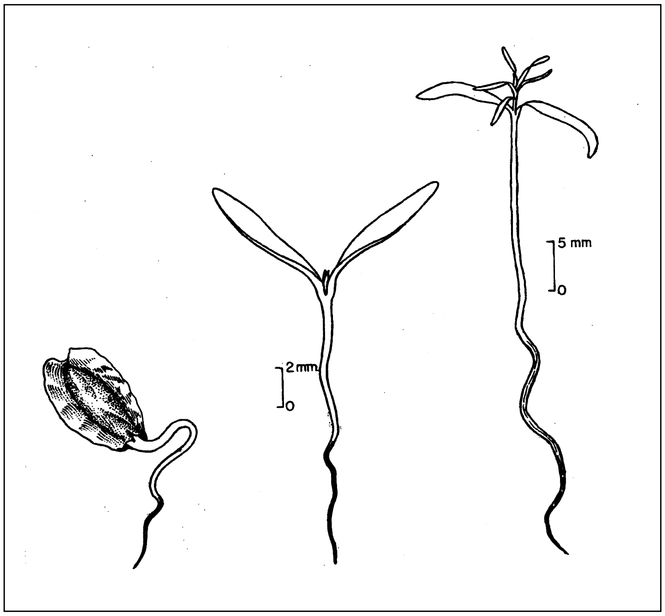
Arborvitae seeds are orthodox in storage behavior. Seeds should be stored in fiber containers with plastic or foil liners (Gordon and others 1991). Seeds stored at a moisture content of 5 to 10% in sealed containers at 0 to 5 °C should remain viable for up to 5 years (Gordon and others 1991). For longer periods, storage at –18 °C is recommended.

Pregermination treatments. The need for stratification to ensure that a high percentage of seeds germinate uniformly is not clear. Some authors state that stratification is not needed. Others recommend stratification for 30 to 60 days in moist medium at 1 to 5 °C (Henchell 1994; Schopmeyer 1974). Dirr and Heuser (1987) report that 2 weeks of stratification will improve germination of Japanese thuja. Germination of northern white-cedar and western redcedar seeds is tested by placing seeds on top of moist germination paper kept at 20 to 30 °C; no pretreatment is recommended. Germination is epigeal (figure 4). The first count of germinated seeds is made after 7 days and the last count after 21 days (ISTA 1993).

Nursery practice and seedling care. Northern white-cedar and western redcedar seedlings are not produced in large numbers but can be grown in both bareroot nurserybeds and in containers. Many ornamental varieties of arborvitae, both native and Asian, are propagated from cuttings or by layering (Dirr and Heuser 1987). Cultural practices vary by nursery.

The irregular shape and small size of western redcedar seeds make it difficult to sow the seeds mechanically. Coating seeds with fine-textured materials such as clay, sand, charcoal, or peat has been attempted to make the seeds more uniform in size and shape (Edwards and Leadem 1988). This process should be done just before sowing,

Figure 4—*Thuja occidentalis*, northern white-cedar: seedling development at 1, 5, and 25 days after germination.



because seed viability is reduced if seeds are stored after being coated (Edwards and Leadem 1988).

In bareroot nurseries, seedlings are grown as 1+1, 2+0, 2+1, and 3+0 stock. Fall-sowing is preferred for northern white-cedar and spring-sowing for western redcedar. Some nurseries soak seeds in water for 24 to 48 hours and then stratify them for 7 to 60 days at 2 °C before sowing. Because of better mycorrhizal colonization, planting western redcedar seeds in nurserybeds that have not been fumigated for 1 year seems beneficial (Henchell 1994). Average seedbed density for western redcedar is about 500 seedlings/m^2 (46/ft^2) but varies from 240 to 1000/m^2 (22 to 93/ft^2) (Edwards and Leadem 1988; Henchell 1994). The wider spacings may produce higher quality seedlings (van den Driessche 1984). Sowing depth varies from 0.3 to 1.0 cm ($^1/_8$ to $^3/_8$ in) (Schopmeyer 1974). In another approach used in Minnesota, VanSickle (1994) sowed northern white-cedar seeds at 0.15 cm ($^1/_{16}$ in) and covered them with a double layer of hydromulch. Western redcedar seeds have also been sown on the surface, pressed into the soil by the packing roller of a seed drill, and covered immediately with shade material (Henchell 1994). First-year northern white-cedar seedlings are grown both with half-shade (Jones 1994) and without shading (VanSickle 1994). Shading (50 to 70%) is recommended for first-year western redcedar seedlings. Soil moisture needs to be monitored closely because seeds and seedlings of western redcedar are sensitive to drying (Henchell 1994).

Container seedlings have become more common in the last decade and can be produced in 1 or 2 years. Various container sizes are used, depending on the desired size of the outplanted stock. Common container volumes used are 66 to 164 ml (4 to 10 in^3) (Olson 1994; Schaefer 1994). Seedlings of northern white-cedar grown from fall-planted seeds are ready for outplanting in May, unless the larger containers are used. Seedlings of western redcedar grown from spring-planted seeds are ready for outplanting in the fall or following spring. Seedlings in larger containers are grown in the greenhouse for 10 to 18 months before outplanting. Seeds sown in the containers are covered with a thin layer (about 0.3 cm, or $^1/_8$ in) of crushed granite (Olson 1994) or quartz (Schaefer 1994). Western redcedar seedlings grown in containers and chemically root pruned by painting the inside of the container with latex paint containing copper carbonate showed good height and volume growth when outplanted (Curran and Dunsworth 1988). In container-grown western redcedar, a mild nitrogen and moisture stress after the seedlings reach 8 to 10 cm (3 to 4 in) produces hardened stock with a balanced root to shoot ratio (Schaefer 1994). Seedlings grown for 1 year in containers and then transplanted to the nursery bed (plug+1 transplants) are well-balanced and have been successful when outplanted (Ramirez 1993).

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References

Bower RC, Dunsworth BG. 1988. Provenance test of western red cedar on Vancouver Island. In: Smith NJ, ed. Western red cedar: does it have a future? 1987 July 13; Vancouver, BC. Vancouver: University of British Columbia: 131–135.

Briand CH, Posluszny U, Larson DW. 1992. Comparative seed morphology of *Thuja occidentalis* (eastern white-cedar) from upland and lowland sites. Canadian Journal of Botany 70: 434–438.

Colangeli AM, Owens JN. 1990. The relationship between time of pollination, pollination efficiency, and cone size in western red cedar (*Thuja plicata*). Canadian Journal of Botany 68: 439–443.

Cope EA. 1986. Native and cultivated conifers of northeastern North America: a guide. Ithaca, NY: Cornell University Press. 231 p.

Curran MP, Dunsworth BG. 1988. Coastal western red cedar regeneration: problems and potential. In: Smith NJ, ed. Western red cedar: does it have a future? 1987 July 13; Vancouver, BC. Vancouver: University of British Columbia: 20–32.

Curtis JD. 1946. Preliminary observations of northern white cedar in Maine. Ecology 27: 23–26.

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

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

Edwards DGW. 1986. Cone production, collection, and processing. In: Shearer RC, comp. Proceedings, Conifer Tree Seed in the Inland Mountain West Symposium; 1985 August 5; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 78–102.

Edwards DGW, Leadem CL. 1988. The reproductive biology of western red cedar with some observations on nursery production and prospects for seed orchards. In: Smith NJ, ed. Western red cedar: does it have a future? 1987 July 13; Vancouver, BC. Vancouver: University of British Columbia: 102–113.

Gordon AG, Gosling P, Wang BSP, ed. 1991. Tree and shrub seed handbook. Zurich: ISTA. 14 chapters.

Harlow WM, Harrar ES, Hardin JW, White FM. 1991. Textbook of dendrology: covering the important forest trees of the United States and Canada, 7th ed. New York: McGraw-Hill. 501 p.

Henchell C. 1994. Personal communication. Carson, WA: USDA Forest Service.

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

Jeffers RM. 1976. Survival and height growth of northern white-cedar from 18 provenances. In: Beineke WF, ed. Proceedings, 10th Central States Forest Tree Improvement Conference; 1976 September 22; West Lafayette, IN. West Lafayette, IN: Purdue University, Department of Forestry and Natural Resources: 152–156.

Johnston WF. 1990. *Thuja occidentalis*. In: Burns RM, Honkala BH, tech. coords). Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 580–589.

Jokela JJ, Cyr CL. 1979. Performance of northern white-cedar in central Illinois. In: Proceedings, 13th Lake States Forest Tree Improvement Conference; 1977 August; Gen. Tech. Rep. NC-50. St. Paul: USDA Forest Service, North Central Forest Experiment Station: 100–106.

Jones B. 1994. Personal communication. Watersmeet, MI: USDA Forest Service.

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

Kartesz JT. 1994b. A synonymized checklist of the vascular flora of the United States, Canada, and Greenland. Volume 2. Portland, OR: Timber Press. 816 p.

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

Little EL Jr. 1971. Atlas of United States trees. Volume 1, Conifers and important hardwoods. Misc. Pub. 1146. Washington, DC: USDA Forest Service.

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

Minore D. 1983. Western redcedar: a literature review. Gen. Tech. Rep. PNW-150. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 70 pages.

Minore D. 1990. *Thuja plicata*. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 590–600.

Olson D. 1994. Personal communication. Brandon, MN: Chippewa Farms.

Owens JN, Molder M. 1984. The reproductive cycles of western redcedar and yellow-cedar. Victoria: British Columbia Ministry of Forests, Information Services Branch. 28 p.

Ramirez T. 1993. Diversity of species at Humbolt Nursery. In: Landis TD. Tech. coord. Proceedings, Western Forest Nursery Association; 1992 September 14; Fallen Leaf Lake, CA. Gen. Tech. Rep. RM-221. Fort Collins, CO: USDA Forest Service: 95–97.

Rushforth KD. 1987. Conifers. New York: Facts On File. 232 pages.

Sakai A, Weiser CJ. 1973. Freezing resistance of trees in North America with reference to tree regions. Ecology 54: 118–126.

Schaefer R, III. 1994. Personal communication. Lewiston, ID: Western Forest Systems, Inc.

Schopmeyer CS. 1974. *Thuja*, arborvitae. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 805–809.

van den Driessche R. 1984. Seedling spacing in the nursery in relation to growth, yield, and performance of stock. Forestry Chronicle 60(6): 345–355.

VanSickle C. 1994. Personal communication. Akeley, MN: Minnesota Department of Natural Resources.

Vidakovic M. 1991. Conifers: morphology and variation. Zagreb, Croatia: Graficki zavod Hrvatske. 754 p.

Wallinger DP. 1986. Aerial cone harvesting in British Columbia. In: Shearer RC, comp. Proceedings, Conifer Tree Seed in the Inland Mountain West Symposium; 1985 August 5; Missoula, MT. Gen. Tech. Rep. INT-203. Ogden, UT: USDA Forest Service, Intermountain Forest and Range Experiment Station: 133–139.

T

Tiliaceae—Linden family

Tilia L.

linden or basswood

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Growth habit, occurrence, and uses. The genus *Tilia* L.—linden or basswood—consists of about 40 species of large or medium-sized, deciduous trees that are indigenous to the temperate Northern Hemisphere. *Tilia* is the only genus of its family, Tiliaceae. Species reach their maximum size in loamy, moist, fertile soil, but they tolerate poor soils, pollution, windy conditions, and transplanting and can be grown in full sun or partial shade (Dirr 1990; Haller 1995; Kunneman and Albers 1991). Lindens possess a well-developed root system and are long lived, with some species living between 500 to 1,000 years (Haller 1995; Kunneman and Albers 1991). Table 1 lists species native to North America as well as widely grown non-native species.

Few shade trees vary so greatly in shape, leaf size, and growth rate as do the lindens (Flemer 1980). They generally possess a uniform globular crown and smooth, silver-gray bark that becomes fissured on old trees (table 2). The winter form is striking, with stiff, erect branches growing upward at 30° angles from a thick trunk (Burgess 1991). Considerable differences in growth habit exist among cultivars of littleleaf linden, ranging from the very dense, formal pyramidal habit of 'Greenspire', the dense upright oval shape of 'Chancellor', to the more open, informal oval habit of 'Fairview' (Pellett and others 1988).

There is much disagreement among taxonomists as to correct identification of species, and there are numerous names in the literature that are no longer recognized by many botanists. For example, *T. monticola* Sarg. and *T. michauxii* (Nutt.) Sarg. are sometimes seen in the literature or listed as specimens in botanical gardens, but they are now considered to be varieties of white basswood—*T. americana* var. *heterophylla* (Venten.) Loud.—recognized previously as *T. heterophylla* Venten. (Ayers 1993; Rehder 1990).

Table 1—*Tilia,* linden: nomenclature, and occurrences

Scientific name & synonym(s)	Common name(s)	Occurrence
***T. americana* L.** *T. glabra* Venten.	**American linden,** basswood, whitewood, American lime, bee-tree	New Brunswick S to Virginia & Texas
***T. americana* var. *caroliniana* (P. Mill.) Castigl.**	**Carolina basswood**	SE US
***T. americana* var. *heterophylla* (Venten.) Loud.**	**white basswood**	West Virginia to Florida, W to Indiana & Alabama
***T. cordata* P. Mill.** *T. parviflora* J. F. Ehrh. ex Hoffm.)	**littleleaf linden,** small-leaved lime, European linden	Europe
***T. euchlora* K. Koch** *T. cordata* x *T. dasystyla*	**Crimean linden,** Caucasian lime	SE Europe & SW Asia
***T. europaea* L.** *T. cordata* x *T. platyphyllos* *T. intermedia* DC. *T. vulgaris* Hayne	**European linden,** common linden, lime	Europe
***T. mexicana* Schldl.**	**Mexican basswood**	Mexico
***T. petiolaris* DC.**	**pendent silver linden,** pendent white lime, weeping lime	SE Europe & W Asia
***T. platyphyllos* Scop.** *T. europaea* var. *grandiflora* Hort.	**bigleaf linden,** large-leaved lime, largeleaf linden	Europe to SW Asia
***T. tomentosa* Moench** *T. argentea* DC.	**silver linden,** European white linden	SW Europe & Asia

Sources: Dirr (1990), LHBH (1976), Plotnik (2000), Rehder (1990), RHS (1994).

Table 2—*Tilia,* linden: growth habit and general comments

Species	Growth habit & maximum height	General comments
T. americana	Tree to 40 m with numerous, slender, low-hung spreading branches; pyramidal when young, crown somewhat rounded at maturity	Flowers pale yellow in summer; bee plant; wood used for making expensive furniture & excelsior, inner bark used for fabric
T. a. var. *caroliniana*	Tree to 20 m; close to habit of *T. americana*	—
T. a. var. *heterophylla*	Tree to 30 m; crown conical	—
T. cordata	Tree to 30 m; pyramidal when young; upright-oval to pyramidal-rounded & densely branched in old age; crown outspread	Widely planted as a street tree; pollution-tolerant; excellent shade tree
T. euchlora	Tree to 20 m	Similar to *T. cordata*
T. europaea	Tree to 37 m	—
T. mexicana	Tree to 20 m	—
T. petiolaris	Tree to 23 m	Sometimes considered as a pendulous selection of *T. tomentosa*
T. platyphyllos	Tree to 40 m; crown conical to broadly conical	Not widely planted in the US
T. tomentosa	Tree to 27 m; pyramidal when young; upright-oval to pyramidal-oval in later years; crown dense	Can be grown effectively as a multi-stemmed specimen to highlight light gray, smooth bark; good street tree, tolerating heat & drought better than other lindens

Sources: Dirr (1990), LHBH (1976), Plotnik (2000), Rehder (1990), RHS (1994).

Lindens are generally not suitable for lumber because the wood is soft and rots easily. However, the soft, straight-grained and even-textured wood is ideal for woodcarving and is utilized to make musical instruments, piano keys, Venetian blinds, and veneer and can serve as a source of fiber (Haller 1995; Kunneman and Albers 1991). The wood does not produce splinters, thus making it ideal for tool handles. The inner bark (or "bast") consists of long, tough fibers that once were used in the production of cordage, mats, and clothing. The common names for the species—basswood, linden, and lime—are derived from this characteristic: *bast* gives us the name bastwood or basswood; *linden* and *lime* are thought to be derived from the Latin word for linen (Haller 1995). In addition, flowers of linden are quite fragrant and produce large quantities of nectar that is very attractive to bees. The flowers of European, bigleaf, and littleleaf lindens are brewed for tea (Bremness 1994). The nectar of some species is so overpowering that bees can be found inebriated on the ground beneath the tree (Haller 1995). The light-colored honey produced is world famous.

Lindens are used primarily as ornamental shade and street trees (table 2), more so in Europe than in the United States. For example, Berlin's most famous boulevard is named *"Unter den Linden"*. They are well-adapted to a broad range of soil and climatic conditions and are relatively free of major disease problems that may threaten the survival or landscape value of established trees (Pellett and others 1988). The European lindens—littleleaf, European, bigleaf, and silver lindens—have greater importance in landscape plantings in the United States because they are more tolerant and ornamental than American species such as American linden (Dirr 1990; Heit 1977). In addition, American linden becomes too large for the average home property and is better left in the forest (Dirr 1990). However, silver linden possesses a shallow root system and its canopy casts dense shade, making it unsuitable for underplanting (Burgess 1991).

Geographic races and hybrids. As mentioned previously, there is much disagreement among taxonomists as to correct identification of species. For example, there is debate whether white basswood is a southern race of American linden or a separate species. Also, hybridization between species occurs naturally and has given rise to variability among seedlings (Kunneman and Albers 1991). Of the more common hybrids, Crimean and European lindens are not considered superior landscape trees relative to littleleaf linden (Dirr 1990).

Flowering and fruiting. Perfect, fragrant, yellowish or whitish flowers that bloom in June or July are borne in short, pendulous cymes with stalks attached to a large thin-textured oblong bract. Trees and clonal groups of trees flower almost simultaneously over the exposed parts of their crowns. In each inflorescence, the terminal flower of the dichasium opens first and in warm weather is followed at intervals of a day by flowers on the branches of successive orders (Pigott and Huntley 1981). Trees usually flower within 5 to 15 years when grown from seed. Shortness of blooming period (several days to 2 weeks, depending on weather conditions) and lack of consistent flowering from year to year are problems for beekeepers harvesting honey (Ayers 1993). In particular, the American lindens have a reputation for not flowering every year. Some of the introduced species are more consistent (Ayers 1993).

Following pollination, temperatures must be > 15 °C for growth of the pollen tube and for fertilization to occur so that fruits will be produced (Pigott and Huntley 1981). Fruits are grayish, nut-like, round to egg-shaped capsules that mature in autumn but may persist on the tree into the winter. Each consists of a woody pericarp enclosing a single seed (but sometimes 2 to 4 seeds) (figures 1 and 2) (Brinkman 1974; Pigott and Huntley 1981). The pericarp consists of an outer layer of loose fibers forming a mat (or tomentum) and a broad region of thick-walled lignified fibers that are responsible for its hard, tough, woody character (Spaeth 1934). Fruits of American linden are tough and leathery, whereas those of littleleaf linden tend to be thinner and rather brittle (Heit 1967). Seeds possess a crustaceous seedcoat; a fleshy, yellowish endosperm; and a well-developed embryo (figures 2 and 3). Natural dispersion is primarily by wind and animals (Brinkman 1974).

Collection of fruits, seed extraction and cleaning. The ideal time to harvest fruits is early fall, when seed moisture content is approximately 16% (Vanstone 1982). During fruit ripening, moisture is lost from the seeds at a rate of 1 to 2% per day, so that seeds must be monitored closely. Pericarp color is a reliable indicator of moisture content in relation to germination. Fruits should be picked when the pericarp is turning from green to grayish-brown and before the pericarp becomes tough and leathery. Otherwise, seeds will require greater efforts during extraction and scarification. There is generally uniform ripening on any individual tree, but the exact date of ripening may vary by several weeks among trees (Vanstone 1978). Because fruits of lin-

Figure 1—*Tilia*, linden: fruits of *T. americana*, American linden (**top**) and *T. cordata*, littleleaf linden (**bottom**).

Figure 2—*Tilia cordata*, littleleaf linden: seed.

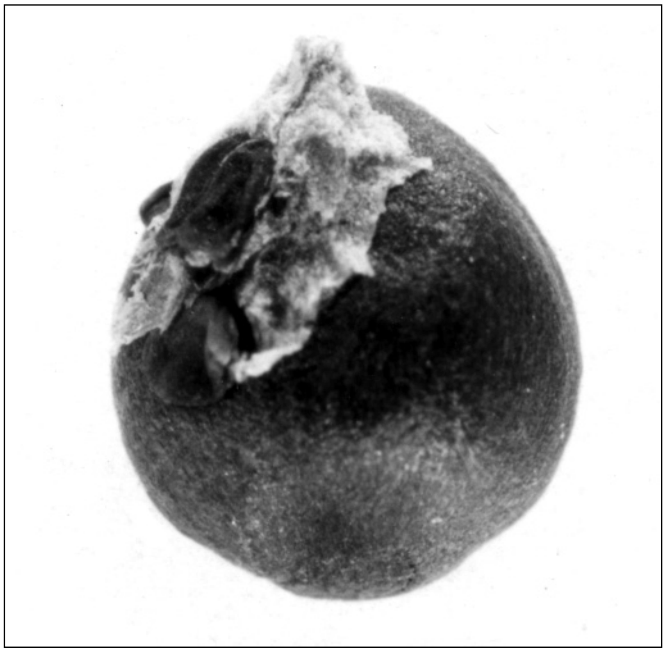
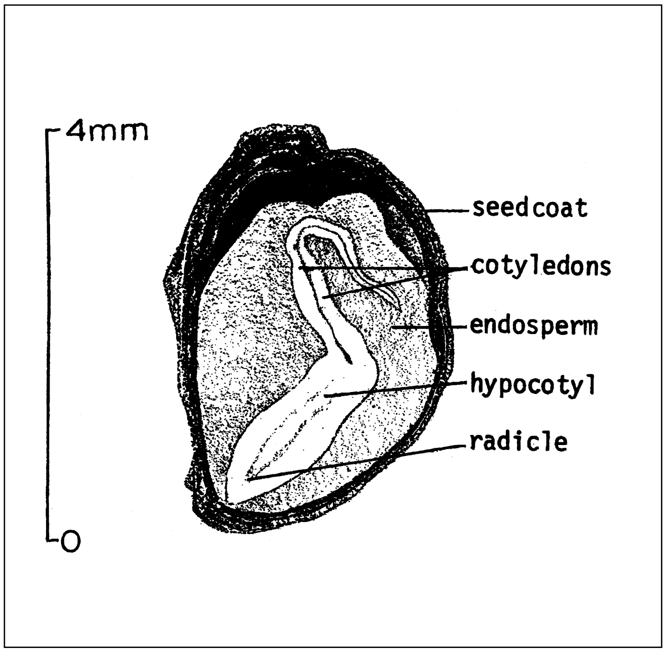


Figure 3—*Tilia americana*, American linden: longitudinal section of a seed.



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den persist on the tree, fruit collection is often postponed until after maturity. After a heavy frost, fruits can be shaken from branches onto a canvas tarp and spread out to dry (Brinkman 1974).

Once fruits have been collected, bracts can be removed by flailing or passing the fruits through a de-winging machine. The hard pericarp must then be removed. Fruits of littleleaf and bigleaf lindens have prominent sutures that are helpful in the extraction process by serving as a breaking point for both mechanical and rubbing techniques (Heit 1977). Fruits of European and silver lindens can be handled similarly, and a combination of sieving, screening, and blowing can readily remove debris (Heit 1977). However, fruits of American linden have a hard, tough, leathery pericarp and must be run through a coffee grinder or a similar device or treated with acid to accomplish its removal (Heit 1977). Mechanical extraction of seeds is often difficult. Any crushing force sufficient to fracture the tough pericarp is likely to exert a shattering pressure on the brittle seedcoat (Spaeth 1934). Seed yields and size vary by species (table 3)

Storage. Seeds of the lindens are orthodox in storage behavior and should be stored in sealed containers at a moisture content of 8 to 12%. Seeds of American linden have retained their viability for 2 years when stored under dry conditions at room temperature and for 5 to 6 years when stored at 1 to 4 °C (Heit 1977).

Pregermination treatments. In addition to their tough pericarps, seeds of linden exhibit double dormancy and thus require both scarification and stratification (moist-prechilling) because of their impermeable seedcoat and dormant embryo, respectively. For seeds of littleleaf linden, Heit (1977) recommended a sulfuric acid treatment of 10 to 50 minutes at a temperature ranging from 23 to 27 °C. Colder temperatures required a longer duration of acid treatment. Because all species of linden and individual seedlots within the same species are variable in their percentage and degree of hardseededness, it is advisable to soak some seeds in water for 1 or 2 days to determine the degree of hardseededness before treating with acid. Ten to 20 minutes of acid treatment may be ideal for some seedlots, but 20 to 50 minutes would produce the best results for others. The degree of hardseededness depends on factors such as seed source, time of collection, and storage conditions, including temperature and relative humidity (Heit 1967, 1977). Other scarification treatments include mechanical scarification and hot water treatments, but neither are as good as acid scarification (Heit 1977). Freezing to –80 and –185 °C had little effect on the permeability of the seedcoat (Spaeth 1934). Surface sterilization with sodium hypochlorite (NaOCl) and ethanol proved to control seed pathogens but lowered germination percentages of littleleaf, bigleaf, and silver lindens (Magherini and Nin 1993).

