Pseudotsuga menziesii (Mirb.) Franco — Douglas-Fir

Pinaceae — Pine family

Richard K. Hermann and Denis P. Lavender

Douglas-fir ***(Pseudotsuga menziesii),*** also called red-fir, Oregon-pine, Douglas-spruce, and piño Oregon (Spanish), is one of the world's most important and valuable timber trees. It has been a major component of the forests of western North America since the mid-Pleistocene *(30).* Although the fossil record indicates that the native range of Douglas-fir has never extended beyond western North America, the species has been successfully introduced in the last 100 years into many regions of the temperate forest zone *(31).* Two varieties of the species are recognized: ***P. menziesii*** **(Mirb.) Franco** var. ***menziesii,*** called coast Douglas-fir, and ***l? menziesii*** var. ***glauca*** (Beissn.) Franco, called Rocky Mountain or blue Douglas-fir.

Habitat

Native Range

The latitudinal range of Douglas-fir (fig. 1) is the greatest of any commercial conifer of western North America. Its native range, extending from latitude 19” to 55” N., resembles an inverted V with uneven sides. From the apex in central British Columbia, the shorter arm extends south along the Pacific Coast Ranges for about 2200 km (1,367 mi) to latitude 34” 44'N., representing the range of the typical coastal or green variety, ***menziesii;*** the longer arm stretches along the Rocky Mountains into the mountains of central Mexico over a distance of nearly 4500 km (2,796 mi), comprising the range of the other recognized variety, *glauca*—Rocky Mountain or blue. Nearly pure stands of Douglas-fir continue south from their northern limit on Vancouver Island through western Washington, Oregon, and the Klamath and Coast Ranges of northern California as far as the Santa Cruz Mountains. In the Sierra Nevada, Douglas-fir is a common part of the mixed conifer forest as far south as the Yosemite region. The range of Douglas-fir is fairly continuous through northern Idaho, western Montana, and northwestern Wyoming. Several outliers are present in Alberta and the eastern-central parts of Montana and Wyoming, the largest being in the Bighorn Mountains of Wyoming. In northeastern Oregon, and from southern Idaho south through the mountains of Utah, Nevada, Colorado, New Mexico, Arizona, extreme western Texas, and northern Mexico, the distribution becomes discontinuous (fig. 1).

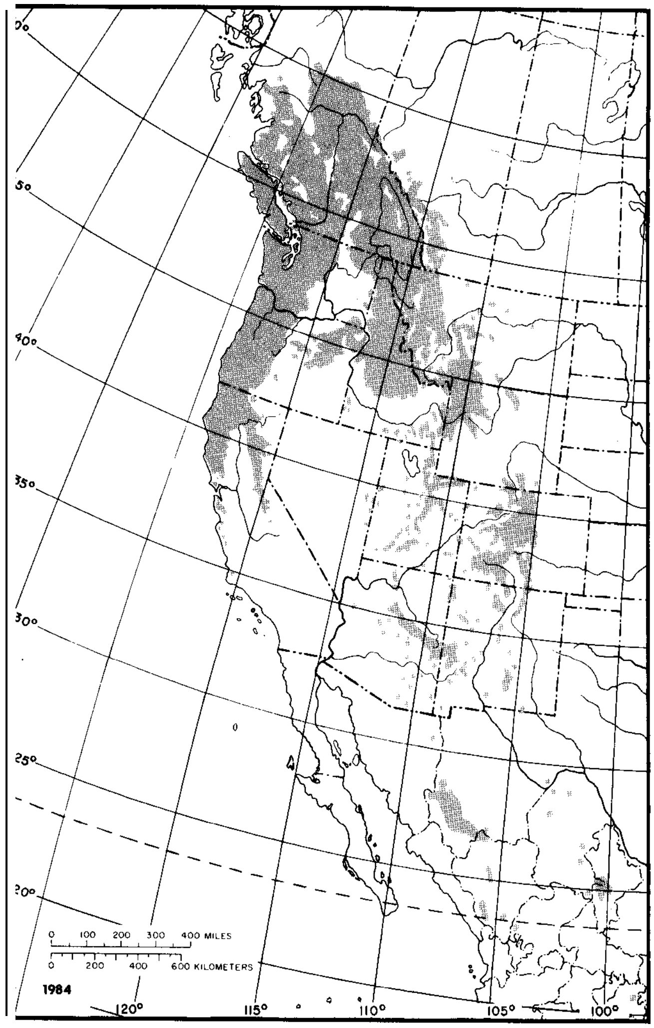

Figure 1-The native range of Douglas-fir.

Climate

Douglas-fir grows under a wide variety of climatic conditions (table 1). The coastal region of the Pacific Northwest has a maritime climate characterized by mild, wet winters and cool, relatively dry summers, a long frost-free season, and narrow diurnal fluctuations of temperature (6” to 8° C; 43” to 46” F).

