Section 4.
Douglas-Fir (*Pseudotsuga menziesii*)

1. Taxonomy

Pseudotsuga menziesii (Mirbel) Franco is generally called Douglas-fir (so spelled to maintain its distinction from true firs, the genus *Abies*). *Pseudotsuga* Carrière is in the kingdom Plantae, division Pinophyta (traditionally Coniferophyta), class Pinopsida, order Pinales (conifers), and family Pinaceae. The genus *Pseudotsuga* is most closely related to *Larix* (larches), as indicated in particular by cone morphology and nuclear, mitochondrial and chloroplast DNA phylogenies (Silen 1978; Wang *et al*. 2000); both genera also have non-saccate pollen (Owens *et al*. 1981, 1994). Based on a molecular clock analysis, *Larix* and *Pseudotsuga* are estimated to have diverged more than 65 million years ago in the Late Cretaceous to Paleocene (Wang *et al*. 2000). The earliest known fossil of *Pseudotsuga* dates from 32 Mya in the Early Oligocene (Schorn and Thompson 1998).

Pseudostuga is generally considered to comprise two species native to North America, the widespread *Pseudostuga menziesii* and the southwestern California endemic *P. macrocarpa* (Vasey) Mayr (bigcone Douglas-fir), and in eastern Asia comprises three or fewer endemic species in China (Fu *et al*. 1999) and another in Japan. The taxonomy within the genus is not yet settled, and more species have been described (Farjon 1990). All reported taxa except *P. menziesii* have a karyotype of 2*n* = 24, the usual diploid number of chromosomes in Pinaceae, whereas the *P. menziesii* karyotype is unique with 2*n* = 26. The two North American species are vegetatively rather similar, but differ markedly in the size of their seeds and seed cones, the latter 4-10 cm long for *P. menziesii* and 9-20 cm for *P. macrocarpa* (Elias 1980; Lipscomb 1993). Although additional species have been described that may occur in Mexico (Flous 1934a, 1934b; Martínez 1963) — *P. flahaultii* Flous, *P. guinieri* Flous, *P. lindleyana* (Roezl) Carr., *P. macrolepis* Flous, *P. rehderi* Flous, these taxa are not broadly recognized due to their overlapping morphological characters which do not correlate with the scattered distribution of Mexican populations of the genus (Farjon 1990; Debreczy and Rácz 1995; Reyes-Hernández *et al*. 2005). Considerable morphological variation has been found among 19 populations sampled from the three major geographical regions of Mexico where *Pseudotsuga* occurs (Reyes-Hernández *et al*. 2005). Strong genetic differentiation for isozymes was found between a northeastern Mexican population of *P. menziesii* at approximately 25° N (2500 m elevation) and 103 other populations of the species sampled rangewide (Li and Adams 1989).

Two botanical varieties of Douglas-fir are commonly recognized: *P. menziesii* var. *menziesii*, called coastal Douglas-fir, and *P. menziesii* var. *glauca* (Beissner) Franco, called Rocky Mountain or interior Douglas-fir (Little 1979; Lipscomb 1993). The two varieties may intergrade in interior British Columbia (Canada) but have geographically separate ranges to the south. The varieties differ in many morphological, physiological and ecological characteristics. The coastal variety has greenish needles and longer seed cones with straight, appressed bracts, whereas the interior variety has bluish-green needles and shorter cones with reflexed bracts. Although the differences are not always obvious, strong differentiation of these varieties has been confirmed with isozymes, and nuclear, mitochondrial, and chloroplast DNA studies (Li and Adams 1989; Aagaard *et al*. 1995, 1998a, 1998b; Klumpp 1999; Nelson *et al*. 2003). Some of these studies have also indicated strong differentiation between the northern and southern subgroups of *P. menziesii* var. *glauca*. Literature particularly from Europe (*e.g.* Göhre 1958;

Klumpp 1999) sometimes recognizes another interior variety for the northern half of the continental range, *P. menziesii* var. *caesia* (Schwerin) Franco. Recently an additional variety, *P. menziesii* var. *oaxacana* Debreczy & Rácz, has been proposed for a few stands of narrow columnar trees with grayish foliage and small cones at the southernmost extent of the species' range (Debreczy and Rácz 1995; Acevedo-Rodríguez 1998).

2. Natural distribution

Douglas-fir is a common western North American species (central to southern area in both the Pacific and the Cordilleran regions), with a very broad latitudinal range extending from 55º N (Klinka *et al*. 2000; Hermann and Lavender 1990) to 16º N (Debreczy and Rácz 1995; Reyes-Hernández *et al*. 2005) (Figure 1). The coastal variety occurs from central British Columbia southward primarily along the Pacific Coast for about 2200 km to 34º44' N, reaching mid-California in the coastal Santa Cruz Mountains yet also occurring inland in the northern Sierra Nevada (Lipscomb 1993). The range of the continental interior variety extends along the Rocky Mountains into the mountains of southern Mexico over a distance of more than 4500 km. In northeastern Oregon, and southern Idaho southward through the mountains of eastern Nevada, Utah, Colorado, Arizona, New Mexico, western Texas and into Mexico, the distribution is discontinuous and fragmented. Disjunct populations are present in Alberta and the eastern-central parts of Montana and Wyoming (Hermann and Lavender 1990; Lipscomb 1993), and as far to the south as 16º22' N in central Oaxaca (Debreczy and Rácz 1995).

Figure 1. The main native range of Douglas-fir
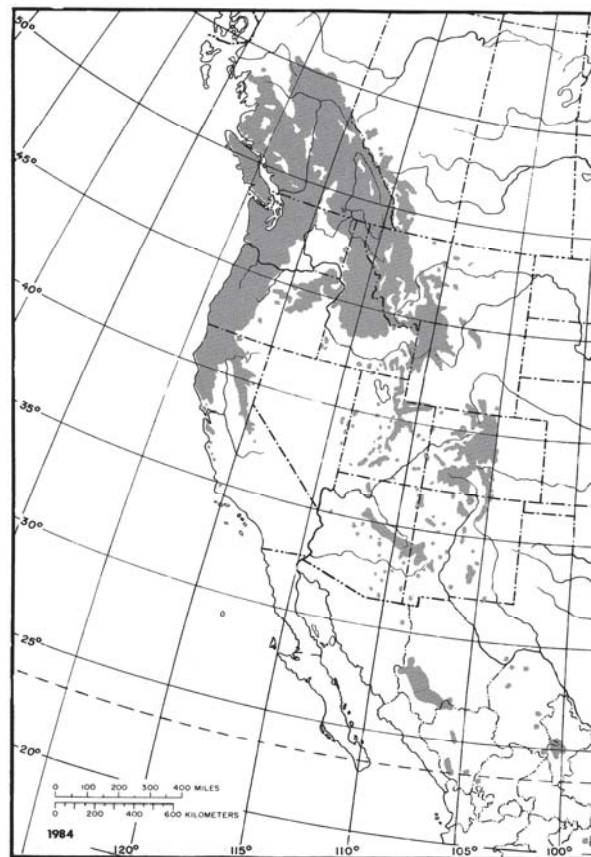
Source: Hermann and Lavender 1990

3. Reproductive biology

3.1. Reproductive development

Douglas-fir is monoecious. Trees commonly reach reproductive maturity at 12 to 15 years of age. Primordia of undifferentiated buds are already present when vegetative buds flush in the spring of the year preceding the cone crop (Hermann and Lavender 1990). By mid-June, vegetative bud primordia, pollen cone primordia (usually clustered near the base of the extending shoot), and seed cone primordia (borne singly near the tip of the shoot) (Allen and Owens 1972) can be separated based on histochemical differences.

The number of lateral buds initiated that differentiate into reproductive buds, rather than aborting or developing into vegetative buds, determines the potential size of the cone crop. Poor seed cone crops in part reflect a high abortion rate of buds during the preceding summer. Large numbers of pollen cone buds or seed cone buds in the fall merely indicate the potential for a heavy cone crop the following year, as buds, cones and seeds can subsequently be damaged by frost and cones and seeds can be damaged or destroyed by seed predation before they mature (Dobbs *et al*. 1974).

Male strobili (pollen cones), generally abundant on year-old shoots especially in the lower crown, are about 2 cm long and yellow to deep red. Their overlapping microsporophylls each have two abaxial microsporangia (pollen sacs), which contain pollen mother cells that undergo meiosis and produce a tetrad of microspores. Each microspore develops into a mature, five-celled pollen grain containing two prothalial cells, a sterile (traditionally "stalk") cell, a generative (or "body") cell and a tube cell (Allen and Owens 1972; Fernando *et al*. 2005). The mature pollen grains are spherical when hydrated but dry and bowl-shaped when shed, have a seemingly smooth exine, and are rather large (90-110 μm diameter), so they do not disperse as far as the pollen of some conifers (Owens 1973; Tsukada 1982; Jackson and Smith 1994; Fernando *et al*. 2005). Under typical weather conditions most pollen is dispersed within ten tree heights, although small amounts can disperse over much greater distances when winds are strong. Pollen dispersal occurs for 20 to 30 days in a stand (Silen 1963).