In addition to scarification, stratification is essential for maximum germination and seedling production. Following scarification, seeds must be either fall-sown immediately or stratified at 1 to 3 °C for about 3 months before spring-sowing. Vanstone (1978) recommends stratification in a 1:1 mixture (by volume) of peat and sand containing 30% moisture by weight. Enzyme activity and levels of soluble proteins and amino acids in the seeds increase gradually during stratification at 4 °C (Pitel and others 1989). Nontreated seeds have been known to lie in the ground for over 5 years without germinating while still maintaining viability (Heit 1967). Bigleaf linden requires 3 to 5 months of warm stratification followed by 3 months of cold, and even this treatment does not guarantee high germination (Dirr and Heuser 1987). Flemer (1980) recommends burying seeds in a wooden box filled with damp sand and leaving the box outdoors during the winter. Boxes are then dug up the following fall and the seeds are sown. Seed treatments that consistently result in

Table 3—*Tilia,* linden: seed yield data

	Seed wt/fruit wt		Cleaned seeds/weight (x1,000)				
			Range		Average		
Species	kg/45.4 kg	lb/100 lb	/kg	/lb	/kg	/lb	Samples
T. americana	—	—	—	—	6.6	3	2
	34.1	75	6.6–17.6	3.0–8.0	11	5	15+
	—	—	20–32.1	9.1–14.6	—	—	—
T. cordata	36.3	80	24.9–38.3	11.3–17.4	30.4	13.8	57+
	—	—	48.8–65.1	22.2–29.6	—	—	—
T. x europaea	—	—	23.3–29.7	10.6–13.5	—	—	—
T. platyphyllos	—	—	25.1–30.6	11.4–13.9	—	—	—
T. tomentosa	—	—	20.0–25.1	9.1–11.4	—	—	—

Sources: Brinkman (1974), Heit (1977).

good germination for all species and seedlots have not been developed. Much variability exists among species and seedlots in regards to permeability of the pericarp and seedcoat, as well as stratification requirements.

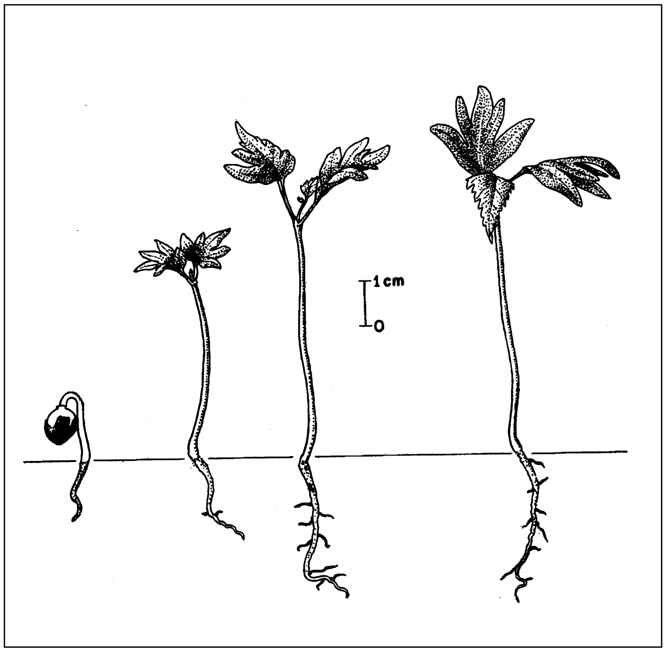
In Europe, dormancy in littleleaf linden is overcome by the use of warm incubation or acid scarification, followed by stratification (Suszka and others 1996). Fully imbibed seeds are first stored for 4 months at 20 to 25 °C (or scarified with concentrated sulfuric acid for 12 minutes), then stratified at 3 °C for 14 to 18 weeks. Stratification should be stopped when the first seeds start to germinate.This complete process may take 8 or 9 months.

Germination tests. Germination is epigeal (figure 4). Optimum germination occurs at temperatures above 20 °C (68 °F), but seeds will germinate at temperatures as low as 2 °C once stratification requirements have been satisfied (Spaeth 1934). Thus, seeds should be checked periodically for radicle emergence during stratification. Light is not required for germination (Heit 1967). The use of any stratification procedure requires far too much time to be used in routine germination testing, however, so rapid estimates of viability are recommended for this purpose. This can be done with tetrazolium staining, indigo-carmine staining, or excised embryo tests (ISTA 1996; Suszka and others 1996). However, these tests require removal of the pericarp and the seedcoat without damaging the embryo. Tetrazolium staining is the most common test. It requires soaking seeds in water for 18 to 24 hours, removing all or a large part of the seedcoat, and soaking the seeds in a 1% tetrazolium solution for 24 to 48 hours at 30 °C.

Pitel and Wang (1988) found that both the rate and percentage of germination of seeds of American linden were increased by treating scarified seeds with a solution of kinetin (1 mg/liter) and gibberellic acid (GA_3, 500 mg/liter. Over 90% germination was obtained after 60 to 80 days at 4 °C. However, GA did not improve germination percentage of seedlots of littleleaf, bigleaf, and silver linden (Magherini and Nin 1993). The conflicting results are likely due to the level of gibberellin present. Natural levels of GA exist in dormant, nonstratified seeds and a sudden increase in the quantity of gibberellin is observed from the sixth week of stratification (Nagy 1980). It is likely that a specific quantity, rather than just the presence of free gibberellins, is required to break dormancy and stimulate germination.

Traditionally, for an accurate germination test, the outer pericarp must be removed and the hard seeds must undergo scarification and stratification. However, excised embryos of American linden that were separated from the seedcoat and endosperm were able to germinate and grow when placed on an agar medium without any pretreatment (Vanstone 1982). If any of the endosperm was retained around the embryo, no growth took place, indicating an apparent lack of embryo dormancy, for the naked embryo will grow when it is separated from other parts of the seed. Some factor that restricts germination seems to be present in the endosperm and must be overcome before an intact seed can germinate. That factor would normally be overcome by stratification. The same result was obtained with bigleaf linden, for germination was induced by removing the endosperm tissue around the radicle (Nagy and Keri 1984).

Figure 4—*Tilia americana*, American linden: seedling development at 1 day and 3, 16, and 19 days after germination.



Nursery practice and seedling care. Most trees in culture are of seedling origin (Kunneman and Albers 1991). However, some are propagated by grafting, chip budding, layering, rooting winter hardwood or leafy softwood cuttings, or tissue culture (Flemer 1980; Howard 1995; Kunneman and Albers 1991). For grafting, seedling rootstocks are used, preferably of the same species as the scion, as incompatibility is a common phenomenon (Kunneman and Albers 1991). Named cultivars are grafted commonly in spring or budded in summer (LHBH 1976). Plants of littleleaf linden have been propagated by somatic embryogenesis initiated from immature zygotic embryos and then established successfully in soil (Chalupa 1990). Except for hybrids such as Crimean and European linden, all can be seed-propagated (Dirr and Heuser 1987).

Production by seed at a specified time is often relatively difficult (Dirr and Heuser 1987; Heit 1967). As described previously, seeds show delayed germination because of a tough pericarp, an impermeable seedcoat, and a dormant embryo. Seeds may remain in the ground for several years and never produce a good stand of seedlings. The degree of seedcoat hardness and embryo dormancy varies within and among seedlots for most species (Hartmann and others 2002). Also, germination is irregular, and unknown seed sources and hybridization between species have given rise to variability among seedlings (Kunneman and Albers 1991). In addition, Heit (1977) found that several lots of seeds of bigleaf and silver lindens from Europe contained high percentages of empty seeds, from 20 to 72% (Heit 1977). This condition should always be checked before sowing or treating seeds.

Mature fall-collected seeds may be sown in spring following scarification and stratification (see Pregermination treatments). An alternate method is to collect seeds early, before the pericarp turns brown and sow in the fall. Early seed collections may result in seeds that have soft seedcoats that do not require scarification (Heit 1977). However, some propagators have harvested early and obtained inconsistent results, with the seeds sometimes decaying. Late-harvested seeds may also be germinated the first season but require more treatment than seeds harvested at the ideal stage of maturity (Vanstone 1978).

Seeds are sown in shallow rows—6 to 13 mm ($^1/_4$ to $^1/_2$ in)—in beds and covered with sand to aid in seedling emergence. The emerging seedlings are very delicate and subject to sun scald, so lathe screens or shade netting over the seedbeds greatly improves seedling stands (Flemer 1980). Fall-sown seedbeds should be mulched, protected from rodent damage, and kept moist until germination begins in the spring (Vanstone 1978). Good stands of littleleaf, bigleaf, and silver lindens are normal, but seeds of American linden exhibit great variation in germination from year to year (Flemer 1980). When poor stands result, seedlings should be removed carefully so as not to disturb the bed, for additional germination often occurs the second year after planting. Seedlings are usually outplanted as 1+0 or 2+0 stock.

References

Ayers GS. 1993. Reconsidering the basswoods: 11. The native American basswoods. American Bee Journal 133(5): 337–340.

Bremness L. 1994. Herbs. London: Dorling Kindersley: 88.

Brinkman KA. 1974. *Tilia* L., basswood, linden. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk 450. Washington, DC: USDA Forest Service: 810–812.

Burgess KS. 1991. *Tilia tomentosa*. Public Garden: Journal of the American Association of Botanical Gardens and Arboreta 6(1): 39.

Chalupa V. 1990. Plant regeneration by somatic embryogenesis from cultured immature embryos of oak (*Quercus robur* L.) and linden (*Tilia cordata* Mill.). Plant Cell Reports 9(7): 398–401.

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

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

Flemer W III. 1980. Linden propagation: a review. Combined Proceedings of the International Plant Propagators' Society 30: 333–336.

Haller JM. 1995. *Tilia americana*, linden: a neglected jewel. Arbor Age 15(7): 32–33.

Hartmann HT, Kester DE, Davies FT Jr, Geneve RL. 2002. Hartmann and Kester's plant propagation: principles and practices. 7th ed. Upper Saddle River, NJ: Prentice-Hall. 880 p.

Heit CE. 1967. Propagation from seed: 7. Successful propagation of six hardseeded group species. American Nurseryman 125(12): 10–12, 37–41, 44–45.

Heit CE. 1977. Propagation from seed: 27. Collecting, testing and growing tilia linden species. American Nurseryman 146(7): 10–11, 100–110.

Howard BH. 1995. Opportunities for developing clonal rootstocks from natural seedlings of *Tilia* spp. Journal of Horticultural Science 70(5): 775–786.

ISTA [International Seed Testing Association]. 1996. International rules for seed testing. Seed Science and Technology 24(suppl.): 335.

Kunneman BPAM, Albers MRJ. 1991. Linden trees (*Tilia* spp.). In: Bajaj YPS, ed. Biotechnology in agriculture and forestry: 16. Trees III Berlin: Springer-Verlag:152–163.

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

Magherini R., Nin S. 1993. Experiments on seed germination of some *Tilia* spp. Acta Horticulturae 331: 251–258.

Nagy M. 1980. Dormancy in fruits of *Tilia platyphyllos* Scop.: 4. Changes in the endogenous gibberellin content during stratification. Acta Agronomica 29: 1–11.

Nagy M., Keri A. 1984. Role of the embryo in the cytolysis of the endosperm cells during the germination of the seeds of *Tilia platyphyllos* Scop. Biochemie und Physiologie der Pflanzen 179: 145–148.

Pellett H, Vogel K, McNamara S, Zuzek K. 1988. Relative growth rate and plant habit of linden taxa. Journal of Environmental Horticulture 6(2): 48–52.

Pigott CD, Huntley JP. 1981. Factors controlling the distribution of *Tilia cordara* at the northern limits of its geographical range: 3. Nature and causes of seed sterility. New Phytologist 87(4): 817–839.

Pitel JA, Cheliak WM, Wang BSP. 1989. Some biochemical changes associated with stratification and germination of basswood seeds. Seed Science and Technology 17(1): 57–71.

Pitel JA, Wang BSP. 1988. Improving germination of basswood (*Tilia americana* L.) seeds with gibberellic acid. Seed Science and Technology 16(1): 273–280.

Plotnik A. 2000. The urban tree book: an uncommon field guide for city and town. New York: Three Rivers Press: 211–215.

Rehder A. 1990. Manual of cultivated trees and shrubs hardy in North America. 2nd ed. Portland, OR: Dioscorides Press. 996 p.

RHS [Royal Horticultural Society]. 1994. The new Royal Horticultural Society dictionary index of garden plants. Griffiths M, ed. London: Macmillan. 1234 p.

Spaeth JN. 1934. A physiological study of dormancy in *Tilia* seed. Cornell University Agricultural Experiment Station Memoir 169: 1–71.

Suszka B, Muller C, Bonnet-Masimbert M. 1996. Seeds of forest broadleaves, from harvest to sowing. Gordon A, trans. Paris: Institut National de la Recherche Agronomique. 294 p.

Vanstone DE. 1978. Basswood (*Tilia americana* L.) seed germination. Combined Proceedings of the International Plant Propagators' Society 28: 566–570.

Vanstone DE. 1982. Seed germination of American basswood in relation to seed maturity. Canadian Journal of Plant Science 62(3): 709–713.

Meliaceae—Mahogany family

Toona ciliata Roemer

Australian toon

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Synonyms. *Toona australis* Harms, *Cedrela toona* var. *australis* (Roxb.) C. DC.

Other common names. toona, Australian redcedar, Burma-cedar.

Growth habit, occurrence, and use. Distributed in a natural range from India to Queensland, Australia (Francis 1951; Webb and others 1984), Australian toon—*Toona ciliata* Roemer—is the only species of *Toona* important in Hawaii and Puerto Rico. It was introduced into Hawaii from coastal rain forest areas of Australia in 1914 (Carlson and Bryan 1959; Streets 1962). Several small plantings of toon of an Indian provenance have reached sawlog size in Puerto Rico. Australian toon is a deciduous timber tree that attains heights of 30 to 43 m. It keeps its leaves longer on moist sites than on drier sites, and sometimes trees are said to be evergreen. Toon has been widely planted because the wood is valued for cabinets, furniture, decorative veneer, boats, and musical instruments (Chudnoff 1984). The red, often highly figured, wood is durable and seasons rapidly (Carlson and Bryan 1959; Francis 1951).

Flowering and fruiting. In Hawaii, Australian toon flowers from April to June. The flowers are bisexual. The 5-valved, teardrop-shaped capsules are 18 to 25 mm long (figures 1 and 2), in pendulous clusters, ripening during July to September. Seeds are disbursed during August to October (Walters 1974). Trees begin to produce seeds as early as 5 years of age, but generally do not do so with regularity or in quantity until they are 10 to 15 years old (Carlson and Bryan 1959).

Collection, extraction, and storage. The capsule turns from green to brown or reddish brown when ripe. When the first capsule in a cluster dehisces, the whole cluster should be picked. Clipping fruited branches using a pruning pole or cherry picker is recommended for seed orchards or open-grown trees. Climbing or felling will be necessary to collect capsules from mature trees in stands. The harvested fruit should be spread on trays in the sun to dry. The light

Figure 1—*Toona ciliata*, Australian toon: seed.

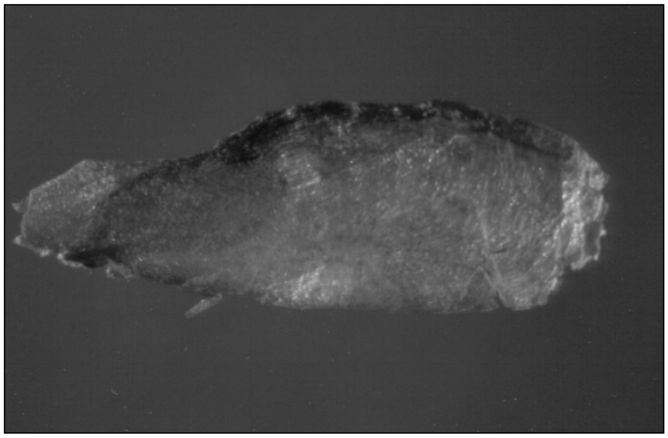
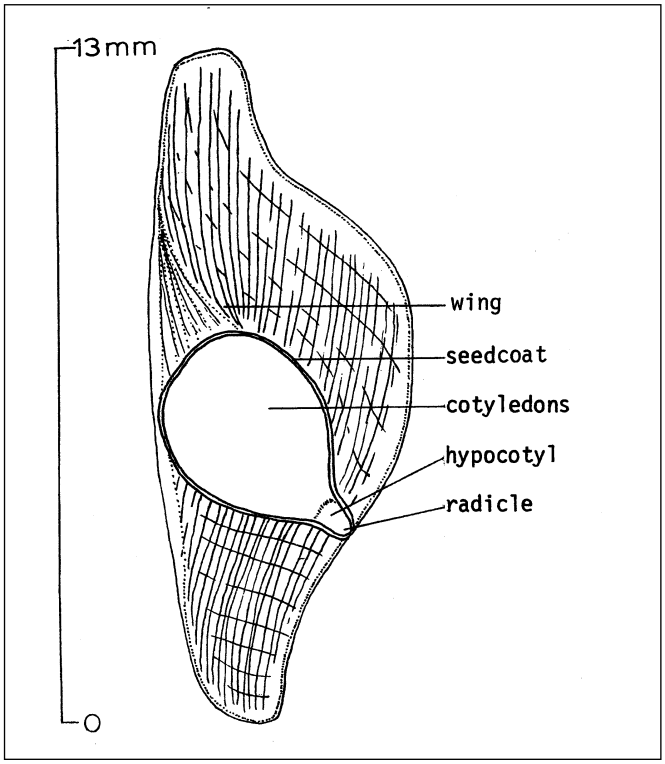


Figure 2—*Toona ciliata*, Australian toon: longitudinal section through a seed with wing attached.



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brown, membranous winged seeds (figures 1 and 2) fall from the capsule as the fruit dehisces. Agitation aids the separation of seeds from the fruits. Various seed cleaners can be used to separate the seeds from chaff. Ten samples showed from 293,000 to 375,000 cleaned seeds/kg (133,000 to 174,000/lb) (Walters 1974). Seed purity was about 84% (Walters 1974). Toon seeds can be stored dry in sealed polyethylene bags at about 1 °C (Walters 1974). Even with this apparent orthodox storage behavior, however, storage life is reported to be only from 6 to 12 months (Webb and others 1984).

Germination. Australian toon seeds germinate without special treatment, but stratification for 30 days at 3 °C in plastic bags greatly increases the speed of germination. A water soak also may speed up germination (Walters 1974). Full germination of 90% of unstratified seedlots occurred in 2 weeks; full germination of 96% of stratified seedlots occurred in 1 week (Walters 1974). Another source (Webb and others 1984) cites 40 to 60% germination of fresh seeds. Germination is epigeal.

Nursery practice. Australian toon seeds can be sown in Hawaii and Puerto Rico during any month of the year, but best results in Hawaii are obtained from March to November sowings and in Puerto Rico from April and May sowings. Seeds for bareroot seedling production are broadcast into precut lines. The lines are about 12 mm deep and about 15 cm apart. Most of the seeds that fall away from the lines are put in place as the lines are covered with soil. The beds are made level to prevent washing. The soil is kept moist by frequent watering. No mulch or shade is used. Seedling density in the beds is about 160 to 270 seedlings/m^2 (15 to 25/ft^2). Seedlings are outplanted as 1+0 or $1^1/_2$+0 stock (Walters 1974). Seedlings are now more frequently grown containerized in plastic nursery bags. Seeds are germinated in germination trays or beds and transplanted to the containers after they have developed 2 or 3 leaves. Seedlings can also be planted as striplings or stumps (Webb and others 1984). Australian toon seedlings grow slowly at first and should be given shade for 2 months. Potted stock reaches plantable size in 18 to 24 months (Webb and others 1984). Attacks of the shootborer *Hypsipyla grandella* (Zeller), which usually prohibits planting *Cedrela* species in the Neotropics, are absent or unimportant in toon plantations (Viga 1976; Whitmore and Medina Gaud 1974).

References

Carlson NK, Bryan, LW. 1959. Hawaiian timber for coming generations. Honolulu: Trustees of the Bernice P. Bishop Estate. 112 p.

Chudnoff M. 1984. Tropical timbers of the world. Agric. Handbk. 607. Washington, DC: USDA Forest Service. 464 p.

Francis WD. 1951. Australian rain-forest trees. Sydney: Commonwealth of Australia, Forestry and Timber Bureau. 469 p.

Streets RJ. 1962. Exotic forest trees in the British Commonwealth. Oxford, UK: Clarendon Press. 765 p.

Viga WM. 1976. Comportamento do 'cedro australiano', *Toona ciliata* M. Roem. var. *australis* (F. & M.) D. DC., face a suceptibilidade do ataque de *Hypsipyla grandella* (Zeller). Silvicultura em São Paulo 10: 109–118.

Walters GA. 1974. *Toona australis*, Australian toon. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 813–814.

Webb DB, Wood PJ, Smith JP, Henman GS. 1984. A guide to species selection for tropical and sub-tropical plantations. Trop. For. Pap. 15. Oxford, UK: Oxford University, Commonwealth Forestry Institute, Unit of Tropical Silviculture. 256 p.

Whitmore JL, Medina Gaud S. 1974. White peach scale attack on toon in Puerto Rico. Journal of Agriculture of the University of Puerto Rico 58(2): 276–278.

Taxaceae—Yew family

Torreya Arn.

torreya

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Growth habit, occurrence, and uses. The genus *Torreya* includes 7 species of conifer trees found in North America and eastern Asia (Little 1979; Price 1990). These species of limited distribution represent a genus that in earlier geologic times was widespread in the Northern Hemisphere—Europe, Greenland, Alaska, British Columbia, Oregon, Colorado, Virginia, and North Carolina (Abrams 1955; Boeshore and Gray 1936; Florin 1963; Schwartz and Hermann 1993a). Two species are native in the United States: Florida torreya is endemic to a small area in Florida and Georgia, and California torreya to central California (table 1). Little genetic variability has been found among populations of Florida torreya in contrast to those of California torreya (Schwartz 1993). Although growing in markedly different climates, the 2 species responded similarly in water stress tests (Schwartz and others 1995).

California torreya is a slow-growing, medium-sized tree found along streams and in canyon bottoms and other moist locations (Griffin and Critchfield 1976; Storer and Usinger 1963; Sudworth 1908). In its shrub form, it is found on serpentine soils and in chaparral. In elevation, California torreya ranges from coastal lowlands to almost 2,130 m in the southern Sierra Nevada. Under very favorable conditions, trees may grow to 23 m or more in height and 60 to 90 cm in diameter (Sudworth 1908). The tallest tree now on record is 29.3 m tall and 638 cm in circumference at 137 cm above ground (AFA 2000).

Florida torreya, also a slow-growing tree, is an endangered species found only at low elevations on ravine slopes 12 to 45 m above constant running streams on the east bank of the Apalachicola River and tributaries in Florida and Georgia and in a colony on low flat land that is 10 km west of the river (Kurz 1938; Nicholson 1990; Schwartz and Hermann 1993a&b). Florida torreya is commonly associated with seepage locations on soils ranging from coarse or fine sand to clay with limestone pebbles (Kurz 1938; USFWS 1986). In their native habitat, mature trees have reached 15 to 20 m in height and 30 to 60 cm in diameter (Harrar and Harrar 1962; Nicholson 1990; Schwartz and others 1995). However, due to severe population decline since the 1950s (the primary cause of this decline is unknown), the 1,500 or fewer immature survivors are generally less than 2 m tall (Bronaugh 1996; Schwartz and Herman 1999; Schwartz and others 1995). The tallest existing trees are found in several plantings outside of the species' endemic habitat; the largest, in North Carolina, measures 13.7 m tall and 277 cm in circumference (AFA 2000).

Because of their low availability, uses of both species of torreya are limited. Their wood is aromatic, rot-resistant, fine-grained, and excellent for cabinet-making (Burke 1975;

Table 1—*Torreya,* torreya: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
***T. californica* Torr.** *T. myristica* Hook. *Tumion californicum* (Torr.) Greene	**California torreya,** California-nutmeg, stinking-yew, stinking-cedar	Central California—scattered in the Coast Ranges and on western slopes of the Cascades & Sierra Nevada
***T. taxifolia* Arn.** *Tumion taxifolium* (Arn.) Greene	**Florida torreya,** Florida-nutmeg, stinking-cedar	E bank of Apalachicola River & tributaries from Decatur Co., Georgia, to Liberty Co., Florida, & an outlying population in Jackson Co., Florida

Sources: Griffin and Critchfield (1976), Kurz (1938), Little (1979), Stalter (1990), Sudworth (1908).