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Table 1-Climatic data for five regional subdivisions of the range of Douglas-fir *(6,62)*

Region	Mean temperature		Frost-free period	Mean precipitation	
	July	January		Annual	Snow fall
	°C	°C	days	mm	cm
Pacific Northwest					
Coastal	20 to 27	-2 to 3	195 to 260	760 to 3400	0 to 60
Cascades and Sierra Nevada	22 to 30	-9 to 3	80 to 180	610 to 3050	10 to 300
Rocky Mountains					
Northern	14 to 20	-7 to 3	60 to 120	560 to 1020	40 to 580
Central	14 to 21	-9 to -6	65 to 130	360 to 610	50 to 460
Southern	7to 11	0 to 2	50 to 110	410 to 760	180 to 300
	°F	°F	days	in	in
Pacific Northwest					
Coastal	68 to 81	28 to 37	195 to 260	34 to 134	0 to 24
Cascades and Sierra Nevada	72 to 86	15 to 28	80 to 180	24 to 120	4 to 120
Rocky Mountains					
Northern	57 to 68	19 to 28	60 to 120	22 to 40	16 to 230
Central	57 to 70	16 to 22	65 to 130	14 to 24	20 to 180
Southern	45 to 52	32 to 36	50 to 110	16 to 30	70 to 120

Precipitation, mostly as rain, is concentrated in the winter months. Climate in the Cascade Range and Sierra Nevada tends to be more severe.

Altitude has a significant effect on local climate. In general, temperature decreases and precipitation increases with increasing elevation on both western and eastern slopes of the mountains. Winters are colder, frost-free seasons are shorter, and diurnal fluctuations of temperature are larger (10° to 16" C; 50" to 61" F). Much of the precipitation is snow. In the northern Rocky Mountains, Douglas-fir grows in a climate with a marked maritime influence. Mild continental climate prevails in all seasons, except midsummer. Precipitation is evenly distributed throughout the year, except for a dry period in July and August. In the central Rocky Mountains, the climate is continental. Winters are long and severe; summers are hot and in some parts of the region, very dry. Annual precipitation, higher on the western sides of the mountains, is mainly snow. Rainfall patterns for the southern Rocky Mountains generally show low winter precipitation east of the Continental Divide but high precipitation during the growing season. West of the Continental Divide, the rainfall is more evenly divided between winter and summer. Frost may occur in any month in the northern part of the range. Length of frost-free periods, however, varies within the central and southern Rocky Mountain regions, even at the same elevations.

Soils and Topography

The variety *menziesii* of Douglas-fir reaches its best growth on well-aerated, deep soils with a pH range from 5 to 6 (fig. 2). It will not thrive on poorly drained or compacted soils. Soils in the coastal belt of northern California, Oregon, and Washington originated chiefly from marine sandstones and shales with scattered igneous intrusions. These rocks have weathered deeply to fine-textured, well-drained soils under the mild, humid climate of the coast. Surface soils are generally acid, high in organic matter and total nitrogen, and low in base saturation. Soils in the Puget Sound area and in southwestern British Columbia are almost entirely of glacial origin. Soils farther inland within the range of the variety *menziesii* are derived from a wide variety of parent materials. These include metamorphosed sedimentary material in the northern Cascades and igneous rocks and formations of volcanic origin in the southern Cascades.

Depth of soils ranges from very shallow on steep slopes and ridgetops to deep in deposits of volcanic origin and residual and colluvial materials. Texture varies from gravelly sands to clays. Surface soils are in general moderately acid. Their organic matter content varies from moderate in the Cascade Range to high in portions of the Coast Range and Olympic Peninsula. Total nitrogen content varies considerably but is usually low in soils of glacial origin. Great soil

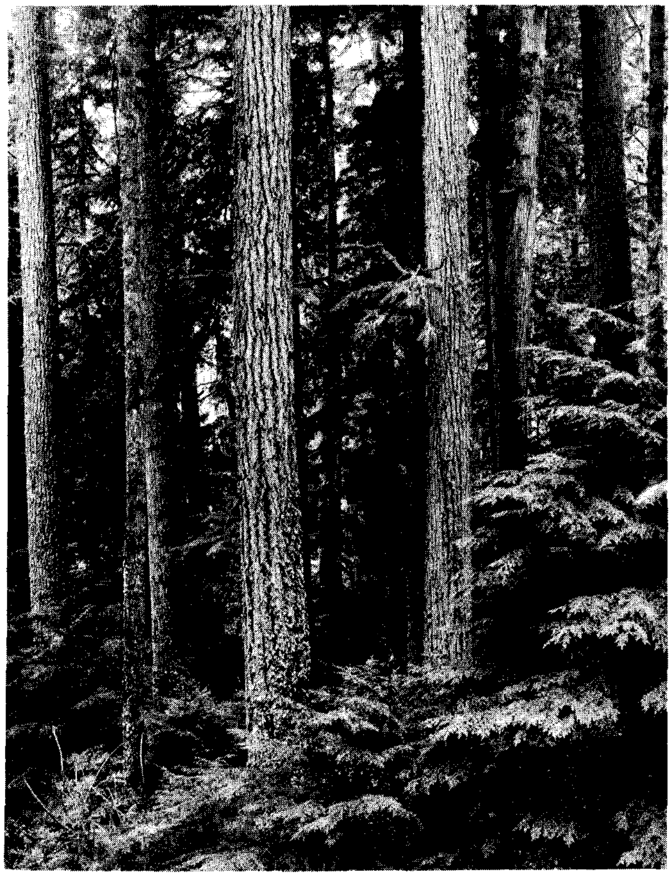

Figure 2—*Dense stand of* **Douglas-fir,** *nearly pure, in Pierce County, WA.*

groups characteristic of the range of coastal Douglas-fir include Haplohumults (Reddish Brown Lateritics) of the order Ultisols, Dystrochrepts (Brown Lateritics), Haplumbrepts (Sols Brims Acides) of the order Inceptisols, Haplorthods (Western Brown Forest soils) of the order Spodosols, Xerumbrepts (Brown Podzolic soils), and Vitrandepts (Regosols) *(63).*