Female strobili (seed cones), occur on year-old lateral shoots usually in the upper half of the crown. They are about 3 cm long, deep green to deep red, and have distinctive narrow trident bracts projecting from between the cone scales. The young cones are erect, and receptive to pollination when emerged (especially halfway or more) from the bud scales, *i.e.* at bud burst, and on average for 6-8 days (Webber and Painter 1996; Stein and Owston 2002). Anthesis and pollination of the coastal variety occur during March and April in warmer areas and as late as May or early June in colder areas. Pollen lands on the bracts and moves downward to the ovuliferous scales and inward to the apices of the inverted ovules (Takaso and Owens 1995). The cones then become larger and pendant, with the cones scales appressed.

Pollen collects on hairs of the integument's bilobed stigmatic tip, which then collapses inward to bring pollen into the micropyle (Allen and Owens 1972; Webber and Painter 1996). Fertilisation occurs about 10 weeks after pollination. *Pseudotsuga* and *Larix* have delayed ovular secretion, with a post-pollination pre-fertilisation drop filling the micropylar canal 5-7 weeks after pollination (von Aderkas and Leary 1999; Gelbart and von Aderkas 2002; Poulis *et al*. 2005). This drop is thought to assist the pollen grain in reaching the ovule and preparing for germination. The generative (body) cell of the pollen grain divides to produce two male gametes prior to fertilisation. After approximately 2 weeks, pollen grains germinate and pollen tubes grow into archegonia, releasing the two male gametes, one of which will fertilise the egg cell. Ovules contain four to six archegonia, thus multiple fertilisations and polyembryony occur, although typically only one embryo survives to maturity (Allen and Owens 1972). The embryo is in a cavity surrounded by the firm, cream-coloured, haploid megagametophyte which forms multinucleate storage cells, thus serving as a food reserve for the germinating embryo (Owens 1973; von Aderkas *et al*. 2005a). Each ovuliferous scale can produce two seeds at its base. Each seed (with the seed coat 5-7 mm long) has a large wing (twice to thrice the body length) consisting of two cell

layers derived from the ovuliferous scale. Mature seeds are dark brown on one side and mottled light brown on the other.

At low and middle elevations, cones mature and seeds ripen from mid-August to mid-September. The bracts turn brown when seeds are mature. Cone scales reflex and seedfall occurs under dry conditions soon after cone maturity, with two-thirds of the total crop typically on the ground by the end of October. Remaining seeds fall during the winter and spring. Reproductive phenology is similar for the interior variety (Baumgartner and Lotan 1991). The degree of dormancy of mature seed and thus the amount of chilling required to break it varies geographically. Chilling requirements are met over the winter and dormancy broken naturally. Dormancy is broken artificially through cold stratification; seeds are soaked in water for 24 hours, then chilled at 2 to 5°C, usually for 21 days. Coastal Douglas-fir generally requires cold stratification, whereas northern Rocky Mountain Douglas-fir may benefit from stratification and southern provenances may not. After dormancy is broken, seed will germinate at temperatures ranging from 10 to 30°C. There is no light requirement for germination. The viability of seed can be maintained for at least several decades when stored under optimal conditions, *i.e.* at 18ºC with a moisture content of 5 to 9% (Stein and Owston 2002).

3.2. Mating system and gene flow

Douglas-fir has a predominantly outcrossing mating system, with selfing rates generally well below 10% in natural populations, selectively harvested stands, and seed orchards (Neale and Adams 1985; Prat and Arnal 1994; Prat 1995; Prat and Caquelard 1995; Burczyk and Prat 1997; Slavov *et al*. 2005). Some trees may have considerably higher selfing rates than average (Stoehr *et al*. 1998).

Seed orchard studies of mating system and pollen contamination from outside stands indicate that two-thirds to half of the pollen received by a mother tree originates from nearby pollen parents, and a third to half comes from more remote sources, either within or outside of the orchard (Burczyk and Prat 1997; Slavov *et al*. 2005). Contamination of orchard seedlots with non-orchard pollen can be as high as 60% within the coastal Douglas-fir range (Adams *et al*. 1997). This contamination can result in decreased genetic gain or increased maladaptation, depending on the location and genetic makeup of the seed orchard (Stoehr *et al*. 1994).

Based on genetic markers, long-distance gene flow appears to be very low between the coastal and interior varieties, and between the northern and southern subgroups of the interior variety (Li and Adams 1989; Mitton 1992; Aagaard *et al*. 1995, 1998a, 1998b; Klumpp 1999; Nelson *et al*. 2003). However, the lack of strong differentiation of populations within the coastal variety (St. Clair *et al*. 2005), and within the northern subgroup of the interior variety, is indicative of higher levels of gene flow within each of these two relatively non-fragmented regions (Li and Adams 1989). Populations within the southern subgroup are much more isolated (Figure 1), although for example during the last glacial period there was considerably less fragmentation in the Colorado Plateau area and Rocky Mountains (Jackson *et al*. 2005).

3.3. Seed production

An old-growth Douglas-fir population may produce 20 to 30 times more cones per hectare than a 50- to 100-year-old second-growth stand. Seed crops occur at irregular intervals — on average, one heavy (mast) crop and one medium crop every 7 years (Owston and Stein 1974; Stein and Owston 2002). Even during heavy seed years, only about 25% of the trees produce an appreciable number of cones (Isaac 1943). Data on seed fall density in an area will vary widely, but most years less than 2.2 kg fall per ha, of which no more than 40% is viable. Years with small seed crops generally have a lower percentage of sound seeds than mast years, perhaps because the low density of seed and pollen-producing trees results in a higher level of self-pollination (Garman 1955).

Seed quality also varies during the annual seedfall period. It is higher in the fall of the year but declines rapidly during winter and spring. This pattern probably results from cone scales in the centre of the cone — where the highest quality seed are borne — opening early, and scales at the tip and base, which bear generally poor quality seeds, opening late (Hermann and Lavender 1990).

Both cones and seeds vary greatly in size with latitude and similarly in both varieties, generally with larger seeds to the south: for example, from coastal Douglas-fir trees, 112,000 cleaned seeds per kg in British Columbia, 70,000 per kg in California; from interior Douglas-fir trees, 110,000 seeds per kg in British Columbia, 71,000 per kg in Arizona (Stein and Owston 2002). Seeds of the coastal variety tend to be larger farther inland than near the coast, and seeds of the interior variety larger than in the coastal variety (*e.g.* 115,000 seeds per kg in western Washington, 88,000 per kg in Montana). Also, seeds sometimes are larger at higher elevations (Stein and Owston 2002). Individual cones can contain up to 52(-63) seeds, but an average of 15 to 20 seeds per cone is more typical in natural populations (Silen 1978; Vargas-Hernández *et al*. 2004). Seed size is determined before fertilisation, so there is no correlation between seed weight and paternity, although seedlings germinating from heavier seeds may be slightly larger during the first few months of growth (Hermann and Lavender 1990).

Predation of seed by insects, mammals and birds is a major factor limiting natural regeneration. Competing plant species and unfavourable abiotic environments also reduce success of regeneration. Although fully stocked stands have been reported 1 to 2 km away from a seed source, the vast majority of seeds fall within 100 m of seed parent trees (Allen 1942; Dobbs *et al*. 1974; Barnhart *et al*. 1996; Thompson and Schorn 1998; Brocano *et al*. 2005; Kennedy and Diaz 2005).

Most seed for artificial regeneration of coastal Douglas-fir now originates from seed orchards. Seed orchard managers promote the differentiation of reproductive buds through applications of synthetic giberellins (particularly giberellic acids GA_4 and GA_7), nitrate fertilisation, and partial girdling of stems in early spring (Silen 1978). Selected parents are grafted into seed orchards; graft incompatibility was a major problem until genetically high compatibility lines of rootstock were developed (Copes 1999). Cooling of orchards to delay heat sum accumulation and reproductive bud break is a common method for reducing pollen contamination in some orchards.

3.4. Natural regeneration

Douglas-fir seed germinate epigeally from mid-March to early April in the warmer regions of the range, and as late as mid-May in the cooler areas. Seedling growth during the first year is indeterminate, relatively slow, and moisture limited. Low moisture availability or a photoperiodic cue can trigger formation of buds and initiation of bud dormancy by mid-summer. Buds remain dormant until a genetically-determined chilling requirement is met sometime in winter, and growth resumes in April or May of the following year (Lavender 1984).

Seedlings of coastal Douglas-fir, particularly in wetter and cooler climates, survive best in high light when the seed germinates on moist mineral soil or thin burnt-over forest floor. In contrast, seedlings of interior Douglas-fir, particularly in drier and warmer climates, establish and survive in low light only on a relatively thick forest floor substrate (Isaac 1943; Schmidt 1957, 1969; Carter and Klinka 1992a). The establishment of seedlings is enhanced by ectomycorrhizal fungi (Horton *et al*. 1999; Cline *et al*. 2005). First-year seedlings on fresh sites may develop shoots 6 to 9 cm long. Growth in subsequent years is largely determinate, although some free growth and lammas growth occur in early years. Primary growth gradually accelerates so that when saplings are 8 to 10 years old, growth of the terminal leader may consistently exceed 1 m per yr on highly productive sites (Hermann and Lavender 1990). Lammas shoots of seedlings and saplings sometimes result in form defects such as forking and ramicorn branching, but these deviations are confined to wet climates with heavy late-summer rainfall (Carter and Klinka 1986; Carter *et al*. 1986; Hermann and Lavender 1990).