Peattie 1953). Both species were used locally for such purposes as shingles, fence posts, and firewood. They grow satisfactorily outside of their native range and have received moderate use as ornamentals (Burke 1975; Sargent 1875; Wilson 1938). Fruits of California torreya were collected for food by native Californians, and the characteristics of its oil compare favorably with those of pine-nut oil for cooking purposes (Burke 1975). Squirrels have been observed eating fruits and seeds of Florida torreya and antler-rubbing scars provide evidence of use by deer (Bronaugh 1996; Nicholson 1990; Schwartz and Hermann 1993a).

Flowering and fruiting. Torreyas are dioecious. The male flowers are small, budlike, and clustered on the under sides of twigs in axils of leaves produced the previous year (Abrams 1955; Jepson 1925; Sargent 1933; Sudworth 1908). The female flowers are less numerous and occur on the lower sides of the current year's twigs. After fertilization, they develop singly into sessile, thin-fleshed arils that mature during the second season as green to purplish drupes 25 to 44 mm long (figure 1). When mature, the leathery cover eventually releases a 25- to 30-mm yellow-brown seed (Munz and Keck 1959) (figure 2). The thick woody inner seedcoat is irregularly folded into the female gametophyte, and the embryo is minute (figure 3).

Both species flower in March and April, with some flowers of Florida torreya appearing as early as January and some of California torreya extending into May (Rehder 1940; Sargent 1933; Stalter 1990; Weidner 1996). Under favorable growing conditions, Florida torreya produces male and female flowers about age 20 (Stalter 1990); in greenhouse conditions, 5-year-old sprouts produced pollen (Schwartz 1996).

Figure 1—*Torreya taxifolia*, Florida torreya: the fruit is sessile and drupe-like.

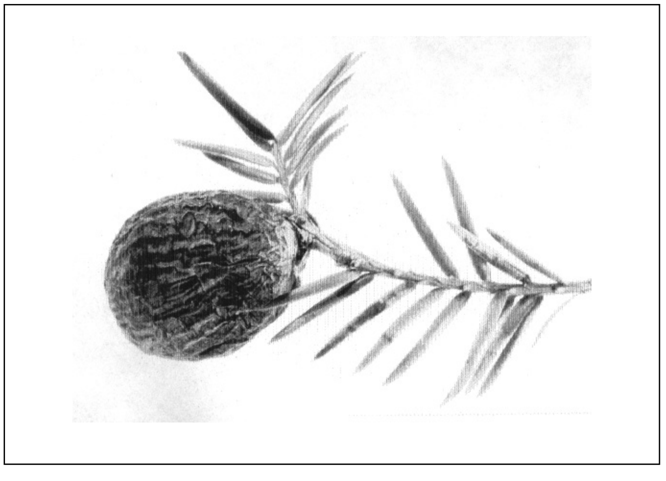


Figure 2—*Torreya*, torreya: large seeds of *T. californica*, California torreya (**left**) and *T. taxifolia*, Florida torreya (**right**).

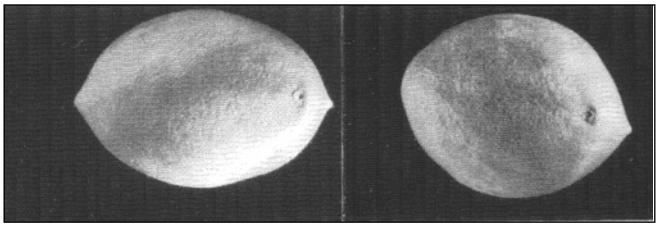
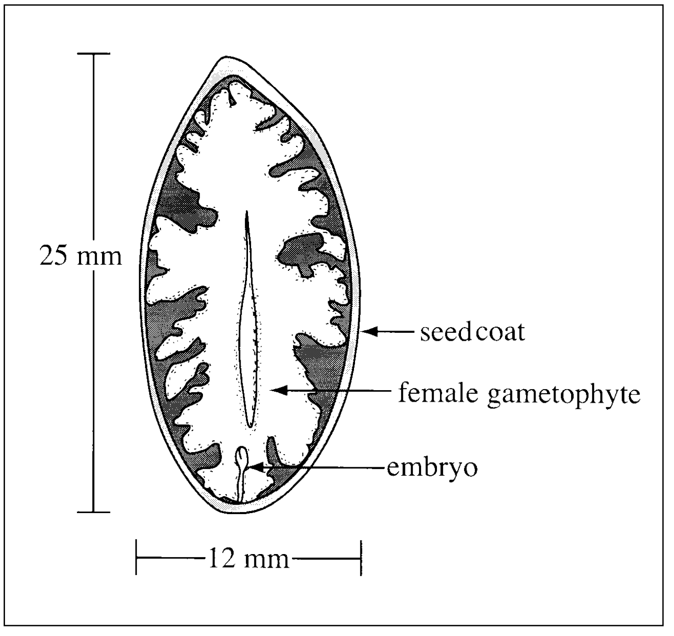


Figure 3—*Torreya californica*, California torreya: longitudinal section through a seed showing the folds of the inner seedcoat extending into the endosperm.



Information on the fruit production characteristics of both torreya species is sparse and inadequate. Fruits mature from August till November (Mirov and Kraebel 1939; Rehder 1940; Stalter 1990). At the Alfred B. Maclay Gardens in Tallahassee, Florida, fruit production from 8 trees was low and varied by tree and year. No fruits were produced in 4 years, and more than 100 fruits were available in 1985, 1986, 1987, and 1989 (Weidner 1996).

Collection, extraction and storage. Collection of Florida torreya fruits from the endemic population is not possible now because there are only scattered sexually mature male trees and no mature females (Bronaugh 1996; Schwartz and Hermann 1993a; Schwartz 1996). Trees in cultivation include less than 2 dozen reproductive females (Bronaugh 1996), so extraordinary diligence is required to collect any seeds that are produced. Fruits have been picked slightly green to gather them before the squirrels do and then held in open storage until the outer cover turned dark; then the pulp was softened in water and removed by rubbing fruits against hardware cloth (Weidner 1996).

Fruit production of California torreya is common and widespread enough to forestall concerns about shortage; several hundred pounds may be collected in single commercial collections (Callahan 1996). The fruits are generally picked from the trees but are sometimes collected after they have been shed. Seed extraction is about the same as for Florida torreya, with the softened pulp removed by water pressure and some hand rubbing (Callahan 1996). Care is needed to avoid damage to the relatively tender seedcoat. Seed quality of California torreya is generally good and can be improved sometimes by separating light seeds through flotation.

Storage experience is short-term and fragmentary because torreya seeds are generally used as available. Based on incidental observations, the seeds may be recalcitrant, as high moisture content appears necessary to maintain their viability. California torreya has been stored in moist vermiculite or sphagnum moss at 2 to 7 °C for up to 3 years (Callahan 1996). Some seeds of both species will germinate in lengthy cool or warm stratification (Callahan 1996; Weidner 1996).

Seeds of California torreya averaged 324/kg (147/lb), with a range of 243 to 421/kg (110 to 191/lb) in 3 samples (Roy 1974). Florida torreya had 496 seeds/kg (225/lb) in 1 sample at a moisture content of 8.6% (Roy 1974).

Pregermination treatments and germination tests. Standard germination test procedures have not been developed yet for torreya seeds. Both species require lengthy after-ripening and stratification, but efforts made to date have not identified methods for timely germination testing of fresh or stored seeds.

As available, fresh seeds of Florida torreya have been tested at Alfred B. Maclay State Gardens according to the 9 variations of methodology specified in the recovery plan for the species (USFWS 1986). Warm stratification in a half and half mixture of Canadian peat and coarse sand for 6 months in a greenhouse at 13 to 18 °C has produced the best results. Gentle cracking of the distal end of the seedcoat before warm stratification produced somewhat higher germination than a preliminary 20-minute soak in 10% chlorine bleach or stratification alone (table 2) (Weidner 1996).

Germination averaged lowest for sowings made directly into outdoor beds. The germination results indicate that seedcrop quality or other factors differed from year to year, and results were also not very consistent for the same pretreatment and germination sequence.

Procedures have been prescribed for determining viability of torreya seeds quickly by a tetrazolium (TZ) test on excised embryos (Moore 1985). Seed preparation involves puncturing the seedcoat, soaking the seeds in water for 18 hours, and then cutting them open to expose nutritive tissue and the distal end of the embryo. The prepared seeds are soaked in a 1% TZ solution for 24 to 48 hours, depending on temperature; nutritive tissue and embryo are then further exposed and evaluated. Viable seeds have a completely stained embryo and nutritive tissue.

Nursery practices. Torreya germination is hypogeal. Both California and Florida torreyas can be reproduced from seeds but quantities grown are so small and infrequent that nursery practices are underdeveloped.

The protocols specified in the recovery plan (USFWS 1986) and the germination resulting therefrom (table 2) are evidently the most recent, systematic, and successful attempts to produce Florida torreya seedlings for outplanting. Seedlings are slow growing and very susceptible to damping-off, so repeated fungicide drenches are necessary.

Seeds of California torreya sown untreated in the fall will germinate late the next summer or in the second spring. Germination can be obtained by April of the first season by sowing in the fall and keeping the seedbed at 7 to 10 °C (Callahan 1996). Seeds generally have high viability—90 to

Table 2—*Torreya,* torreya: germination of *T. taxifolia* seeds

Pre-germination treatment*	Germination by seed year 1985	1990	1993	Average
6 months of warm stratification	69	13	80	54.0
Bleach + 6 months of warm stratification	77	0	85	54.0
Cracking + 6 months of warm stratification	100	25	86	70.3
3 mon of warm, then 3 months of cold stratification	85	38	58	60.3
Bleach + 3 months of warm, then 3 months of cold stratification	77	25	44	48.7
Cracking + 3 months of warm, then 3 months of cold stratification	62	38	35	45.0

Source: Weidner (1996).

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98% germination. In a test of seeds stratified for 3 months, 92% germinated in 232 days after sowing (Mirov and Kraebel 1939). Two growing seasons are required to produce seedlings 15 to 25 cm tall (Callahan 1996; Wilson 1996).

Both species sprout from stumps or root crowns and can be propagated vegetatively. Metcalf (1959) described sprouting of California torreya as vigorous—"like redwood." Stalter (1990), Godfrey (1988), and others indicated that the current endemic Florida torreya population probably originated largely from vegetative propagation, but Schwartz and Hermann (1993a) concluded that most originated from seeds.

The urgency of conserving Florida torreya has stimulated development of its reproduction by cuttings (Bailo and others 1998; Nicholson 1988, 1993). Up to 91% of cuttings collected in November from trees throughout the species' native range rooted in a mixture of pumice, peat, and perlite mixture. The cuttings were potted and grown for 2 years and then shipped to botanic gardens and research institutions. A database on living Florida torreya material is maintained by The Center for Plant Conservation, headquartered at the Missouri Botanical Garden, St. Louis, Missouri.

References

Abrams L. 1955. Illustrated flora of the Pacific states: Washington, Oregon, and California. Volume I. Stanford, CA: Stanford University Press. 538 p.

AFA [American Forestry Association]. 2000. The national register of big trees 2000–2001. American Forests 106(1): 22–64.

Bailo BG, Determann R, Nicholson R, Sojkowski S. 1998. The ex situ conservation of stinking cedar. Public Garden 13(3): 9–11.

Boeshore I, Gray WD. 1936. An Upper Cretaceous wood: *Torreya antiqua*. American Journal of Botany 23: 524–528.

Bronaugh W. 1996. Champions on the brink. American Forests 102(1): 16–19.

Burke JG. 1975. Human use of the California nutmeg tree, *Torreya californica*, and of other members of the genus. Economic Botany 29: 121–139.

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

Florin R. 1963. The distribution of conifer and taxad genera in time and space. Acta Horti Bergiani 20(4): 121–312 [Torreya: 262–266].

Godfrey RK. 1988. Trees, shrubs, and woody vines of northern Florida and adjacent Georgia and Alabama. Athens, GA: University of Georgia Press. 734 p.

Griffin JR, Critchfield WB. 1976. The distribution of forest trees in California. Res. Pap. PSW-82 (reprinted with supplement). Berkeley, CA: USDA Pacific Southwest Forest and Range Experiment Station. 118 p.

Harrar ES, Harrar JG. 1962. Guide to southern trees. 2nd ed. New York: Dover. 709 p.

Jepson WL. 1925. A manual of the flowering plants of California. Berkeley: University of California. 1238 p.

Kurz H. 1938. *Torreya* west of the Apalachicola River. Proceedings of the Florida Academy of Sciences 3: 66–77.

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

Metcalf W. 1959. Native trees of the San Francisco Bay region. Berkeley: University of California Press. 72 p.

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

Moore RP, ed. 1985. Handbook on tetrazolium testing. Zurich: International Seed Testing Association: 73.

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

Nicholson R. 1990. Chasing ghosts: the steep ravines along Florida's Apalachicola River hide the last survivors of a dying tree species. Natural History 12/90: 8, 10–13.

Nicholson R. 1993. Rooting *Torreya taxifolia*, an endangered conifer of the Florida panhandle. Botanic Gardens Conservation News 2(2): 1–3.

Nicholson RG. 1988. Propagation of some woody endemic plants of eastern North America. Combined Proceedings of the International Plant Propagators' Society 37: 468–473.

Peattie DC. 1953. A natural history of western trees. Boston: Houghton Mifflin. 751 p.

Price RA. 1990. The genera of Taxaceae in the southeastern United States. Journal of the Arnold Arboretum 71: 69–91.

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

Roy DF. 1974. *Torreya* Arn., torreya. In: Schopmeyer CS, tech coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 815–816.

Sargent CS. 1933. Manual of the trees of North America (exclusive of Mexico). 2nd ed. Cambridge, MA: Riverside Press. 910 p.

Sargent HW. 1875. A treatise on the theory and practice of landscape gardening adapted to North America. New York: Orange Judd Co. 592 p.

Schwartz MW. 1993. Allozyme variation of the endangered Florida torreya (*Torreya taxifolia*). Canadian Journal of Forest Research 23: 2598–2602.

Schwartz MW. 1996. Personal communication. Davis: University of California.

Schwartz MW, Hermann SM. 1993a. The continuing population decline of *Torreya taxifolia* Arn. Bulletin of the Torrey Botanical Club 120(3): 275–286.

Schwartz MW, Hermann SM. 1993b. The population ecology of *Torreya taxifolia*: habit evaluation, fire ecology, and genetic variability. Final Rep. Tallahassee: Florida Game and Fresh Water Fish Commission, Nongame Wildlife Program. 76 p.

Schwartz MW, Hermann SM. 1999. Is slow growth of the endangered *Torreya taxifolia* (Arn.) normal? Journal of the Torrey Botanical Society 126(4): 307–312.

Schwartz MW, Hermann SM, Vogel CS. 1995. The catastrophic loss of *Torreya taxifolia*: assessing environmental induction of disease hypotheses. Ecological Applications 5(2): 501–516.

Stalter R. 1990. *Torreya taxifolia* Arn., Florida torreya. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Agric. Handbk. 654. Volume 1, Conifers. Washington, DC: USDA Forest Service: 601–603.

Storer TI, Usinger RL. 1963. Sierra Nevada natural history. Berkeley: University of California Press. 374 p.

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

USFWS [USDI Fish and Wildlife Service]. 1986. Florida torreya (*Torreya taxifolia*) recovery plan. Atlanta: USDI Fish and Wildlife Service. 42 p.

Weidner B. 1996. Personal communication. Tallahassee: Florida Department of Environmental Protection, Alfred B. Maclay State Gardens.

Wilson A. 1938. The California nutmeg tree in cultivation. Madroño 4: 166–167.

Wilson B. 1996. Personal communication. San Luis Obispo, CA: Los Pilitas Nursery.

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Euphorbiaceae—Spurge family

Triadica sebiferum (L.) Small

tallowtree

Franklin T. Bonner

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Synonym. *Sapium sebifera* (L.) Roxb.

Other common name. Chinese tallowtree.

Growth habit, occurrence, and use. Tallowtree—*Triadica sebiferum* (L.) Small—is a small deciduous tree that attains heights of about 10 m at maturity. A native of China, the species has been widely planted in the coastal plain from South Carolina and Florida to Texas, Oklahoma, and Arkansas. The bright red fall foliage makes the tree a popular ornamental, and the seeds have some value as wildlife food. In Asia, oils are extracted from the seeds and waxes from the seedcoats for use in a wide variety of products, including diesel fuel additives, soaps, candles, and cloth dressings (Bringi 1988; Samson and others 1985; Singh and others 1993; Vines 1960). Tallowtree readily escapes from cultivation and is common along roadsides of the Gulf Coast, where many consider it a pest species.

Flowering and fruiting. Both pistillate and staminate flowers are borne on the same yellowish green spike in the spring. The fruit, ripening in October to November, is a rounded, 3-lobed capsule, 8 to 13 mm in diameter (Vines 1960). Its greenish color changes to a brownish purple at maturity (Bonner 1974). There are 1 to 3 white waxy seeds per capsule (figures 1 and 2). In India, this species bears fruit as early as the third year after planting, and mature trees can yield 20 to 25 kg (Singh and others 1993).

Collection, cleaning, and storage of seeds. The dry capsules can be collected from the trees by hand after dehiscence (fruit-splitting) has started. Seeds can be removed from the capsules by gentle flailing in burlap bags or by being run through macerators at slow speeds. On a sample of capsules from a tree in central Mississippi, the following data were obtained (Bonner 1974):

Capsules per volume	30,300/hl (10,700/bu)
Seeds per weight	6,100/kg (2,780/lb)
Moisture content of seeds (% of fresh weight)	6
Sound seeds (% of total seeds)	90

Figure 1—*Triadica sebiferum*, tallowtree: seed.

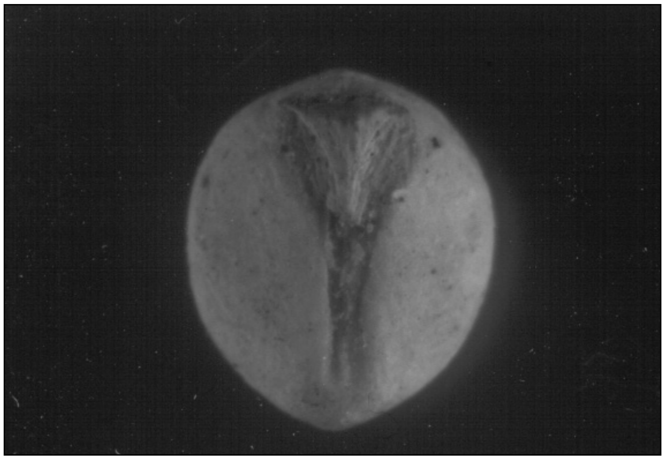
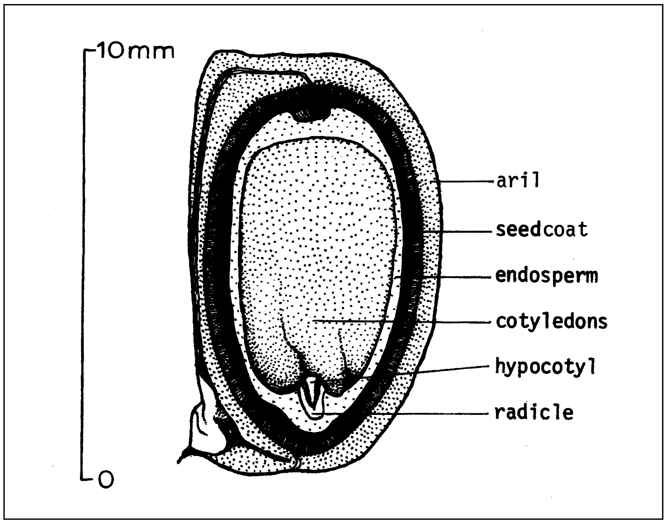


Figure 2—*Triadica sebiferum,* tallowtree: longitudinal section through a seed.



There are no known storage tests with seeds of tallow tree, but drying the sample noted above to 6% without killing the seeds indicates that they are orthodox in storage behavior. Short-term storage at low temperatures and seed moisture contents should be no problem. The seeds have a lipid content of about 20% (Zubair and others 1978), how-

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ever, so sub-freezing temperatures should be used for any storage over 5 years.

Germination tests. Seeds of tallowtree are not dormant and do not typically require pretreatment. Germination results of 60 to 62% in germination beds have been reported from India (Singh and others 1993). Fresh seeds from the Mississippi collection had a laboratory germination of 38% after 30 days on moist Kimpak at day-night temperatures of 30 and 20 °C. The seeds received 8 hours of light during the day temperature. Moist stratification at 2 °C for 34 days increased the rate of germination but did not boost the percentage. Sixty days of stratification apparently induced a deep secondary dormancy (Bonner 1974). Tallowtree can also be propagated by cuttings from root suckers (Singh and others 1993).

References

Bonner FT. 1974. *Sapium sebiferum* (L.) Roxb., tallowtree. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 540. Washington, DC: USDA Forest Service: 760.

Bringi NV. 1988. Progress in the chemistry and technology of non-traditional oilseeds/oils. Journal of the Oil Technologists' Association of India 20(1): 1–9 [Seed Abstracts 16: 392; 1993].

Samson WD, Vidrine CG, Robbins JWD, Case JI. 1985. Chinese tallow seed oil as a diesel fuel extender. Transactions of the American Society of Agricultural Engineers 28: 1406–1409.

Singh K, Kapur SK, Sarin YK. 1993. Domestication of *Sapium sebiferum* under Jammu conditions. Indian Forester 119: 36–42.

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

Zubair MU, Oppal M, Zaheer Z. 1978. New possible indigenous source of fat. Pakistan Journal of Scientific and Industrial Research 21(3/4): 136–137 [Biological Abstracts 67(9): 53823; 1979].

Pinaceae—Pine family

Tsuga Carr.

hemlock

Jill R. Barbour, Robert H. Ruth, and Robert P. Karrfalt

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Growth habit, occurrence, and use. Trees of the hemlock genus—*Tsuga* spp.—are tall, straight, late successional climax evergreens with conical crowns and slender, horizontal to pendulous branches. Fourteen species have been reported; 4 of these are native to the United States and the others to the Himalayas, China, Taiwan, and Japan. The name *tsuga* is a Japanese word meaning "tree-mother" (Dirr 1998). Native American names for the North Country (that is, Canada), *hoe-nadia*, and for the lands of upper New York, *oh-neh-tah,* both mean "land of the hemlock" (Dirr 1998).

Of the 4 native species in the United States (table 1), both eastern and western hemlocks are used commercially for lumber and pulpwood. The bark of eastern hemlock has been a source of tannin for the leather industry. In central and southern Oregon and some other areas, mountain hemlock has become an important part of the softwood sawtimber volume.

Much of eastern hemlock has been severely affected by the hemlock woolly adelgid—*Adelges tsugae* Annand—in New England and the mid–Atlantic region (Dirr 1998). The hemlock woolly adelgid has also been noted on Carolina hemlock in the Tallulah Gorge in northeastern Georgia (Price 2002). Although the hemlock woolly adelgid occurs on mountain and western hemlocks from southern California to southeastern Alaska, these 2 species are resistant to the insect (McClure and others 2001).

Carolina hemlock overlaps the southern range of eastern hemlock, but it is a smaller tree with longer needles and cones. The wood serves the same uses as eastern hemlock, but the species is not abundant and of only minor commercial importance. Carolina hemlock is especially suitable for ornamental plantings.

Mountain hemlock is important mainly for watershed protection and the scenic beauty it adds to subalpine environments of Pacific Northwest mountain ranges. Its populations are disjunct due to the physical separation of its high-elevation sites. Due to the disjunct nature of its distribution, mountain hemlock was included in a world list of threatened species (Farjon and others 1993). It varies in size from a sprawling shrub at the timberline to a medium-sized forest tree.

Geographic races. Eastern, western, and mountain hemlocks have long north–south ranges and grow in a variety of habitats. Through natural selection, they apparently have developed numerous genetic types, each adapted to its local habitat.

Table 1—*Tsuga*, hemlock: nomenclature and occurrence

Scientific name	Common name(s)	Occurrence
T. canadensis **(L.) Carr.**	**eastern hemlock,** Canada hemlock, hemlock	Nova Scotia to S Ontario, S to N Georgia & Alabama
T. caroliniana **Engelm.**	**Carolina hemlock**	Mountains of Virginia to South Carolina to Georgia & Tennessee
T. heterophylla **(Raf.) Sarg.**	**western hemlock,** Pacific hemlock, hemlock	Pacific Coast from Alaska to Washington, Oregon, & California & in mtns of N Idaho & NW Montana
T. mertensiana **(Bong.) Carr.**	**mountain hemlock,** black hemlock	Pacific Coast regions from Cook Inlet, Alaska, to central California & to W Montana

Source: Ruth (1974)

A series of experiments with eastern hemlock (Baldwin 1930; Nienstaedt 1958; Olson and others 1959; Stearns and Olson 1958) showed that seedlings grown from southern seed sources tend to harden-off and go dormant later in the autumn and make more total growth (and the seeds requires less stratification) than those from northern sources. Southern seeds germinate best when temperatures approach 21 °C, whereas northern seeds do best near 13 °C. Seedlings from southern sources planted in Wisconsin grew late into the fall and were damaged more severely by frost than were their northern counterparts.