Soils within the range of Rocky Mountain Douglas-fir originated also from a considerable array of parent materials. In south-central British Columbia, eastern Washington, and northern Idaho, soils vary from basaltic talus to deep loess with volcanic ash to thin residual soil over granitic or sedimentary rocks. They are mostly Vitrandepts and Xerochrepts. Parent materials in Montana and Wyoming consist of both igneous and sedimentary rocks, and locally of glacial moraines. Soils derived from noncalcareous substrates are variable in texture but consistently gravelly and acidic. A significant portion of the sedimentary rocks is limestone, which gives rise to neutral or alkaline soils ranging in texture from gravelly loams to gravelly silts. Limestones often weather into soils that are excessively well drained. Soils are Cryoboralfs of the order Alfisols, and Cryandepts and Cryochrepts of the order Inceptisols. Soils in the central and southern Rocky Mountains are very complex. They developed from glacial deposits, crystalline granitic rocks, conglomerates, sandstones, and, in the Southwest, limestones. These soils are Alfisols (Gray Wooded soils), Mollisols (Brown Forest soils), Spodosols (Brown Podzolic soils, Podzols), and Entisols *(2,46).*

Altitudinal distribution of both varieties of Douglas-fir *(menziesii* and *glauca)* increases from north to south, reflecting the effect of climate on distribution of the species. The principal limiting factors are temperature in the north of the range and moisture in the south. Consequently, Douglas-fir is found mainly on southerly slopes in the northern part of its range, and on northerly exposures in the southern part. At high elevations in the southern Rocky Mountains, however, Douglas-fir grows on the sunny slopes and dry rock exposures (56).

Generally, the variety *glauca (fig. 3) grows* at considerably higher altitudes than the coastal variety of comparable latitude. Altitudinal limit for Douglas-fir in central British Columbia is about 760 m (2,500 ft) but rises to 1250 m (4,100 ft) on Vancouver Island. In Washington and Oregon, the species generally occurs from sea level to 1520 m (5,000 ft), although locally it may occur higher. In the southern Oregon Cascades and in the Sierra Nevada, the altitudinal range is between 610 and 1830 m (2,000 and 6,000 ft). In river valleys and canyon bottoms, the species may occasionally occur at elevations of 240 to 270 m (800 to 900 ft). Near the southern limit of its range in the Sierra Nevada, the species grows to elevations of 2300 m (7,500 ft). The inland variety grows at elevations from 550 to 2440 m (1,800 to 8,000 ft) in the northern part of its range. In the central Rocky Mountains, Douglas-fir grows mostly at elevations between 1830 and 2590 m (6,000 and 8,000 ft), and in the southern Rocky Mountains, between 2440 and 2900 m (8,000 and 9,500 ft). In some localities in southern and central Arizona, Douglas-fir may be found as low as 1550 m (5,100 ft) in canyon bottoms. The highest elevation at which Douglas-fir grows in the Rocky Mountains is 3260 m (10,700 ft) on the crest of Mount Graham in southeastern Arizona.

Associated Forest Cover

Periodic recurrence of catastrophic wildfires created vast, almost pure stands of coastal Douglas-fir throughout its range north of the Umpqua River in Oregon, Although logging has mainly eliminated

Figure *3-A good stand of second-growth Rocky Mountain* Douglas-fir *covering the hillside behind a mature tree.*

the original old-growth forest, clear-cutting combined with slash burning has helped maintain Douglas-fir as the major component in second-growth stands. Where regeneration of Douglas-fir was only partially successful or failed, red alder *(Alnus rubra)* has become an associate of Douglas-fir or has replaced it altogether.

Rocky Mountain Douglas-fir grows in extensive pure stands, uneven- and even-aged, in southern Idaho and northern Utah and in western Montana as a broad belt between ponderosa pine and spruce–fir zones. At high elevations or northerly latitudes, more cold-tolerant mountain hemlock *(Tsuga mertensiana)*, whitebark pine *(Pinus albicaulis)*, true firs *(Abies* spp.), Engelmann spruce *(Picea engelmannii)*, western white pine *(Pinus monticola)*, and lodgepole pine *(Pinus contorta)* gradually replace Douglas-fir. Douglas-fir yields to ponderosa pine *(P. ponderosa)*, incense-cedar *(Libocedrus decurrens)*, Oregon white oak *(Quercus garryana)*, California black oak *(Q. kelloggii)*, canyon live oak *(Q. chrysolepis)*, and interior live oak *(Q. wislizeni)* on droughty sites, and to western redcedar *(Thuja plicata)*, maples *(Acer* spp.), red alder, black cottonwood *(Populus trichocarpa)*, and other broad-leaved species on poorly drained sites.

