Pseudotsuga Carr.

Douglas-fir

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Growth habit, occurrence, and uses. Seven species are currently included in the genus *Pseudotsuga*—Douglas-fir (*P. menziesii* (Mirb.) Franco) and bigcone Douglas-fir (*P. macrocarpa* (Vasey) Mayr) in North America; *P. japonica* (Shirasawa) Beissner*, P. wilsoniana* Hayata, *P. sinensis* Dode, *P. forrestii* Craib, and *P. gausseni* Flous in eastern Asia (Hermann 1982; Little 1979). The generic name—*Pseudotsuga,* meaning "false hemlock"—reflects the difficulties taxonomists had in classifying the genus (Little 1952).

Fossil records indicate that *Pseudotsuga* has been present in western North America since the Early Tertiary Epoch, and later also in Japan and perhaps in Europe (Hermann 1985). Its limited early range in North America expanded during interglacial intervals to approximately its current range.

Only 1 species, Douglas-fir, is widely distributed; the other 6 species are relatively sparse and their natural distributions are narrow and restricted. The range of Douglas-fir extends from latitude 19E N in central Mexico to 55E N in central British Columbia, and from longitude 97E W in Mexico northwesterly to the Pacific Ocean and to 128E W in British Columbia (Little 1971; Silen 1978). Two varieties are recognized—coast or green Douglas-fir (var. *menziesii*) and Rocky Mountain or blue Douglas-fir (var. *glauca*) (table 1). The 2 varieties adjoin and introgress in British Columbia (Li and Adams 1989; Rudloff 1972) but occur in separate territories from southern British Columbia southward. Bigcone Douglas-fir occurs only in southwestern California and is separated by 34 km from the southernmost known locality for coast Douglas-fir (Griffin 1964). Both North American species have been propagated successfully in Europe but only Douglas-fir has gained worldwide prominence. It is the most important exotic grown in western and central Europe and is also very important in Chile, New Zealand, and Australia (Kleinschmit and Bastien 1992), becoming naturalized in several countries (Jones 1946; Ledgard 1988).

In North America, Douglas-fir naturally occupies a wide span of elevations and climatic conditions. Coast Douglas-fir is found on soils derived from marine, glacial, and volcanic origins at elevations from sea level to 1,250 m in the north to 2,300 m near its southern limits in the Sierra Nevada (Hermann and Lavender 1990). Rocky Mountain Douglas-fir is found on soils derived from many parent materials at elevations from 550 to 2,440 m in the north and from 1,550 to 3,260 m in southern Arizona. Bigcone Douglas-fir is also found on a wide variety of soils at elevations from 275 to 2,400 m on gentle to steep slopes (McDonald 1990). The altitudinal distribution of these species shifts from southerly slopes at high elevations or in northern parts of their ranges to northerly slopes in the southern parts in response to the interacting limitations of temperature and moisture. The presence of large canyon live oaks─*Quercus chrysolepis* Liebm.─apparently modifies fire intensity and appears to be a third crucial influence on distribution of bigcone Douglas-fir (Minnich 1977, 1980).

Both species are found in pure and mixed stands, generally as dominants or codominants, and grow to large sizes that vary by elevation and site. On favorable sites, mature bigcone Douglas-fir trees average 24 to 30 m tall and 61 cm or more in dbh; the largest living individual is 44.2 m tall and 213 cm dbh (AFA 2000). Rocky Mountain Douglas-fir trees average 30 to 37 m tall and 38 to 102 cm dbh; the largest individual now on record is 42.4 m tall and 255 cm dbh (AFA 2000). Coast Douglas-fir grows much larger; heights of 76 m and diameters of 150 to 180 cm are common on favorable sites. The largest living tree is 85.6 m tall and 408 cm in diameter (AFA 2000). The lifespan of bigcone and Rocky Mountain Douglas-firs is up to 400 years and that for coast Douglas-fir about 500 years (Hermann and Lavender 1990; McDonald 1990). The recorded maximums are 622 years for bigcone Douglas-fir and 1,400 years for coast Douglas-fir (McArdle and others 1961; McDonald 1990).

Because of its wide distribution and many desirable characteristics, Douglas-fir is a major factor in timber production, watershed protection, wildlife habitat, and aesthetics whereas bigcone Douglas-fir's contribution is primarily local and limited. Douglas-fir is the premier species used where strength is needed in construction─laminated beams and arches, timbers, poles, piling, and structural plywood─and also for general construction, fiberboard, millwork, furniture, and specialty products. It is also the leading species used in the West for sulfate pulp (Panshin and Zeeuw 1970) and for Christmas trees.

To further its propagation within and beyond its native range, Douglas-fir's genetic and regeneration traits have been studied intensively. Clinal genetic variation has been demonstrated in both the coast and Rocky Mountain varieties for many traits, including survival, growth, form, phenology, insect and disease resistance, cold hardiness, wood characteristics, and chemical composition (Campbell 1986; Campbell and Sorensen 1978; Campbell and Sugano 1993; Ching and Bever 1960; Griffin and Ching 1977; Joly and others 1989; Li and Adams 1989; Read and Sprackling 1976; Rehfeldt 1979, 1989; Schowalter 1988; Silen 1978; Sorensen 1983; St. Clair and Adams 1991; Strauss and Tsai 1988). Because the survival and growth of Douglas-fir at a given location varies by the genetic source used, much effort has been expended in defining guidelines and zones for informed use of seeds and stock beyond the local geographic and climatic area of origin (Campbell 1991; Kleinschmit and Bastien 1992; Randall 1996; Rehfeldt 1981, 1983a & b). Inspection systems have been developed to ensure that Douglas-fir seedlots and stock are correctly labeled and their origins certified (Portlock 1992; Schrumpf and Pfeifer 1993).

Efforts to genetically improve Douglas-fir began over 50 years ago (Isaac 1949) and have developed into large long-term cooperative programs in western North America and abroad. In the Pacific Northwest, most of the seeds used in reforestation of coast Douglas-fir now come from seed orchards (Daniels 1995). The species' use in the breeding zone of origin and other breeding zones is guided by results of outplanting tests and general rules for seed transfer (Randall 1996). A 10% gain in juvenile height growth is predicted for selections representing 6 low-elevation breeding zones in western Oregon and Washington (Stonecypher and others 1996). An international program for genetic improvement of Douglas-fir was started in 1967 and is continuing under IUFRO agencies involving 59 institutions in 36 countries (Kleinschmit and Bastien 1992). Other genetic improvement efforts involve selection for Christmas trees (Douglass and TerBush 1975; Silen 1978) hybridization (Rehfeldt 1977), and clonal propagation (Silen 1978). Many cultivars of Douglas-fir have been propagated by horticulturists (Hermann 1982).

Flowering and fruiting. Male and female strobili burst bud during late winter and spring (table 2), about a year after their initiation as axillary bud primordia (Allen and Owens 1972). Male strobili are generally borne abundantly over much of the crown on the proximal half of year-old shoots; these strobili become somewhat pendant when mature and are about 2 cm long. Female strobili develop more distally on year-old shoots that are located primarily in the upper half of the crown. The female strobili are erect at the time of pollen shedding and measure about 3 cm long; their appearance is dominated by large trident bracts (Allen and Owens 1972). The color of female strobili (seed cones) ranges from deep green to deep red, and that of male strobili from yellow to deep red. Strobili of the same sex tend to be of uniform color on individual trees, but the color of the males and females may differ (Griffith 1968).