Similar results were obtained with western hemlock from 18 western provenances planted at various sites in Great Britain. Western hemlock seedlings from southern parts of this species' native range grew faster and set terminal buds later in the season than those from the North. However, when planted in northern Great Britain, they suffered severe damage from frost and cold winds. Frost damage was reduced if seedlings were planted under a high forest cover (Lines and Aldhous 1962, 1963; Lines and Mitchell 1969). Seed weight was found to decrease significantly from south to north, with collections from Alaska expected to have at least 110,000 more seeds/kg (50,000/lb) than western hemlock seeds from Oregon (Buszewicz and Holmes 1961). Kuser and Ching (1981) found significant differences among provenances in 100-seed weights, but there were only low correlations of seed weight with latitude, elevation, or distance from the Pacific Ocean. An increase in elevation on Vancouver Island, British Columbia, tended to increase germination rate and total germination (Edwards 1973).

Provenances of western hemlock with the fastest growing seedlings are from the southern part of the range; those with the slowest growing seedlings are from the northern part of the range as well as from the upper elevational extremes in the Rocky Mountains (Kuser and Ching 1981). In the case of western hemlock, the tree seed zones delineated by the Western Forest Tree Seed Council (WFTSC 1966b) may be used in Oregon and Washington. Those developed by the Organization for Economic Cooperation and Development (Piesch and Phelps 1970) may be used in British Columbia. A seed transfer zone map has been published for Oregon (Randall 1996).

Jeffrey hemlock—*Tsuga* × *jeffreyi* (Henry) Henry—has been reported as a cultivated hybrid of western and mountain hemlocks (Little 1979; Means 1990; Rehder 1949). Some French taxonomists proposed that mountain hemlock itself is an intergeneric hybrid of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and western hemlock and they renamed it *Tsuga–Picea hookeriana* (Campo-Duplan and Gaussen 1948; Vabre-Durrieu 1954a&b). They considered a California form of mountain hemlock known as *Tsuga crassifolia* Flous to be a cross of mountain hemlock and Engelmann spruce (*Picea engelmannii* Parry ex Engelm). These hypotheses were rejected by American foresters, largely because of the absence of backcrosses and hybrid swarms in the field (Duffield 1950; Means 1990).

Many horticultural varieties of hemlock, including compact, weeping, spreading, and columnar forms, have been described (Dallimore and Jackson 1957; den Ouden and Boom 1965; Rehder 1940, 1949; Swartley 1945). They are widely planted as ornamentals throughout the temperate parts of the Northern Hemisphere.

Flowering and fruiting. Hemlocks are monoecious plants. Male and female strobili develop in clusters near the ends of lateral branches; each one consists of a central axis with spirally arranged microsporophylls. The male sporangia open transversely and the pollen is simple (Radford and others 1968). In mountain hemlock, pollen release is both protogynous and synchronous with female receptivity (Means 1990). The pollen is extremely sensitive to drying, which can prevent seed development in eastern hemlock (Godman and Lancaster 1990).

Ovulate strobili are erect, with nearly orbicular scales (each scale has 2 basal ovules), subtended by a membranous bract about the same length as the scale; they occur terminally on the lateral shoots of the previous year. In western hemlock, the total number of ovuliferous scales per cone is about 23 and about 70% of the scales are fertile (Colangeli and Owens 1989a). High temperatures in July the year before cone production favor flower initiation in mountain hemlock (Means 1990).

Hemlock is the only genus of the Pine family in which the mechanism of pollination involves nonmicropylar germination. Because of this difference, western hemlock seed cones are receptive for a much longer period than those of other conifers. Cones are receptive from shortly after bud burst until cone closure. The average number of days between bud burst and cone closure for western hemlock was 34 days in 1983 and 23 days in 1984 (Colangeli and Owens 1989a). Maximum pollination and seed efficiency (filled seed divided by the potential number of seeds per cone) is obtained when 50 to 75% of the cones have emerged beyond the cone scales (Bramlett and others 1977; Colangeli and Owens 1989a).

Hemlock pollen does not enter the cone micropyle but attaches to the waxy layer of the exposed portion of the bracts and ovuliferous scales. The bracts of western hemlock can trap more than 100 pollen grains, the average pollen grain count per bract from controlled pollinations being 34, with a range from 2 to 116 (Colangeli and Owens 1989a). The ovuliferous scales elongate over the bracts, trapping the pollen between the bracts and scales. About 4 to 7 days after pollen germination, the pollen tubes grow into the micropyles; usually 1 to 6 pollen tubes and sometimes up to 10 pollen tubes have been found in each micropyle (Colangeli and Owens 1989a). In western hemlock, pollen is not essential for seed cone enlargement and unpollinated ovules can continue seedcoat development, but the seed will not have an embryo or gametophytic tissue (Colangeli and Owens 1990a).

Cones mature in 1 season and are small, pendant, globose to ovoid or oblong, with scales longer than the bracts (figure 1). Carolina hemlock has the largest seeds of the native hemlocks, followed by mountain hemlock and eastern hemlock, with western hemlock having the smallest seeds (table 2; figure 2). Eastern hemlock has the smallest cones; they measure 1.5 to 2.5 cm by 1 to 1.5 cm. Eastern hemlock trees grown from eastern and southern sources have larger cones than do those grown from northern and western sources (Godman and Lancaster 1990). Western hemlock cones measure 1 to 3.0 cm by 1to 2.5 cm; Carolina hemlock cones measure 2.5 to 4 cm by 1.5 to 2.5 cm. Mountain hemlock have the largest cones, which measure 3 to 6 cm by 1.5 to 3 cm (FNAEC 1993; Harlow and Harrar 1968; Hough 1947; Sargent 1933).

Cone production of hemlock usually begins when trees are 20 to 30 years of age, a little later if trees are shaded. All 4 species of hemlock bear some cones almost every year and large crops are frequent (table 3). Cones often remain on the hemlocks well into the second year, being especially conspicuous on the tops of mountain hemlock. Wisconsin had good eastern hemlock cone crops on 61% of the 32 years recorded (Godman and Lancaster 1990). Eastern hemlock trees as old as 450 years have been seen bearing cones. Western hemlock bear cones every year with heavy crops every 3 to 4 years; in Alaska good crops occur every 5 to 8 years (Packee 1990). In Washington and Oregon, mountain hemlock trees 175 to 250 years old bear medium to heavy cone crops at 3-year intervals (Means 1990). Despite the frequency of cone crops, seed viability in hemlocks is generally low. Less than half the seeds in a cone are viable (Burns and Honkala 1990).

The period of dissemination of western hemlock seeds (table 4) can extend over a full year but the seeds are only viable during their first growing season (Packee 1990; Harris 1969). Most western hemlock seeds fall within 610 m from the tree, whereas eastern hemlock seeds fall within tree height due to their small wings (Godman and Lancaster 1990). Seeds remaining in cones are usually sterile in eastern hemlock.

Figure 1—*Tsuga*, hemlock: cones of *T. canadensis*, eastern hemlock (**upper left**); *T. mertensiana*, mountain hemlock (**lower left**); *T. carolina*, Carolina hemlock (**center**); and *T. heterophylla*, western hemlock (**right**).

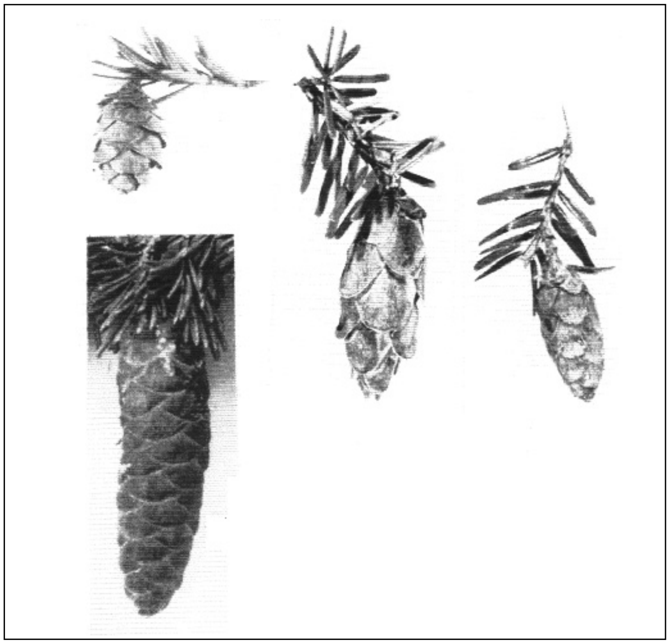


Table 2—*Tsuga*, hemlock: seed yield data

	Seeds (x1,000)/weight				
	Range		Average		
Species	/kg	/lb	/kg	/lb	Samples
T. canadensis	273–794	124–360	412	187	69
T. caroliniana	167–213	76–97	—	—	2+
T. heterophylla	417–1,120	189–508	573	260	106
T. mertensiana	132–459	60–208	251	114	6

Sources: Burns and Honkala (1990); Buszewicz and Holmes (1961), Hill (1969), Rafn (1915), Toumey and Korstian (1952), Toumey and Stevens (1928), Ruth (1974).

Table 3—*Tsuga*, hemlock: height, seed-bearing age, seedcrop frequency, and cone ripeness criteria

Species	Height at maturity (m)	Year first cultivated	Minimum seed-bearing age (yr)	Years between large seed-crops	Cone ripeness criteria: Pre-ripe color	Cone ripeness criteria: Ripe color
T. canadensis	18–30	1736	20–30	2–3	Yellow-green	Purple-brown
				15	Green	Tan to brown
T. caroliniana	12–21	1881	—	—	Purple	Light brown
T. heterophylla	18–75	1851	20–30	5–8	Green with purple tips	Brown with red-brown tips
T. mertensiana	7.5–45	1854	20–30	1–5	Yellow-green to brown	Brown

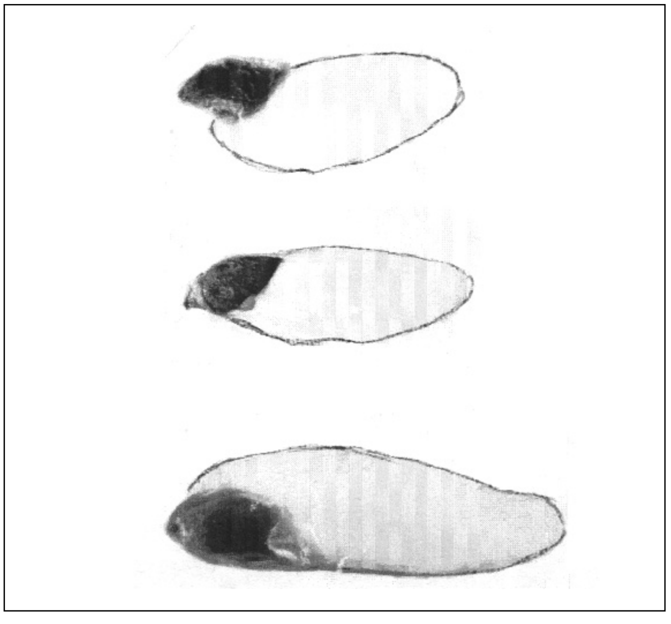
Sources: Burns and Honkala (1990), den Ouden and Boom (1965), Franklin (1968), Frothingham (1915), Harlow and Harrar (1968), Harris (1969), Hough (1947), Merrill and Hawley (1924), Olson and others (1959), Ruth (1974), Ruth and Berntsen (1955), Sudworth (1908).

Table 4—*Tsuga,* hemlock: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal
T. canadensis	Southern range to northern range	Apr–early June	Sept–Oct	Sept–winter
T. caroliniana	North Carolina to South Carolina	Mar–Apr	Aug–Sept	—
T. heterophylla	Oregon to Washington	Apr–May	Sept–Oct	Oct–May
	S British Columbia	—	Sept 15	Oct–June
	SE Alaska	Late May-June	Sept–Oct	Oct
	W central Oregon	Mid to late Apr	—	Sept–May
	Idaho	May 27–June 5	Aug	Sept 17–winter
T. mertensiana	Oregon	June	Late Sept–Oct	—
	British Columbia, Alaska	June–mid-July	Late Sept-Nov	—
	Bitterroot Mtns, Idaho	Aug	—	—

Sources: Allen (1957), Burns and Honkala (1990); Ebell and Schmidt (1963), Frothingham (1915), Garman (1951), Gashwiler (1969), Godman (1953), Green (1939), Harris (1967), Harris (1969), Heusser (1954), Hough (1947), James (1959), Leiberg (1900), Radford and others (1964), Ruth (1974), Ruth and Berntsen (1955).

Figure 2—*Tsuga*, hemlock: seeds of *T. canadensis*, eastern hemlock (**top**); *T. heterophylla*, western hemlock (**center**); and *T. carolina*, Carolina hemlock (**bottom**).

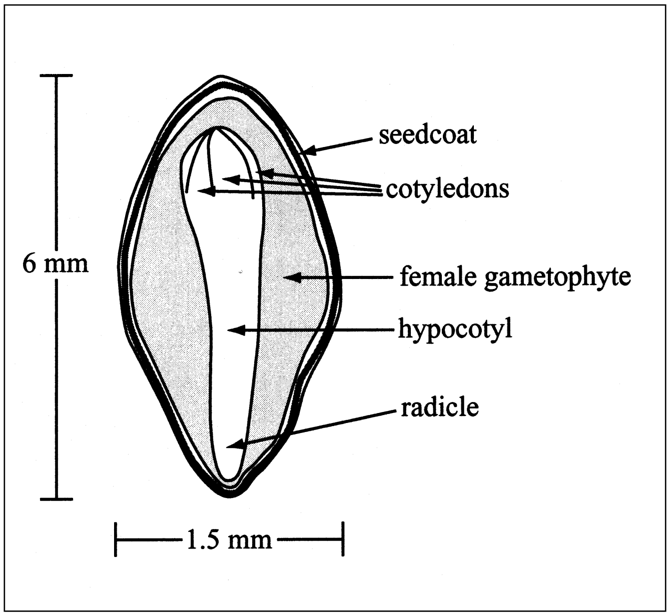


Western hemlock generally produces less than 40 seeds per cone; usually less than 20 of these are filled (Edwards 1976). At a clone bank in Victoria, British Columbia, the average number of seeds per cone was 34, and 22 seeds were filled when counted in 1983 and 1986 (Colangeli and Owens 1990b). The number of filled seeds counted on the exposed cut-face of a cone is a good predictor of total filled seeds per cone (Meagher 1996). The number of cones needed to estimate total filled seeds within ± 5 seeds ranged from 3 to 60 cones (Meagher 1996).

Prepollination ovule abortion produces small, flat seeds. Colangeli and Owens (1990b) found that it accounted for an average of 11 and 14% reduction in filled-seed yield in 1983 and 1986, respectively. Postpollination ovule abortion occurred in about 4% of the ovules, corresponding to less than 1 seed per cone (Colangeli and Owens 1990b). Insufficient pollination—which is usually the reason for low seed set—resulted in 25% empty seeds in 1983 and 66% empty seeds in 1986 (Colangeli and Owens 1990b).

Embryos have 3 to 6 cotyledons (figure 3) (Sargent 1933). Kuser and Ching (1981) found provenance variation

Figure 3—*Tsuga mertensiana*, mountain hemlock: longitudinal section through a seed.



in cotyledon number in western hemlock. Seedlots from the Rocky Mountains produced higher frequencies (15%) of 4-cotyledon seedlings than those from the Cascade Mountains or coastal zones (11%). The embryo extends the full length of the seed. Olson and others (1959) reported that embryos from eastern hemlock are about 3 mm long and 0.5 to 0.7 mm in diameter.

Collection of fruits. Hemlock cones are small and, therefore, more difficult to harvest than the larger cones of many conifers. They are most easily collected from tops of trees felled during harvest cuttings, but it is important that seeds from such collections are checked for maturity. Usually cone collection is delayed until shortly before seed dispersal to ensure full maturity of the seeds. Cones also can be harvested by the use of ladders, pole pruners, and various kinds of climbing equipment.

Based on a study of western hemlock in southern British Columbia, Allen (1958) recommended September 15th as a suitable date to begin cone collection even though cones are still green and hard. Seeds collected earlier (August 30th) had lower total germination. The germination rate of seeds collected September 15th was improved by storage and stratification. Seeds of western hemlock cones that are stored for 3 to 6 months before seed extraction had higher percentages of germinating seeds (91%) than did seeds from cones stored for 1 month before extraction (75%) (Leadem 1980). Also working with western hemlock, Harris (1969) found a few seeds viable when extracted as much as 70 days before seed dispersal. When cones were left on the tree, the percentage viability increased gradually until almost dispersal time.

Extraction and storage of seeds. Handling procedures for hemlock cones and seeds follow those of other conifers. Usually cones are stored—often for several weeks and sometimes months—in permeable sacks in open-sided cone drying sheds while awaiting processing. This covered storage serves as a preliminary curing process. Green cones tend to mold during storage, especially if stored without surface drying. Adequate air circulation is needed around each sack to minimize heating and mold buildup. Under proper conditions, western hemlock seeds may remain in the cones up to 6 months without detrimental effects upon seed quality. Leadem (1980) found that seeds from cones refrigerated at 2 °C had no better quality than seeds from cones stored outdoors.

An additional, or sometimes alternate, procedure is to place cones in a heated room for up to 36 hours before actually placing them in a drying kiln. This avoids exposing seeds that are nearly saturated with water to high kiln temperatures, a procedure that damages some conifer seeds. It also reduces kiln time and cost.

There are few problems in extracting seeds from hemlock cones. According to Baldwin (1930), mature hemlock cones need little artificial heat to open. Kiln-drying temperatures range from 31 to 43 °C, with drying time about 48 hours (Deffenbacher 1969; Isaacson 1969; Ruth 1974; Ward 1969). In the West, few hemlock cones are processed, and kiln schedules generally follow those for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and pine (*Pinus* spp.).

Eastern hemlock cones that are picked green, and thus are difficult to open, usually can be opened by exposure to repeated cycles of moistening followed by drying at 38 °C. Eastern hemlock cones collected just as they turn tan will open readily upon drying (Olson and others 1959). Mold-infested cones often open poorly, making seed extraction difficult. Seeds are extracted by tumbling or shaking the cones during or immediately after kiln-drying. On the tree, western hemlock cones open and close readily in response to changing moisture conditions and require many flexings of the cone scales before all seeds are dislodged; with kiln-drying and tumbling or shaking, a single opening of the cone scales appears sufficient for good seed extraction (Harris 1969).

Seeds are nearly surrounded by their wings (figure 2). Unlike the seeds of fir, Douglas-fir, and some pines, hemlock seeds have an entire wing that can be detached without serious damage to the seeds themselves (AOSA 2001).

Seeds are de-winged, and wing parts and foreign matter removed in a fanning mill or gravity separator. Minimum standards of 90% purity and 60% viability have been established for seedlots of western hemlock (WFTSC 1966a). The low viability often reported for eastern hemlock may be due to the difficulty of separating out low-quality seeds (Olson and others 1959). Care should be taken during processing to minimize the seed mortality that results from bruising or cracking the seedcoat.

For eastern hemlock, 0.35 hl (1 bu) of cones weigh about 15.5 kg (34 lb) or 1 liter (1 qt) of cones weights 0.44 kg (1 lb) (Eliason 1942) and yields 0.6 to 0.7 kg (1.4 to 1.5 lb) of seeds with a moisture content of 7.1% (Hill 1969; Toumey and Korstian 1952). Eastern hemlock seed yield per 100 kg (220 lb) of cones is 3.1 kg to 6.2 kg (6.8 to 13.6 lb) of seeds (Barton 1961; Ruth 1974). For western hemlock, there were 20,000 cones in 0.35 hl (1 bu) (Kummel and others 1944) and 0.45 kg (1 lb) of seeds was extracted from 0.35 hl (1 bu) of cones (Toumey and Korstian 1952).

Annual seeding and planting programs are dependent on successful seed storage (table 5). Western hemlock seeds keep best below freezing, and general practice is to store them at –18 °C. Barton (1954a) showed that viability was maintained better at this temperature than at –11 or –4 °C, with distinct differences showing up after only 2 years of storage. Viability can be maintained for at least 5 years, and this generally bridges the gap between large seedcrops.

Eastern hemlock seeds are stored both above and below freezing. They have been kept for 2 to 4 years in jars or plastic bags in a refrigerator maintained a few degrees above freezing, but retention of viability varied between seedlots (Olson and others 1959).

Mountain hemlock seeds are also stored at –18 °C. Mountain hemlock seedlots vary in their ability to withstand short-term stress, indicating that the genetic makeup of the seedlot may affect long-term seed storage. Accelerated aging (37.5 °C) treatments, varying from 0 to 21 days at 3-day intervals on mountain hemlock seeds, resulted in a complete loss of viability for stratified seeds at 12 days and for unstratified seeds at 18 days (El-Kassaby and Edwards 1998). The average viability for stratified seedlots decreased from 88% before aging to 3.6% after 9 days of aging. The average viability for unstratified seedlots decreased from 91% to 2% over the same time period (El-Kassaby and Edwards 1998).

Table 5—*Tsuga,* hemlock: seed storage conditions

Species	Seed moisture (%)	Temp (°C)	Viable period (yrs)
T. canadensis	—	5	4
	6–8	1–3	—
	—	–3	—
T. heterophylla	7–9	–18	5–7
	6–8	0	—
	8	–18	5+
	8	–18	3+
	—	21	2–3

Sources: Allen (1957), Barton (1954b, 1961), Jones (1962), Ruth (1974).

Moisture content of hemlock seeds in storage should be maintained between 6 and 9%. In longevity tests of seedlots stored at 5 °C with 6 to 10% moisture contents, a seedlot of western hemlock had 13% germination after 15 to 16 years, and another of mountain hemlock had 2% after 11 to 20 years (Schubert 1954). A study with western hemlock (Lavender 1956) demonstrated that temperatures and humidity levels generally experienced between removal of seeds from storage and seeding operations or testing procedures do not appreciably reduce viability. There was good viability retention of seeds removed from storage and stored at 20 °C and 30% relative humidity for as much as 11 weeks.

Pregermination treatments. Dormancy is variable in hemlock, with some seedlots requiring pregermination treatment and others germinating satisfactorily without treatment (Baldwin 1934; Bientjes 1954; Olson and others 1959). Because cold stratification (1 to 4 °C) of mature seeds shortens incubation time and may substantially increase germination, cold stratification is recommended prior to testing (except for seeds known to be nondormant) (table 6).

Stratification clearly accelerates and improves total germination of eastern hemlock (Baldwin 1930, 1934; Stearns and Olson 1958). For eastern hemlock seeds that have not been stratified, germination is improved by exposing seeds to 8- to 12-hour photoperiods at a temperature of about 21 °C alternating with dark periods at about 13 °C (Olson and others 1959). A long stratification period (70 days) increased germination percentages for Coffman (1975), who germinated seeds at 18 °C in darkness or with a $^1/_2$ hour of red light daily (615 nm, 0.056 g-cal/cm^2/min). Viable stratified, irradiated seeds showed 58% germination; viable stratified, non-irradiated seeds showed only 37%. Coffman also found that gibberillic acid (GA), kinetin, or a mixture of the two, inhibited the effect of prechilling, even in the presence of red light. There was nearly a complete lack of germination of unstratified eastern hemlock seedlots kept under red light (Coffman 1975).

Table 6—*Tsuga*, hemlock: stratification treatments

Species	Medium	Temp (°C)	Time (days)
T. canadensis	Moist sand or peat	1–5	30–120
T. caroliniana	Peat moss	3–5	30–90
T. heterophylla	Moist sand	1–5	21–90
	Plastic bag*	1–2	21–56
T. mertensiana	Moist sand	5	90

Sources: Allen (1958), Babb (1959), Deffenbacher (1969), Devitt and Long (1969), Eide (1969), Olson and others (1959), Ruth (1974), Swingle (1939), Walters and others (1960), Ward (1969), Weyerhaeuser (1969).
* Seeds were presoaked in tap water for 24 to 36 hours.

Germination of eastern hemlock seeds declines depending on the frequency and degree of drying following the imbibition phase and on the intensity of light. Eastern hemlock seeds incubated in open petri dishes at a low light level (645 lux) showed various germination values, from 50.2% with decomposed birch medium to 0% with filter paper. Seeds incubated in open petri dishes with decomposed birch medium that were exposed to a moderate light level (4,682 lux) exhibited delayed initial germination and significantly reduced total germination to half that at low light conditions (Coffman 1978). The intensity of light had no effect on seeds in covered petri dishes where a high moisture content was maintained.