First-year germinants have higher survival and growth under light shade, especially on southerly exposures, but older seedlings require full sunlight, particularly on fresh and moist sites, where Douglas-fir has low shade tolerance (Carter and Klinka 1992a). Competing vegetation decreases light levels and limits Douglas-fir regeneration. On water-deficient sites, graminoids and shrubs also compete strongly with Douglas-fir seedlings for available moisture. Leaves and other organic debris from *Pteridium aquilinum* (northern bracken fern) and *Chamerion angustifolium* (narrow-leaf fireweed) can smother small seedlings. Regeneration may be more reliable after fire, which can destroy the seed bank of potential competing species, while forest harvesting can leave areas suitable for the establishment and growth of herbaceous and woody competitors (Burns 1983; Hermann and Lavender 1990).

Historically, large burned areas (including post-harvest burns) within the range of coastal Douglas-fir have naturally regenerated to nearly pure stands of Douglas-fir. On fresh sites, where Douglas-fir is considered an early seral and shade-intolerant species, this process occurred over a relatively short period, whereas on water-deficient and moist sites, regeneration has required more than 50 years. Regeneration on water-deficient sites in warmer and drier climates, where Douglas-fir is moderately shade-tolerant and considered a climax species, occurs under the forest canopy; in fact, temporary protection from the open-area climate is necessary for successful establishment (Daubenmire 1943; Krajina 1965; Ryker 1975; Hermann and Lavender 1990; Klinka *et al*. 1990).

From 1950 to 1970, large areas of cutover and burnt forest land in the Pacific Northwest were aerially seeded for reforestation. With the increase in forest nursery capacity and the ability to better control the success and density of regeneration through planting, direct seeding became rare (Schubert and Adams 1971; Cleary *et al*. 1978). One major problem with direct seeding is high seed predation by rodents and birds, although this problem can be reduced by seeding Douglas-fir seed mixed with a larger amount of desirable food such as sunflower seeds or oats (Sullivan and Sullivan 1984). Taking into account the range of sites on which Douglas-fir may grow and its variation in shade tolerance, it can be maintained using a wide variety of silvicultural systems — including clearcutting, seed-tree, shelterwood and selection systems. Although success of natural regeneration may be high, the advantage of planting is the opportunity for much greater initial stocking control and genetic improvement, particularly on productive sites. An adequate seed source, appropriate seedbed, and suitable microsite are all necessary for successful natural regeneration.

3.5. Vegetative reproduction

Douglas-fir does not reproduce vegetatively in nature. Reliable rooting of cuttings is limited to material collected from trees less than 10 years old, or from trees that have been subjected to repeated hedging which produces material with a juvenile habit. A second major impediment to the use of cuttings is that much of this material can have a lengthy period of plagiotropic growth before an erect habit is assumed (Hermann and Lavender 1990; Ritchie *et al*. 1994, 1997; Fennessy *et al*. 2000). Plagiotropic rooted cuttings become orthotropic more readily when grown outdoors than when maintained in a greenhouse; the reasons for this are not clear (Ritchie *et al*. 1997). Both rooted cuttings and plants produced through tissue culture of cotyledons appear more physiologically mature than seedlings of the same size (Ritchie *et al*. 1994). The rooting of stem cuttings is promoted through application of auxins, either IBA (24.6 mM) or NAA (2.5-7.4 mM) (Copes and Mandel 2000).

Methods for cloning Douglas-fir genotypes through somatic embryogenesis have been developed and are entering operational phases (Gadgil *et al*. 1998; Taber *et al*. 1998; Zhang *et al*. 1999; Benowicz *et al*. 2002). These methods allow for the development of clonal forestry programs, providing the technology to capture non-additive genetic variation, the opportunity to deploy clonal blocks for specific end uses, and a regeneration system for propagating genetically transformed material.

4. Genetics

4.1. Cytology

The 2C nuclear DNA content of *Pseudotsuga menziesii* is 38.10 picograms (O'Brien *et al.* 1996). The cell nuclear volumes are greater in northern provenances than southern provenances, and in the coastal variety than the interior variety (El-Lakeny and Sziklai 1971). Unlike all other species of the Pinaceae, the haploid number of chromosomes in Douglas-fir is 13. Whereas 5 metacentric and 6 submetacentric chromosomes appear karyotypically similar to those of other studied *Pseudotsuga* species, Douglas-fir has 2 telocentric chromosomes instead of a sixth large metacentric chromosome as in the other *Pseudotsuga* species. Moreover, the chromomycin A_3-banding pattern of Douglas-fir chromosomes is different from the quite similar banding patterns of the two Asian species (Hizume and Kondo 1992). Experimentally, polyploid Douglas-fir seedlings have been produced (using colchicine) but they were slow-growing and short-lived (Silen 1978).

In Douglas-fir, as in other species of the Pinaceae, inheritance of chloroplasts is predominantly paternal (Neale *et al.* 1986). In contrast, mitochondrial inheritance is maternal (Marshall and Neale 1992; Aagaard *et al.* 1998a).

4.2. Genetic variation

4.2.1.   Population-level variability

Douglas-fir has substantial among-population variation both for quantitative traits and genetic markers. Population differentiation for quantitative traits related to adaptation to climate can be considerably stronger than that observed for selectively neutral genetic markers. For example, seedling studies including samples from a wide range of source environments have found that 13 to 20% of the total genetic variation for timing of bud set, 11 to 13% of the variation in timing of bud flush, and 47% of the variation for cold hardiness are attributable to differences among populations within varieties, which is higher than the average population differentiation for genetic markers (F_{ST}) (Table 1) (Howe *et al.* 2003). Short-term seedling genecological nursery studies have found significant differentiation of populations, particularly for bud phenology traits, over distances of only a few km or 100 m of elevation (Rehfeldt 1974, 1979a, 1979b; Campbell 1979, 1986). This variation is associated primarily with temperature of source environments, and generally reflects a tradeoff between growth rate and cold hardiness, which are negatively correlated among populations. The importance of this variation at local scales to the health and productivity of operational plantations has been a subject of debate in practice and the literature. Long-term field provenance trials within the native range and elsewhere have generally failed to show the fine-grained geographic patterns of variation observed in detailed seedling genecological trials (White and Ching 1985), fuelling a debate over the need to manage Douglas-fir genetic resources on a local scale (Stonecypher *et al.* 1996; Johnson 1997).

Field provenance trials have shown weaker geographic patterns than seedling studies. In a synthesis of the results from fifteen (mostly European) countries that established provenance trials from 1967 IUFRO seed collections, Breidenstein and collaborators (1990) identified four groups of provenance sites based on principal components analysis of climatic data: (1) sites in northeastern Europe with continental climates; (2) sites in northwestern British Columbia and Norway, along with a few locations in France and Spain, with cold maritime climates; (3) sites in southwestern British Columbia and northwestern Europe with moderate maritime climates; and (4) sites in southern Europe with warm maritime climates. Mortality was higher on sites in groups 1 and 2, and lower on sites in groups 3 and 4. There was substantial provenance variation in mortality among site groups, with trees from southern coastal Oregon suffering the highest mortality rates on the coldest (group 1) sites, and provenances from the interior of British Columbia having the highest mortality on the mildest (group 4) sites (Breidenstein *et al.* 1990).

However, surviving trees from low-elevation coastal and Cascade provenances in Washington State (USA) were surprisingly consistent in having the most rapid growth over most sites, showing broad adaptability, although mortality was high on some colder sites (Kleinschmit and Bastien 1992). Growth generally decreased with increasing source elevation of provenances. Some northern Oregon provenances from west of the Cascades as well as a few southwestern British Columbia sources also had high productivity across much of Europe. Only in continental climates, *e.g.* in Sweden, Finland and the Czech Republic, did *P. menziesii* var. *glauca* provenances outperform *P. menziesii* var. *menziesii*. However, marked changes in provenance performance between the ages of 17 and 60 in one of the oldest provenance trials, likely due to cumulative effects of small injuries as well as extreme climatic effects, caution against over-reliance on early field results (Silen 1978).

Table 1.   Genetic diversity and population differentiation estimates for Douglas-fir

Marker type, and Population sampled	Expected heterozygosity (H_e) within populations	Population differentiation within races (G_{ST})	Population differentiation between races (G_{ST})	Reference
Allozymes				

Rangewide n=104
var. *menziesii* n=43
var. *glauca*:
  northern subgroup n=36
  southern subgroup n=24
	0.164
	
	0.150
	0.077
		0.07
		
		0.04
		0.12
			0.23	Li and Adams 1989

RAPD nuclear markers				

Rangewide n=6
var. *menziesii* n=2
var. *glauca*:
  northern subgroup n=2
  southern subgroup n=2
	0.26
	
	0.25
	0.15
		0.05
		
		0.07
		0.25
			0.25	Aagaard *et al*. 1998a

RAPD mitochondrial markers				

Rangewide n=6
var. *menziesii* n=2
var. *glauca*:
  northern subgroup n=2
  southern subgroup n=2
	0.01
	
	0.04
	0.03
		0.04
		
		0.75
		0.84
			0.72	Aagaard *et al*. 1998b

Although marker-based studies find less among-population variation than provenance and genecological studies, they confirm that Douglas-fir populations are relatively highly differentiated compared to various other tree species. A comprehensive rangewide survey of allozyme variation found that coastal and interior varieties were clearly differentiated, with an average Nei's genetic distance of 0.083, as were the interior variety's populations in northern and southern regions, separated by an average genetic distance of 0.034 (Li and Adams 1989). G_{ST} averaged 0.23 between varieties, 0.07 among populations within the coastal variety, 0.04 for the northern region of the interior variety, and 0.12 for the southern region of the interior variety (Table 1). These corresponded to average Nei's genetic distances among populations of respectively 0.015, 0.008, and 0.012. One of two Mexican populations was clearly distinct from all the other populations sampled. The strong differentiation of the coastal and interior varieties has been confirmed with nuclear RAPD (randomly amplified polymorphic DNA) markers. Mitochondrial RAPD markers exhibited even higher levels of racial and population differentiation (Aagaard *et al*. 1995, 1998a, 1998b), and restriction digestion of a region of chloroplast DNA also has shown strong racial differentiation (Nelson *et al*. 2003). Chloroplast restriction

fragment length polymorphisms (cpRFLPs) revealed less population differentiation (Ponoy *et al.* 1994). Chloroplast simple sequence repeats (cpSSRs) exhibited no differentiation among coastal British Columbia populations, presumably due to the recent migration into the region after glacial retreat and the long-distance gene flow *via* pollen within the region (Viard *et al.* 2001; Nelson *et al.* 2003).