Seed cones become receptive to pollination when they have emerged by half to two-thirds from the bud scales, and they remain so for at least 6 to 10 days (Ho 1980; Owens and others 1991; Silen 1978). Pollen dispersal occurs for 20 to 30 days in a given locality (Silen 1963). Seed cones soon become pendant, and fertilization takes place about 10 weeks after pollination (Allen and Owens 1972). Seeds develop through late spring and summer, reaching maturity in August or early September. Cones generally begin to dry and turn brown in August or September, and most seeds are released in September and October (table 2).

Calendar dates for phenological events vary with latitude and elevation (Silen 1963), between individual trees in a locality (Orr-Ewing 1956), and by position within the crown (Orr-Ewing 1956; Roeser 1942). Timing also varies from year to year, depending on weather conditions. Because cones open by drying, time of seed dispersal is particularly influenced by low humidity and drying winds in late summer and fall.

The mature cones of Douglas-fir are readily identified by their 3-lobed bracts, which protrude beyond the cone scales (figure 1). On each scale are 2 seeds that have relatively large wings (figure 2). One side of the seed is variegated light brown; the other is more glossy and dark brown. Embryos are linear (figure 3). The number of filled seeds per cone varies widely and tends to be greater for large cones (Willis 1917). In Rocky Mountain Douglas-fir, filled-seed numbers ranged from 20 to 30 per cone in some collections (Owston and Stein 1974). For coast Douglas-fir, filled-seed numbers ranged from 4 to 54 per cone in 309 collections from individual 35-year-old trees in northwestern Oregon (Olson and Silen 1975). Numbers averaged 16 per cone in collections from 127 individual trees in 10 westside areas located from north-central Washington to south-central Oregon (Willis and Hofmann 1915) and 19.4 per cone (range 2 to 35) in collections made between 1966 and 1978 from 923 individual trees with sparse to good crops in 95 coastal and Cascade stands in Oregon and Washington (Sorensen 1997).

The seeds of Douglas-fir are disseminated by gravity and wind; their distribution varies widely—it is influenced by crop abundance, tree height and position, wind velocity, and other factors (Isaac 1930). Most seeds of bigcone Douglas-fir fall beneath the tree of origin; wider dissemination occurs primarily during high winds (McDonald 1990). Some Douglas-fir cones remain attached to the tree for a year or more after seed dispersal.

Seed production in Douglas-fir is highly variable from tree to tree. In a good seed year, an average mature, forest-grown coast Douglas-fir produces about 0.45 kg (1 lb) of cleaned seeds (Isaac 1943), whereas widely spaced trees may produce 0.91 kg (2 lb) or more (Allen 1942; Isaac 1943). Because not all trees produce seeds, stand production averages considerably less than 0.45 kg (1 lb) of seeds per tree (Isaac 1943). Trees 100 to 200 years old are most prolific, but cones on younger trees are larger and contain more viable seeds (Willis 1917; Willis and Hofmann 1915). In young stands, seed production of coast Douglas-fir begins at 7 to 10 years of age and somewhat later for Rocky Mountain Douglas-fir (table 3). When cultural and chemical techniques are used to stimulate precocious flowering, seeds have been produced on 2- to 5-year-old Douglas-firs, but pollen production is sparse (Silen 1978). Bigcone Douglas-firs may bear cones beginning about age 20, but they are rare on trees less than 40 years old (McDonald 1990).

Generally, some seeds are produced annually by coast Douglas-fir except for about 1 year in any 4- to 5-year period (Isaac 1943; Reukema 1982); however, higher crop failure rates have been reported (McDonald 1992). Stand conditions as well as environmental and internal factors make the crop cycle erratic (Baron 1969; Eis 1973; Lowry 1966; Owens and others 1991). Abundant crops have occurred from 2 to 11 years apart (table 3). The seed production cycle for Rocky Mountain Douglas-fir is quite similar. Bigcone Douglas-fir usually has small cone crops; abundant crops occur infrequently and usually only in localized areas (USDA FS & CDF 1955–1971).

The existence of a cone crop cannot be confirmed until about 2 months before seedfall; pollination, frost, cone abortion, insects, and other factors may cause widespread failure after cones are visible (Owens and others 1991). Although forecasts of crop potential are possible 12 months in advance of seedfall by counts of female buds (Allen 1941) or 17 months in advance by counts of male buds (Silen 1967), bud counts are more accurate in predicting crop failures than in forecasting successful crops.

The high economic value of Douglas-fir seeds, especially genetically improved seeds, has prompted many useful studies, including the following: (1) factors affecting seed set (Owens and others 1991); (2) effects of inbreeding level on filled seed production (Woods and Heaman 1989); (3) influence of reproductive phenology on genetic diversity of seed crops (Copes and Sniezko 1991; El-Kassaby and Askew 1991); and (4) differences in fruitfulness between clonal and seedling orchards (El-Kassaby and others 1989). Cultural practices to stimulate seed production in natural stands or seed orchards include thinning and spacing (Reukema 1982, Williamson 1983); fertilization (Edwards 1986); girdling (Wheeler and others 1985; Woods 1989); top pruning (Copes 1973); and use of growth regulators alone (Ross and others 1980) or in combination with girdling, root pruning, top-pruning, and branch thinning (Ross and Bower 1991; Ross and Currell 1989; Ross and others 1985). In 1990, Cress and Daniels (1990) reported that existing coast Douglas-fir seed orchards had the production potential to reforest 11 million acres with genetically improved stock by the year 2000.

Hedlin and others (1980) have developed a key for the many insects that damage cones and seeds of Douglas-fir. The Douglas-fir cone moth (*Barbara colfaxiana* Kearfott) causes major damage throughout the range of Douglas-fir, but is most persistent in dry areas (Miller and Ruth 1989). As few as 3 larvae can destroy all of the seeds in a cone. The Douglas-fir cone gall midge (*Contarinia oregonensis* Foote) is another major destroyer of seeds, particularly in wet areas; severe infestations can destroy an entire crop. The Douglas-fir seed chalcid (*Megastigmus* *spermotrophus* Wachtl.) is found on both Douglas-fir and bigcone Douglas-fir and frequently destroys 2 to 15% of the crop. Other insect pests include the western flower thrips (*Frankliniella occidentalis* Pergande), which feeds on Douglas-fir pollen in California; Douglas-fir cone scale midge (*Contarinia washingtonensis* Johnson); coneworms (*Dioryctria abietivorella* Groté, *D. pseudotsugella* Munroe, and *D. reniculelloides* Mutuura and Munroe); western conifer seed bug (*Leptoglossus occidentalis* Heidemann); and the fir cone looper (*Eupithecia spermaphaga* Dyar). The western spruce budworm (*Choristoneura occidentalis* Freeman) has also caused heavy damage to flower buds, flowers, and developing cones (Dewey 1970; Frank and Jenkins 1987).