Seeds of western hemlock stratified for 3 weeks at 1 °C germinated faster than untreated seeds; longer stratification periods caused additional but smaller increases in the rate of germination (Bientjes 1954; Ching 1958). Stratification of western hemlock seeds apparently has its main effect on speed of germination; it has only a minor effect on total germination percentage. Seedlots stratified for 1 week reached R_{50} (the number of days to reach 50% germination) 2.5 days sooner than did unstratified seedlots. Seedlots stratified for 4 weeks reached R_{50} 4.5 days sooner, and seedlots stratified for 16 weeks reached R_{50} 10.5 days sooner than did unstratified seedlots (Edwards 1973). Unstratified seedlots of western hemlock required nearly 2.5 weeks (18 days) to produce the same number of germinants as did seedlots stratified for 3 months in 10 days (Edwards 1973). Western hemlock seeds stratified for 1 week in plastic bags germinated about 1 day sooner than seeds stratified on filter paper (Edwards 1973). Presoaking the seeds for 48 hours was as effective in reducing the germination rate as was 1 week of stratification on filter paper (Edwards 1973). Immature western hemlock seeds tend to have lower total germination as a result of stratification (Allen 1958).

Experiments in Great Britain showed slightly increased rates of germination following stratification when western hemlock seeds were exposed to light but none when they were germinated in darkness (Buszewicz and Holmes 1961). Stratified western hemlock seeds tended to reduce the sensitivity to photoperiod (Edwards and Olsen 1973). Germination rate increased under a 4-hour photoperiod (300 to 350 foot candles or 3,228 lux); whereas 16 hours or more of photoperiod depressed germination rate below those in complete darkness at a constant 20 °C temperature (Edwards and Olsen 1973). Eight hours of light did not have a difference in germination from the no light treatment (Edwards and Olsen 1973).

Light significantly reduces germination rate for mountain hemlock seeds regardless of stratification. Unstratified and stratified seeds germinated in 8 hours of light (100 lux at filter paper surface) a week later than seeds grown in darkness (Edwards and El-Kassaby 1996). The R_{50} values for seeds incubated in light was almost double (6 days more) that of seeds incubated in darkness (Edwards and El-Kassaby 1996). Stratification increased the speed of germination slightly, but it did not alleviate the light effect nor did it effect total germination (Edwards and El-Kassaby 1996). Mountain hemlock seeds germinated 91% in the dark and 90% with light: mountain hemlock seeds can germinate as well or better without light (Edwards and El-Kassaby 1996).

Germination may begin while seeds are still in stratification if kept too long, with subsequent problems of drying out and mechanical damage during sowing. Careful regulation of seed moisture content and temperature can prevent germination from beginning in stratification. Seeds need to be kept at full imbibition but surplus water should be totally or mostly removed. Radicals will only elongate with surplus water present. Keeping temperatures closer to freezing and constant is also a good precaution. Temperature in the 1 to 2 °C range will retard germination more effectively than allowing temperatures to rise to near 5 °C. Personnel should limit entry into the stratification cooler to minimize temperature fluctuations.

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Germination tests. The Association of Official Seed Analysts (AOSA 2001) have prescribed standard germination test conditions for eastern and western hemlocks (table 7). It is recommended that eastern hemlock seeds be prechilled for 28 days at 3 to 5 °C followed by 28 days in a germinator at 15 °C. The rules call for placing western hemlock seeds directly in germinators at 20 °C for 28 days. Stratification is not required as part of the standard germination test procedure for western hemlock seeds but a paired germination test with 21 days of stratification can be performed and it is common practice to stratify seeds prior to nursery sowing. Seeds of both species should be exposed to light no more than 8 hours daily during this period. A tetrazolium staining technique for estimating seed viability may be used on western hemlock, but results may tend to underestimate seed quality (Buszewicz and Holmes 1957).

The International Seed Testing Association (ISTA 1999) rules used for exporting seeds are similar to domestic rules except that the germination test period for western hemlock is extended to 35 days. Standard procedures have not been developed for Carolina and mountain hemlock, so test conditions follow those for the associated eastern or western hemlocks.

Mountain hemlock seed germination is very sensitive to the total accumulation of heat even though it has been known to germinate on snow but much more slowly (Franklin and Krueger 1968). Stratification as long as 120 days does not compensate for sub-optimal temperatures. For mountain hemlock seed testing germination, stratification for 90 days at 4.5 °C is recommended with germination temperature set at a constant 20 °C (480° daily heat sum) (table 6).

In a laboratory study, as the heat sums rose from 280 to 440% daily heat sums the germination rate increased but final germination was not affected by temperature (El-Kassaby and Edwards 2001). Heat sum is the addition of temperatures above 0 °C for 24 hours. The threshold heat sum for mountain hemlock seed germination lies close to 400% daily heat sum which does not occur at high elevations until August in British Columbia, Canada (El-Kassaby and Edwards 2001). Stratification treatments did not have a significant effect on rate or final germination (El-Kassaby and Edwards 2001).

Correlations between latitude and total germination (r= 0.482) and between mountain hemlock seed weight and latitude (r = – 0.482) were found to be significant (*p* less than

Table 7—*Tsuga*, hemlock: stratification period, germination test conditions, and results

	Cold strati-fication*	Daily light period	Germination test condions†					Germin-ation	
			Temp (°C)			Germination rate			
Species	(days)	(hrs)	Day	Night	Days	(%)	(days)	(%)	Samples
T. canadensis	60–120	—	30	20	60	10–55	15–30	38	15
	0–30	—	22	22	—	6–62	28	10–66	9–12
	21–30	8	16	16	28	—	—	—	—
	20	8	15	15	28	—	—	60	3
	40	8	15	15	28	—	—	45	3
	90	8	15	15	28	—	—	61	9
T. caroliniana	0	8	30	20	28	—	—	40–80	9
	21–30	8	30	20	28	—	—	51–57	3
	0–120	16	22	22	34	—	—	82–91	5
T. heterophylla	0	8	20	20	28–35	49	21	53	146
	0–90	—	16	11	30	38	20–30	56	25
	0	8	15	15	35	—	—	86	44
	28	8	15	15	35	—	—	86	43
T. mertensiana	0–90	—	30	20	25–30	62–75	16–20	47	4
	—	Dark	20	20	28	—	—	91	19
	—	8	20	20	28	—	—	90	19
	90	—	30	20	60	61	16	62	1
	0	8	20	20	28	—	—	81	4
	28	8	20	20	28	—	—	97	3
	90	8	20	20	28	—	—	72	5

Sources: AOSA (2001), Buszewicz and Holmes (1961), Edwards and El-Kassaby 1996, Hill (1969), ISTA (1999), Ruth (1974), USDA FS (2002)
* Temperatures were –16 to –15 °C.
† Moisture-holding media were either blotters, Kimpak®, sand, or peat.

or equal to 0.05) (Edwards and El-Kassaby 1996). As seed source was moved further north in latitude, the seed weight decreases because the seeds are smaller. Germination parameters are under strong genetic control with broad sense heritabilities, h_2, ranging from 0.30 to 0.85 for stratified seeds and 0.45 to 0.84 for unstratified seeds (El-Kassaby and Edwards 1998).

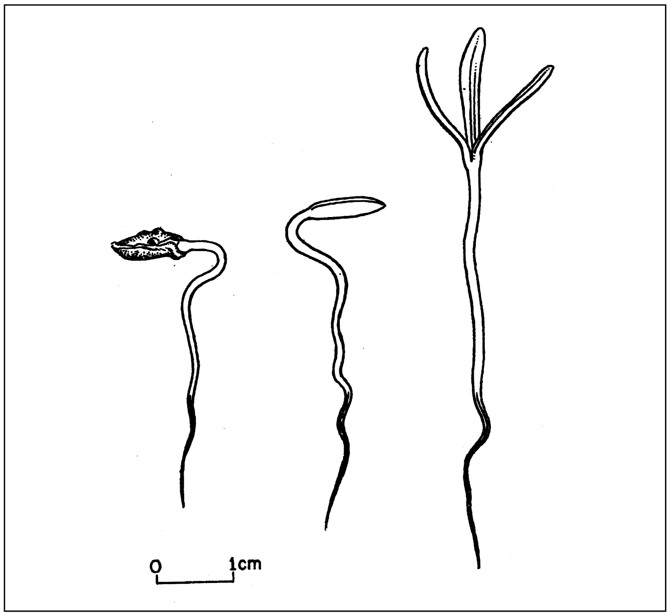
Final germination percentage of western hemlock seeds is affected by germination temperature. Greater total germination occurred at a constant temperature of 20 °C than under lower, higher, or alternating temperatures (Bientjes 1954; Buszewicz and Holmes 1961; Ching 1958). When alternating temperatures are used, keeping seeds in the dark improves germination (Buszewicz and Holmes 1961).

Western hemlock seeds from northern populations tended to germinate early, by about 4 days/degree of latitude, at 7 °C after 10 days of chilling (Campbell and Ritland 1982). Western hemlock seeds from high-elevation populations in the coast range germinated more rapidly than seeds from low or middle elevation population. For populations in the Cascades, seeds from both high- and low-elevation sources germinated more rapidly than seeds from middle elevations (Campbell and Ritland 1982). Lengthening stratification tended to decrease differences among provenances.

Observations of eastern hemlock (Olson and others 1959) illustrate ontogeny of seed germination, which is epigeal (figure 4). The first indicator of a viable seed is splitting of the seedcoat for half to two-thirds of its length, followed by the appearance of the pointed, bright-red root tip. The root grows at the rate of 2 to 3 mm/day, curving abruptly after emergence. After a few days, the hypocotyl also begins to grow, reaching 2 to 3 cm in length in 1 to 3 weeks. Normally, there is a pause in development after the cotyledons open, which may arbitrarily be considered the end of germination.

Nursery practice. Hemlock seedlings are difficult to grow in the nursery. They are easily damaged in the hot sun, and their small size the first year makes them particularly susceptible to frost heaving. Because of these difficulties, natural regeneration has in the past been favored over planting seedlings. Natural regeneration of western hemlock usually has been adequate, and a common procedure for mixed stands is to plant or seed associated species and expect hemlock to come in on its own, which it usually does. With increasing intensity of management, demand for western hemlock seedlings has increased, and production procedures were developed (Deffenbacher 1969; Devitt and Long 1969; Eide 1969; Isaacson 1969; Ward 1969; Weyerhaeuser 1969).

Figure 4—*Tsuga canadensis*, eastern hemlock: seedling development at 2, 4, and 7 days after germination.



At some nurseries (Eide 1969; Weyerhaeuser 1969), western hemlock seeds are soaked for 24 to 36 hours prior to stratification. The speed of germination was increased by soaking seeds in tap-water for 33 hours at room temperature (Bientjes 1954). Prolonged soaking for 96 to 120 hours, however, reduced the germination rate (Ching 1958).

Most nursery managers stratify western hemlock seeds and sow them in the spring. Seeds are moistened, excess water drained off, then the seeds are stratified at 1 to 2 °C from 21 to 42 days in a polyethylene bag. No stratification medium is used. Seed moisture content for optimum germination should be about 60% (Devitt 1969). Soil moisture content should be high but with drainage adequate to keep the ground water level below the rooting zone. Seedbeds may need screening to protect seeds from birds and rodents.

At one nursery (Eide 1969), seeds were sown on the surface and covered with burlap and sprinkled as needed to maintain moisture. After germination and penetration of the radicle into the soil, the burlap is removed and seedlings are mulched with peat moss. Additional peat moss is added during the growing season. Seedlings go into the winter with 13 to 19 mm ($^1/_2$ to $^3/_4$ in) of mulch to minimize frost heaving. About 50% shade is provided the first season.

For nursery production of eastern hemlock seedlings, spring-sowing of stratified seed is preferred over fall-sowing (Hill 1969; Olson and others 1959). Good eastern hemlock seeds planted under favorable conditions usually survive superficial contamination with mold, and use of fungicides is not recommended unless serious contamination is present. Nursery seedlings are very subject to damping-off by *Rhizoctonia* spp. during the first few months after germination and this can be aggravated by over-fertilization. It can be prevented (and weed seeds killed) with fumigation. Damping-off after germination can be controlled with fungicide (Olson and others 1959). One nursery growing western hemlock treats seedbeds when necessary with captan or thiram and has not had a serious problem with damping-off diseases. They also have treated hemlock seedlings with animal repellant to protect them from damage after outplanting (Eide 1969).

In nursery experiments in Great Britain, partial soil sterilization with formalin drench or chloropicrin injection improved growth of western hemlock. Moderate to large height increases were obtained with either treatment. Both sterilants used together often gave even better growth response, although treatment effects were not additive (Benzian 1965).

Only a few reports are available on nutrient requirements of hemlock. Western hemlock in British Columbia requires a well-drained acid soil with pH about 4 to 5 and an organic matter content of 5 to 6% (Devitt 1969). In Washington, it grows well at pH 5.3 to 5.4 with at least 15% soil organic matter (Eide 1969). In Great Britain, western hemlock made maximum growth on acid soil at about pH 4.5 and responded favorably to fertilization with nitrogen, phosphorus, and potassium. It showed a definite tip burn when suffering a copper deficiency, but seedlings recovered when sprayed with Bordeaux mixture. Water deficits during a dry summer apparently prevent response to nitrogen fertilization (Benzian 1965), but on the other hand, late summer watering can delay hardening-off and may increase the risk of frost damage (Olson and others 1959).

Seedlings are small at the end of the first growing season in the nursery and usually are held over and lifted after the second or third season. Seedlings frequently are transplanted for 1 year and then outplanted as 2+1 or 3+1 planting stock (Devitt and Long 1969; Olson and others 1959; Ward 1969). To overcome the difficulties of germination and frost heaving in the bareroot bed, plug+1 or plug+2 seedlings are used more commonly now than directly sowing seeds in the nurserybed (Romeriz 1997). In this system, a miniplug seedling is started in the greenhouse and then transplanted to the bareroot nurserybed.

Desired densities range from 323 to 538 seedlings/m^2 (30 to 50/ft^2) and tree percentages run from 15 to 50 (Deffenbacher 1969; Devitt and Long 1969; Eide 1969; Isaacson 1969; Ward 1969; Weyerhaeuser 1969). Experience in Great Britain indicates that a large proportion of losses in the nursery occur before seedling emergence. A high variability in tree percentage requires large safety factors in nursery sowings, resulting in an occasional surplus of seedlings (Buszewicz and Holmes 1961). The use of western hemlock plug transplants (Klappart 1988) reduces the number of seeds used and produces a larger, higher quality seedling in less time (Smith 1997). The production of container seedlings for outplanting is also widely practiced for western hemlock (Smith 1997).

Most hemlocks are now grown in containers in greenhouses under intensive culture instead of in bareroot nurseries. Styrofoam® blocks are the most common containers used and the sizes vary from 60, 77, to 112 trees/block with 77 trees/block the most commonly used. There are two outplanting regimes that dictate the propagation procedure in the greenhouse. The spring-planting regime requires that seeds be sown around February 1st, with the seedlings outplanted in the spring of the next year. Seeds are sown around January 15th for the summer-planting regime, with the seedlings being outplanted in the summer of the same year (Girard 2002).

Seeds are stratified for 21 days before sowing to achieve rapid, uniform germination and are germinated at 20 to 25 °C with light. It is the usual practice to sow with equipment more than 1 seed per cavity when germination falls below 90%. Once the seeds are fully germinated the photoperiod is increased to 20 hours/day and maintained until late April to keep the terminal bud from setting prematurely. The container medium is usually peat moss that may be amended with perlite or fir sawdust. Containers are lightly filled with medium to allow hemlock's large root system to grow. Controlled-release fertilizer is added to the medium at 4 kg/m^3 of medium in addition to lime to raise the pH and trace elements. The seeds are lightly covered with a sandy grit. A complete soluble fertilizer is added to the irrigation water every time the seedlings are watered. Frequency of irrigation is determined by weighing the containers after watering and then re-irrigating once the container weight drops below the target level (Girard 2002).

The seedlings are induced to set a terminal bud in the greenhouse by photoperiod reduction achieved through retractable darkout systems. Western hemlock seeds from southern sources require about a 4-week darkout period of 10 hours/day of light and 14 hours/day darkness. Seeds from northern sources only require about 2 weeks of darkness in the July following sowing to set buds. The short-day induction period is not begun until the trees have reached a minimum height of 15 cm (77 cavities/block). Seedlings will continue height growth during the short-day treatment so it is important to initiate bud induction early enough to maintain a good shoot to root ratio. Following the darkout period, seedlings are subjected to moderate moisture stress to maintain budset. Nurseries favor greenhouse systems that have roofs that open to subject the planting stock to full light conditions following budset. In nurseries lacking those systems, containers are usually moved outside growing compounds (Girard 2002).

For 77 cavities/block stocktypes, the target seedling height for outplanting is 30 cm (12 in), with no more than a maximum of 40 cm (16 in) height. The minimum caliper for outplanting is 3 mm and the target is 3.5 mm. It takes about 25 weeks from sowing to grow a target seedling. For spring-planted crops, ambient greenhouse temperatures are reduced to about 2 °C in the late fall to further develop dormancy. A frost hardiness test is performed to determine dormancy before the seedlings are lifted for cold storage. A sample of seedlings are frozen to –15 °C and injury is determined through variable chlorophyll inflorescence (Girard 2002).

For extraction of seedlings from the growing containers, most nurseries use automatic pin extractor machines. The containers are laid on their sides and metal pins push the plugs out of the containers and the seedlings are then graded for quality. For summer outplanting (late August and early September), seedlings are not stored before planting. The seedlings are lifted while still growing, shipped, and planted within 24 hours (Girard 2002).

Spring-outplanted seedlings are lifted from containers in December and stored for up to 3 months in cold storage at –2 to –5 °C. Seedlings are placed in an upright position within a waxed cardboard box. Boxes filled with seedlings to be stored frozen have a brown paper liner with an inner plastic membrane to retain moisture. Frozen seedlings are allowed to thaw 3 to 5 days in a thawing shed before they are shipped to the field for planting (Girard 2002).

Eastern hemlock is sometimes propagated vegetatively. Dormant cuttings taken in January to mid-February should be placed in beds with bottom heat, but results can be variable (Dirr and Heuser 1987).

References

Allen GS. 1957. Storage behavior of conifer seeds in sealed containers held at 0 °F, 32 °F, and room temperature. Journal of Forestry 55: 278–281.

Allen GS. 1958. Factors affecting the viability and germination behavior of coniferous seed: 1. Cone and seed maturity, *Tsuga heterophylla* (Rafn) Sarg. Forestry Chronicle 34: 266–274.

AOSA [Association of Official Seed Analysts]. 2001. Rules for testing seeds. Association of Official Seed Analysts. 126 p.

Babb MF. 1959. Propagation of woody plants by seed. Alaska Agricultural Experiment Station Bulletin 26: 1–11.

Baldwin HI. 1930. The effect of after-ripening treatment on the germination of eastern hemlock seed. Journal of Forestry 28: 853–857.

Baldwin HI. 1934. Further notes on the germination of hemlock seed. Journal of Forestry 32: 99–100.

Barton LV. 1954a. Effect of subfreezing temperatures on viability of conifer seeds in storage. Contributions of the Boyce Thompson Institute 18: 21–24.

Barton LV. 1954b. Storage and packeting of seeds of Douglas-fir and western hemlock. Contributions of the Boyce Thompson Institute 18: 25–37.

Barton LV. 1961. Seed preservation and longevity. New York: Interscience Publishers. 216 p.

Benzian B. 1965. Experiments on nutrition problems in forest nurseries. Volume 1. For. Comm. Bull. 37. London: Her Majesty's Stationery Office. 251 p.

Bientjes W. 1954. The effects of temperature, seed moisture, and stratification on the germination behavior of western hemlock seed. For. Club Res. Note 11. Vancouver: University of British Columbia. 7 p.

Bramlett DL, Belcher EW, DeBarr GL, Hartel GD, Karrfalt RP, Lantz CW, Miller T, Ware KD, Yates HO. 1977. Cone analysis of southern pines: a guidebook. Gen. Tech. Rep. SE-13. Asheville, NC: USDA Forest Service, Southeastern Forest Experiment Station.

Burns RM, Honkala BH. 1990. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service. 1675 p.

Buszewicz G, Holmes GD. 1957. Seven years seed testing experience with the tetrazolium viability test for conifer species. In: Report of the Forestry Research Committee. Great Britain Forestry Commission (London) 1957: 142–151.

Buszewicz G, Holmes GD. 1961. A summary of ten years' seed testing experience with western hemlock, *Tsuga heterophylla*. In: Report of the Forestry Research Committee. Great Britain Forestry Commission (London) 1959–60: 110–119.

Campbell RK, Ritland SM. 1982. Regulation of seed-germination timing by moist chilling in western hemlock. New Phytologist 92: 173–182.

Campo-Duplan V, Gaussen H. 1948. Sur quatre hybrides de genres chez les Abietinees. Travaux du Laboratoire Forestier de Toulouse Tome I (4)24: 1–14.

Ching TM. 1958. Some experiments on the optimum germination conditions for western hemlock (*Tsuga heterophylla* Sarg.). Journal of Forestry 56: 277–279.

Coffman MS. 1975. *Tsuga canadensis* (L.) Carr. germination stimulated by red light while inhibited by gibberellin and kinetin. Res. Note 13 (May 1975). L'Anse, MI: Michigan Technology University, Ford Forestry Center. 12 p.

Coffman MS. 1978. Eastern hemlock germination influenced by light, germination media, and moisture content. Michigan Botanist 17: 99–103.

Colangeli AM, Owens JN. 1989a. Postdormancy and seed-cone development and the pollination mechanism in western hemlock (*Tsuga heterophylla*). Canadian Journal of Forest Research 19: 44–53.

Colangeli AM, Owens JN. 1989b. Cone and seed development in a wind-pollinated, western hemlock (*Tsuga heterophylla*) clone bank. Canadian Journal of Forestry 20: 1432–1437.

Dallimore W, Jackson AB. 1957. A handbook of Coniferae and Ginkgoaceae. 4th ed. Harrison SG, rev. New York: St. Martin's Press. 729 p.

Deffenbacher FW. 1969. Personal correspondence. Carson, WA: USDA Forest Service, Wind River Nursery.

den Ouden P, Boom BK. 1965. Manual of cultivated conifers hardy in the cold-and warm-temperate zones. The Hague: Martinus Nijhoff. 526 p.

Devitt B. 1969. Nursery procedures and problems in growing western hemlock planting stock. Proceedings, 8th Annual Reforestation Board Workshop, Tree Farm Forestry Committee (BC). 5 p.

Devitt B, Long J. 1969. Personal correspondence. Victoria: British Columbia Forest Service Reforestation Division.