4.2.2.   *Variation among individuals within populations*

Levels of within-population variation are also high. The average expected heterozygosity (H_e) based on allozymes is high for coastal Douglas-fir (0.16) and the northern subgroup of interior Douglas-fir (0.15), but is half that for the more isolated southern interior subgroup (Li and Adams 1989) (Table 1). In contrast, for chloroplast DNA markers, levels of within-population variation are higher for interior populations than coastal populations (Ponoy *et al.* 1994). Mitochondrial RAPD markers revealed relatively low levels of within-population variation compared to nuclear RAPD markers, for which within-population variation was similar to allozymes (Aagaard *et al.* 1998b). The proportion of total genetic variation due to within-population variation is considerably higher for presumably selectively neutral molecular markers than for adaptive traits such as bud phenology (as predicted by theory) (Howe *et al.* 2003).

Table 2. Examples of individual heritability (h_i^2) estimates for quantitative traits in Douglas-fir

Trait	Variety	h_i^2 estimate, mean or range	Reference
Height 1 year	*menziesii*	0.60	Christophe and Birot 1979
Height 2 years	*menziesii*	0.46	Christophe and Birot 1979
Height 4 years	*menziesii*	0.26	Christophe and Birot 1979
Height 12 years	*menziesii*	0.15 (0.12-0.17)	Adams and Joyce 1990; Stonecypher *et al.* 1996
DBH 12 years	*menziesii*	0.08	Adams and Joyce 1990
Stem volume 12 years	*menziesii*	0.08	Adams and Joyce 1990
Lammas growth occurrence	*menziesii*	0.45	Aitken and Adams 1995a
	glauca	0.32	Rehfeldt 1983
Date of bud break	*menziesii*	0.87 (0.45-1.0)	Christophe and Birot 1979; Li and Adams 1993; El-Kassaby&Park 1993; Aitken&Adams 1995a
	glauca	0.52	Rehfeldt 1983
Date of bud set	*menziesii*	0.70 (0.15-0.81)	Li&Adams 1993; Aitken&Adams 1995a, 1995b
	glauca	0.25	Rehfeldt 1983
Fall cold hardiness	*menziesii*	0.29 (0.21-0.37)	Aitken and Adams 1996; Aitken *et al.* 1996; O'Neill *et al.* 2001
Winter cold hardiness	*menziesii*	0.11 (0.0-0.35)	Aitken and Adams 1995b
Spring cold hardiness	*menziesii*	0.62 (0.36-1.0)	Aitken and Adams 1997; O'Neill *et al.* 2001
Cambial growth initiation	*menziesii*	0.23	Li and Adams 1994
Cambial growth cessation	*menziesii*	0.11	Li and Adams 1994
Overall wood density	*menziesii*	0.59	Vargas-Hernandez and Adams 1991
Earlywood density	*menziesii*	0.47	Vargas-Hernandez and Adams 1991
Latewood density	*menziesii*	0.36	Vargas-Hernandez and Adams 1991
Latewood proportion	*menziesii*	0.24	Vargas-Hernandez and Adams 1991
Intra-ring density variation	*menziesii*	0.25	Vargas-Hernandez and Adams 1991
Graft incompatibility	*menziesii*	0.81	Copes 1973

The amount of genetic variation and the degree of genetic control of polygenic traits of economic or adaptive interest within populations of Douglas-fir have been studied extensively (Table 2). Generally, growth traits and fall cold hardiness are under relatively weak genetic control (individual heritability $h_i^2 < 0.3$) whereas bud phenology, spring cold hardiness, wood density and graft incompatibility are

under relatively strong genetic control ($h_i^2 \geq 0.5$). The polygenic control of bud phenology and cold hardiness traits has been verified through quantitative trait loci (QTL) mapping in a three-generation pedigree, with 11 QTL for fall cold hardiness, 15 for spring cold hardiness, and 33 for the timing of bud flush (Jermstad *et al*. 2001a, 2001b).

4.3. Inbreeeding depression and genetic load

Douglas-fir has a very high genetic load, with an estimated 10 lethal equivalents per genome (Sorensen 1969). Controlled outcrossing results in an average of 40 seeds per cone, whereas matings between half-sibs (inbreeding coefficient F=0.125) produce 31 seeds per cone, full-sib and parent-offspring matings (F=0.25) produce 23 seeds per cone, and self-pollination (F=0.50) averages just over one seed per cone (Sorensen and Cress 1994). Growth of seedlings and young trees is reduced by about 7% for every 0.1 increase in F (Sorensen 1997).

5. Hybridisation

Experimental hybrids between *Pseudotsuga menziesii* and *P. macrocarpa* have been reported (Ching 1959; Gause 1966; Orr-Ewing 1966a, 1966b). The present natural ranges of these species do not overlap, being about 35 km apart. Attempts to hybridise *P. menziesii* with generally accepted Asian species of the genus have failed, producing only empty seeds (Orr-Ewing 1966a, 1966b, 1971; Silen 1978). This failure is likely because of the different number of chromosomes in *P. menziesii* ($2n = 26$) from the diploid $2n = 24$ present in other species of the genus, but does not explain the interspecific crossing success with *P. macrocarpa* (Silen 1978). Attempts to hybridise *P. macrocarpa* with *P. japonica* and *P. sinensis* also have failed, producing only empty seeds (Orr-Ewing 1975).

Experimental crosses made in British Columbia of *Pseudotsuga flahaultii* (from western Chihuaua, Mexico) with *P. menziesii* var. *glauca* and *P. menziesii* var. *menziesii* (Orr-Ewing *et al*. 1972) were successful. The two generally accepted Douglas-fir taxa *P. menziesii* var. *menziesii* and *P. menziesii* var. *glauca* are completely interfertile experimentally. Intervarietal hybrids and F_2 crosses of such hybrids combine high growth rates with good frost resistance, and have been used in breeding programs in Germany (Braun 1992, 1999). Natural introgression of these two varieties may take place where their present ranges meet, for example in the interior of British Columbia (von Rudloff 1972; Li and Adams 1989), but in other areas of proximity the populations may remain distinct, possibly because of their local adaptation (*e.g*. St. Clair *et al*. 2005). When British Columbia was covered by the Cordilleran ice sheet 18,000 years ago, the varieties were isolated from each other farther to the south as coastal and Rocky Mountain populations; their convergence in interior British Columbia may have taken place no earlier than 7000 years ago (Tsukada 1982; Bartlein *et al*. 1998).

6. Ecology

This section focuses on the ecological information from Canada and the United States.

6.1. Autecology

Douglas-fir has an extensive geographical and elevational range, with the broadest ecological amplitude of all the western North American tree species. It grows in a wide variety of climates (arranged here in order of increasing frequency of presence): subalpine boreal, boreal, semiarid, temperate, and mesothermal (Hermann and Lavender 1990; Klinka *et al*. 2000). The Pacific region has a maritime climate with cool, relatively dry summers and wet, mild winters, with a long frost-free period and relatively narrow diurnal temperature fluctuations (6 to 8ºC). Precipitation falls mostly as rain, and is concentrated in the winter. The interior, Cordilleran region has a continental climate. In the northern part of the range of interior Douglas-fir, frost can occur in any month of the year. Precipitation in the northern

Rocky Mountains is relatively evenly distributed throughout the year, with the exception of a dry period during July and August. In the central Rocky Mountains, summers are hot and very dry in some areas, and winters are long and severe. The southern Rocky Mountains east of the Continental Divide generally have high rainfall during the growing season but low winter precipitation; west of the Continental Divide, the rainfall is bimodal, being more evenly divided between winter and summer. In the Sierra Madre Occidental of northern Mexico, the precipitation is primarily in the summer months, with occasional winter rainfall (but sometimes severe drought), average low temperature in January below freezing at higher elevations, and a spring dry period (Fulé and Covington 1999; Cleaveland *et al*. 2003; González-Elizondo *et al*. 2005).