A variety of efforts have been made to assess and curb insect damage to cones and seeds of Douglas-fir. The effects of cone and seed insects were evaluated in natural stands (Shearer 1984) and in Douglas-fir seed orchards (Schowalter and Haverty 1989; Schowalter and others 1985). Dombrosky and Schowalter (1988) suggested an inventory monitoring system to better identify causes of seed loss, and Miller (1986) described damage prediction systems to judge the need for protection from the Douglas-fir cone gall midge and other insects. Rappaport and Volney (1989) found that control of one pest resulted in increased damage from another. Insecticide treatments have been tested for protecting against all cone and seed insects (Stein and Koerber 1989; Stein and Tilden 1987; Summers and Miller 1986), and specifically from the cone gall midge and seed chalcid (Stein and Markin 1986) and the western spruce budworm (Stipe and Green 1981). The role of 2 recently identified pests, the Douglas-fir twig mining beetle (*Pityophthorus orarius* Bright) and a flightless weevil (*Lepesoma lecontei* (Casey), have also been investigated (Rappaport and Wood 1989; Sexton and Schowalter 1991).

Douglas-fir flowers, cones, and seeds are also affected by frost, small mammals, and birds. Buds, flowers, and conelets are periodically damaged by spring frosts (Roeser 1942; Silen and Keene 1969; Timmis 1977). Squirrels start clipping cones early, but they cut cones in large quantities mainly after seeds mature (Lavender and Engstrom 1956; Moore 1940; White and White 1985).

Collection of cones. Douglas-fir cones are collected from untended natural stands, from natural stands tended for seed production; from seed orchards; and even from trees growing in yards, playgrounds, and parks. The scope of collection ranges from a few cones for scientific or personal purposes to region-wide collections to achieve technical or commercial objectives. Thus, collection techniques range from simple hand methods to highly mechanized efforts with commensurate preharvest planning and organization (Brown 1983; Maxwell and Aldhous 1967). Whatever the size of the collection, the same key considerations are involved—where, when, and how to collect and how to care for the cones afterward.

With 2 varieties to choose from and demonstrated genetic, geographic, and ecologic adaptation within each, choosing the right source from which to collect Douglas-fir cones is complex. Fortunately, the general axiom to collect seeds from sources ecologically similar to where they are to be used has been implemented by designation of seed zones (Rudolf 1974; Stein and others 1986) and development of seed transfer guidelines (Campbell 1986, 1991; Campbell and Sugano 1993; Randall 1996; Rehfeldt 1981, 1983a,b). Though much less is known about genetic variation in bigcone Douglas-fir, the same attention should be given to ecologically matching the seed source to the planting location.

Seeds are sufficiently ripe and ready for collection from 3 to 4 weeks before cones begin to open and shed seeds (Allen 1958a; Finnis 1950; Rediske 1969). This short collection period may start as early as August at low elevations and latitudes and as late as October at high elevations and latitudes (table 2), and it also varies with yearly weather conditions and from tree to tree (Allen 1958a; Brown 1983).

In general, cone color is not a good indicator of seed ripeness; browning of the external bracts is more diagnostic (Ching and Ching 1962). Ripeness is best determined by cutting cones open to reveal the seeds' color and appearance. The seedcoat should be golden brown to dark brown and the seed-wing light brown to tan; the endosperm should be full and firm; and the embryo should be yellowish green and fill most of its cavity (Brown 1983; Ching and Ching 1962; Finnis 1950; Willis 1917). Sample cones are cut longitudinally to check on seed ripeness and estimate seed yield. The count of filled seeds visible on one cut surface multiplied by 4.5 approximates the number of filled seeds per cone (Olson and Silen 1975). An average of 5 filled seeds per cut surface is generally needed for an economic large-scale harvest; lesser yields may be sufficient when supplies are scarce or only minor quantities are needed (Douglass and TerBush 1975; Portlock 1996; Schaefer and Miller 1985).

Douglas-fir cones are collected from standing trees, from felled trees or tops, and from squirrel caches. A whole array of spurs, ladders, cable methods, lifts, and axillary devices are used to assist climbers in getting into the crowns of tall trees and safely collecting cones (Matusz 1964; Portlock 1996). Vehicle-mounted lifts are often used in seed orchards. Shaking the cones from trees has been accomplished without serious crown damage (Copes 1985; Copes and Randall 1983; USDA FS 1972). Cost-effective methods have been devised to aerially rake crowns or clip tops by helicopter (Camenzind 1990; Wallinger 1985). Gathering squirrel-cut cones from the ground or from caches is still a key method of obtaining cones from tall trees in natural stands (Brown 1983; Maxwell and Aldhous 1967; White and White 1985). Squirrel caches provide a means of extending the harvest season as the cones are usually cached in moist areas and remain closed. However, damage from molds may be greater than in cones harvested from trees. Silvicultural and practical advantages and disadvantages of each collecting method have been summarized by Edwards (1985).

Picked cones are bagged, then transported either first to a collection station or directly to a processing plant where they may be held before seeds are extracted, cleaned, and stored. Two concerns are paramount: keeping the collected cones adequately identified, and ensuring good ventilation to prevent killing seeds from overheating or molding. A label on the inside and outside of each bag or container should at least indicate the species, geographic location, elevation, date, and signature of the collector (Stein and others 1986). Plastic mesh bags are preferred over burlap sacks because of better aeration and thus decreased likelihood of contamination by molds. To facilitate air circulation and cone expansion, bags are usually filled only half full, loosely tied, and kept in shade on racks at field sites, collection stations, and even during transport (Brown 1983).

Cones may be stored for 2 to 4 months under dry, well-ventilated conditions without impairing seed viability (Bloomberg 1969; Lavender 1958; Rediske 1961; Rediske and Shea 1965). In fact, under good cone storage conditions, seeds may benefit from after-ripening (Bloomberg 1969; Rediske 1961), whereas lengthy storage of green cones under warm moist conditions can result in severe seed losses from increased molding (Rediske and Shea 1965). Because of tree-to-tree variation in time of seed ripening, any broad-scale collection contains cones with immature seeds that need after-ripening (Allen 1958a; Olson and Silen 1975; Rediske

1961; Silen 1958). Currently, some processors after-ripen cones in well-ventilated, refrigerated vans at temperatures of 7 to 10 EC (Lippitt 1996). Air-drying cones in protected, well-ventilated storage for several weeks or longer is more common, however (Brown 1983; Schaefer and Miller 1985).

Extraction, cleaning, and storage of seeds. At most extractories, Douglas-fir cones are at least partially air-dried during storage, then kiln-dried to fully open them. Where warm, low-humidity conditions prevail, air-drying may be sufficient, but in much of the West, some supplemental heat is necessary. Slow drying at moderate temperature is recommended (table 4), as high heat applied to green cones and seeds of high moisture content can be very damaging (Allen 1958b; Hall 1984; Morris 1936; Willis 1917). Cones may be moistened just before kiln-drying to overcome any case-hardening and to facilitate a uniform rate of drying (Brown 1983). Cones of coast Douglas-fir open fully with loss of 35 to 51% of their wet weight (Willis 1917).

Seeds are extracted from fully open cones in a variety of tumbling devices, ranging from a hand-turned, screen-covered wooden frames to large rotary combination dryer-tumblers (Stein and others 1974). Because both heat and sharp impacts can damage Douglas-fir seeds (Allen 1958b), loose seeds are often removed at several stages of processing─before kiln-drying, during drying, and during tumbling. A seed moisture content of 7.5% (wet weight basis) or less is sought during kiln-drying or by later supplemental conditioning (Brown 1983).