Dirr MA. 1998. Manual of woody landscape plants: their identification, ornamental characteristics, culture, propagation and uses. 5th ed. Champaign, IL: Stipes Publishing. 1187 p.
Dirr MA, Heuser Jr. CW. 1987. The reference manual of woody plant propagation: from seed to tissue culture. Athens, GA: Varsity Press. 239 p.
Duffeld JW. 1950. Review of "Sur quatre hybrides de genres chez les Abietinees" [On four intergenus hybrids in the Abietineae, by Mme. Van Campo-Duplan and H. Gaussen]. Journal of Forestry 48(6): 440.
Ebell LF, Schmidt RL. 1963. The influence of meteorological factors upon dispersal of conifer pollen on Vancouver Island, British Columbia. British Columbia Forest Service Technical Publication 54: 1–28.
Edwards DGW. 1973. Effects of stratification on western hemlock germination. Canadian Journal of Forest Research 3: 522–527.
Edwards DGW, Olsen PE. 1973. A photoperiod response in germination of western hemlock seeds. Canadian Journal of Forest Research 3: 146–148.
Edwards DGW. 1976. Seed physiology and germination in western hemlock. In: Atkinson WA, Zasoski RJ, eds. Proceedings, Western Hemlock Management Conference. Seattle: University of Washington, College of Forest Resources: 87–102.
Edwards DGW, El-Kassaby YA. 1996. The effect of stratification and artificial light on the germination of mountain hemlock seeds. Seed Science and Technology 24: 225–235.
Eide R. 1969. Personal correspondence. Canby, OR: Indian Forestry Association, Canby Forest Nursery.
Eliason EJ. 1942. Data from cone collections of various species in New York. Notes on Forest Inventory No. 39, 1 p.
El-Kassaby YA, Edwards DGW. 1998. Genetic control of germination and the effects of accelerated aging in mountain hemlock and its relevance to gene conservation. Forest Ecology and Management 112: 203–211.
El-Kassaby YA, Edwards DGW. 2001. Germination ecology in mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.). Forest Ecology and Management 144: 183–188.
FNAEC [Flora of North America Editorial Committee]. 1993. Flora of North America: north of Mexico. Volume 2, Pteridophytes and Gymnosperms. New York: Oxford University Press. 475 p.
Farjon A, Page CN, Schellevis N. 1993. A preliminary world list of threatened conifer taxa. Biodiversity and Conservation 2: 304–326.
Franklin JF. 1968. Cone production by upper-slope conifers. Res. Pap. PNW-60. Corvallis, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 21 p.
Franklin JF, Krueger KW. 1986. Germination of true fir and mountain hemlock seed on snow. Journal of Forestry 66: 416–417.
Frothingham EH. 1915. The eastern hemlock. Bull. 152. Washington, DC: U.S. Department of Agriculture. 43 p.
Garman EH. 1951. Seed production by conifers in the coastal region of British Columbia related to dissemination and regeneration. Tech. Bull. T-35. Victoria: British Columbia Forest Service: 1–47.
Gashwiler JS. 1969. Seed fall of three conifers in west central Oregon. Forest Science 15: 290–295.
Girard M. 2002. Personal communication. Vancouver Island, BC: Malaspina College.
Godman RM. 1953. Seed dispersal in southeast Alaska. Tech. Note. Juneau: USDA Forest Service, Alaska Forest Research Center: 2 p.
Godman RM, Lancaster K. 1990. *Tsuga canadensis* (L.) Carr., eastern hemlock. In: Burns RM, Honkala BH. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 604–612.
Green CH. 1939. Trees of the South. Chapel Hill: University of North Carolina Press. 551 p.
Harlow WM, Harrar ES. 1968. Textbook of dendrology. 5th ed. New York: McGraw-Hill Book Co. 512 p.
Harris AS. 1967. Natural reforestation on a mile-square clearcut in southeast Alaska. Res. Pap. PNW-52. Corvallis, OR: USDA Forest Service, Pacific Northwest Forest and Range Research Center. 16 p.
Harris AS. 1969. Ripening and dispersal of a bumper western hemlock–Sitka spruce seed crop in southeast Alaska. Res. Note PNW-105. Corvallis, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 11 p.
Heusser CJ. 1954. Alpine fir at Taku Glacier, Alaska, with notes on its postglacial migration to the territory. Bulletin of the Torrey Botanical Club 81: 83–86.
Hill J. 1969. Personal correspondence. Mont Alto: Pennsylvania Department of Forests and Waters, Mont Alto State Forest Nursery.
Hough RB. 1947. Handbook of trees of the northern states and Canada east of the Rocky Mountains. New York: Macmillian. 470 p.
ISTA [International Seed Testing Association]. 1999. International rules for seed testing rules 1999. Seed Science and Technology 27 (Suppl.): 1–333.
Isaacson JA. 1969. Personal correspondence. Coeur d'Alene, ID: USDA Forest Service, Coeur d'Alene Nursery.
James GA. 1959. Seed production in a scrub stand. Tech. Note 43. Juneau: USDA Forest Service, Alaska Forest Research Center: 1–3.
Jones L. 1962. Recommendations for successful storage of tree seed. Tree Planters' Notes 55: 9–20.
Klappart RA. 1988. Greenhouse transplants for bareroot stock production. In: Landis TD, tech coord. Proceedings, Combined Meeting of the Western Forest Nursery Council, Forest Nursery Association of British Columbia, and Intermountain Forest Nursery Association; 1988 August 8–11; Vernon, BC. Gen. Tech. Rep. RM-167. Fort Collins, CO: USDA Forest Service, Rocky Mountain Forest and Range Experiment Station: 165–167.
Kummel JF, Rindt CA, Munger TT. 1944. Forest planting in the Douglas-fir region. [Corvallis, OR]: USDA Forest Service, North Pacific Region. 154 p.
Kuser JE, Ching KK. 1981. Provenance variation in seed weight, cotyledon number, and growth rate of western hemlock seedlings. Canadian Journal of Forest Research 11(3): 662–670.
Lavender DP. 1956. Western hemlock seed germination after exposure to varying temperatures and humidities. Res. Note 26. Oregon State Board of Forestry. 4 p.
Leadem C. 1980. Seed viability of *Abies, Picea*, and *Tsuga* after storage in the cones. Proceedings of the International Symposium on Forest Tree Seed Storage: 1980 Sept. 23–27. Chalk River, ON: Petawawa National Forestry Institute: 57–67.
Leiberg JB. 1900. The Bitterroot Forest Reserve. In: 20th Annual Report, 1898–1899, Part 5, Forest Reserves. Washington, DC: U.S. Geological Survey: 317–410.
Lines R, Aldhous JR. 1962. Provenance studies. Forestry Committee (London) Report on Forest Research for the year ended March 1961. Great Britain Forestry Commission: 37–41.
Lines R, Aldhous JR. 1963. Provenance. Forestry Committee (London) Report on Forest Research for the year ended March 1962. Great Britain Forestry Commission: 32–36.
Lines R, Mitchell AF. 1969. Provenance: Forestry Committee (London) Report on forest research for the year ended March 1969. Great Britain Forestry Commission: 42–49.
Little EL Jr. 1979. Checklist of United States Trees (native and naturalized). Agric. Handbk 541. Washington, DC: USDA Forest Service. 375 p.
McClure MS, Salom SM, Shields KS. 2001. Hemlock woolly adelgid. Forest Health Technology Enterprise Team FHTET-2001–03, March 2001. Morgantown, WV: USDA Forest Service, 14 p.
Meagher MD. 1996. Estimating the number of filled seeds per cone of western hemlock from coastal British Columbia. Western Journal of Applied Forestry 11(2) p. 44-49.
Merrill PH, Hawley RC. 1924. Hemlock: its place in the silviculture of the southern New England forest. Bull. 12. New Haven, CT: Yale University School of Forestry. 68 p.
Nienstaedt H. 1958. Height growth is indicative of the relative frost resistance of hemlock seed sources. Tech. Note 525. St. Paul: USDA Forest Service, Lakes States Forest Experiment Station. 2 p.
Olson JS, Stearns FW, Nienstaedt H. 1959. Eastern hemlock seeds and seedlings: response to photo period and temperature. Bull. 620. Hamden: Connecticut Agricultural Experiment Station. 70 p.
Packee EC. 1990. *Tsuga heterophylla* (Raf.) Sarg., western hemlock. In: Burns RM, Honkala BH. Silvics of North America. Volume 1, Conifers. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 613–622.
Piesch RF, Phelps VH. 1970. Certification of source-identified British Columbia tree seed under the O.E.C.D. scheme. Info. Rep. BC-X-49. Victoria, BC: Canadian Forestry Service, Pacific Forest Research Centre. 8 p.
Price T. 2002. Personal communication. Macon: Georgia Forestry Commission,
Radford AE, Ahles HE, Bell CR. 1968. Guide to the vascular flora of the Carolinas. Chapel Hill: University of North Carolina Book Exchange. 383 p.
Rafn J. 1915. The testing of forest seeds during 25 years, 1887–1912. Copenhagen: Langkjaers Bogtrykkeri. 91 p.
Randall W. 1996. Personal communication. Corvallis, OR: USDA Forest Service.
Rehder A. 1940. Manual of cultivated trees and shrubs hardy in North America. New York: Macmillan. 996 p.
Rehder A. 1949. Bibliography of cultivated trees and shrubs hardy in the cooler temperate regions of the Northern Hemisphere. Cambridge, MA: Harvard University Press. 825 p.
Romeriz A. 1997. Personal communication. Webster: Washington State Department of Natural Resources.

Ruth RH. 1974. *Tsuga*, hemlock. In: Schopmeyer CS, tech. cord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 819–827.

Ruth RH, Berntsen CM. 1955. A 4-year record of Sitka spruce and western hemlock seed fall. Res. Pap. 12. Corvallis, OR: USDA Forest Service Pacific Northwest Forest and Range Experiment Station. 13 p.

Sargent CS. 1933. Manual of the trees of North America. Boston: Houghton Mifflin. 910 p.

Schubert GH. 1954. Viability of various coniferous seeds after cold storage. Journal of Forestry 52: 446–447.

Smith M. 1997. Personal communication. Olympia: Washington Department of Natural Resources, Webster Forest Nursery.

Stearns F, Olson J. 1958. Interactions of photo period and temperature affecting seed germination in *Tusga canadensis*. American Journal of Botany 45: 53–58.

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

Swartley JC. 1945. Variations and uses of Canada hemlock. Cornell Plantations 2: 3–6.

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

Toumey JW, Korstian CF. 1952. Seeding and planting in the practice of forestry. 3rd ed. New York: John Wiley & Sons. 520 p.

Toumey JW, Stevens CL. 1928. The testing of coniferous tree seeds at the School of Forestry, Yale University, 1906–1926. For. Bull. 21. New Haven, CT: Yale University School of Forestry. 46 p.

USDA Forest Service. 2002. Official seed testing results. Dry Branch, GA: National Tree Seed Laboratory.

Vabre-Durrieu A. 1954a. L'hybride *Tsuga–Picea hookeriana* et ses parents: des plantules. Travaux du Laboratoire Forestier de Toulouse. Tome 1 (vol 5, art. 15) 8 p.

Vabre-Durrieu A. 1954 b. L'hybride *Tsuga–Picea hookeriana* et ses parents: 'etude chromosomique et caryologique. Travaux du Laboratoire Forestier de Toulouse, Tome 1 (vol 5, art. 17) 4 p.

Walters J, Soos J, Haddock PG. 1960. The selection of plus trees in the University of British Columbia Research Forest, Haney, B.C. Res. Pap. 33. Vancouver: University of British Columbia Faculty of Forestry. 12 p.

Ward H. 1969. Personal correspondence. Olympia: Washington State Department Natural Resources, L.T. "Mike" Webster State Forest Nursery,

WFTSC [Western Forest Tree Seed Council]. 1966a. Sampling and service testing western conifer seeds. Western Reforestation Coordinating Committee of the Western Forestry and Conservation Association. 36 p.

WFTSC [Western Forest Tree Seed Council]. 1966b. Tree seed zone map. Portland, OR: Western Forest Tree Seed Council.

Weyerhaeuser Co. 1969. Written correspondence. Tacoma, WA.

Fabaceae—Pea family

Ulex europaeus L.

common gorse

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Growth habit, occurrence, and use. Gorse is a leafless, spined shrub introduced from western Europe. In its homeland, it grows 1 to 2 m tall and is primarily a non-aggressive invader of disturbed areas that is recognized as useful for wildlife protection, soil stabilization, and revegetation. It has also been cultivated as an ornamental and as forage for livestock, which feed on the soft, new growing shoots. Its major use in the past, however, was for hedgerows to contain livestock before barbed wire (Jobson and Thomas 1964). As a useful plant, European settlers carried gorse to many parts of the world where it quickly escaped from cultivation and formed aggressive feral populations. These feral plants grow 3 to 5 m tall in dense, spiny, impenetrable stands that exclude desirable vegetation in pasture lands (Hill 1983; Sandrey 1985) and, in open forests, interfere with reforestation and forest management (Balneaves and Zabkiewicz 1981; Zabkiewicz 1976). Gorse is presently recognized as one of the worst weeds in New Zealand, Chile, and Tasmania and is recognized as a weed in at least 15 other countries or island groups around the world (Holm and others 1979).

In North America, gorse is still used to a limited extent as an ornamental for its dense yellow flowers. In the eastern United States, scattered feral populations have been recorded, but apparently these are not of an aggressive nature. By contrast, along the Pacific Coast, gorse is found scattered along the coastline from San Francisco, California, north to Vancouver, British Columbia (Markin and others 1994). Through most of this area, it is found in small, scattered populations that are usually targeted for intensive control programs to keep them from expanding. The major outbreak along the southwestern coast of Oregon covers at least 15,000 ha and is a major problem in forest management. This gorse population interferes with reforestation and, because of the plant's highly flammable nature, creates an extreme fire hazard (Herman and Newton 1968). Gorse also infests 14,000 ha at higher elevations on the islands of Hawaii and Maui in Hawaii (Markin and others 1988).

As a useful agricultural and ornamental plant in its native range, methods for propagating gorse have been developed in Europe (Rudolf 1974). As a major weed through the rest of the world, no effort has been made to propagate it for sale or outplanting. However, very extensive work has been done in studying the regeneration, reproduction, and propagation of this plant for research purposes and to develop control methods, particularly in New Zealand. A more recent need has been to propagate gorse to be used as food for insects being tested as potential biocontrol agents (Markin and Yoshioka 1989).

Flowering and fruiting. The small, bright yellow, pea-like flowers (Whitson and others 1991) are very similar in size and appearance to those of the closely related Scotch broom—*Cytisus scoparius* (L.) Link—with which it shares much of its range on the Pacific Coast. In Europe, gorse blooms in late spring, usually for 1 month; depending upon the latitude, this can occur from late February to early June. On the Oregon coast, gorse blooms from February to early May; in Hawaii, it blooms from December to May, peaking in February and April. Flowers may be solitary or in clusters, but because they are often synchronized in blooming, an entire plant will sometimes be covered with thousands of blooms. The flowers are insect-pollinated and require a large insect that, while probing for nectar, can trip and release the stamens held in the keel on the lower surface of the flower. The major pollinator in North America and Hawaii is the common honey bee (*Apis mellifera* L.). When massive blooms occur in areas where feral bees are scarce, poor pod set may be seen in limited areas (a desirable feature for land managers). Beekeepers, however, recognize the bloom as an excellent source of early spring pollen that can be used to build up their hives, and they usually move hives in to take advantage of the bloom, resulting in adequate pollination (Sandrey 1985). One method of control that has been used in Hawaii is restricting commercial bees in an effort to reduce seed production.

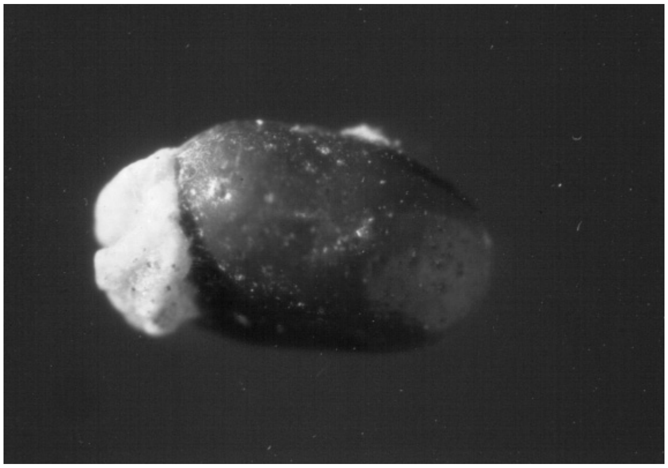
The mature fruit is a typical, small (1 to 1.5 cm), black legume (pod) that contains 1 to 12 seeds, although the average is 4 to 5. After pollination, a legume requires 2 months to mature, so peak legume set occurs 2 months after peak flowering. In Oregon, this is mid-May through July; in Hawaii, peak legume set is in May and is finished by the first of July. On maturing and drying, the legumes open violently (dehisce), naturally dispersing the seeds 1 to 3 m out from the parent plant. In Oregon and Hawaii, natural germination usually occurs during the wetter winter and spring months.

Fruit collection; seed extraction and storage. As an aggressive, noxious weed, there is no demand for the commercial collection of seeds. Researchers obtain the seeds they need by collecting the mature black legumes individually or by cutting a branch containing them. When allowed to dry out in a cloth sack at room temperature, the legumes naturally dehisce, releasing the seeds. The mature brown seeds are generally spherical, 1.25 to 2 mm in diameter (figure 1). Each seed initially contains an elaiosome, a yellow, fleshy appendage, rich in oil and protein (Pemberton and Irving 1990) that attract ants; this is another method of seed dispersal (Weiss 1909). The gorse seedcoat is notorious for its hardness (it is water impermeable), which gives the seeds a very long field life and has created major problems in managing this weed (Butler 1976; Chater 1931; Moss 1959). Seed numbers range from 145,000 to 159,000/kg and average about 150,000/kg (66,000 to 72,000/lb and average about 68,000/lb) (Rudolf 1974). The seeds are orthodox in storage behavior and can be kept indefinitely in ordinary cool, dry storage.

Pregermination treatments. Germination of mature, well-dried seeds varies greatly according to the literature but can be as low as 10 to 30% in 6 months. In the field, the seeds have a long life; it has been estimated that they can remain viable for up to 26 years or more (Moss 1959).

Because of the seedcoat's hardness, a number of different pregermination treatments have been tried. In the field, the most common method to trigger germination is fire. When a gorse area burns, the seeds in the top centimeter or two of duff are destroyed, but the deeper seeds survive and most of these are often triggered into germinating (Rolston and Talbot 1980; Zabkiewicz and Gaskin 1978). In the laboratory, this can be duplicated by heating the seeds from 60 to 80 °C for 30 minutes in an oven (Butler 1976; Moss 1959). Placing gorse seeds in boiling water for 30 seconds and then cooling them in cold water can increase germination to over 90% (Millener 1961).

Figure 1—*Ulex europaeus*, common gorse: seed.



Other methods of germination include soaking in concentrated sulfuric acid for $^{1}/_{2}$ to $1^{1}/_{2}$ hours, and mechanical scarification (Buttler 1976), most simply done with emery paper (Moss 1959).

Germination tests. Because of the noxious nature of gorse in North America, standardized germination tests for quality control have not been developed. In Europe, where gorse is a beneficial native plant, germination tests at one time were apparently developed in which seeds were tested in germinators or sand flats at 20 °C for 30 days using 400 pretreatment seeds/test (Rudolf 1974). Researchers have reported no problem in obtaining germination by planting scarified seeds 1 cm deep in different media. First signs of germination are usually seen within 10 days of planting. In 15 to 25 days, seedlings are small rosettes with true leaves, approximately 1.5 cm in diameter. Small leaves continue to form until the plant is approximately 5 cm tall, at which time the first spines are produced. During the remainder of its life, the plant produces no more leaves, only spines. The juvenile stage of the plant, from seed germination until spines begin to form, requires 4 to 6 months in the field. In Europe, large-scale germination in pots and direct seeding into the field have been practiced in the past (Rudolf 1974).

U

References

Balneaves JM, Zabkiewicz JA. 1981. Gorse control: a review. In: Chavasse CGR, ed. Proceedings, Forest Nursery and Establishment Practice in New Zealand; 1982 March 23–27; Rotorua, NZ: New Zealand Forest Service, Forest Research Institute: 92–105.

Butler JHB. 1976. A preliminary investigation of the hard seed characteristics of *Ulex europaeus* with emphasis on laboratory scarification treatments [thesis]. Palmerston North, New Zealand: Massey University. 82 p.

Chater EH. 1931. A contribution to the study of the natural control of gorse. Bulletin of Entomological Research 22: 225–235.

Hermann RK, Newton M. 1968. Tree plantings for control of gorse on the Oregon coast. Res. Pap. 9. Corvallis: Oregon State University, Forestry Research Laboratory. 12 p.

Hill RL 1983. Prospects for the biological control of gorse. New Zealand Weed and Pest Control Conference: 56–58.

Holm L, Pancho JV, Herberger JP, Plucknett DL. 1979. A geographical atlas of world weeds. New York: Wiley-Interscience: 373 p.

Jobson HT, Thomas B. 1964. The composition of gorse (*Ulex europaeus*). Journal of the Science of Food and Agriculture 15: 652–656.

Markin GP, Yoshioka ER. 1989. Present status of biological control of the weed gorse (*Ulex europaeus* L.) in Hawaii. In: Delfosse ES, ed. Proceedings, 7th Symposium on Biological Control of Weeds; 1988 March 6–11; Rome. East Melbourne, Australia: CSIRO Publications: 357–362.

Markin GP, Yoshioka ER, Brown RE. 1994. Gorse. In: Nechols JR, ed. Biological control in western United States. Pub. 3361. Oakland: University of California, Division of Agriculture and Natural Resources: 299–302.

Markin GP, Dekker LA, Lapp JA, Nagata RF. 1988. Distribution of the weed gorse (*Ulex europaeus* L.) a noxious weed in Hawaii. Newsletter of the Hawaiian Botanical Society 27: 110–117.

Millener LH. 1961. Day length as related to vegetative development in *Ulex europaeus* L. New Phytologist 60: 339–354.

Moss GR. 1959. The gorse seed problem. Proceedings of the New Zealand Weed and Pest Control Conference 12: 59–64.

Pemberton RW, Irving DW. 1990. Elaiosomes on weed seeds and the potential for myrmecochory in naturalized plants. Weed Science 38: 615–619.

Rolston MP, Talbot J. 1980. Soil temperatures and regrowth of gorse burnt after treatment with herbicides. New Zealand Journal of Experimental Agriculture 8: 55–61.

Rudolf PO. 1974. *Ulex europaeus* L., common gorse. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 828.

Sandrey RA. 1985. Biological control of gorse: an ex-ante evaluation. Res. Rep. 172. Lincoln College: New Zealand Agricultural Economics Research Unit. 97 p.

Weiss FE. 1909. The dispersal of the seeds of the gorse and the broom by ants. New Phytologist 8(3): 81–89.

Whitson TD, Burrill LC, Dewey SA, Cudney DW, Nelson BE, Lee RD, Parker R. 1991. Gorse. In: Weeds of the West. Jackson, WY: Western Society of Weed Science and Western United States Land Grant Universities Cooperative Extension Service: 348–349.

Zabkiewicz JA. 1976. The ecology of gorse and its relevance to new forestry. In: The use of herbicides in forestry in New Zealand. New Zealand Forest Research Institute Symposium 18: 63–68.

Zabkiewicz JA, Gaskin RA. 1978. Effect of fire on gorse seeds. Proceedings of the New Zealand Weed and Pest Control Conference 31: 47–52.

U

Ulmaceae—Elm family

Ulmus L.

elm

Jill R. Barbour and Kenneth A. Brinkman

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Growth habit, occurrence, and use. About 20 species of elm—the genus *Ulmus*—are native to the Northern Hemisphere. There are no native elms in western North America but some are found in northeastern Mexico (Johnson 1973). American elms are much loved as street trees for their arching branches and most elms species are valued for their hard, tough wood and many have been planted for environmental purposes. The natural ranges of 13 of the more important species are listed in table 1.

Since the 1930s, however, most elms in North America have been killed by the Dutch elm fungus, *Ophiostoma ulmi* (Buisman) Nannf., or by phloem necrosis, which is caused by a microplasma-like organism (Sinclair and others 1987). The Dutch elm disease was discovered in 1930 in Ohio. Dutch elm disease is transmitted when the European elm beetle, *Scolytus multistriatus* (Marsham), and the native elm bark beetle, *Hylurgopinus rufipes* Eichoff, feed on the tree (Burns and Honkala 1990). Phloem necrosis is spread by the

Table 1—*Ulmus,* elm: nomenclature and occurrence

Scientific name & synonym(s)	Common name(s)	Occurrence
U. alata **Michx.**	**winged elm,** cork elm, wahoo	Virginia to Missouri, S to Oklahoma & E Texas, E to central Florida
U. americana **L.**	**American elm,** water elm, soft elm, white elm	Quebec to E Saskatchewan, S to North Dakota, Oklahoma, & Texas, E to central Florida
U. crassifolia **Nutt.**	**cedar elm,** basket elm, red elm, southern rock elm	SW Tennessee, Arkansas, & S Oklahoma to S Texas, Louisiana & W Mississippi
U. glabra **Huds.** *U. scabra* Mill. *U. montana* With. *U. cammpestris* L. in part	**Scots elm,** Scotch elm, Wych elm	N & central Europe & Asia Minor
U. japonica **(Sarg. ex Rehd.) Sarg.** *U. campestris* var. *japonica* Rehd. *U. davidiana* var. *japonica* (Rehd.) Nakai	**Japanese elm**	Japan & NE Asia
U. laevis **Pall.** *U. pedunculata* Pall. *U. effusa* Willd.; *U. racemosa* Borkh.	**Russian elm,** spreading elm, European white elm'	Central Europe to W Asia
U. minor **Mill.** *U. carpinifolia* Gled.	**Smoothleaf elm,** field elm,	Central & S Europe, England, Algeria, & Near East
U. parvifolia **Jacq.** *U. chinensis* Pers.	**Chinese elm,** leatherleaf elm, lacebark elm	N & central China, Korea, Japan, & Formosa
U. procera **Salisb.**	**English elm**	S & central England, NW Spain
U. pumila **L.**	**Siberian elm,** Chinese elm, dwarf Asiatic elm	Turkestan, E Siberia, & N China
U. rubra **Mühl.** *U. fulva* Michx.	**slippery elm,** grey elm, red elm, soft elm (lumber)	SW & Quebec to E North Dakota, S to W Oklahoma & SE & E Florida
U. serotina **Sarg.**	**September elm,** red elm	Kentucky and S Illinois, S to N Alabama & NW Georgia; also in Arkansas & E Oklahoma
U. thomasii **Sarg.** *U. racemosa* Thomas	**rock elm,** cork elm	Vermont to S Ontario, central Minnesota & SE South Dakota, S to E Kansas, E to Tennessee & New York

Sources: Brinkman (1974), Maisenhelder (1966), Rudolf (1937).

whitebanded elm leafhopper, *Scaphoideus luteolus* (Van Duzee) and root grafts (Burns and Honkala 1990). Only Chinese, Japanese, and Siberian elms (Krüssman 1960) are resistant to these diseases. Although American elms now are only a small percentage of the large-diameter trees in mixed forest stands, beautiful old specimens of American elm still exist in some isolated city parks and along streets, for example, in Central and Riverside Parks in Manhattan (Barnard 2002).

Flowering and fruiting. Elm flowers are perfect. Selfing rarely occurs in elms due to their high degree of self-incompatibility, with the exception of Siberian elm, which is self-compatible (Townsend 1975). American elm has twice as many chromosomes (2n = 56) as the other elm species common to North America, making it hard to cross-pollinate different species to impart disease resistance to American elm (Burns and Honkala 1990).