Within these large regions the climate also varies considerably, which is readily notable with elevation. In general, temperature decreases and precipitation increases with increasing elevation throughout the Coastal ranges, Sierra Nevada, and Rocky Mountains. At middle and high elevations particularly north of Mexico, the winters are colder, the frost-free season is shorter, diurnal temperature fluctuations are larger (10 to 16ºC), and much of the precipitation falls as snow.
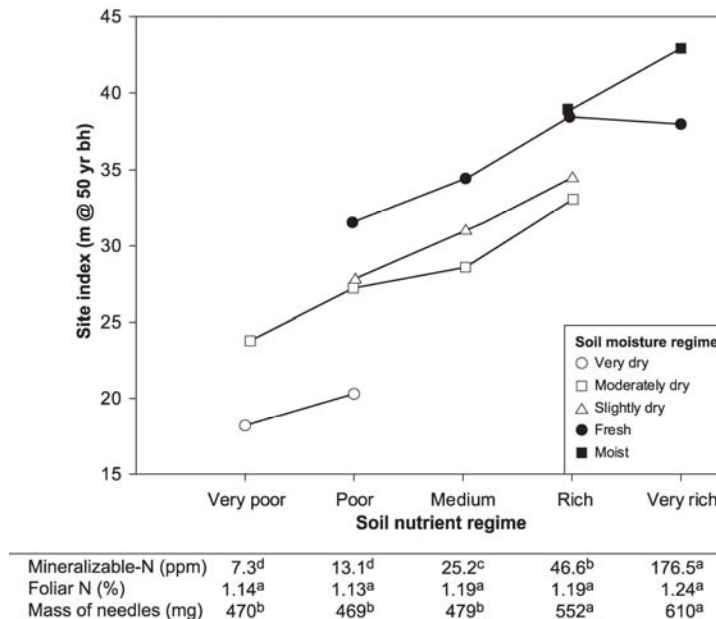
Douglas-fir grows across nearly the entire range of conditions of soil moisture (very dry to very moist) and soil nutrients (very poor to very rich), but the most productive growth occurs on fresh to moist, nitrogen-rich soils. Douglas-fir has a greater tolerance of water- and nutrient-deficient soils than many other native tree species (Krajina 1969; Klinka *et al*. 2000).

Site index is an expression of site productivity, based on the height of dominant or codominant trees at a standard base age (usually 50 years). Relationships between potential site index of the coastal variety and analytical and categorical measures of site quality have been quantified in the Coastal Western Hemlock zone of British Columbia (Klinka and Carter 1990). Site index increased with increasing soil water supply, peaked between fresh and moist sites, and then decreased with increasing water surplus. Site index also increased with increasing nitrogen availability, even on water-deficient sites (Figure 2). All the trends in site index – site quality relationships are supported by regression analysis indicating that each soil moisture and soil nutrient regime had a strong relationship with site index. The best quantitative soil measures related to site index were water deficit and mineralisable nitrogen in the first 30 cm of mineral soil, which together accounted for 63% of the Douglas-fir site index variability.

Both soil moisture and soil nitrogen are major determinants of Douglas-fir growth in the Coastal Western Hemlock zone (British Columbia) and likely in other environments (Carter and Klinka 1992b). Douglas-fir will respond to nitrogen fertilisation, with the magnitude of response decreasing with increasing soil water surplus and the available nitrogen (Carter *et al*. 1998) (Figure 3).

Coastal Douglas-fir reaches its best growth on well-aerated, deep soils with a pH from 5 to 6. In coastal northern California, Oregon and Washington, soils originated chiefly from marine sandstone and shales with scattered igneous intrusions. Surface soils are generally acidic, low in base saturation, and high in organic matter and total nitrogen. Soils supporting coastal Douglas-fir have textures ranging from gravelly sands to clays. Soil depth varies from very shallow on steep slopes and ridgetops, to deep where there are deposits of volcanic origin as well as residual and colluvial materials. Soil orders characteristic of the range of coastal Douglas-fir include Ultisols, Inceptisols, Spodosols and Entisols (Heilman *et al*. 1979).

**Figure 2. Douglas-fir site index relative to soil moisture and soil nutrient regimes in a dry,
cool mesothermal climate of coastal British Columbia, Canada**

	Very poor	Poor	Medium	Rich	Very rich
Mineralizable-N (ppm)	7.3[d]	13.1[d]	25.2[c]	46.6[b]	176.5[a]
Foliar N (%)	1.14[a]	1.13[a]	1.19[a]	1.19[a]	1.24[a]
Mass of needles (mg)	470[b]	469[b]	479[b]	552[a]	610[a]

Relationships between soil nutrient regimes and several empirical variables (site n=149). Different superscripts within rows indicate significant differences among the soil nutrient regimes (p<0.05, Tukey's test) (from Carter and Klinka 1990)

**Figure 3. Edatopic grid showing pre-treatment foliar nitrogen (N, %) and sulphate-sulphur (SO4-S, ppm),
and isolines of relative basal-area response, indicating 3rd-year response of Douglas-fir
to nitrogen fertilisation**
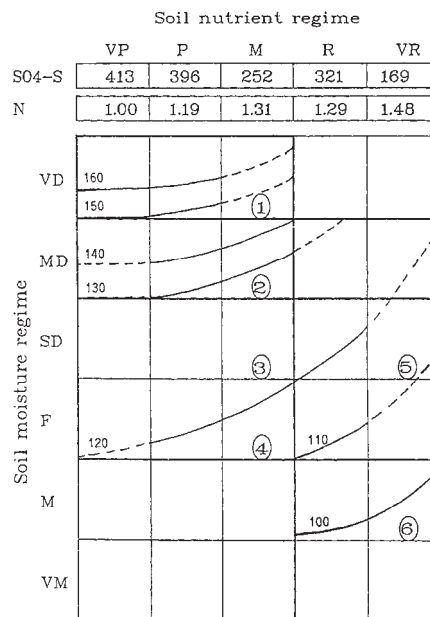
Dashed isolines are extrapolations. Soil nutrient regimes (detailed in Figure 2) are: VD=very dry, MD=moderately dry, SD=slightly dry, F=fresh, M=moist, and VM=very moist. Encircled numbers are site units: 1=Cladonia spp., 2=Gaultheria shallon, 3=Rhytidiadelphus loreus, 4=Blechnum spicant, 5=Tiarella trifoliata, and 6=Athyrium filix-femina (from Carter and Klinka 1992b)

Soils in the range of interior Douglas-fir originated from an array of parent materials ranging from basaltic talus and deep loess with volcanic ash to thin residual soil over sedimentary or granitic rocks. The soils are mostly Alfisols, Inceptisols, Mollisols, Spodosols and Entisols. Limestone comprises a significant portion of the sedimentary rock, and gives rise to neutral or alkaline soils ranging in texture from gravelly silts to gravelly loams (Alexander 1974; Pfister *et al*. 1977).

The elevational distributions of both coastal and interior Douglas-fir decrease from south to north, reflecting the effect of latitude on temperature. Principal limiting factors are low temperature in the northern, high temperature in the far southern portions of the range, and low moisture especially in the southern portion (*e.g.* Adams and Kolb 2005; Case and Peterson 2005). Interior Douglas-fir generally grows at considerably higher elevations than coastal Douglas-fir at comparable latitudes. The highest elevation where interior Douglas-fir grows north of Mexico is 3260 m, on the crest of Mount Graham in southeastern Arizona (Hermann and Lavender 1990). Populations in Mexico generally occur between 2000-3600 m, on northern exposures (Acevedo-Rodríguez *et al*. 2006).

In summary, Douglas-fir tolerates water- and nutrient-deficient soils but not water-surplus and flooded soils (Krajina 1969; Klinka *et al*. 2000). In the Pacific Northwest and Intermountain Northwest, nitrogen is the only nutrient in forest soils that has been shown to limit the growth of Douglas-fir (Miller *et al*. 1986; Moore 1988).

Juvenile life-history characteristics are described above in Section III, Subsection D (Natural regeneration). Coastal Douglas-fir can reach reproductive maturity at 7 to 10 years of age, whereas Rocky Mountain Douglas-fir is slower to reproduce (Stein and Owston 2002). Sapling-age trees produce relatively few cones, investing most energy in rapid height growth under competition for light. Maximum fecundity occurs between 100 and 200 years, but younger trees produce fewer, larger cones and more viable seeds per cone (Stein and Owston 2002). The species produces relatively fewer cones in most years but large crops at intervals of 2 to 7 years (Owens 1973).

Coastal Douglas-firs commonly reach maximum heights of 76 m and diameters (dbh) of 150-180 cm. Among the living trees, one of the largest on record (1998) reached 85.6 m in height and 408 cm dbh, with a crown spread of 22 m, and wood volume of 308 m^3 (AFA 2000). The most massive recorded tree (1998) had a wood volume of 349 m^3 (height 73.8 m, dbh 423 cm, crown spread 23 m); and the tallest living tree (1998) reached 99.4 m (dbh 354 cm) (Van Pelt 2001). Historically, purportedly larger trees were reported, with heights of 115-127 m. Douglas-fir thus remains among the world's few tallest species. The lifespan of coastal Douglas-fir typically reaches some 500 years, with the oldest known tree attaining about 1350 years (McArdle *et al*. 1961; Hermann and Lavender 1990). Rocky Mountain Douglas-firs are smaller, averaging 30-37 m in height and 38-102 cm dbh, with one of the most massive recorded being 42.4 m in height and 255 cm dbh, and the tallest reaching 67.4 m with 179 cm dbh. The interior variety typically lives to around 400 years, although relatively frequent fires often kill trees at a younger age (Hermann and Lavender 1990); they can attain a known lifespan of some 1275 years. The Douglas-fir generations in an area can be overlapping or discrete, and long or short, depending on the agents of disturbance and whether the stands were even-aged or uneven in age.