Post-extraction processing of seeds usually includes (1) screening to separate seeds from cone scales, dirt, and debris, (2) de-winging, and (3) fanning or blowing to remove hollow seeds, wings, and dust. Vibrating, air, or gravity separators; soaking and drying, and other methods may be used to get seedlots extra clean (Hergert and others 1971; Lowman 1975; Sweeney and others 1991). Elimination of small seeds by sizing is not recommended, however, as this reduces genetic diversity (Silen and Osterhaus 1979). In every stage of cleaning, sharp impacts need to be minimized to produce Douglas-fir seedlots of highest quality (Allen 1958b). An attainable processing standard for Douglas-fir is 98% for purity and 80% or higher for viability (Brown 1983; Lippitt 1996; Stein and others 1986).

Cone sizes and seed weights of Douglas-fir vary by variety, year, geographic location, elevation, aspect, stand age and density, tree and family, and time of collection (Hermann and Lavender 1968; Kozak and others 1963; Olson and Silen 1975; Silen and Osterhaus 1979; Sorensen 1967, 1980, 1983; St. Clair and Adams 1991; Willis and Hofmann 1915). Bigcone Douglas-fir has much larger cones and yields more seeds per weight of cones (table 4). Its smallest seeds average 5 times the weight of the largest seeds of Rocky Mountain and coast Douglas-firs (table 5).

For coast Douglas-fir, the number of cones per volume ranged from 977 to 5,067/hl (344 to 1,784/bu) in collections from 309 individual 35-year-old trees (Olson and Silen 1975); in collections from 127 individual 15- to 600-year-old trees, cones per volume ranged from 1,988 to 5,441/hl (700 to 1,916/bu) (Willis and Hofmann 1915). For both coast and Rocky Mountain Douglas-fir, size of seeds tends to decrease from southern to northern latitudes, that is, to increase in number per weight (table 5). Douglas-fir seeds near the coast tend to be smaller than those further inland, and seeds from lower elevations are sometimes smaller than those from higher elevations (Griffin and Ching 1977; Hermann and Lavender 1968; Lippitt 1996; Sorensen 1967, 1983; Sorensen and Miles 1978; Sweet 1965). Seeds produced in a seed orchard from trees of coastal Oregon origins were similar in weight to those produced by trees in untended stands (table 5).

Seeds of Douglas-fir are usually stored at or near ! 18 EC at moisture contents of 5 to 9% (wet weight basis) in sacks or plastic-lined fiberboard drums (Brown 1983; Stein and others 1986). Viability of good seedlots can be maintained for many years under these storage conditions; 85 to 87% germination of several coast Douglas-fir seedlots has been maintained for 27 years (Lippitt 1996). Moderate to good seed viability has been maintained for varying lengths of storage around 0 to 5 EC, but viability declines rapidly in storage at room temperature and at high moisture content (Allen 1957, 1962a; Barton 1954; Schubert 1954).

Pregermination treatments and germination tests. Pregermination treatment of Douglas-fir seeds strongly influences their subsequent response to various germination conditions. Most seedlots benefit from stratification, but some do not require stratification, some are harmed by it, and some that need it are harmed by too lengthy stratification (Allen 1960; Allen and Bientjes 1954; Gosling 1988; Jensen and Noll 1959; Taylor and others 1993). Based on accumulated experience, seeds of coast Douglas-fir generally require or benefit from stratification, those of Rocky Mountain Douglas-fir from northern sources may benefit, those from southern sources may not benefit, and the response to stratification by bigcone Douglas-fir is unknown (Allen 1960, 1962c; Heit 1968).

Stratification overcomes different degrees of seed dormancy that may be related to seed source and family, year of collection, cone and seed drying conditions, length and kind of storage, and other causes (Allen 1960; Allen and Bientjes 1954; El-Kassaby and others 1992; Jensen and Noll 1959; Sorensen 1991). Several pretreatments used with or in lieu of stratification also stimulate germination or reduce pathogen damage. These include a light rinse with cold or hot water, fungicide, bleach, hydrogen peroxide, ethanol, polyethylene glycol, or ethylene (Borno and Taylor 1975; Ching 1959; Dumroese and others 1988; James and others 1988; Li and others 1994; Paci 1987; Shearer and Tackle 1960; Trappe 1961; Wenny and Dumroese 1987).

For seedlots that benefit, stratification speeds the rate of germination; for many, it also increases total germination (table 6). Although the increase in total germination was often not large, it occurred in 76.1% of samples submitted for standard service testing (Jensen and Noll 1959). The increase in germination may be substantial after lengthy stratification when seeds are tested at low temperatures or have been produced in seed orchards (Allen 1960, 1962c; Campbell and Sorensen 1984; Jones and Gosling 1994; Muller and others 1999; Sorensen 1991). Even small gains are important when using valuable improved seeds.

Douglas-fir seeds are usually stratified "naked," that is, without medium. For testing, dry seeds are often placed directly on the moistened substratum in a closed dish, or soaked in tap water for 24 hours, drained, and then placed in a closed container or bag to prechill at 2 to 5 EC for 3 weeks (AOSA 2001).

The official germination test procedures for both coast and Rocky Mountain Douglas-firs require paired samples—one prechilled for 21 days at 2 to 5 EC and one not—then subjected to alternating day and night temperatures of 30 EC for 8 hours and 20 EC for 16 hours, with light at least during the high temperature period (AOSA 2001; ISTA 1996). Test duration is 21 days. A variety of absorbent blotters and other materials may be used as substratum—Sponge Rok, vermiculite, Terralite, and mixtures with sand. Alternating temperatures are prescribed because these yielded the highest and most consistent germination in comparison tests (Jensen and Noll

1959). But given appropriate prechilling and germinating periods, Douglas-fir will germinate with or without light in constant temperatures from 10 to 30 EC but higher temperatures cause damage (Allen 1960, 1962c; Gosling 1988; Jones and Gosling 1994; Sorensen 1991; Wright 1931). Seed position influences rate of germination; when the side of the seed that developed against the cone scale is on top, 50% germination on a moist surface is obtained in 4.6 days versus 6.3 days for those of opposite orientation, and response varies among seeds of different geographic origin (Sorensen and Campbell 1981). Rate of germination also varies among seedlots and is not directly linked with total viability (Thomson and El-Kassaby 1993). Average germination and germinative energy data from source-paired comparisons and other test experiences are listed in table 6.

Germination conditions for bigcone Douglas-fir are relatively untested (table 6). Techniques that work well for the other Douglas-fir species may prove satisfactory.

Several methods are used to quickly appraise the quality and vitality of Douglas-fir seeds when approximations are adequate or time is too short for germination tests. Determining viability by a tetrazolium (TZ) test is officially recognized and standard procedures have been designated (AOSA 2000). Seeds are soaked in water at room temperature (20 to 25 EC) overnight, then sliced longitudinally, soaked in a 1% TZ solution at 0 to 25 EC for 4 to 6 hours (or longer at lower temperatures), and evaluated. Healthy endosperm and embryo tissue stains uniformly pink to red. Vitality can also be determined by 2 other tests. In the first test, embryos are excised and placed in conditions favorable for growth for several days (Heit 1955); in the second test, radicle tips are cut and the seeds soaked in weak hydrogen peroxide solution under conditions that promote radicle elongation (Ching and Parker 1958). In an additional test, the oldest and simplest, seeds are cut open to determine if they are full or empty, insect damaged, or shriveled and their quality judged by the appearance and color of the endosperm and embryo; this test is still useful for a quick evaluation, particularly in the field. Seeds can be evaluated non-destructively from x-ray views, which can reveal full, empty, shriveled, and insect-filled contents, as well as any damage to the seedcoat and interior (Belcher and Vozzo 1979). Estimates of Douglas-fir seed viability are now similar if measured by germination, X-radiographic, TZ, or hydrogen peroxide tests (Hardin 1981).