Most of the elms commonly grown in North America have protogynous flowers, where the stigma becomes receptive to pollen before the male anthers dehisce (Burns and Honkala 1990). Three species—rock, Siberian and Russian elms—have protandrous flowers, where the male anthers dehisce before the stigma is receptive. The elms are one of the few tree genera where the normal flowering period varies more than 2 to 3 weeks among species that are sexually compatible (Santamour 1989). Five floral stages have been identified: (1) stigma visible; (2) stigma lobes reflexed above anthers; (3) anthers dehiscing; (4) anther dehiscence complete and stigma wilting; (5) stigma shriveled, ovule green, and enlarged (Lee and Lester 1974). Pollination at stage 2 yielded the most viable seed (81%) followed by stage 1, stage 3, stage 4, and finally stage 5 (Lee and Lester 1974).

The perfect, rather inconspicuous inflorescences usually are borne in the spring before the leaves appear except for cedar, lacebark, and red elms, which flower in the fall (table 2). The inflorescences are fascicles, racemes, or racemose cymes measuring <2.5 up to 5 cm long (Fernald 1970). American, Scots, and rock elms have pendulous inflorescences (FNAEC 1997). Individual flowers are borne on pedicels measuring 0.4 to 1 cm long. The flowers have a calyx with 3 to 9 lobes, 3 to 9 stamens, and white stigmas with 2 styles (Fernald 1970; Radford and others 1968). Most of the elm species have reddish anthers,which gives the trees their characteristic flower color (FNAEC 1997; Johnson 1973).

The fruit is a 1-cell samara that ripens a few weeks after pollination and consists of a compressed nutlet surrounded by a membranous wing (figures 1 and 2). Winged, cedar, slippery, red, and rock elm seeds have pubescent samaras (Hora 1981). The seed is centrally located within the wing for slippery, Siberian, lacebark, and Scots elms (Hora 1981). The apex of the wing can be shallowly or deeply notched (FNAEC 1997). American elm seeds have 2 inward curving beaks at the wing's apex (Dirr 1998). Elm seeds have no endosperm and are dispersed by wind, water, or animals (Burns and Honkala 1990). Most species produce good seedcrops at 2- or 3-year intervals (table 3).

Collection of fruits. Elm seeds can be collected by sweeping them up from the ground soon after they fall or by beating or stripping the seeds from the branches. The large seeds of rock elm are greatly relished by rodents (Dore 1965), however, and usually must be picked from the trees. American elm samaras fall within 91 m of the parent tree (Burns and Honkala 1990). Rock elm samaras are carried no more than 40 to 45 m from the parent tree, but their buoyant

Table 2—*Ulmus,* elm: phenology of flowering and fruiting

Species	Location	Flowering	Fruit ripening	Seed dispersal	Seed size (mm)
U. alata	—	Feb–Apr	Apr	Apr	6–8
U. americana	From S to Canada	Feb–May	Late Feb–June	Mid-Mar–mid-June	13
U. crassifolia	SE US	Aug–Sept	Sept–Oct	Oct	6–13
U. glabra	Europe & Asia Minor	Mar–Apr	May–June	May–June	15–25
U. japonica	Japan	Apr–May	June	—	—
U. laevis	Massachusetts	Apr–May	May–June	May–June	10–15
U. parvifolia	NE US	Aug–Sept	Sept–Oct	Sept–Oct	10
U. pumila	E central US	Mar–Apr	Apr–May	Apr–May	10–14
U. rubra	F S to Canada	Feb–May	Apr–June	Apr–June	12–18
U. serotina	SE US	Sept	Nov	Nov	10–13
U. thomasii	NE US	Mar–May	May–June	May–June	13–25

Sources: Asakawa (1969), Brinkman (1974), Burns and Honkala (1990), Dirr (1998), FNAEC (1997), Hora (1981), Little and Delisle (1962), Loiseau (1945), Pammel and King (1930), Petrides (1958), Rehder (1940), Spector (1956), Stoeckeler and Jones (1957), Sus (1925) ,Vines (1960),Wappes (1932),Wyman (1947).

Figure 1—*Ulmus*, elm: samaras of *U. alata*, winged elm (**top left**); *U. americana*, American elm (**top right**); *U. parvifolia*, Chinese elm (**middle left**); *U. pumila*, Siberian elm (**middle center**); *U. rubra*, slippery elm (**middle right**); *U. crassifolia*, cedar elm (**bottom left**); and *U. thomasii*, rock elm (**bottom right**).

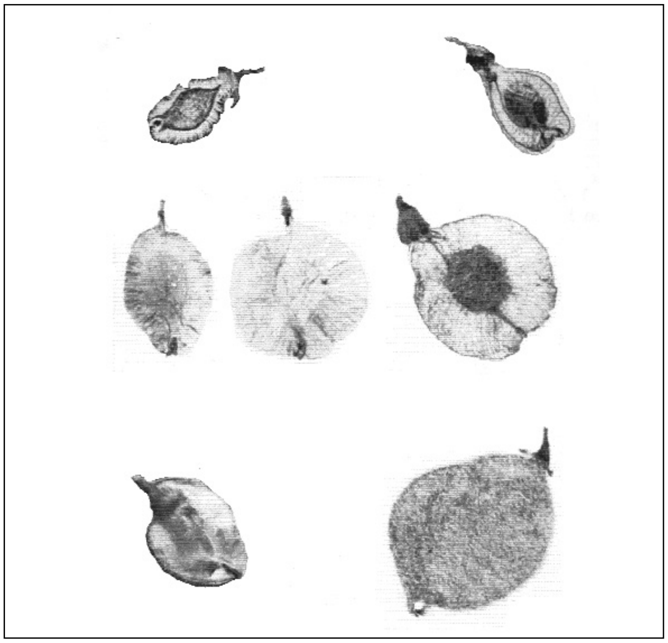


Figure 2—*Ulmus alata*, winged elm: longitudinal section through a seed.

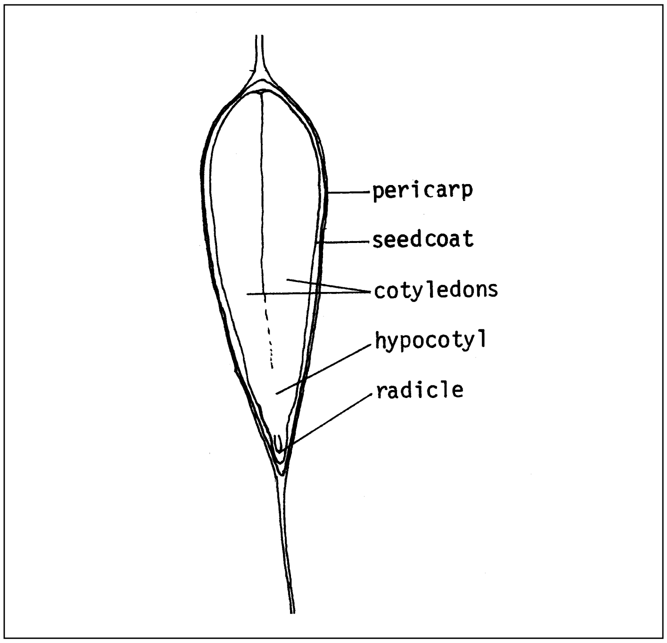


Table 3—*Ulmus,* elm: height, seed-bearing age, seed crop frequency, and fruit ripeness criteria

Species	Height at maturity (ft)	Year first cultivated	Minimum seed-bearing age (yr)	Years between large seedcrops	Ripe fruit color when ripe
U. alata	50	1820	—	—	Reddish green
U. americana	120	1752	15	—	Greenish brown
U. crassifolia	100	—	—	—	Green
U. glabra	130	Long cultivated	30–40	2–3	Yellow-brown
U. japonica	100	1895	—	2	—
U. laevis	100	Long cultivated	30–40	2–3	Yellow-brown
U. parvifolia	80	1794	—	—	Brown
U. pumila	80	1860	8	45	Yellow
U. rubra	70	1830	15	2–4	Green
U. serotina	60	1903	—	2–3	Light green to brownish
U. thomasii	100	1875	20	3–4	Yellow or brownish

Sources: Brinkman (1974), Burns and Honkala (1990), Dore (1965), FNAEC (1997), George (1937), Little and Delisle (1962), McDermott (1953), Van Dersal (1938), Vines (1960), Wappes (1932).

samaras can be carried by water and are frequently found along stream and lake banks (Burns and Honkala 1990). In rock elm, 90 to 100% of the mature seeds are viable and the seeds ripen about 2 to 3 weeks after American elm seeds (Burns and Honkala 1990).

Storjohann and Whitcomb (1977) collected lacebark elm seeds at Oklahoma State University and found that 75 to 80% of the seeds were empty. They also found that lacebark elm seeds are the most viable if collected before a hard freeze. Freshly collected fruits should be air-dried for a few days before being sown or stored. The number of seeds per weight varies widely, even within species (table 5).

Extraction and storage of seeds. Although the fruits can be de-winged by putting them into bags and beating with flails, this has been found to damage the seeds of American and Siberian elms (Cram and others 1966; George

1937). Elm seeds can be cleaned with an air-screen cleaner in a reverse procedure—blowing out the seeds, and catching the heavier leaves and twigs (Myatt 1996) with the air vents wide open on both sides of the cleaner. A large round-holed 9.9-mm screen (#25) is placed on top of the cleaner to separate the seeds from the leaves and a small round-holed 2.4-mm screen (#6) is placed on the bottom to separate the twigs from the seeds (Myatt and other 1998). Only 3 to 7% of the seeds blown out of the air chute in the back of the air-cleaner were good seeds (Myatt and others 1998).

Fruits usually are sown or stored with the wings attached. Elm seeds are orthodox in storage behavior and should be stored at low temperatures and moisture contents in sealed containers (table 4). Dessication of smoothleaf elm seeds to 3.3% moisture content did not reduce germination (Tompsett 1986). When the temperature of storage was increased at constant moisture contents, seed longevity was reduced within the range of –13 to 52 °C. Smoothleaf elm seeds stored at 22% moisture content (fresh-weight basis) died after 7 days at –75 C°, but seeds stored at 19% moisture content lost no germination ability. Lowering the storage temperature from –13 to –75 °C did not increase seed longevity. Tompsett (1986) found that a 5% moisture content and a temperature of –20 °C or lower maintains the long-term seed viability for smoothleaf elm seeds. Tylkowski (1989) reported that Russian elm seeds dried to 10% moisture could be stored at –1 to –3 °C for 5 years without losing any viability; however, after 6 years of storage, a 20% decrease in germination was observed. Siberian elm seeds with 3 to 8% moisture content have been stored at 2 to 4 °C in sealed containers for 8 years (Dirr and Heuser 1987). Air-dried Scots elm seeds stored at 1 to 10 °C were only viable for 6 months (Dirr and Heuser 1987).

Dried American elm seeds stored at 0, 10, and 20 °C declined from 65 to 70% germination before storage to less than 10% after 10.5 months of storage (Steinbauer and Steinbauer 1932). Another lot of dried American elms seeds stored at 20 °C exhibited a steady, continuous decline in germination when stored for 14 to 51 weeks compared to fresh seed germination values (Steinbauer and Steinbauer 1932). Barton (1939, 1953) found that a 75% germination value for American elm seeds was retained after 15 years of seed storage at –4 °C with a 3% seed moisture content .

Pregermination treatments. Under natural conditions, elm seeds that ripen in the spring usually germinate in the same growing season; seeds that ripen in the fall germinate in the following spring. Although seeds of most elm species require no presowing treatment, practically all the seeds in some seedlots of American elm remain dormant until the second season (Rudolf 1937). Dormant American elm seedlots should receive cold stratification for 2 to 3

Table 4—*Ulmus,* elm: seed storage conditions

Species	Seed moisture (%)	Storage temp (°C)	Viable period (yr)
U. alata	Air-dried	4	1
U. americana	3–4	–4	15
	Air-dried	4	2
U. crassifolia	Air-dried	4	1
U. glabra	Air-dried	1–10	0.5
U. laevis	Air-dried	22	0.5
U. parvifolia	10–15	0	0.5
U. pumila	3–5	2–4	8
U. thomasii	Air-dried	Cold	—

Sources: Barton (1939, 1953), Brinkman (1974), Heit (1967a&b), Kirby and Santelmann (1964), Rohmeder (1942), Sus (1925).

Table 5—*Ulmus,* elm: seed yield data

Species	Place collected	Fruit/vol kg/hl	Fruit/vol lb/bu	Cleaned seeds (x1,000)/weight: Average /kg	Average /lb	Range /kg	Range /lb	Samples
U. alata	Mississippi	—	—	245	112	222–269	101–119	4
U. americana	—	5.8	4.5	156	71	106–240	48–109	14
U. crassifolia	Mississippi	—	—	147	67	130–135	59–61	5
U. glabra	Europe	4–6.5	3–5	88	40	66–99	30–45	12+
U. japonica	Japan	—	—	12.8	6	—	—	2+
U. laevis	Russia	—	—	140	63	117–205	53–93	20+
U. parvifolia	US, Japan	—	—	265	121	250–372	114–169	6+
U. pumila	—	—	—	158	72	88–261	40–119	35+
U. rubra	—	—	—	90	41	77–119	35–54	10
U. serotina	—	—	—	328	149	—	—	—
U. thomasii	—	7.7–10.3	6–8	15	7	11–15	5–7	5

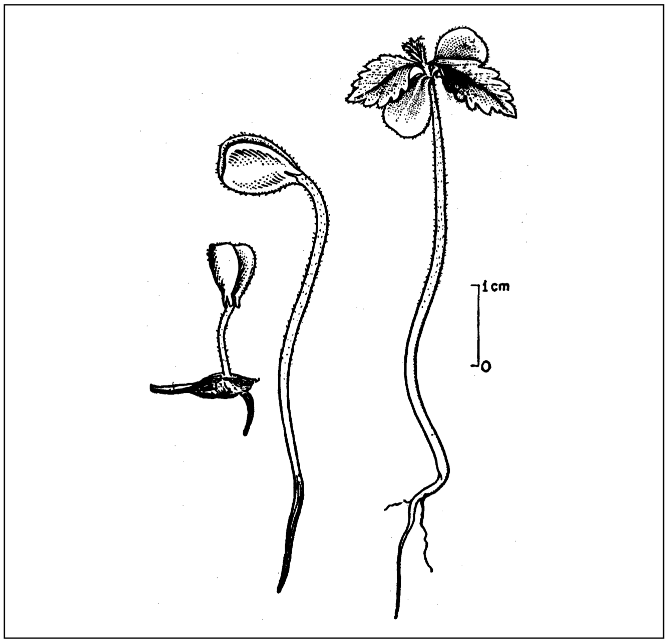
Sources: Asakawa (1969), Brinkman (1974), Engstrom and Stoeckeler (1941), Goor (1955), Gorshenin (1941), Heit (1969), Rafn and Son (1928), Stoeckeler and Jones (1957), Sus (1925), Swingle (1939), Taylor (1941), Van Dersal (1938), Wappes (1932).

months (Dirr and Heuser 1987). Seeds of slippery elm, especially from northern sources, also may show dormancy; 70% of fresh seeds germinated and 57% germinated after 2 months of cold, moist stratification (Dirr and Heuser 1987). Stratification at 5 °C for 60 to 90 days before sowing improves germination of cedar, smoothleaf, and September elms (Brinkman 1974; Dirr and Heuser 1987; Maisenhelder 1968).

Winged, Scots, Japanese, English, Russian, Siberian, and rock elms have no pregermination requirements (Dirr and Heuser 1987). Fresh seedlots of Scots elm germinated at 98%, but after 2 months of cold, moist stratification, only 88% germinated (Dirr and Heuser 1987). English elm rarely produces seeds, but fresh seeds will germinate at 100% with or without 2 months of stratification (Dirr and Heuser 1987). Fresh Siberian elm seeds germinated 96% and cold stratification did not improve germination (Dirr and Heuser 1987). Fresh lacebark elm seeds will germinate without pretreatment, but once dried they require 1 to 2 months of cold, moist stratification (Dirr and Heuser 1987).

Germination tests. Official testing rules for American elm call for alternating temperatures of 30 °C (day) for 8 hours and 20 °C (night) for 16 hours for 14 days on wet blotters and 10 days at a constant 20 °C for Chinese and Siberian elms (AOSA 2001). American elm seeds can also germinate well at alternating temperatures of 21 °C (day) and 10 °C (night) (Burns and Honkala 1990). The International Seed Testing Association (1999) suggests testing for 14 days on wet blotters for all 3 species. ISTA also suggests removal of the pericarp if germination is slow. Germination tests of most species may also be made on sand or peat in germinators at alternating temperatures of 30 °C (day) and 20 °C (night). Rock elm seeds germinated 70 to 80% in a peat moss medium (Burns and Honkala 1990). Light requirements may vary among species (table 6). American elm can germinate in darkness but germination is increased with the addition of light (Burns and Honkala 1990).

Figure 3—*Ulmus americana*, American elm: seedling development at 1, 3, and 21 days after germination.



Germination is epigeal (figure 3); it usually peaks within 10 days. Seedlots of stratified seeds complete germination in 10 to 30 days. With American elm seeds, germination can extend up to 60 days; seeds can lay on flooded ground for a month without adversely affecting germination (Burns and Honkala 1990). Radicles of rock elm emerge in 2 to 3 days in a petri dish and are 2.5 to 3.8 cm (1 to 1.5 in) long by the 5th day; cotyledons opened about the 5th or 6th day (Burns and Honkala 1990). Winged elms cotyledons are oval with shallowly notched apexes and heart-shaped bases and may persist 1 to 2 months on the seedling with primary leaves appearing 1 week after germination in natural forest conditions (Burns and Honkala 1990).

Nursery practice. Seeds of elm species ripening in the spring are usually sown immediately after collection, whereas seeds of fall-ripening species or of species requiring stratification are usually planted the following spring (table 7). Beds should be kept moist until germination is complete; shading is not usually necessary. From 5 to 12% of the viable cedar elm seeds sown can be expected to produce plantable stock (Burns and Honkala 1990). One-year-old seedlings usually are large enough for field planting. Rock elm seedlings have a persistent dormant bud, so seedlings rarely develop more than a single pair of true leaves in the first growing season (Burns and Honkala 1990). In northern Wisconsin, rock elm 1.5+0 nursery stock averaged 27 cm (10.6 in) in height 5 years after planting and 52 cm (20.5 in) in height 10 years after planting; first-year survival was 85% and 10th-year survival was 32% (Burns and Honkala 1990). To improve survival in semiarid regions, trees often are transferred into containers after 1 year in the seedbeds (Goor 1955). Slippery elm is commonly used as rootstock when grafting hybrid elms (Burns and Honkala 1990).

Table 6—*Ulmus,* elm: germination test conditions and results

Species	Germination test conditions*				Germinative energy	Germinative capacity			
		Temp (°C)							
	Medium	Day	Night	Days	Amount (%)	Period (days)	Avg (%)	Samples	Purity (%)
U. alata	Soil	32	21	15	76	7	91	6	—
U. americana	Paper pads	30	20	14	—	—	—	—	—
	Kimpak	30	20	28	—	—	67	1	—
	—	—	—	13–60	55	7	64	15	92
U. crassifolia	Soil	32	21	80	56	78	56	2	—
U. glabra	Germinator or sand	21–30	20–25	30–60	—	—	44	72+	—
U. laevis	Germinator or sand	21	21	30	—	—	65	22+	85
U. parvifolia	Paper pads	20–29	20	10–60	—	—	55	2+	64
U. pumila	Paper pads	—	—	10	—	—	—	—	—
	Kimpak	30	20	28	—	—	81	1	—
	Germinator or sand	20–30	20	30	55	10	76	48	90
U. rubra	Sand	30	20	60	21	10	23	5	94
U. serotina	Soil	32	21	30	68	20	72	1	—
U. thomasii	Sand or petri dish	30	20	30	77	8	81	11	95

Sources: Arisumi and Harrison (1961), AOSA (2001), Engstrom and Stoeckeler (1941), Gorshenin (1941), Heit (1967a&, 1968), ISTA (1999), Johnson (1946), Kirby and Santelman (1964), Maisenhelder (1968), McDermott (1953), NBV (1946), Rafn and Son (1928), Rohmeder (1942), Spector (1956), Stoeckeler and Jones (1957), Sus (1925), Swingle (1939), USDA FS (2002), Wappes (1932).

* Light for 8 hours or more per day is recommended for American elm (AOSA 2001; ISTA 1999; McDermott 1953). Light is neither required nor inhibitory for germination of winged elm (Loiseau 1945), and Chinese and Siberian elms (AOSA 2001; ISTA 1999).

Table 7—*Ulmus,* elm: nursery practice

Species	Sowing season*	Seedlings/area		Sowing depth		Tree percent	Out-planting age (yrs)
		/m²	/ft²	mm	in		
U. alata	Summer	—	—	0–6.4	0–1/4	—	1
U. americana	Spring	5	2	6.4	1/4	12	1
U. crassifolia	Spring	—	—	0–6.4	0–1/4	—	1
U. glabra	Summer	—	—	0–6.4	0–1/4	—	—
U. laevis	Summer	—	—	0-6.4	0–1/4	6	1–2
U. parvifolia	Spring	25–30	2–3	4.8–6.4	3/16–1/4	12–20	1–2
U. pumila	Summer	—	—	6.4	1/4	3–7	1–2
U. rubra	Spring	25	2	6.4	1/4	—	1
U. serotina	Spring	—	—	0–6.4	0–1/4	—	1
U. thomasii	Spring	15–38	1–4	6.4	1/4	—	2

Sources: Baker (1969), Deasy (1954), Engstrom and Stoeckeler (1941), George (1937), Kirby and Santelman (1964), Rohmeder (1942), Stoeckeler and Jones (1957), Sus (1925), Swingle (1939), Toumey and Korstian (1942).

* Spring-sowing was preceded by stratification in sand or in a plastic bag at 4 to 5 °C for 60 days.

References

Arisumi T, Harrison JM. 1961. The germination of rock elm seeds. American Nurseryman 114(7): 10.

Asakawa S. 1969. Personal correspondence. Meguro, Japan: Ministry of Agriculture and Forestry.

AOSA [Association of Official Seed Analysts]. 2001. Rules for testing seeds. Association of Official Seed Analysts. 126 p.

Baker LA. 1969. Personal correspondence. Elkton, OR: Oregon State Forestry Department, Dwight L. Phipps Forest Nursery.

Barnard ES. 2002. New York City trees: a field guide for the metropolitan area. New York: Columbia University Press: 212.

Barton LV. 1939. Storage of elm seeds. Contributions of the Boyce Thompson Institute 10(2): 221–233.

Barton LV. 1953. Seed storage and viability. Contributions of the Boyce Thompson Institute 17(2): 87–103.

Brinkman KA. 1974. *Ulmus* L., elm. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk 450. Washington, DC: USDA Forest Service: 829–834.

Burns RM, Honkala BH. 1990. Silvics of North America. Volume 2, Hardwoods. Agric. Handbk 654. Washington, DC: USDA Forest Service. 877 p.

Cram WH, Lindquist CH, Thompson AC. 1966. Seed viability studies: American and Siberian elm. Summary Report Tree Nursery Saskatchewan. 1965: 8–9.

Deasy JJ. 1954. Notes on the raising of forest trees in the nursery. Irish Forestry 11(1): 10–19.

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

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

Dore W. 1965. Ever tried rock elm seeds for eating? Canada Audubon 27(3): 90–91.

Engstrom HE, Stoeckeler JH. 1941. Nursery practice for trees and shrubs. Misc. Pub. 434. Washington, DC: USDA Forest Service. 159 p.

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

FNAEC [Flora of North America Editorial Committee]. 1997. Flora of North America north of Mexico. Volume 3, Magnoliophyta: Magnoliidae and Hamamelidae. New York: Oxford University Press. 590 p.

George EJ. 1937. Storage and dewinging of American elm seed. Journal of Forestry 35(8): 769–772.

Goor AY. 1955. Tree planting practices for arid areas. For. Dev. Pap. 6. Rome: FAO. 126 p.

Gorshenin NM. 1941. Agrolesomelioratsiya [in Russian: Agro-forest melioration]. 392 p.

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

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

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

Heit CE. 1969. Personal communication. Geneva, NY: New York State Agricultural Experiment Station.

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

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

Johnson H. 1973. The international book of trees. New York: Simon and Schuster. 288 p.

Johnson LPV. 1946. Effect of humidity on the longevity of *Populus* and *Ulmus* seeds in storage. Canadian Journal of Research 24(Sec. C): 298–302.

Kirby B, Santelmann PW. 1964. Germination and emergence of winged elm seed. Weeds 12(4): 277–279.

Krüssmann G. 1960. Die Nadelgehölze. 2nd ed. Berlin. 335 p.

Lee MT, Lester DT. 1974. Floral receptivity in American elm. Canadian Journal of Forest Research 4: 416–417.

Little EL Jr, Delisle AL. 1962. Time periods in development: forest trees, North American. In: Altman PL, Dittmer D, eds. Biological handbook on growth. Washington, DC: Federation of American Societies for Experimental Biology: Table 104.

