Pinaceae—Pine family

# *Tsuga* Carr.

## hemlock

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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 derived from 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 saw-timber 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.

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 EC, whereas northern seeds do best near 13 EC. 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 Hjeffreyi* (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 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..

Western hemlock generally produces less than 40 seeds per cone of which usually less than 20 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 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 EC 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 EC, 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 EC. 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 EC. 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 seed crops.

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 EC. 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 EC) 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).

Moisture content of hemlock seeds in storage should be maintained between 6 and 9%. In longevity tests of seedlots stored at 5 EC 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 EC 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 EC) 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 EC alternating with dark periods at about 13 EC (Olson and others 1959). A long stratification period (70 days) increased germination percentages for Coffman (1975), who germinated seeds at 18 EC in darkness or with a ½ 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).

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 EC 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 EC 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 or 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 EC range will retard germination more effectively than allowing temperatures to rise to near 5 EC. Personnel should limit entry into the stratification cooler to minimize temperature fluctuations.

**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 EC followed by 28 days in a germinator at 15 EC. The rules call for placing western hemlock seeds directly in germinators at 20 EC 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 EC is recommended with germination temperature set at a constant 20 EC (480E daily heat sum) (table 6).

In a laboratory study, as the heat sums rose from 280 to 440E 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 $^{E}$C for 24 hours. The threshold heat sum for mountain hemlock seed germination lies close to 400E 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 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 EC 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 EC 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).

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 EC 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 (½ to ¾ 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 rhen 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 nursery bed (Romeriz 1997). In this system, a miniplug seedling is started in the greenhouse and then transplanted to the bareroot nursery bed.

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 seedling faster and a 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 which dictate the propagation procedure in the greenhouse. The spring planting regime requires that seeds be sown around February 1st, then the seedlings are 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 EC 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 photo period is increased to 20 hours/day and maintained until late April to keep the terminal bud from prematurely setting. The container medium is usually peat moss which 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 to a target level (Girard 2002).

The seedlings are induced to set a terminal bud in the greenhouse by photo period 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 which have roofs that open that subject the planting stock to full light conditions following budset. 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 plant crops ambient greenhouse temperatures are reduced to about 2 EC 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 EC 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 where 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 EC. 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).

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**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)

**Table 2—***Tsuga*, hemlock: seed data (thousands of cleaned seeds per unit weight)

| Species | Range (thousands) | | Average (thousands) | | |
|---|---|---|---|---|---|
| | /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, seed crop frequency, and cone ripeness criteria

| Species | Height at maturity (m) | Year first cultivated | Minimum seed-bearing age (yr) | Interval btw large seed-crops (yr) | Cone ripeness criteria | |
|---|---|---|---|---|---|---|
| | | | | | Pre-ripe color | 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 dates | Fruit ripening dates | Seed dispersal dates |
|---|---|---|---|---|
| *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).

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

| Species | Seed moisture (%) | Temp (EC) | 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).

**Table 6—***Tsuga*, hemlock: stratification treatments

| Species | Medium | Temp (EC) | Time (day) |
| --- | --- | --- | --- |
| *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.

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

| Species | Cold strati-fication* (days) | Daily light period (hrs) | Germination test cond† Temp (EC) Day | Night | Duration (days) | Germination rate (%) | (days) | Germin-ation (%) | 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 EC.

† Moisture-holding media were either blotters, Kimpak®, sand, or peat.

**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**).

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

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

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