Nursery practices. Millions of Douglas-fir seedlings are grown in both bareroot and container nurseries. Bareroot production predominates in the United States; container production predominates in Canada. Many sizes of seedlings are produced, including from small 1+0 to 3+0 bareroot stock; 1-year-old container (plug) stock; and 1+1, 1+2, 2+1, 2+2, or plug+1 transplants. Use of 1+1 transplants is now very common and plug+'s are gaining attention. Extra large stock is often used to combat animal damage or competing vegetation and for restoration plantings in riparian areas.

Technology for the production of Douglas-fir seedlings is detailed and varies by nursery and the type and size of stock to be produced. Careful management of growing-medium fertility and drainage in both bareroot and container nurseries is critical for growth and hardiness of Douglas-fir. The factors and specific techniques involved in producing bareroot Douglas-fir seedlings are presented in the Forest Nursery Manual (Duryea and Landis 1984); those for containers in the multiple-volume Container Tree Nursery Manual (Landis and others 1989, 1990a & b, 1992, 1995). The concept and practices for producing seedlings with morphological and physiological characteristics targeted for specific field conditions were brought together in a symposium (Rose and others 1990).

Production and grading practices have the potential of influencing the genetic composition as well as the physical characteristics of the seedling populations produced (Campbell and Sorensen 1984; El-Kassaby and Thomson 1996; Sorensen and Campbell 1993; St. Clair and Adams 1993). Thus, every nursery practice needs scrutiny to avoid severely altering the intrinsic characteristics for which each seedlot is valued.

Both bareroot and container nurseries usually sow stratified seeds as early in late winter or spring as possible to maximize growth and vigor of first-year seedlings (Sorensen 1996). Fall-sowings can produce even larger seedlings, but the risk of seed losses over winter from natural causes is usually too great (Duryea 1984). Before sowing outdoors or in containers, seeds are commonly soaked in tap water at 10 to 22 EC for 24 to 48 hours, drained of excess water, perhaps surface-dried, and then prechilled in 2-kg (5-lb) quantities per plastic bag in a cooler at 1 to 5 EC (Allen 1962b; Allen and Bienjes 1954; Johnson 1983; Tanaka 1984). A breather tube may be inserted in the neck of the bag and such intermediate tending as rinsing, addition of water, and turning may be done during 28 to 60 or even 90 days of stratification. Results from germination tests help guide the choice and length of pretreatments applied to individual seedlots.

When necessary, stratified Douglas-fir seeds can be stored for later use. Stratified seeds that were air-dried and stored at relatively high moisture content at 2 EC for 3 months or oven-dried to 7 to 15% moisture content and stored at ! 7 to 3 EC for 9 months or more retained the viability and stratification effect (Allen 1962b; Belcher 1982; Danielson and Tanaka 1978; Jones and Gosling 1994; Muller and others 1999). In other trials, viability was retained by partial drying of stratified seeds followed by low temperature storage, but the stratification effect was lost (Hedderwick 1970; Malavasi and others 1985). Seeds cannot be held in stratification indefinitely; seeds of some lots will deteriorate and those of others will germinate (Allen 1960; Danielson and Tanaka 1978; Sorensen 1980, 1991).

For bareroot production, most Douglas-fir seeds are drill-sown at a depth of 3 to 6 mm (0.1 to 0.2 in). The larger seeds of bigcone Douglas-fir are usually sown at a depth of 13 mm (0.5 in). Seedbed density varies depending on the stock size desired. For 2+0 Douglas-fir stock, seedling densities vary from 161 to 323/m^2 (15 to 30/ft^2); for 1+1's, bed densities of first-year seedlings range from 538 to 753/m^2 (50 to 70/ft^2) (Thompson 1984). Seedbed density has more effect on size of seedlings produced, and on their subsequent field survival and growth, than does irrigation frequency or undercutting and wrenching (Stein 1988).

Irrigation is used in bareroot nurseries to supply moisture to seeds and seedlings, prevent overheating or frost damage, promote growth, and augment other practices such as fertilizing and root wrenching (Duryea 1984). Carefully planned irrigation regimes are also used to control moisture stress, harden seedlings, and initiate dormancy. Specific irrigation regimes should be developed for each nursery and kind of stock—seedlings can be harmed by either too much or too little water.

The fertilizer mix and the timing and number of applications must also be developed for each bareroot nursery. Physical and chemical characteristics of the soil and irrigation water and the density of the seedling crop are critical influencing factors. A pH of 5.0 to 6.0 has been suggested for Northwest nurseries and 5.5 to 6.5 for Intermountain nurseries as well as concomitant target levels for key mineral elements (Youngberg 1984). Most nurseries stop fertilizing in July or early August to promote seedling hardening (Duryea 1984).

Almost all bareroot nurseries undercut Douglas-fir seedlings to stimulate root growth in the upper soil layers (Duryea 1984). Timing, frequency, and depth vary by nursery and stock type. Eighty percent of nurseries in the Pacific Northwest also wrench the roots of Douglas-fir seedlings to promote fibrous root systems, stress and harden seedlings, control shoot height, and aerate the soil.

Many other cultural techniques including transplanting, weed and pest control, top pruning, and mycorrizhal inoculation are used to condition bareroot Douglas-fir seedlings for specific field conditions. Emphasis continues on fine tuning and evaluating seedling quality. Thus, an array of morphological and physiological tests have been developed to assess the quality of Douglas-fir seedlings (Duryea 1985; Jenkinson and others 1993; Rose and others 1993, 1997). Grading criteria and target sizes have been recognized for different types of stock (Iverson 1984), but more importantly, the trend is to specify seedlings by height and stem caliper as well as by stock type.

In containers, plantable stock can be produced in one season in greenhouses, outdoors under shade, or in the open. Douglas-fir grows well in the containers commonly used in forestry. High-quality, well-stratified seeds are particularly important in producing container-grown Douglas-fir. Other important considerations include keeping the pH of the potting mixture between 4.5 and 6.0; using growing practices that produce seedlings with tops and roots in balance; and hardening the seedlings to withstand direct sunlight and cold.

Fast growth of Douglas-fir is achieved in containers by providing greater control of the growth environment than possible in a bareroot nursery (Landis and others 1995). A precise growing regime must be developed suited to the capabilities at the individual container facility and the requirements of the stock to be produced. For example, Wenny and Dumroese (1992) describe a regime for producing Rocky Mountain Douglas-fir container stock at a facility in Idaho. Producing this variety in a single season requires use of artificial light to lengthen the photoperiod early in the growing season.

To produce extra hardy, compact stock, seedlings are grown in containers for the first year and in outdoor beds for a second year. The resulting plug+1 stock has a very fibrous root system and is usually larger and sturdier than 1+1 stock (Iverson 1984).