Loiseau J. 1945. Les arbres et la fôret. Paris. 204 p.

Maisenhelder LC. 1966. Unpublished data. Stoneville, MS: USDA Forest Service, Southern Forest Experiment Station.

Maisenhelder LC. 1968. Unpublished data. Stoneville, MS: USDA Forest Service, Southern Forest Experiment Station.

Myatt A. 1996. Personal communication. Washington, OK: Oklahoma Forestry Division.

Myatt A, Huffman G, Odell, J Sr. 1998. Seed processing manual. Washington, OK: Oklahoma Department of Agriculture, Forestry Division, Forest Regeneration Center.

McDermott RE. 1953. Light as a factor in the germination of some bottomland hardwood seeds. Journal of Forestry 51: 203–204.

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

Pammel LH, King CM. 1930. Germination and seedling forms of some woody plants. Iowa Academy of Science Proceedings 37: 131–141.

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

Radford AE, Ahles HE, Bell CR. 1968. Guide to the vascular flora of the Carolinas. Chapel Hill: University of North Carolina Book Exchange. 383 p.

Rafn J & Son. [nd, circa 1928]. Skovfrökontoret's Fröanalyser gennem 40 Aar, 1887–1927. Udfort paa Statsfrokontrollen i Köbenhavn. 5 p.

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

Rohmeder E. 1942. Keimversuche mit *Ulmus montana* With. Forstwissenschaftliches Centralblatt 64: 121–135.

Rudolf PO. 1937. Delayed germination in American elm. Journal of Forestry 35: 876–877.

Santamour FS Jr. 1989. Flowering and fertility of hybrids between spring- and fall-flowering elms. Horticultural Science 24(1): 139–140.

Sinclair WA, Lyon HH, Johnson WT. 1987. Diseases of trees and shrubs. Ithaca, NY: Comstock Press: 366–388.

Spector WS, ed. 1956. Handbook of biological data. Philadelphia: Saunders. 584 p.

Steinbauer CE, Steinbauer GP. 1932. Effects of temperature and dessication during storage on germination of seeds of the American elm (*Ulmus americana* L.). Proceedings of the American Society for Horticultural Science 28: 441–443.

Stoeckeler JH, Jones GW. 1957. Forest nursery practice in the Lake States. Agric. Handbk 110. Washington, DC: USDA Forest Service. 124 p.

Storjohann A, Whitcomb CE. 1977. Collection and storage of *Ulmus parvifolia*, lacebark elm seed. Res. Rep. Pap. 760. Stillwater: Oklahoma Agricultural Experiment Station: 86.

Sus NI. 1925. Pitomnik [in Russian: The forest nursery]. 227 p.

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

Taylor CA. 1941. Germination behavior of tree seeds as observed in the regular handling of seed at the seed extractory and nursery. Norfolk, NE: USDA Forest Service, Prairie States Forestry Project. 63 p.

Tompsett PB. 1986. The effect of temperature and moisture content on the longevity of seed of *Ulmus minor* and *Terminalia brassii*. Annals of Botany 57: 875–883.

Toumey JW, Korstian CF. 1942. Seeding and planting in the practice of forestry. New York: John Wiley & Sons. 520 p.

Townsend AM. 1975. Crossability patterns and morphological variation among elm species and hybrids. Silvae Genetica 24(1): 18–23.

Tylkowski T. 1989. Storing of Russian elm (*Ulmus laevis* Pall.) seed over many years. Arboretum Kornicke 32: 297–305.

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

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

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

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

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

Lauraceae—Laurel family

Umbellularia californica (Hook. & Arn.) Nutt.

California-laurel

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Growth habit, occurrence, and uses. The genus *Umbellularia* contains a single species—*Umbellularia californica* (Hook. & Arn.) Nutt.—that has many common names (Coombes 1992; Stein 1990), the best known being California-laurel, California-olive, Oregon-myrtle, myrtlewood, bay, laurel, and pepperwood. California-laurel is a broad-leaved evergreen that matures either as a shrub or tall forest tree. Over much of its range, it attains heights of 12 to 24 m and diameters of 46 to 76 cm, but near the ocean, in the chaparral, and on other severe or rocky sites it is confined to prostrate or shrub sizes (Harlow and others 1979; Jepson 1910). In the protected bottomlands of southern Oregon and northern California, mature trees are 91 to 305 cm in diameter and 30 or more m tall (Harlow and others 1979). A maximum circumference of 1,387 cm at 137 cm above ground (AFA 2000) and a maximum height of 53.3 m have been reported (Sargent 1961).

Several racial variations are recognized. *Umbellularia californic*a forma *pendula* Rehd. is an uncommon, broad-spreading tree distinctive for its pendulous branchlets that contrast strongly with typically ascending branch growth (Jepson 1910; Rehder 1940). *U. californica* var. *fresnensis* Eastwood has fine white down on the lower surfaces of leaves and branches of the panicle (Eastwood 1945). Several forms that Jepson (1910) describes—gregarious, rockpile, dwarf, and prostrate—may indicate other varietal differences.

The range of California-laurel spans more than 11 degrees of latitude, from near the 44th parallel in the Umpqua River Valley of Douglas County, Oregon, south beyond the 33rd parallel in San Diego County, California, nearly to the Mexican border. California-laurel is widely distributed in the coast ranges and less abundantly in inland valleys and the Siskiyou and Sierra Mountains (Sudworth 1908). It may be found from sea level to 1,220 m in much of its range, and from 610 to 1,520 m in southern California (Jepson 1910). Pure, dense stands of California-laurel develop in some areas, but more often it is intermixed with other tree and shrub species. It grows in many kinds of soils under both cool-humid and hot-dry atmospheric conditions (Stein 1990). In xeric climates, it is most prominent where soil moisture is favorable—on alluvial deposits or protected slopes, along watercourses, near springs and seeps—but in its shrub form, it also is found on dry slopes and is a common component of chaparral (Sampson and Jespersen 1963).

All parts of the tree have served human needs. Wood of this species compares favorably in machining quality with the best eastern hardwoods (Davis 1947) and is used for woodenware, interior trim, furniture, paneling, veneer, and gunstocks. Burls and other growths with distorted grain are especially prized for making the gift and novelty items that are marketed extensively as "myrtlewood." Dried leaves are used for seasoning meats and soups (McMinn 1970). In an earlier day, Hudson Bay Company trappers brewed a comforting tea from the leaves to overcome chill (Ross 1966). David Douglas learned that hunters made a drink from the bark and declared it "by no means an unpalatable beverage" (Harvey 1947). Native Americans ate substantial quantities of the fruit and seeds, made a drink from the bark of the roots, and used the leaves for several internal and external medicinal purposes, including vermin control (Chesnut 1902).

Extracts of the leaves, seeds, and wood have strong chemical properties and should be used with caution. Vapor from the aromatic leaves can cause sneezing, headache, sinus irritation, other severe discomforts, and even unconsciousness (Drake and Stuhr 1935; Peattie 1953). The leaves contain considerable menthol (Stein 1974) and the ketone umbellulone, which when extracted from the leaf oil, interferes strongly enough with respiration, heartbeat, and blood circulation to cause death in laboratory animals (Drake and Stuhr 1935). Umbellulone also has fungicidal and germicidal properties (Drake and Stuhr 1935). Oils from the wood, leaves, and seeds have been sold for pharmaceutical purposes such as treating catarrh, nervous disorders, rheumatism, meningitis, intestinal colic, and dyspepsia (Peattie 1953; Sargent 1895; Stuhr 1933).

California-laurel is used to a moderate extent as an ornamental evergreen. It has thick, glossy, medium-to-dark green persistent leaves that turn orange or yellow before they drop individually and contrasting pale yellow flowers. The very dense aromatic foliage often shapes naturally into a pleasing, symmetrical, rounded crown. Since it was first cultivated in 1829 (Rehder 1940), it has demonstrated the ability to grow well far outside its natural range (Stein 1958). It can be grown as a decorative potted plant for lobbies and patios and will tolerate moderate pruning (Kasapligil and Talton 1973).

California-laurel also has wildlife values—young sprouts are choice browse in spring and summer. Year-long use is rated by Sampson and Jespersen (1963) as good to fair for deer (*Odocoileus* spp.) and fair to poor for cattle, sheep, and goats. Longhurst and others (1952) list it as a principal browse species for deer in the north coastal ranges of California. Silver gray-squirrels (*Sciurus griseus*), dusky-footed wood rats (*Neotoma fuscipes*), and Steller's jays (*Cyanocitta stelleri*) feed on the seeds extensively (Bailey 1936; Van Dersal 1938). Hogs eat both seeds and roots (Jepson 1910; Van Dersal 1938).

Flowering and fruiting. California-laurel flowers regularly and often profusely. The small, pale yellow, perfect flowers grow on short-stemmed umbels that originate from leaf axils or near the terminal bud (figure 1). Flower buds develop early; those for the following year become prominent as current-year fruits are maturing. Within its long north–south range, California-laurel has been reported to flower in all months from November to May, beginning before new leaves appear (Jepson 1910; Kasapligil and Talton 1973; Rehder 1940; Unsicker 1974). The flowering period may stretch into late spring and summer with the occasional appearance of flowers originating in axils of the current year's developing leaves (Sargent 1895). California-laurel flowers at an early age; flowers have been observed on short whiplike shrubs and on 1-year-old sucker growth that originated on a long broken stub. Small insects appear to be the chief pollinaters (Kasapligil 1951).

Seedcrops are abundant in most years (Stein 1974). Although umbels bear 4 to 9 flowers each, generally only 1 to 3 fruits set (Jepson 1910). The age when a tree first bears fruit, the age for maximum production, and the average quantity produced have not been reported. Seeds are produced in abundance after trees are 30 to 40 years old (Harlow and others 1979). Damage to developing seedcrops by insects, birds, or diseases has not been reported.

Collection, extraction, and storage. The fruits—acrid drupes each containing a single, large, thin-shelled seed—ripen in the first autumn after flowering (Rehder 1940; Sargent 1895; Sudworth 1908). As the drupes mature, their thin, fleshy hulls change from medium green to speckled yellow green (Britton 1908; Sudworth 1908) (figure 1), pale yellow (Eliot 1938), or various other hues, ranging from yellow-green tinged with dull red or purple (Peattie 1953; Sargent 1895) through purplish brown (Jepson 1910; Kasapligil 1951) to purple (Kellogg 1882; Sargent 1892; Torrey 1856). Ripe drupes may be yellow-green on one tree and dark purple on an adjacent tree (Stein 1974).

Drupes fall stemless to the ground in late autumn or winter and are dispersed by gravity, wind, animals, and water (McBride 1969). Seeds are collected simply by gathering fallen drupes—if squirrels and other animals don't get there first. Shaking ripe drupes from the tree should provide a good means for making quick, efficient collections.

When soft, the fleshy hulls are readily removed from the seeds by hand. The hulls can also be removed easily by machines used for de-pulping drupes if quantity processing is required. Mirov and Kraebel (1937) obtained about 300 cleaned seeds (figure 2) from 0.45 kg (1 lb) of drupes. For 8 samples processed at Davis, California (Lippitt 1995), the seed count averaged 547/kg (248/lb) and ranged from 403 to 675/kg (183 to 306/lb).

Figure 1—*Umbellularia californica*, California-laurel: yellow-green mature drupe suspended from its conical capula.

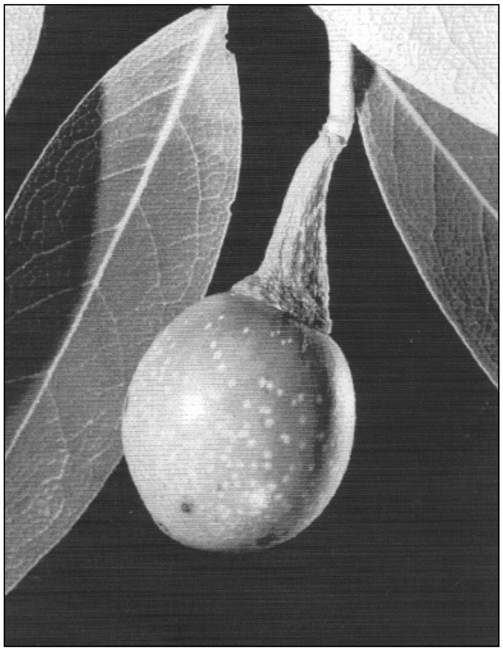


Figure 2—*Umbellularia californica*, California-laurel: exterior views of cleaned seeds.

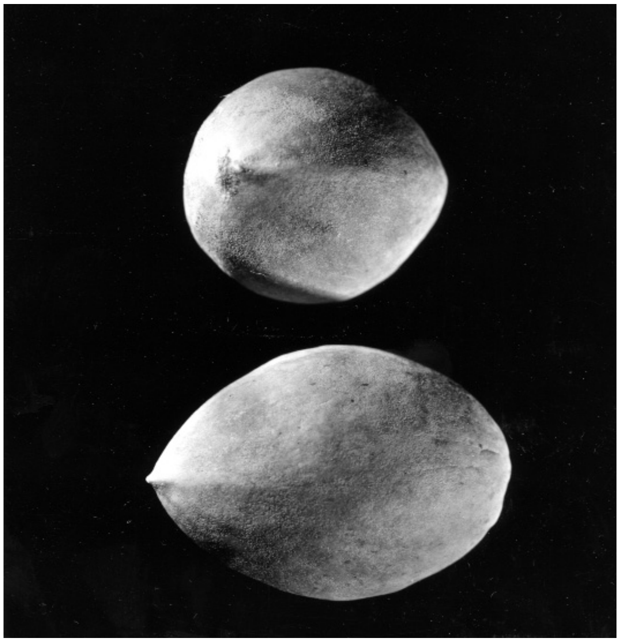
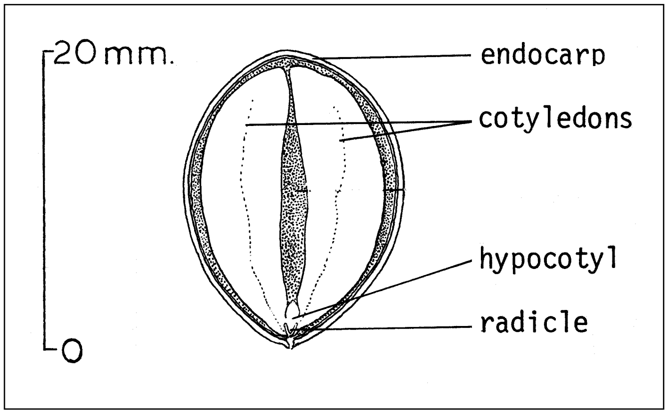


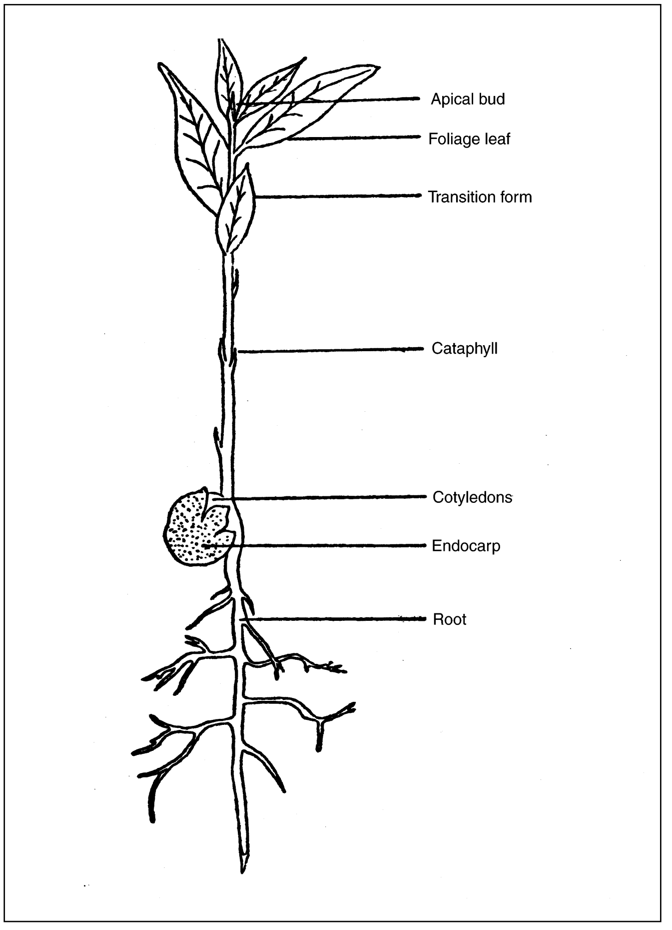
Figure 3—*Umbellularia californica*, California-laurel: tudinal section through a seed.



Seeds of California-laurel have lost viability in storage even at low temperatures, so yearly collection of fresh seeds is advised (Stein 1974). Viability has been maintained for 6 months when seeds were stored at 3 °C in wet, fungicide-treated vermiculite (McBride 1969). Storage trials have been very limited and tests of cool, moist storage at different moisture contents are needed. Highest germination (81%) was obtained from a seedlot with 32% moisture content (Lippitt 1995). Under favorable natural conditions, seeds on the ground retain their viability over winter, but under adverse conditions, viability may prove transient.

Seed treatment and germination. Fresh untreated seeds will germinate under room or outdoor conditions in peat moss, sawdust, vermiculite, or light-textured soil but may require 3 months or longer (Kasapligil 1951; Mirov and

Figure 4—*Umbellularia californica*, California-laurel: 4-month-old seedling (from Stein 1974, courtesy of Baki Kasapligil 1951).



Kraebel 1937; Stein 1974). Germination can be speeded by scarifying, cracking, or removing the endocarp or by stratifying the seeds, but it still may require about 2 months (Kasapligil 1951; McBride 1969; Stein 1974). In light soil, 20 to 25% of untreated seeds germinated; with stratification, germination nearly doubled (Stein 1974). In 16 lots of seeds collected in 1969 from Oregon and California sources, germination by the end of March ranged from 0 to 82% after January planting deep in pots of peat or vermiculite. Parts of seedlots held in a refrigerator at 4.4 °C from November to January germinated somewhat better than those immediately planted outdoors in a peat–vermiculite mixture. The better seedlots germinated equally well in several contrasting test conditions (Stein 1974).

In comparison tests made in petri dishes, California-laurel germination was highest in 30 days under a temperature regime of 16 °C day, 7 °C night, and when evaporative stress was minimal (McBride 1969). Germination did not appear affected by light level but was highest in soil with moisture tension at 4 to 10 atmospheres.

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Seedling development and nursery practice. Under forest conditions, germination has been reported to take place in autumn soon after seedfall (Harlow and others 1979; Sargent 1895; Sudworth 1908) or in late winter and spring (Stein 1958, 1974). Covered seeds germinate best, but the large seeds do not bury readily without ground disturbance or silt deposition by high water. Seedling establishment is uncommon in the drier parts of California except in protected areas and where the ground is disturbed (Jepson 1910).

Germination is hypogeal, and the fleshy cotyledons remain within the endocarp and attached to the seedling until midsummer, when the plant may be 15 to 20 cm tall (Kasapligil 1951; Sargent 1895). Generally, there are 2 large cotyledons, sometimes 3, and no endosperm (figure 3) (Kasapligil 1951).

Young California-laurel seedlings appear flexible in their growth requirements. In the first 120 days, seedlings potted in vermiculite grew well at several levels of temperature, evaporative stress, soil moisture, and soil nutrients (McBride 1969). Seedlings grown at 18% or more of full sunlight produced the most dry weight. Seedlings produce leaves of several transitional forms as they develop (figure 4) and do not branch until they are 2 or 3 years old unless so induced by removal of the terminal bud (Kasapligil 1951). They soon develop a moderately stout taproot and are difficult to transplant if more than 1 year old unless grown in containers. Recovery after transplanting is often slow, and height growth may be limited for several seasons.

California-laurel may also be reproduced by cuttings (Stein 1974). Under field conditions, it sprouts prolifically from the root collar, stump, and fallen or standing trunk.

References

AFA [American Forestry Association]. 2000. The national register of big trees, 2000–01. American Forests 106 (1): 22–64.
Bailey V. 1936. The mammals and life zones of Oregon. North American Fauna 55. Washington, DC: USDA Bureau of Biological Survey. 416 p.
Britton NL. 1908. North American trees. New York: Henry Holt & Co. 894 p.
Chesnut VK. 1902. Plants used by the Indians of Mendocino County, California. United States National Herbarium Contributions 7(3): 295–408.
Coombes AJ. 1992. Trees: eyewitness handbook. New York: Dorling Kindersley: 189.
Davis EM. 1947. Machining of madrone, California laurel, tanbark oak, and chinquapin. Pub. R1727. Madison, WI: USDA Forest Service, Forest Products Laboratory. 6 p.
Drake ME, Stuhr ET. 1935. Some pharmacological and bactericidal properties of umbellulone. Journal of the American Pharmaceutical Association 24(3): 196–207.
Eastwood A. 1945. New varieties of two well-known Californian plants. Leaflets of Western Botany 4(6): 166–167.
Eliot WA. 1938. Forest trees of the Pacific Coast. New York: G. P. Putnam's Sons. 565 p.
Harlow WM, Harrar ES, White FM. 1979. Textbook of dendrology. 6th ed. New York: McGraw-Hill Book Co. 510 p.
Harvey AG. 1947. Douglas of the fir. Cambridge, MA: Harvard University Press. 290 p.
Jepson WL. 1910. The silva of California. Memoirs of the University of California 2: 1–480.
Kasapligil B. 1951. Morphological and ontogenetic studies of *Umbellularia californica* Nutt. and *Laurus nobilis* L. University of California Publications in Botany 25(3): 115–239.
Kasapligil B, Talton B. 1973. A flowering calendar for native California shrubs in the San Francisco Bay region. California Horticultural Journal 34(1): 12–30.
Kellogg A. 1882. California laurel or bay tree. In: Forest trees of California. Sacramento: California State Mining Bureau: 137–140.
Lippitt L. 1995. Personal communication. Davis: California Department of Forestry and Fire Protection, Lewis A. Moran Reforestation Center.
Longhurst WM, Leopold AS, Dasmann RF. 1952. A survey of California deer herds, their ranges and management problems. Game Bull. 6. Sacramento: California Department of Fish and Game. 136 p.
McBride JR. 1969. Plant succession in the Berkeley Hills [PhD thesis]. Berkeley: University of California.
McBride JR. 1974. Plant succession in the Berkeley Hills, California. Madroño 22(7): 317–329.
McMinn HE. 1970. An illustrated manual of California shrubs. Berkeley: University of California Press. 663 p.
Mirov NT, Kraebel CJ. 1937. Collecting and propagating the seeds of California wild plants. For. Res. Note 18. Berkeley: USDA Forest Service, California Forest and Range Experiment Station. 27 p.
Peattie DC. 1953. A natural history of western trees. Boston: Houghton Mifflin. 751 p.
Rehder A. 1940. Manual of cultivated trees and shrubs hardy in North America. 2nd ed. New York: Macmillan. 996 p.
Ross CR. 1966. Trees to know in Oregon. Coop. Ext. Bull. 697 (rev.). Corvallis: Oregon State University. 96 p.
Sampson AW, Jespersen BS. 1963. California range brushlands and browse plants. Pub. 4010. Berkeley: University of California, Division of Agriculture and Natural Resources. 162 p.
Sargent CS. 1892. *Umbellularia*. Garden and Forest 5: 349–350, 355.
Sargent CS. 1895. The silva of North America. Volume 7, Lauraceae–Juglandaceae. Boston: Houghton Mifflin. 173 p.
Sargent CS. 1961. Manual of the trees of North America (exclusive of Mexico). Volume 1, 2nd corrected ed. New York: Dover. 433 p.
Stein WI. 1958. Silvical characteristics of California-laurel. Silvical Ser. 2. Portland, OR: USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. 16 p.
Stein WI. 1974. *Umbellularia* (Nees) Nutt., California-laurel. In: Schopmeyer CS, tech. coord. Seeds of woody plants in the United States. Agric. Handbk. 450. Washington, DC: USDA Forest Service: 835–839.
Stein WI. 1990. *Umbellularia californica* (Hook.& Arn.) Nutt., California-laurel. In: Burns RM, Honkala BH, tech. coords. Silvics of North America. Volume 2, Hardwoods. Agric. Handbk. 654. Washington, DC: USDA Forest Service: 826–834.
Stuhr ET. 1933. Manual of Pacific coast drug plants. Lancaster, PA: Science Press Printing Co. 189 p.
Sudworth GB. 1908. Forest trees of the Pacific slope. Washington, DC: USDA Forest Service. 441 p.
Torrey J. 1856. Lauraceae. Pacific Railroad Report 4 (Bot. Pt.): 133.
Unsicker JE. 1974. Synecology of the California bay tree, *Umbellularia californica* (H.& A.) Nutt., in the Santa Cruz Mountains [PhD thesis]. Santa Cruz: University of California.
Van Dersal WR. 1938. Native woody plants of the United States: their erosion-control and wildlife values. Misc. Pub. 303. Washington, DC: USDA. 362 p.