6.2. Synecology

Depending on site and disturbance history, Douglas-fir can grow in even- or uneven-aged stands and in monospecific or mixed-species stands. It may be present in all seral stages of secondary succession, and can form old-growth stands on some sites.

As a result of its wide climatic amplitude, Douglas-fir is a minor or major component in many regional ecosystems (climatic or vegetation zones): for example, in British Columbia it occurs in 10 of the 12 forested zones. It is the major late seral species in the Interior Douglas-fir zone and Coastal Douglas-fir zone (Krajina 1965, 1969; Meidinger and Pojar 1991; Klinka *et al*. 2000). Given

its relatively wide edaphic amplitude, Douglas-fir can be a minor or major, temporary or self-perpetuating component of local ecosystems (plant associations, site types, habitat types, or forest cover types), but it is absent on wet sites, sites with a strongly fluctuating water table, and sites affected by ocean spray (Krajina 1969; Klinka *et al*. 2000).

The major associates of coastal Douglas-fir may include *Abies amabilis* (Pacific silver fir), *A. grandis* (grand fir), *A. concolor* (white fir), *Acer macrophyllum* (bigleaf maple), *Alnus rubra* (red alder), *Arbutus menziesii (*Pacific madrone), *Chamaecyparis lawsoniana* (Port Orford-cedar), *Libocedrus decurrens* (incense-cedar), *Picea sitchensis* (Sitka spruce), *Pinus monticola* (western white pine), *Quercus chrysolepis* (canyon live oak), *Q. garryana* (Garry oak), *Q. kelloggii* (California black oak), *Q wislizeni* (interior live oak), *Sequoia sempervirens* (coast redwood), *Thuja plicata* (western redcedar) and *Tsuga heterophylla* (western hemlock)*. Those species above that also occur in the Cordilleran region are also associated with interior Douglas-fir. Its other major associates are *Abies lasiocarpa* (subalpine fir), *Larix occidentalis* (western larch), *Picea glauca* (white spruce), *Pinus contorta* (lodgepole pine), *P. ponderosa* (ponderosa pine) and *Populus tremuloides* (trembling aspen) (Franklin and Dyrness 1973; Eyre 1980; Hermann and Lavender 1990).

Coastal Douglas-fir is a major component of four forest cover types (Eyre 1980): Pacific Douglas-fir (229), Douglas-fir−Western Hemlock (230), Port Orford Cedar (231) and Pacific Ponderosa Pine−Douglas-fir (244). It is a minor component of the following ten cover types: Red Alder (221), Sitka Spruce (223), Western Hemlock (224), Western Hemlock−Sitka Spruce (225), Coastal True Fir−Hemlock (226), Western Redcedar−Western Hemlock (227), Western Redcedar (228), Redwood (232), Oregon White Oak (233) and Douglas-fir−Tanoak−Pacific Madrone (234).

Interior Douglas-fir is a principal species in three forest cover types (Eyre 1980): Interior Douglas-fir (210), Western Larch (212) and Grand Fir (213). It is a minor component in five cover types: Engelmann Spruce−Subalpine Fir (206), White Fir (211), Western White Pine (215), Aspen (217) and Lodgepole Pine (218).

The cover and composition of understory vegetation within forest cover types vary depending on site (climate and soil), associated tree species, stand developmental stage, and stand density. Relative to other tree species, light interception by the canopy of Douglas-fir is intermediate, thus providing light conditions for the development of diverse understory vegetation.

Plantations of Douglas-fir in Europe, Argentina, Chile and New Zealand have been sources of natural reproduction for the naturalisation of Douglas-fir (MacLaren 1996; Knoerzer 1999; Ledgard and Langer 1999; Simberloff *et al*. 2003; Brocano *et al*. 2005). The rapid growth that has made Douglas-fir an exotic species of economic value with plantations in many areas may, in some cases, result in ecological problems as it can out-compete native species and potentially become invasive. There is some concern that conversion of native hardwood or grassland ecosystems to Douglas-fir dominated forests may result in changes in species composition, including insect communities, and soil acidity, fertility or nitrification (Alfredsson *et al*. 1998; Knoerzer 1999; Knoerzer and Reif 2001; Gossner and Simon 2002).

6.3. Stand dynamics

Periodic recurrence of major wildfire events has sometimes created large, rather pure stands of Douglas-fir, more so in the Pacific region than the Cordilleran region (*e.g.* Winter *et al*. 2002a, 2002b; Briles *et al*. 2005; Brunelle *et al*. 2005). The species' rapid growth and longevity, with thick corky bark of lower boles and main roots of older trees (*cf.* Kuiper and Coutts 1992; McConnon *et al*. 2004), and epicormic branching (Ishii and Ford 2001) are main adaptations that have enabled Douglas-fir to remain a dominant element in Pacific Northwest forests. Without major fire or other severe disturbance, Douglas-fir would gradually be replaced throughout much of this range by more shade-tolerant conifers. Although harvesting has reduced the area of the original old-growth forest, clearcutting with slash

burning followed by natural regeneration and/or planting has helped maintain Douglas-fir as the major component in second-growth stands. Where regeneration has been only partially successful or failed, *Pinus contorta*, broad-leaved trees or shade-tolerant conifers have become associates of Douglas-fir or replaced it altogether (Hermann and Lavender 1990). On the other hand, the historically recent lack of landscape-scale fire in some other areas of the western United States is causing encroachment of Douglas-fir into grasslands (Arno and Gruell 1986; Barnhart *et al*. 1996; Kennedy and Diaz 2005).

In Mexico, *Pseudotsuga* is a minor component in mixed-pine and *Abies* forests (*e.g.* Acevedo-Rodríguez 1998; Aguirre-Calderón *et al*. 2003; Domínguez-Álvarez *et al*. 2004). For example, it occurs in the Sierra Madre Oriental in *Abies vejarii* forests, and in Central Mexico with *A. religiosa*, and it is also found in association with *Pinus ayacahuite* and *P. hartwegii*.

The variation in shade tolerance of Douglas-fir from intolerant to moderately tolerant (Krajina 1965, 1969; Klinka *et al*. 1990; Carter and Klinka 1992a) is reflected in stand dynamics. In wetter and cooler climates (predominantly in the Pacific region, except on very dry sites in the rain shadow of the Olympic Mountains and southwestern Oregon and northern California), shade-intolerant Douglas-fir can be a minor or major but persistent seral species. Over several hundred years in the absence of stand-destroying events, it is replaced by shade-tolerant *Abies amabilis*, *Thuja plicata* and/or *Tsuga heterophylla* (Franklin and Dyrness 1973; Hermann and Lavender 1990). In drier and warmer climates (predominantly in the Cordilleran region, except the interior wet belt), moderately shade-tolerant Douglas-fir is a minor or major climax species: it is self-perpetuating under its own canopy. It replaces species such as *Pinus ponderosa*, *P. contorta* and *Larix occidentalis*. However, in the interior wet belt it functions as a minor or major seral species and is gradually replaced by shade-tolerant *Abies grandis*, *A. lasiocarpa*, *Picea engelmannii*, *Thuja plicata* and/or *Tsuga heterophylla* (Daubenmire 1943; Krajina 1969; Alexander 1988).

6.4. Damaging agents

Throughout life Douglas-fir is subject to damage from a variety of agents. It is host to hundreds of fungi, but relatively few cause serious damage. Over sixty species of insects attack Douglas-fir cones, but only a few result in significant damage to seed crops. Seed and cone insects include *Contarinia oregonensis* (Douglas-fir cone gall midge) and *C. washingtonensis* (Douglas-fir cone scale midge) (Diptera: Cecidomyiidae); *Leptoglossus occidentalis* (western conifer seed bug) (Hemiptera: Coreidae); *Megastigmus spermotrophus* (Douglas-fir seed chalcid) (Hymenoptera: Torymidae) (von Aderkas *et al*. 2005b); *Eupithecia spermaphaga* (fir cone looper) (Lepidoptera: Geometridae); *Dioryctria abietivorella*, *D. pseudotsugella* and *D. reniculelloides* (coneworms) (Lepidoptera: Pyralidae); *Barbara colfaxiana* (Douglas-fir cone moth) (Lepidoptera: Yponomeutidae); and *Frankliniella occidentalis* (western flower thrip) (Thysanoptera: Thripidae) (Hedlin *et al*. 1980). The damage by insects is frequently more pronounced during the years of light or moderate seed crops that follow mast crops (Furniss and Carolin 1977).

Various species of *Pythium* and *Rhizoctonia* (Peronosporales: Pythiaceae) and *Phytophthora*, *Fusarium* and *Botrytis* (Incertae sedis) fungi may cause significant seedling mortality in nurseries (Peterson and Smith 1975; Sutherland and van Eerden 1980). The root rots *Rhizina undulata* (Pezizales: Rhizinaceae), *Armillaria ostoyae* (Agaricales: Marasmiaceae) and *Phellinus weirii* (Hymenochaetales: Hymenochaetaceae) cause significant damage in plantations. The latter two fungi represent a serious threat to the management of young stands — trees either die or are weakened and blown over. The only effective control measures include removing infected stumps and introducing non-host species, and preclude continuous crop rotations of Douglas-fir. Many heart-rot fungi infect Douglas-fir; of these the most damaging and widespread is *Phellinus pini*, but *Phaeolus schweinitzii* (Polyporales: Polyporaceae) also causes serious problems. The main entry points for infection are knots and scars caused by fire, lightning and falling trees. Losses from heart rots far exceed those from any other type of decay

(Hermann and Lavender 1990). Other fungi found predominantly on dead wood of Douglas-fir include *Fomitopsis cajanderi* and *F. pinicola* (Polyporales: Fomitopsidaceae) (Hepting 1971).