Toward the fog belt of the Pacific coast, Douglas-fir gives way to Sitka spruce *(Picea sitchensis)*, western hemlock *(Tsuga heterophylla)*, and western redcedar. The variety *menziesii* is a major component of four forest cover types *(20)*: Pacific Douglas-Fir (Society of American Foresters Type 229), Douglas-Fir–Western Hemlock (Type 230), Port Orford-Cedar (Type 231), and Pacific Ponderosa Pine-Douglas-Fir (Type 244). It is a minor component of the following types:

221 Red Alder
223 Sitka Spruce
224 Western Hemlock
225 Western Hemlock-Sitka Spruce
226 Coastal True Fir-Hemlock
227 Western Redcedar-Western Hemlock
228 Western Redcedar
232 Redwood
233 Oregon White Oak
234 Douglas-Fir-Tanoak-Pacific Madrone

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

Wherever Douglas-fir grows in mixture with other species, the proportion may vary greatly, depending on aspect, elevation, kind of soil, and the past history of an area, especially as it relates to fire. This is particularly true of the mixed conifer stands in the southern Rocky Mountains where Douglas-fir is associated with ponderosa pine, southwestern white pine *(Pinus strobiformis),* corkbark fir *(Abies lasiocarpa* var. *arizonica),* white fir *(Abies concolor),* blue spruce *(Picea pungens),* Engelmann spruce, and aspen *(Populus* spp.).

The most important shrubs associated with coastal Douglas-fir *(21)* through its central and northern range are vine maple *(Acer circinatum),* salal *(Gaultheria shallon),* Pacific rhododendron *(Rhododendron macrophyllum),* Oregongrape *(Berberis nervosa),* red huckleberry *(Vaccinium parvifolium)*, and salmonberry *(Rubus spectabilis).* Toward the drier southern end of its range, common shrub associates are California hazel *(Corylus cornuta* var. *californica)*, oceanspray *(Holodiscus discolor),* creeping snowberry *(Symphoricarpos mollis)*, western poison-oak *(Toxicodendron diversilobum),* ceanothus *(Ceanothus* spp.), and manzanita *(Arctostaphylos* spp.).

Principal understory species associated with variety *glauca* differ within its range (3). In the northern part, they are common snowberry *(Symphoricarpos albus)*, white spirea *(Spirea betulifolia),* ninebark *(Physocarpus malvaceus),* and pachistima *(Pachistima myrsinites).* In the central part, they are true mountain-mahogany *(Cercocarpus montanus),* squaw currant *(Ribes cereum),* chokeberry *(Prunus virginiana),* big sagebrush *(Artemisia tridentata)*, western serviceberry *(Amelanchier alnifolia),* and bush rockspirea *(Holodiscus dumosus);* in the southern part they are New Mexico locust *(Robinia neomexicana),* Rocky Mountain maple *(Acer glabrum),* and oceanspray *(3).*

Life History

Reproduction and Early Growth

Flowering and Fruiting-Douglas-fir is monoecious; trees commonly begin to produce strobili at 12 to 15 years of age, although observations of younger seedlings bearing ovulate strobili have been reported.

Primordia of both pollen and seed cone buds are present when the vegetative bud breaks in the spring of the year before the cone crop. But neither can be distinguished from primordia of vegetative buds for the first 10 weeks of their existence. By mid-June, histochemical differences separate the pollen cone primordia, which are usually clustered near the base of the extending shoot, from the seed cone primordia, which are borne singly near the acropetal end of the shoot, and from the vegetative bud primordia *(5).* These three primordia may be microscopically identified in mid-July; by September, the egg-shaped pollen cone buds are easily distinguished by the naked eye from the darker vegetative buds and the larger seed cone buds.

The size of the cone crop is determined by the number of primordia that differentiate and develop into buds, not by the number formed. Poor cone crops, then, reflect a high abortion rate of primordia the preceding year. Large numbers of pollen or seed cone buds in the fall merely indicate the potential for a heavy cone crop the following year. Damaging frost during cone anthesis or depredations by insects may destroy most of the cones and seeds before they mature *(19).*

Male strobili are about 2 cm (0.8 in) long and range from yellow to deep red. Female strobili are about 3 cm (1.2 in) long and range from deep green to deep red (45). They have large trident bracts and are receptive to pollination soon after emergence.

Anthesis and pollination of variety *menziesii* occur during March and April in the warmer part of the range and as late as May or early June in the colder areas. At low and middle elevations, Douglas-fir cones mature and seeds ripen from mid-August in southern Oregon to mid-September in northern Washington and southern British Columbia. Mature cones are 8 to 10 cm (3 to 4 in) long. The bracts turn brown when seeds are mature (45). Seedfall occurs soon after cone maturity with, generally, two-thirds of the total crop on the ground by the end of October. The remaining seeds fall during winter and spring months. In British Columbia, seedfall starts later and lasts longer-less than half the seeds fall by late October and more than one-third fall after March 1. In general, Douglas-fir seedfall in the fog belt of western North America is more protracted than in the drier areas east of the summit of the Coast Ranges.

The phenology of flowering is similar for variety *glauca;* early flowering occurs in mid-April to early May in Colorado and as late as early May to late June in northern Idaho. Cone ripening varies from late July at the lower elevations (about 850 m or 2,800 ft) in Montana to mid-August in northern Idaho. Seed dispersal of *glauca* begins in mid-August in central Oregon and occurs as late as mid-September at higher elevations (about 1710 m or 5,600 ft) in Montana (45).