Douglas-fir is also propagated commercially by adventitious rooting of cuttings (Myers and Howe 1990; Ritchie 1991). Cuttings are rooted in 1 season, transplanted to a bareroot nursery in the fall to overwinter, and then grown for 1 year as bareroot stock. Over 5 years, stock from cuttings has performed similarly to 1+1 transplants. Cuttings from juvenile wood root better than those from older wood and have less plagiotropic tendencies (Copes 1992). Juvenile meristems are produced in quantity by accelerating first-year growth of stock plants (Ritchie 1994) or by maintaining juvenility on older trees by pruning (Copes 1992). Limited numbers of Douglas-fir emblings are produced by micropropagation techniques (Gupta and Grob 1995; Hutzell and Durzan 1993; Tabor and others 1998). Rapid multiplication of superior genetic strains is made possible by practical vegetative propagation.

Seedling care. Whether bareroot or container-grown, Douglas-fir stock is best able to withstand the shock of lifting, storage, and outplanting when dormant, that is, after adapting to winter conditions. Midseason reductions in applying water and fertilizer, root wrenching, and other techniques are used to slow growth and enhance the normal climatic progression toward dormancy.

Because Douglas-fir seedlings are quite vulnerable, great care should be taken to minimize mechanical damage, desiccation, and molding during lifting, processing, storage, transportation, and planting. Protective practices include hydrating seedlings before lifting; minimizing exposure of lifted seedlings to direct sunlight, temperature extremes, and wind; preventing metabolic over-heating; misting during processing; storing and transporting them at low temperatures in bags or cartons with vapor barriers; and minimizing handling and exposure during field planting (Burdett and Simpson 1984).

Properly hardened Douglas-fir nursery stock can be stored for lengthy periods at temperatures just above or below freezing (Burdett and Simpson 1984; Hee 1986). Freezer storage prevents molding and some dormancy developments that would occur if seedlings were exposed outdoors (Ritchie 1987). Frozen bareroot and container seedlings should be thawed before they are planted (Hee 1986; Rose and Hause 1997).

Douglas-fir is usually outplanted any time from late fall through spring, depending on local climate. Winter and early spring plantings are usually best in areas with mild winters west of the Cascade Mountains. The planting season may extend into early summer in interior regions and at high elevations where snow lingers. Seedlings are extracted from most types of containers either before storage or before shipment to the field. Bigcone Douglas-fir was planted periodically from 1905 to 1975 in Los Angeles County, California, but results are unknown (McDonald 1990); in contrast, there is overwhelming evidence on successful plantings of coast and Rocky Mountain Douglas-fir.

Nursery managers are dedicated to producing the size and vigor of Douglas-fir stock needed for an extremely wide range of field conditions. In many instances, the kind of stock required and the nursery practices needed to produce it are well defined; in some instances, however, either the stock or the field practices need improvement. Specific trials testing variations in a nursery's practices for producing stock of different sources may be needed, for example, "lifting windows" as investigated by Jenkinson and others (1993).

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Table 1—*Pseudotsuga,* Douglas-fir: nomenclature and occurrence

Scientific name & synonyms	Common name	Occurrence
***P. macrocarpa* (Vasey) Mayr** *Abies douglasii* var. *macrocarpa* Torr. *A. macrocapa* Vasey	**bigcone Douglas-fir**, bigcone-spruce, desert-fir	Mtns of SW California
***P. menziesii* var. *glauca* (Beissn.) Franco** *P. douglasii* var. *glauca* Mayr *P. menziesii* var. *caesia* (Schwerin) Franco *P. taxifolia* var. *glauca* (Beissn.) Sudworth	**Rocky Mountain Douglas-fir,** interior Douglas-fir, blue Douglas-fir, Colorado Douglas-fir, inland Douglas-fir	Central British Columbia & SW Alberta, S in mtns to N & central Mexico, from E Washington, Oregon, Nevada, & W Arizona to E Montana, Wyoming, Colorado, New Mexico, & NW Texas
***P. menziesii* var. *menziesii* (Mirb.) Franco** *P. douglasii* var. *viridis* Schwerin *P. menziesii* var. *viridis* (Schwerin) Franco *P. mucronata* (Raf.) Sudworth *P. taxifolia* (Lamb.) Britton	**coast Douglas-fir,** Douglas-fir, Oregon Douglas-fir, green Douglas-fir, Douglas-spruce	SW BritishColumbia through W Washington & Oregon to central California, E into Cascade & Sierra Nevada ranges to W Nevada

Sources: Griffin and Critchfield (1976), Hermann (1982), Hermann and Lavender (1990), Little (1952, 1971, 1979), McDonald (1990), Minnich (1982).

Table 2—*Pseudotsuga,* Douglas-fir: phenology of flowering and fruiting

Species	Location	Flowering	Cone ripening	Seed dispersal
P. macrocarpa	S California	February–mid-Apr	Early Aug–early Oct	Late Aug–late Oct
P. menziesii var. *glauca*	Central Colorado (elev. 2,060–2,880 m)	Mid-Apr–early May	—	—
	Montana (elev. 700–1,700 m)	Late May–early June	Late July–early Aug	Late Aug–mid-Sept*
	Northern Idaho (elev. 820–1,000 m)	Early May–late June	Mid-Aug	Early Sept*
	Central Oregon	Mid-May–mid-June	—	Mid-Aug–mid-Sept*
P. menziesii var. *menziesii*	Coastal British Columbia	Late Mar–mid-May	Aug	Sept–late Mar
	W-central Oregon & W Washington	Mid-Mar–early June†	Aug	Late Aug–late Mar‡
	S Oregon	Early Apr–early May	—	Mid-Aug*
	N California	—	August	Sept–early winter§

Sources: Allen (1942), Allen and Owens (1972), Ching and Ching (1962), Gashwiler (1969), Gause (1966), Griffith (1968), Isaac (1943), McDonald (1990, 1992), Morris (1952), Owston and Stein (1974), Roeser (1942), Silen (1963), Sorensen and Campbell (1971), Sudworth (1908).

* Beginning dates only.

† Upslope progression in pollen shedding and female receptivity averaged 23.5 m of elevation per day on four transects in western Oregon and Washington (Silen 1963).

‡ About 70 to 90% of the seeds usually disperse in September and October; most of the remainder disperse between November and March (Allen 1942; Isaac 1943).

§ Seedfall usually greatest in October (McDonald 1992).

Table 3—*Pseudotsuga,* Douglas-fir: height, seed-bearing age, crop frequency, and cone length

Species	Mature height (m)	Minimum seed- bearing age (yr)	Interval (yr) between large seed crops	Cone length (cm)
P. macrocarpa	9–30	20*	—	11–17
P. menziesii				
var. *glauca*	23–49	20	3–10	4–7
var. *menziesii*	27–91	7–10†	2–11	6–10

Sources: Allen (1942), Boe (1954), Gause (1966), Hermann and Lavender (1990), Lowry (1966), McArdle and others (1961), McDonald (1990), Roeser (1942), Sudworth (1908).

* Occasionally earlier on good, open sites (Gause 1966).

† The minimum age for commercial collections has been considered 20 to 25 years (Allen 1942).