Among needle diseases the most conspicuous is needle cast caused by *Rhabdocline pseudotsugae* (Heliotiales: Hemiphacidiaceae). It mainly affects younger trees, and typically only causes substantial damage after prolonged periods of rain while new needles are emerging. *Phaeocryptopus gaeumannii* (Pleosporales: Venturiaceae) needle blight is a serious problem in off-site plantations, especially in southern coastal Oregon. Serious stem deformities in the dry southern interior are caused by the dwarf mistletoe *Arceuthobium douglasii* (Santalales: Viscaceae), which occurs throughout most of the range of Douglas-fir (Hawksworth and Wiens 1996).

On interior Douglas-fir the most damaging instects are *Orgyia pseudotsugata* (Douglas-fir tussock moth) (Lepidoptera: Lymantriidae) and *Choristoneura fumiferana* (western spruce budworm) (Lepidoptera: Tortricidae). Both of these insects can attack trees of all ages at recurrent intervals (*e.g.* Campbell *et al*. 2005), and often result in severe defoliation. *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae) is a destructive bark beetle in old-growth stands of both coastal and interior Douglas-fir, but its impact is declining with the conversion to second-growth management and rotations of less than 100 years (Furniss and Carolin 1977).

Consumption of Douglas-fir seeds by small mammals and birds further impacts the quantity of seed available for regeneration. As most seedfall occurs at least 150 days before the germination period, the rodent *Peromyscus maniculatus* (deer mouse), can consume a great majority of the seed on the ground (Hermann and Lavender 1990). Browsing and clipping of seedlings and saplings by *Lepus americanus* (snowshoe hare), *L. townsendii* (jackrabbit), *Aplodontia rufa* (mountain beaver) and *Thomomys talpoides* (pocket gopher) often cause injury. *Odocoileus* spp. (deer) and *Cervus elaphus* (elk or wapiti) can also injure young trees (Black *et al*. 1979). In the Cordilleran region, domestic livestock can damage seedlings considerably through trampling and browsing.

High winds occasionally cause extensive blowdown of coastal Douglas-fir in the Pacific Northwest, particularly when following heavy rain. Scattered breakage of tree tops in dense, young stands can result from heavy snow and ice storms. Seedlings are vulnerable to both late spring and early fall frost events (Timmis *et al*. 1994). Interior Douglas-fir is less cold hardy than most sympatric conifers. Cold injury can be a concern with exotic plantations, for example in Europe and New Zealand (Hermann and Lavender 1999). In North America, crown fires can destroy stands of all ages; however, older Douglas-fir trees with thick bark are resistant to ground fires (Hermann and Lavender 1990).

7. Forestry practices

7.1. Deployment of reforestation materials

Douglas-fir is one of the most commonly regenerated trees in western North America, with the area planted now surpassing that regenerated naturally. Douglas-fir is grown in monospecific stands or mixed-species stands with shade-tolerant or shade-intolerant species. Depending on site and management objectives, clearcutting, seed-tree, shelterwood, and selection reproduction cuttings are effective silvicultural systems for its establishment and growth (Burns 1983). Propagation by seed is the primary method for regenerating the species. An overview of techniques for collection, processing, testing and storage of seed is in Stein and Owston (2002). Bare-root seedlings are predominantly used for artificial regeneration in the United States, and containerised seedlings in Canada. Most seed used for reforestation of coastal Douglas-fir comes from seed orchards. Interior Douglas-fir is largely regenerated by planting seedlings grown from wild-collected seed or is regenerated naturally, although young seed orchards will be providing more seed for the northern portion of the range (FGCBC 2001). Detailed information for pollen management is provided by Webber and Painter (1996).

Pseudotsuga menziesii has been a major component of western North American forests since the mid-Pleistocene (Hermann 1985). The known fossil record indicates that the species' native range did not extend beyond western North America, although *Pseudotsuga* fossils have been found in Alaska, Beringia and East Asia (Bartlein *et al*. 1998; Schorn and Thompson 1998). The arrival of David Douglas at Fort Vancouver (Washington State, USA) in April 1825 to collect seeds and plants for the Horticultural Society of London marked the beginning of the introduction of many North American species into Europe. He sent home many seeds and specimens, including Douglas-fir. Of all the North American species introduced into Europe, none has become more important (Hermann 1987; de Champs 1997). Plantations exist in many European countries ranging from Portugal to Russia, and Italy to Finland. The countries with the largest area of Douglas-fir plantations are France, where it is predicted to cover about 500,000 ha by 2010-2020, and Germany and Great Britain, where stands currently occupy about 80,000 ha and 50,000 ha, respectively. In the last 100 years Douglas-fir has been successfully introduced into many regions of the world's temperate forest zones, where it is grown in forests, arboreta and parks (Hermann 1987; Hermann and Lavender 1999).

7.2. Provenance transfer

The early introductions of Douglas-fir to Europe originated from coastal (*Pseudotsuga menziesii* var. *menziesii*) provenances, whereas some later seed imports from more interior regions (likely *P. menziesii* var. *glauca*) produced less successful plantations (Kleinschmit and Bastien 1992). Field provenance trials were first established in 1912 in Germany (Stimm and Dong 2001), and in 1913 in the Pacific Northwest (Munger and Morris 1936; Irgens-Möller 1968; Ching and Hermann 1977). Subsequently provenance trials were established in locations including Europe (Göhre 1958), New Zealand (Sweet 1964), Michigan (Steiner 1979), California (Griffin and Ching 1977), the Pacific Northwest (Ching and Bever 1960; Ching 1965; Rowe and Ching 1973; White and Ching 1985) and British Columbia (Haddock *et al*. 1967). The early literature on provenance variation was compiled by Hermann and Ching (1975). The early trials generally included relatively few provenances planted on relatively few sites, but still showed strong differentiation between the coastal and interior varieties in growth rate, frost hardiness, drought resistance and resistance to needle cast diseases (including *Rhabdocline pseudotsugae* and *Phaeocryptopus gaeumannii*) (Kleinschmit and Bastien 1992), which indicated the need for controlled seed transfer. Seed zones and seed transfer guidelines are designed to promote the utilisation of local, well-adapted and productive seedlots for reforestation by limiting movement of seed from the place of collection to the site for reforestation. Seed zones usually require that seedlots are collected and used within the same defined geographic area and elevational range, whereas seed transfer rules limit movement to some maximum latitudinal, longitudinal and elevational distance. For use as an exotic for reforestation or afforestation, seed transfer regulations define the area within the native range from which seed can be obtained.

In 1966 the International Union of Forest Research Organizations (IUFRO) initiated a systematic rangewide collection of 182 provenances of Douglas-fir, with seed distributed to 59 organisations in 36 countries to develop seed transfer rules for Europe (Kleinschmit and Bastien 1992). Provenance trials established from this collection varied in experimental design, number of provenances, and year planted, but have generated a wealth of information on optimal seed sources for use as an exotic (*e.g.* Breidenstein *et al*. 1990; Kleinschmit and Bastien 1992; Beran 1995; Kleinschmit *et al*. 1995; Kranenborg and de Vries 1995; Orlić and Ocvirek 1995; Vega *et al*. 1995). The results of these trials (summarised in Section IV. Genetics) have been used to develop seed transfer rules for European countries based on North American seed zones, to ensure that plantations are established from well-adapted, productive provenances (Kleinschmit and Bastien 1992). There is also considerable within-provenance variation for breeding programs to utilise, indicating that productive landraces can be developed from a range of provenances. Potential seed-collection areas for European forestry were defined following the IUFRO provenance trial (Fletcher *et al*. 1981; Fletcher and Bastien 1988, 1989 –

cited in Kleinschmit and Bastien 1992). The emphasis of Douglas-fir programs in western Europe has shifted from provenance selection to breeding programs using select genotypes from a range of appropriate sources.

Seed zones and seed-transfer guidelines for Douglas-fir within its native range are among the most conservative for western North American conifers. The guidelines are based in part on the relatively fine-scale geographic variation observed in seedling genecological trials (Rehfeldt 1974; Campbell 1979; Rehfeldt 1979a, 1979b; Campbell 1986). Field provenance trials have not shown the degree of local adaptation or the steepness of genetic clines that these seedling experiments have displayed. It is not clear if the differences in results between nursery and field trials are due to tree age, test environment, sampling issues, or experimental design problems (White and Ching 1985).

In coastal Oregon and Washington State, seed zones have recently been expanded slightly (Randall 1996; Randall and Berrang 2002). Douglas-fir still has more seed zones, and narrower elevational bands within zones (150 to 600 m), than other sympatric conifers in this region. In British Columbia, the seed planning zones are generally larger than in USA, and they are larger in the coastal region than the interior region. The maximum permitted distances for seed transfers of wild-stand seedlots of coastal Douglas-fir for reforestation within seed planning zones in British Columbia are up to 3° latitude to the north, up to 2° latitude to the south, within long (north to south) and narrow (east to west) seed planning zones, and 350 m up or down in elevation (BCMF 1995). Comparable maximum transfers for interior Douglas-fir within seed planning zones are 2° latitude north and 1° south, 3° longitude west and 2° east, and 200 m up in elevation and 100 m down.