Seed quality varies during the seedfall period. It is high in the fall but declines rapidly during winter and spring. This pattern probably reflects the fact that cone scales in the center of the cone, where the highest quality seed are borne, open early and scales at the tip and base of the cone, which bear generally poorly formed seeds, open late.

Both cones and seeds vary greatly in size; the smaller seeds (about 132,000/kg or 60,000/lb) occur on trees in British Columbia and the larger seeds (about 51,000/kg or 23,000/lb), on trees in California. Seeds of variety *glauca* are slightly heavier and more triangular in shape than seeds of *menziesii.* Size is determined before fertilization, so there is no correlation between weight of seed and genetic vigor, although seedlings germinated from heavier seeds may be slightly larger the first few months of growth than those grown from lighter seeds. Because the range in seed size from any one tree is relatively small, however, fractionation of seed lots to segregate the heavier seed may reduce the genetic variation and actually eliminate traits from certain populations.

Douglas-fir seed crops occur at irregular intervals-one heavy and one medium crop every 7 years on the average; however, even during heavy seed years, only about 25 percent of the trees produce an appreciable number of cones (34). Trees 200 to 300 years old produce the greatest number of cones. For example, a stand of old-growth Douglas-fir may produce 20 to 30 times the number of cones per hectare that a second-growth stand 50 to 100 years old produces.

Seed Production and Dissemination-Major deterrents to natural regeneration of Douglas-fir include limited seed supply; consumption of seed by insects, animals, and birds; competing plant species; and unfavorable environments. Although reports of fully stocked stands resulting from seedfall from sources 1 to 2 km (0.6 to 1.2 mi) distant are not rare, the great majority of Douglas-fir seeds fall within 100 m (330 ft) of a seed tree or stand edge *(18).*

Data describing the quantities of seeds that may fall vary widely, but most years are characterized by less than 2.2 kg/ha (2 lb/acre), of which no more than 40 percent is sound. Years with poor seed crops generally have a lower percentage of viable seeds, perhaps because the low incidence of fruiting trees may favor a higher level of selfing (25).

Seedling Development-Douglas-fir germination is epigeal. Seed germinates in mid-March to early April in the warmer portions of the range and as late as mid-May in the cooler areas. Seedling growth the first year is indeterminate but relatively slow and limited generally by moisture, which triggers initiation of dormancy in midsummer. The dormant period normally extends from midsummer until April or May of the following year *(37).* Douglas-fir can produce lammas shoots, but this habit is confined to either the more moist portion of the range or to years with abnormally heavy summer rainfall. This habit is probably most pronounced in the southern Rockies, where the summer period is characterized by irregular, heavy rainstorms. In any event, the great majority of the annual shoot growth occurs during the initial flush. First-year seedlings on better sites in the Pacific Northwest may develop shoots 6 to 9 cm (2.5 to 3.5 in) long. Growth in subsequent years is determinate and gradually accelerates so that when saplings are 8 to 10 years old, terminal growth may consistently exceed 1 m (3.3 ft) per year on the more productive sites.

Seedlings of the variety *menziesii* normally survive best when the seed germinates on moist mineral soil, but *menziesii* will tolerate a light litter layer. Seedlings do not survive well, however, on heavy accumulations of organic debris. In contrast, seedlings of the variety *glauca* are favored by a duff layer, especially in the larch forests of northwestern Montana (53).

First-year seedlings survive and grow best under light shade, especially on southerly exposures, but older seedlings require full sunlight. Particularly in the fog belt, competing vegetation such as alder, maple, salmonberry, and thimbleberry *(Rubus parviflorus)* limits Douglas-fir regeneration by creating intolerable levels of shade; plants such as grasses, manzanita, ceanothus, and oak compete strongly for available moisture; and plants such as bracken *(Pteridium aquilinum)* and vetch *(Vicia* spp.) smother small seedlings with leaves and other debris. Successful regeneration of variety *menziesii* often depends on weed control in the commercial range of Douglas-fir because many associated plant species have growth rates much greater than that of juvenile Douglas-fir *(8).* For this reason, regeneration may be more reliable after a wildfire, which destroys the reservoir of potential competitive species, than after a harvest operation, which leaves areas well suited to the rapid proliferation of the herbaceous and woody competitors of Douglas-fir.

In the Rocky Mountains, competing vegetation may promote the establishment of variety *glauca* seedlings by reducing temperature stress and may inhibit seedling growth by competing strongly for moisture. The latter effect is most pronounced in the southern portions of *glauca's* range.

Microsites with adverse moisture and temperature conditions frequently limit establishment of both *menziesii* and *glauca* seedlings on southerly aspects (32). Soil surface temperatures in excess of 65" C (149" F) are prevalent in the southern Cascade Range and Siskiyou Mountains and are common in the Cascades even as far north as Mount Rainier. Prolonged droughts, which may extend from May through September, are frequent in southern Oregon and northern California, and low annual precipitation and high evaporation stress greatly limit the distribution of *glauca* in the Rocky Mountains.