Table 4— *Pseudotsuga,* Douglas-fir: cone drying schedules and seed yield data

Species	Cone drying schedule: Air-drying (days)	Kiln-drying: Time (hr)	Kiln-drying: Temp (EC)	Cone wt/cone vol: kg/hl	Cone wt/cone vol: lb/bu	Seed yield: Seed wt/cone vol: kg/hl	Seed yield: Seed wt/cone vol: lb/bu	Seed yield: Seed wt/cone wt ratio
P. marocarpa	8–10	—	—	32–39	25–30	1.02	0.8	2.8
P. menziesii								
var. *glauca*	4–60	2–10	38–43	32–7	25–60	0.30–1.02	0.5–0.8	1.0–1.3
var. *menziesii*	8–60	16–48	32–43	39–64	30–50	0.12–1.02	0.2–0.8	0.5–2.0

Sources: Brown (1983), Owston and Stein (1974), Radcliffe (1952), Swingle (1939).

Table 5—*Pseudotsuga,* Douglas-fir: cleaned seeds per weight

Species & location	Average /kg	Average /lb	Range /kg	Range /lb	Samples
P. macrocarpa					
S California	8,685	3,940	7,620–11,120	3,460–5,045	8
P. menziesii var. *glauca*					
Arizona	70,768	32,100	52,911–75,619	24,000–34,300	8
New Mexico	83,555	37,900	72,312–90,830	32,800–41,200	8
Colorado	85,539	38,800	73,414–96,122	33,300–43,600	33
Montana	88,405	40,100	79,807–99,869	36,200–45,300	14
E Washington	102,354	46,427	101,834–103,093	46,191–46,762	3
British Columbia	109,845	52,315	85,465–142,635	38,705–64,700	42
P. menziesii var. *menziesii*					
Coastal California					
Fog-belt	86,882	39,409	80,257–104,058	36,404–47,200	4
Inland	70,028	31,764	55,618–78,493	25,228–35,604	5
California	71,752	32,546	33,951–116,845	15,400–53,000	41
N California	67,250	30,504	40,858–109,171	18,409–49,519	20
California					
Zones 090	72,305	32,797	63,268–93,268	28,698–42,605	62
Zones 300	65,538	30,181	54,780–81,359	24,848–36,904	29
Zones 500	56,906	25,812	48,028–69,867	21,785–31,691	37
Oregon	97,165	44,075	68,770–169,495	31,195–76,880	374
Oregon & Washington	85,300	38,700	73,634–125,664	33,400–57,000	224
Coastal Oregon (seed orchard)	87,268	39,584	76,128–110,972	34,531–50,336	23
Washington Cascades	81,183	36,824	75,074–87,336	34,053–39,615	2
W Washington	115,185	52,245	82,260–150,770	37,315–68,385	48
British Columbia	112,050	50,825	92,500–145,740	41,960–66,105	41

Sources: Allen (1942), Bialobok and Mejnartowicz (1970), Ching and Bever (1960), Griffin and Ching (1977), Heit (1968), Lippitt (1996), Olson and Silen (1975), Owston and Stein (1974), Rafn (1915), Randall (1997), St. Clair and Adams (1991), Sweet (1965), Willis and Hofmann (1915).

Table 6—*Pseudotsuga,* Douglas-fir: stratification periods, germination conditions, and results

	Stratifi-	Germination conditions				Germinative energy				
	cation*	Moist	Temp (EC)		Amount	Time	Germ. capacity (%)			
Species	(days)	medium	Day	Night†	Days	(%)	(days)	Ave.	Range	Samples
P. macrocarpa	28	Vermiculite	30	20	28	—	—	31	—	3
	—	—	—	—	100	14	60	28	14–36	3
	—	Sand	27	21	20–90	—	—	30	15–57	5
P. menziesii	21	Sponge Rok	30	20	14–21	60	9	68	24–83	8
var. *glauca*	0	Sponge Rok	30	20	21–35	40	12	60	27–75	8
	30	Paper	30	20	17	70	10	78	—	3‡
	0	Paper	30	20	29	76	9	84	—	3‡
	20–40	Vermiculite	25	25	30	—	—	95	86–100	6
	0	Vermiculite	25	25	50	—	—	93	88–98	6
P. menziesii	21	Sponge Rok	30	20	14–35	55	10	81	38–95	194
var. *menziesii*	0	Sponge Rok	30	20	28–35	54	17	75	29–93	194
	20–40	Vermiculite	25	25	30	—	—	87	34–100	20
	0	Vermiculite	25	25	50	—	—	84	42–100	20
	28	—	30	20	28	—	—	84	66–98	129

Sources: Allen (1962c), Lippitt (1996), Owston and Stein (1974), Rafn (1915).

* Seeds stratified "naked" (Allen and Bientjes 1954) or on moist Sponge Rok, vermiculite, or paper at 0 to 5 EC.

† Alternating temperatures included 8 hours of light during the high temperature period; light apparently was provided with constant temperature.

‡ Var. *glauca* from north-central Colorado seed sources.

Figure 1— *Pseudotsuga menziesii* var. *menziessii*, coast Douglas-fir: mature, closed cones have characteristic 3-lobed protruding bracts, H 0.5.

Figure 2—*Pseudotsuga,* Douglas-fir: seeds with intact wings, H 1. The 2 varieties of *P. menziesii*, coast Douglas-fir and Rocky Mountain Douglas-fir, bear seeds similar in appearance and anatomy.

Figure 3—*Pseudotsuga menziesii,* Douglas-fir: longitudinal section through a seed showing fully developed embryo, H 8.

Figure 4—*Pseudotsuga menziesii* var. *menziesii*, coast Douglas-fir: epigeal seedling development 2, 5, 8 and 22 days after emergence from a peat moss–vermiculite potting mixture, H 0.5.

Table 1—*Pseudotsuga,* Douglas-fir: nomenclature and occurrence

Scientific name & synonyms	Common name	Occurrence
***P. macrocarpa* (Vasey) Mayr** *Abies douglasii* var. *macrocarpa* Torr. *A. macrocapa* Vasey	**bigcone Douglas-fir**, bigcone-spruce, desert-fir	Mtns of SW California
***P. menziesii* var. *glauca* (Beissn.) Franco** *P. douglasii* var. *glauca* Mayr *P. menziesii* var. *caesia* (Schwerin) Franco *P. taxifolia* var. *glauca* (Beissn.) Sudworth	**Rocky Mountain Douglas-fir,** interior Douglas-fir, blue Douglas-fir, Colorado Douglas-fir, inland Douglas-fir	Central British Columbia & SW Alberta, S in mtns to N & central Mexico, from E Washington, Oregon, Nevada, & W Arizona to E Montana, Wyoming, Colorado, New Mexico, & NW Texas
***P. menziesii* var. *menziesii* (Mirb.) Franco** *P. douglasii* var. *viridis* Schwerin *P. menziesii* var. *viridis* (Schwerin) Franco *P. mucronata* (Raf.) Sudworth *P. taxifolia* (Lamb.) Britton	**coast Douglas-fir,** Douglas-fir, Oregon Douglas-fir, green Douglas-fir, Douglas-spruce	SW BritishColumbia through W Washington & Oregon to central California, E into Cascade & Sierra Nevada ranges to W Nevada

Sources: Griffin and Critchfield (1976), Hermann (1982), Hermann and Lavender (1990), Little (1952, 1971, 1979), McDonald (1990), Minnich (1982).