7.3. Breeding programs

Breeding programs for coastal Douglas-fir are among the oldest and are the largest in the Pacific Northwest, with large numbers of progeny tests and seed orchards (Adams *et al*. 1990). Like seed zones, breeding zones for coastal Douglas-fir are generally long north-south and narrower east-west, reflecting coastal climatic gradients. The appropriate geographic size of breeding zones for coastal Douglas-fir has been controversial, due to the conflicting provenance and genecological test results described above. Some programs, such as the Pacific Northwest Tree Improvement Cooperative program, started with many small breeding zones based on the fine-scaled geographic variation observed in provenance trials and seedling genecological studies (Silen and Wheat 1979), and reinforced by quantification of substantial genotype-by-environment interaction in progeny trials (Campbell 1992). Other programs have delineated much larger breeding zones based on a lack of genotype-by-environment interaction in the field growth of highly ranked families and a lack of correspondence between genotype-by-environment interaction and variation in physical environments between test sites (Stonecypher *et al*. 1996; Johnson 1997).

Early breeding programs focused on obtaining genetic gain through intensive phenotypic selection in wild stands. This resulted in gains of a few percent for juvenile growth (Stonecypher *et al*. 1996). Subsequent progeny testing and selection resulted in gains of around 10% for growth rate in the first generation. Some breeding programs used open-pollinated progeny trials, whereas others had progeny testing of extensive partial diallel matings. In the latter, the amount of non-additive genetic variation for traits of interest was found to be about half that of additive genetic variation (Stonecypher *et al*. 1996), although this varies greatly among sets of genotypes (Yanchuk 1996). Thus, programs focus primarily on utilising additive variation. As cloning technology improves (*e.g.* somatic embryogenesis), interest may increase in capturing some non-additive variation through deployment of clones in some situations.

The objectives for these selective breeding programs are to increase volume growth while maintaining quality traits including stem form, wood density and branch diameter. In western Europe, increasing spring cold hardiness through delaying bud burst is also of interest (*e.g,.* Heois 1994). Most programs are currently in the second generation of breeding and testing. Selection for faster growth

can lead to a greater frequency of lammas growth on highly productive sites, and this can produce forking and ramicorn branching defects (Adams and Bastien 1994; Schermann *et al*. 1997), so lammas growth is selected against in some programs. Some breeding lines within multiple-population breeding programs focus on increasing wood density. Stem volume and wood density are moderately negatively genetically correlated, so simultaneous improvement of these traits is difficult. Breeding efforts for interior Douglas-fir in British Columbia, Idaho and Montana are more recent and smaller in scale than their coastal counterparts, but also focus on increasing wood volume, with wood density as a secondary consideration (FGCBC 2001). Cooperative European breeding efforts have arisen from the IUFRO provenance trial among France, Belgium, Spain and Germany, with a base population of 10 provenances and 50 open-pollinated progeny from each (Kleinschmit and Bastien 1992).

Estimates of the optimum age for genetic selection for increased growth rate have ranged from 4 years in highly cultivated, intensive farm field tests up to 7 to 18 years in some field trials (Magnussen and Yanchuk 1994; Woods *et al*. 1995; Johnson *et al*. 1998). Seedlings 1 or 2 years of age can be used to identify the poorest families and cull genotypes prior to establishing progeny trials, but the best families cannot be identified in early tests (Adams *et al*. 2001). Final selections have typically been made in field trials at 12 to 15 years. Spacing of trees or testing genotypes in mixtures *versus* pure blocks does not significantly affect estimation of genetic parameters or genotype rankings (St. Clair and Adams 1991; El-Kassaby and Park 1993).

7.4. Conservation of genetic resources

The inherently high genetic diversity of Douglas-fir, both within and among populations, is being conserved both *in situ* in natural parks, ecological reserves and other protected areas across most of the species' range, and *ex situ* in seed orchards, breeding archives and genetic field tests. Geographic information system-based spatial analyses of the adequacy of *in situ* protection of Douglas-fir in parks have recently been conducted in British Columbia, Washington and Oregon, and its ecological envelope has also been modelled in relation to protected areas (Coulston and Riitters 2005). In British Columbia, *in situ* protection was analyzed for each of twelve Seed Planning Units (SPUs) used for managing seed transfer and breeding programs (Hamann *et al*. 2004). Only protected areas over 250 ha with at least 5000 mature-equivalent individuals were considered adequate reserves. The number of protected areas meeting these criteria in each SPU ranged from two to sixty. Nearly all of the SPUs appeared to have sufficient conservation populations, with the Cariboo Transition SPU near the northern edge of the *Pseudotsuga menziesii* var. *glauca* range being the only area judged to need field verification of adequacy of protection.

In Washington and Oregon, the analyses were conducted based on both seed zones and ecoregions. The conservation threshold set was that at least 5000 reproductively mature individuals be protected in parks and ecological reserves in each spatial unit (Lipow *et al*. 2004). Of 204 seed zone-by-elevation bands in Washington and western Oregon, 198 were well protected. The primary *in situ* conservation gap was in the Puget Lowlands of western Washington State (Lipow *et al*. 2004; Coulston and Riitters 2005), an area of high forest productivity. Fortunately genotypes from this region are well represented in *ex situ* collections (Lipow *et al*. 2004). Provenances from the region are well represented and important in breeding populations in western Europe (Kleinshmidt and Bastien 1992). In eastern Oregon, 14 of 18 breeding zone-by-elevation bands were also considered well protected; conservation gaps were identified in the Fort Rock and Chiloquin breeding zones, but unprotected stands of Douglas-fir in these mid-southern areas were considered unlikely to be harvested. Additional protected areas were considered desirable for the species in northwestern California (Coulston and Riitters 2005), and greater protection for populations in Mexico (Vargas-Hernández *et al*. 2004).

In addition to *in situ* conservation reserves and extensive *ex situ* resources in seed banks, provenance and progeny trials, and breeding populations within the native range, there are considerable *ex situ*

collections of Douglas-fir in both North America and Europe. In France, Germany and Belgium, over 1000 ha of *ex situ* gene conservation plantations have been established from provenances of interest in USA (Kleinschmidt and Bastien 1992). The widespread use of relatively local seed and breeding zones to control the movement of seed for reforestation within the native range also maintains adaptation and geographic variation in reforested areas.

Many studies have evaluated genetic diversity of Douglas-fir resulting from forest management practices, and generally have found little change relative to wild populations. Alternative regeneration methods have been compared, including shelterwood systems, group selection and clearcutting followed by natural regeneration or planting (Adams *et al*. 1998). In general, harvesting and regeneration methods had little effect on genetic diversity, although harvesting from below (removing smaller trees) in the shelterwood method resulted in removal of some rare, possibly deleterious alleles. Similarly, the silvicultural system had little effect on the mating system (Neale and Adams 1985). First-generation and second-generation domesticated populations of coastal Douglas-fir in British Columbia and Washington have similar or higher levels of genetic diversity than wild populations, although second-generation populations differ slightly for some allele frequencies from wild populations (El-Kassaby and Ritland 1996a, 1996b). It has been suggested that slightly higher levels of genetic diversity would be maintained through nursery production of seedlings if single seeds were sown from bulked seedlots or if individual families were managed separately (El-Kassaby and Thomson 1996).

8. Summary

Douglas-fir is one of the most important and valuable timber species globally. Its wood is moderately heavy and hard, and exceptionally strong. It is a source of wood for both lumber and pulp, and used for structural purposes, in shipbuilding, and in the production of items such as laminated beams and interior and exterior finishing, boxes, railway ties, and when impregnated with a preservative, in piling and decking for marine structures. Douglas-fir is also grown for seasonal Christmas trees, and as an ornamental.

Across its native range in western North America, Douglas-fir is a long-lived and ecologically important species. It is a seral species in wet and cool climates, and a fire-adapted climax species in dry and warm climates. Because of its rapid growth rate, it produces a higher volume of wood sooner than many of its associates, and is valuable as an exotic plantation species in many temperate regions. It has moderate nutrient requirements and is easy to regenerate and grow. The ecology of Douglas-fir is diverse, in keeping with its large geographical distribution. It may grow in pure, single-storied, even-aged stands as well as in multi-aged and multi-storied stands. It is associated with many softwood and hardwood species in diverse ecosystems throughout a considerable range of climatic zones. Douglas-fir is also a major tree species in critical watersheds and in many scenic and recreational areas. It is a component of a very large area of wildlife habitat, and is widely associated with grazing and range allotments.

Douglas-fir has very high levels of genetic diversity, and this variation represents an important resource. Genetic clines are strong, related primarily to environmental gradients in temperature, but also to moisture. There is a lack of consensus on how narrowly populations are adapted, and thus at what geographic scale they should be managed. Genetic diversity in this species is fairly well protected in most regions, both *in situ* and *ex situ*, and potential conservation gaps in the northernmost and northwestern portions of the range have been assessed. Breeding programs, particularly for the coastal variety, are large and well into the second generation of domestication. Selective breeding is increasing growth rate while maintaining the stem form and wood quality that make this such a desirable timber species. New cloning technologies, primarily somatic embryogenesis, allow for consideration of clonal strategies for improving this species.

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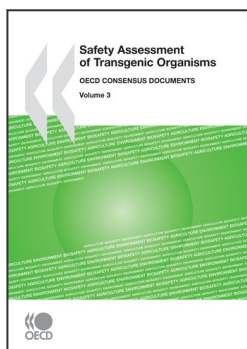
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