Like nearly all perennial woody plants, Douglas-fir is dependent on a mycorrhizal relationship for efficient uptake of mineral nutrients and water. Approximately 2,000 species of fungi have been identified as potential symbionts with Douglas-fir, and both ectomycorrhizal and ectendomycorrhizal structures have been observed on this species (59). Occasionally, nursery practices result in seedlings with few mycorrhizae, but no deficiencies in mycorrhizal infection have been reported for natural seedlings.

Historically, large burned or cleared areas in the range of variety *menziesii,* such as those on Vancouver Island *(52),* have naturally seeded into nearly pure stands of Douglas-fir. On mesic to moist sites this process may occur over a relatively short period, perhaps 10 to 15 years. On drier sites, such regeneration may be quite protracted and require a hundred or more years. Stocking of harvested areas has been extremely variable during the past 30 years, and large tracts in the drier or cooler portions of the range are covered by brush species such as manzanita, ceanothus, salmonberry, salal, or lower value hardwoods, such as alder, maple, and oak.

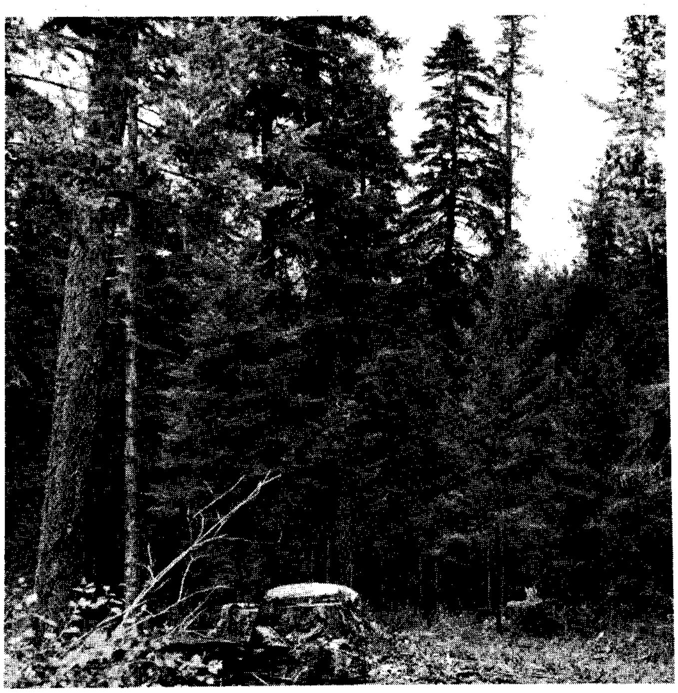

Figure *4-Thrifty young trees and good reproduction in a cutover Douglas-fir forest in New Mexico.*

Regeneration of variety *glauca* in the Rocky Mountains (fig. 4) has also been variable. In general, *glauca* may be considered a seral species in moist habitats and a climax component in the warmer, drier areas. Regeneration is favored where Douglas-fir is seral, especially in northern Idaho and western Montana where a strong maritime influence modifies the generally continental climate that prevails in the central and southerly Rocky Mountains. In contrast, regeneration of Douglas-fir is poor where the species has attained climax status (49).

From 1950 until about 1970, large areas of cutover and burned-over forest land in the Pacific Northwest were aerially seeded. Direct seeding suffers from the same deficiencies as natural regeneration, however; that is, stands produced are often uneven in stocking and require interplanting or precommercial thinning, and animals destroy a large proportion of the seeds. With the advent of greatly increased forest nursery capacity, direct seeding is much less common *(13,54).*

Vegetative Reproduction-Douglas-fir does not naturally reproduce vegetatively. Substantial research to develop cuttings as a regeneration procedure has demonstrated that 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 shearing to regenerate material with a juvenile habit. A second major impediment to the use of cuttings as a regeneration technique for this species is that most such material has a period of plagiotropic growth, which may be lengthy, before the erect habit is assumed.

Research with tissue culture techniques has demonstrated substantial promise, but widespread use of this technique in reforestation of the Douglas-fir region is, at best, a future possibility.

Sapling and Pole Stages to Maturity

Growth and Yield-Natural stands of coastal Douglas-fir normally start with more than 2,500 trees per hectare (1,000/acre). Planted stands generally have between 750 and 1,500/ha (300 and 600/acre) at the beginning (9). Annual height increment is relatively slow the first 5 years but then begins to accelerate. Coastal Douglas-fir attains the largest height increments between 20 and 30 years of age but retains the ability to maintain a fairly rapid rate of height growth over a long period. Douglas-fir in high-elevation forests of the Oregon–Washington Cascade Range can continue height growth at a substantial rate for more than 200 years

(15). Height growth of Douglas-fir on dry sites at mid-site indices in the Cascade Range of western Oregon is similar to that of upper-slope Douglas-fir in the Washington and Oregon Cascade Range. At higher site indices, however, height growth on dry sites is initially faster but slower later in life; at lower site indices, it is initially slower but faster later in life *(40).*

On a medium site (III) at low elevations, height growth, which averages 61 cm (24 in) annually at age 30, continues at a rate of 15 cm (6 in) per year at age 100, and 9 cm (3.6 in) at age 120 *(18,39).* Trees 150 to 180 cm (60 to 72 in) in diameter and 76 m (250 ft) in height are common in old-growth forests *(22).* The tallest tree on record, found near Little Rock, WA, was 100.5 m (330 ft) tall and had a diameter of 182 cm (71.6 in). Coastal Douglas-fir is very long lived; ages in excess of 500 years are not uncommon and some have exceeded 1,000 years. The oldest Douglas-fir of which there is an authentic record stood about 48 km (30 mi) east of Mount Vernon, WA. It was slightly more than 1,400 years old when cut (39).