Table 2—*Pseudotsuga,* Douglas-fir: phenology of flowering and fruiting

Species	Location	Flowering	Cone ripening	Seed dispersal
P. macrocarpa	S California	February–mid-Apr	Early Aug–early Oct	Late Aug–late Oct
P. menziesii var. *glauca*	Central Colorado (elev. 2,060–2,880 m)	Mid-Apr–early May	—	—
	Montana (elev. 700–1,700 m)	Late May–early June	Late July–early Aug	Late Aug–mid-Sept*
	Northern Idaho (elev. 820–1,000 m)	Early May–late June	Mid-Aug	Early Sept*
	Central Oregon	Mid-May–mid-June	—	Mid-Aug–mid-Sept*
P. menziesii var. *menziesii*	Coastal British Columbia	Late Mar–mid-May	Aug	Sept–late Mar
	W-central Oregon & W Washington	Mid-Mar–early June†	Aug	Late Aug–late Mar‡
	S Oregon	Early Apr–early May	—	Mid-Aug*
	N California	—	August	Sept–early winter§

Sources: Allen (1942), Allen and Owens (1972), Ching and Ching (1962), Gashwiler (1969), Gause (1966), Griffith (1968), Isaac (1943), McDonald (1990, 1992), Morris (1952), Owston and Stein (1974), Roeser (1942), Silen (1963), Sorensen and Campbell (1971), Sudworth (1908).

* Beginning dates only.

† Upslope progression in pollen shedding and female receptivity averaged 23.5 m of elevation per day on four transects in western Oregon and Washington (Silen 1963).

‡ About 70 to 90% of the seeds usually disperse in September and October; most of the remainder disperse between November and March (Allen 1942; Isaac 1943).

§ Seedfall usually greatest in October (McDonald 1992).

Table 3—*Pseudotsuga,* Douglas-fir: height, seed-bearing age, crop frequency, and cone length

Species	Mature height (m)	Minimum seed- bearing age (yr)	Interval (yr) between large seed crops	Cone length (cm)
P. macrocarpa	9–30	20*	—	11–17
P. menziesii				
var. *glauca*	23–49	20	3–10	4–7
var. *menziesii*	27–91	7–10†	2–11	6–10

Sources: Allen (1942), Boe (1954), Gause (1966), Hermann and Lavender (1990), Lowry (1966), McArdle and others (1961), McDonald (1990), Roeser (1942), Sudworth (1908).
* Occasionally earlier on good, open sites (Gause 1966).
† The minimum age for commercial collections has been considered 20 to 25 years (Allen 1942).

Table 4— *Pseudotsuga,* Douglas-fir: cone drying schedules and seed yield data

Species	Cone drying schedule					Seed yield		
		Kiln-drying						
	Air-drying	Time	Temp	Cone wt/cone vol		Seed wt/cone vol		Seed wt/cone
	(days)	(hr)	(EC)	kg/hl	lb/bu	kg/hl	lb/bu	wt ratio
P. marocarpa	8–10	—	—	32–39	25–30	1.02	0.8	2.8
P. menziesii								
var. *glauca*	4–60	2–10	38–43	32–7	25–60	0.30–1.02	0.5–0.8	1.0–1.3
var. *menziesii*	8–60	16–48	32–43	39–64	30–50	0.12–1.02	0.2–0.8	0.5–2.0

Sources: Brown (1983), Owston and Stein (1974), Radcliffe (1952), Swingle (1939).

Table 5—*Pseudotsuga,* Douglas-fir: cleaned seeds per weight

Species & location	Average /kg	Average /lb	Range /kg	Range /lb	Samples
P. macrocarpa					
S California	8,685	3,940	7,620–11,120	2,800–3,681	8
P. menziesii var. *glauca*					
Arizona	70,768	32,100	52,911–75,619	24,000–34,300	8
New Mexico	83,555	37,900	72,312–90,830	32,800–41,200	8
Colorado	85,539	38,800	73,414–96,122	33,300–43,600	33
Montana	88,405	40,100	79,807–99,869	36,200–45,300	14
E Washington	102,354	46,427	101,834–103,093	46,191–46,762	3
British Columbia	109,845	52,315	85,465–142,635	38,705–64,700	42
P. menziesii var. *menziesii*					
Coastal California					
Fog-belt	86,882	39,409	80,257–104,058	36,404–47,200	4
Inland	70,028	31,764	55,618–78,493	25,228–35,604	5
California	71,752	32,546	33,951–116,845	15,400–53,000	41
N California	67,250	30,504	40,858–109,171	18,409–49,519	20
California					
Zones 090	72,305	32,797	63,268–93,268	28,698–42,605	62
Zones 300	65,538	30,181	54,780–81,359	24,848–36,904	29
Zones 500	56,906	25,812	48,028–69,867	21,785–31,691	37
Oregon	97,165	44,075	68,770–169,495	31,195–76,880	374
Oregon & Washington	85,300	38,700	73,634–125,664	33,400–57,000	224
Coastal Oregon (seed orchard)	87,268	39,584	76,128–110,972	34,531–50,336	23
Washington Cascades	81,183	36,824	75,074–87,336	34,053–39,615	2[d]
W Washington	115,185	52,245	82,260–150,770	37,315–68,385	48[f]
British Columbia	112,050	50,825	92,500–145,740	41,960–66,105	41

Sources: Allen (1942), Bialobok and Mejnartowicz (1970), Ching and Bever (1960), Griffin and Ching (1977), Heit (1968), Lippitt (1996), Olson and Silen (1975), Owston and Stein (1974), Rafn (1915), Randall (1997), St. Clair and Adams (1991), Sweet (1965), Willis and Hofmann (1915).

Table 6—*Pseudotsuga,* Douglas-fir: stratification periods, germination conditions, and results

Species	Stratification* (days)	Germination conditions				Germinative energy				
		Moist medium	Temp (EC)		Amount	Time	Germ. capacity (%)			
			Day	Night†	Days	(%)	(days)	Ave.	Range	Samples
P. macrocarpa	28	Vermiculite	30	20	28	—	—	31	—	3
	—	—	—	—	100	14	60	28	14–36	3
	—	Sand	27	21	20–90	—	—	30	15–57	5
P. menziesii	21	Sponge Rok	30	20	14–21	60	9	68	24–83	8
var. *glauca*	0	Sponge Rok	30	20	21–35	40	12	60	27–75	8
	30	Paper	30	20	17	70	10	78	—	3‡
	0	Paper	30	20	29	76	9	84	—	3‡
	20–40	Vermiculite	25	25	30	—	—	95	86–100	6
	0	Vermiculite	25	25	50	—	—	93	88–98	6
P. menziesii	21	Sponge Rok	30	20	14–35	55	10	81	38–95	194
var. *menziesii*	0	Sponge Rok	30	20	28–35	54	17	75	29–93	194
	20–40	Vermiculite	25	25	30	—	—	87	34–100	20
	0	Vermiculite	25	25	50	—	—	84	42–100	20
	28	—	30	20	28	—	—	84	66–98	129

Sources: Allen (1962c), Lippitt (1996), Owston and Stein (1974), Rafn (1915).

* Seeds stratified “naked” (Allen and Bientjes 1954) or on moist Sponge Rok, vermiculite, or paper at 0 to 5 EC.

† Alternating temperatures included 8 hours of light during the high temperature period; light apparently was provided with constant temperature.

‡ Var. *glauca* from north-central Colorado seed sources.