Information about yields of coastal Douglas-fir under intensive management for an entire rotation is still limited. It is therefore necessary to rely either on estimates based on yields from unmanaged stands, or on yields from intensively managed stands in regions where Douglas-fir has been introduced as an exotic *(12)*, or on growth models *(16).* If measured in cubic volume of wood produced, range in productivity between the best and poorest sites is more than 250 percent. Depending on site quality, mean annual net increments at age 50 vary from 3.7 to 13.4 m^3/ha (53 to 191 ft^3/acre) in unmanaged stands (39). Estimates of gross yields may increase these values as much as 80 percent, depending on mensurational techniques and assumptions. Comparisons of gross yields from unmanaged stands with those from managed stands of the same site indexes in Europe and New Zealand suggest that yields in managed stands will be considerably higher than would be indicated by estimates based on yields in unmanaged stands. Presumably, managed stands of coastal Douglas-fir can produce mean annual increments of 7 m^3/ha (100 ft^3/acre) on poor sites and exceed 28 m^3/ha (400 ft^3/acre) on the highest sites under rotations between 50 and 80 years *(55).* Although information on productivity of Douglas-fir in terms of total biomass production is still limited, indications are that it may reach 1000 t/ha (447 tons/acre) on high sites (22).

The interior variety of Douglas-fir does not attain the growth rates, dimensions, or age of the coastal variety. Site class for Rocky Mountain Douglas-fir is usually IV or V (site index 24 to 37 m or 80 to 120 ft at age 100) when compared with the growth of this species in the Pacific Northwest *(1,43).* On low sites, growth is sometimes so slow that trees do not reach saw-log size before old age and decadence overtake them. Interior Douglas-fir reaches an average height of 30 to 37 m (100 to 120 ft) with a d.b.h. between 38 and 102 cm (15 and 40 in) in 200 to 300 years. On the best sites, dominant trees may attain a height of 49 m (160 ft) and a d.b.h. of 152 cm (60 in) (23). Diameter growth becomes extremely slow and height growth practically ceases after age 200. Interior Douglas-fir, however, appears capable of response to release by accelerated diameter growth at any size or age (35). The interior variety is not as long lived as the coastal variety and rarely lives more than 400 years, although more than 700 annual rings have been counted on stumps (23).

Gross volume yields for Douglas-fir east of the Cascades in Oregon and Washington range from 311 m^3/ha (4,442 ft^3/acre) for site index 15.2 m or 50 ft (at age 50) to 1523 m^3/ha (21,759 ft^3/acre) for site index 33.5 m (110 ft) *(14).* In the northern Rocky Mountains, estimates of yield capabilities of habitat types where Douglas-fir is climax range from about 1.4 to 7 m^3/ha (20 to 100 ft^3/acre) per year to more than 9.8 m^3/ha (140 ft^3/acre) per year in some of the more moist habitat types where Douglas-fir is seral *(46).*

Information on yields of Douglas-fir in the southern Rocky Mountain region is scant. In New Mexico, a virgin stand of Douglas-fir (61 percent) and associated species averaged 182 m^3/ha (13,000 fbm/acre). Occasionally, stands yield as high as 840 m^3/ha (60,000 fbm/acre). Annual growth rates from 2.0 to 3.9 m^3/ha (140 to 280 fbm/acre) after partial cutting have been reported in New Mexico *(17).*

Rooting Habit-Although Douglas-fir is potentially a deep-rooting species, its root morphology varies according to the nature of the soil. In the absence of obstructions, Douglas-fir initially forms a tap root that grows rapidly during the first few years. In deep soils (69 to 135 cm, 27 to 53 in), it was found that tap roots grew to about 50 percent of their final depth in 3 to 5 years, and to 90 percent in 6 to 8 years; however, boulders or bedrock close to the soil surface result in quick proliferation of the original tap root. Platelike root systems develop when Douglas-fir grows in shallow soils or soils with a high water table. Main lateral branches develop during the first or second growing season as branches of the tap root. These structural roots tend to grow obliquely into deeper soil layers and contribute to anchoring a tree. The majority of roots in the surface soil are long ropelike laterals of secondary and tertiary origin. Fine roots, those less than 0.5 cm (0.2 in) in diameter, develop mostly from smaller lateral roots and are concentrated in the upper 20 cm (8 in) of soil *(29)*. Fine roots have a short lifespan, ranging in general from a few days to several weeks. Cyclic death and replacement of fine roots changes seasonally, reflecting changes in environmental conditions *(51)*.

Size of the root system appears to be related to size of the crown rather than the bole. In British Columbia, ratios of root spread to crown width averaged 1.1 for open- and 0.9 for forest-grown Douglas-fir, but greater lateral spread has been observed on poorly drained sand and sandy gravel soils. The radial symmetry of root systems seems to be readily distorted by slope, proximity to other trees, and presence of old roots. Observations in the Pacific Northwest and the Rocky Mountains indicate that roots of Douglas-fir extend farther downslope than upslope.

The proportion of root biomass decreases with age and may vary from 50 percent at age 21 to less than 20 percent in stands older than 100 years (29). Root grafting is very common in stands of Douglas-fir, often leading to a system of interconnected roots in older stands *(36)*.

Reaction to Competition-Except in its youth, when it is reasonably tolerant of shade, coastal Douglas-fir is classed as intermediate in overall shade tolerance, below most of its common associates in tolerance to shade (42). Of these associates, ponderosa pine, Jeffrey pine *(Pinus jeffreyi)*, incense-cedar, noble fir ***(Abies procera)***, and red alder are more demanding of light. In its interior range, Douglas-fir ranks intermediate in tolerance among its associates, being more tolerant than western larch, ponderosa pine, lodgepole pine, southwestern white pine, and aspen (23).

The coastal variety is a seral species, except on extremely dry sites in southwestern Oregon and northern California. In its interior range, Douglas-fir is both a climax and a seral species. In the northern Rocky Mountains, it replaces ponderosa pine, lodgepole pine, and western larch above the ponderosa pine belt, and in turn is replaced by western redcedar, western hemlock, Engelmann spruce, grand fir, and subalpine fir on cooler and wetter sites. In the southern Rocky Mountains, Douglas-fir is a climax species in several habitat types of mixed conifer forest and a seral species in the spruce-fir forests (4).

The natural occurrence of Douglas-fir in extensive stands is mainly a consequence of forest fires. The species' rapid growth and longevity, the thick corky bark of its lower boles and main roots, combined with its capacity to form adventitious roots, are the main adaptations that have enabled Douglas-fir to survive less fire-resistant associates and to remain a dominant element in western forests. Without fire or other drastic disturbance, Douglas-fir would gradually be replaced throughout much of its range by the more tolerant hemlock, cedar, and true fir. Old-growth forests of Douglas-fir tend to show wide ranges in age structure-rather than being even-aged— which indicates that Douglas-fir was not established over short periods after major fires or other disturbances (22).

Stands of vigorous Douglas-fir can be successfully regenerated by any of the even-aged methods. Clear cutting in combination with planting is the most widely used method. In stands infected with dwarf mistletoe ***(Arceuthobium*** spp.), clearcutting is the best alternative for eliminating the disease. If clear-cutting on good sites results in establishment of red alder, Douglas-fir is at a severe disadvantage. Alder has very rapid juvenile growth on high sites and can easily over top and suppress Douglas-fir. If Douglas-fir is released in time, however, its subsequent development will actually benefit from the nitrogen fixed by red alder. Nitrogen is the only nutrient in forest soils of the Pacific Northwest *(41)* and Inter-mountain Northwest (44) that has been shown to be limiting to growth of Douglas-fir.

Because of its ability to tolerate shade in the seedling stage, the shelterwood system is a feasible alternative to clearcutting in coastal stands (64). Shelterwood cutting has been practiced only on a limited scale in the Pacific Northwest, however, where the large dimensions of old-growth timber, danger of blowdown to the residual stand, and probability of brush encroachment limit its use. In the Rocky Mountains, shelterwood cutting has been more commonly applied and with good results *(50)*. Where interior Douglas-fir is climax, the true selection method can be used. It is unsuitable for coastal Douglas-fir.

Although Douglas-fir may be regenerated either naturally or artificially from seed, the erratic spacing characteristic of many naturally regenerated stands and the general lack of reliability of this system have resulted in legislation (Forestry Practices Acts) in Washington, Oregon, and California that virtually mandates artificial regeneration. And, because direct seeding also produces variable results, the regeneration system uses 2-year-old bare root seedlings, 3-year-old transplants, year-old container-grown seedlings, or 2-year-old transplants that were grown the first year in containers (9). Such planting stock may be affected by agents discussed here under the heading "Damaging Agents" or may suffer mortality from a lack of vigor occasioned by improper production and harvest practices, from poor planting practices, and from frost damage incurred either in nursery beds or after planting *(13).*

When Douglas-fir develops in a closed stand, the lower limbs die rapidly as they are increasingly subjected to overhead shade. Nevertheless, natural pruning is exceedingly slow because even small dead limbs resist decay and persist for a very long period. On the average, Douglas-fir is not clear to a height of 5 m (17 ft) until 77 years old, and to 10 m (33 ft) until 107 years. Obviously, natural pruning will not produce clear butt logs in rotations of less than 150 years. Artificial pruning will greatly reduce the time required to produce clear lumber but may result in severe grain distortion and brittle grain structure around pruning wounds *(10).*

Seedlings and saplings of Douglas-fir respond satisfactorily to release from competing brush or overstory trees if they have not been suppressed too severely or too long. Trees of pole and small sawtimber size in general respond very well to thinning. Trees that have developed in a closed stand, however, are poorly adapted to radical release, such as that occasioned by very heavy thinning. When exposed, the long slender boles with short crowns are highly susceptible to damage from snowbreak, windfall, and sunscald. Sudden and drastic release of young Douglas-fir may cause a sharp temporary reduction in height growth (57). Application of a nitrogen fertilizer in combination with thinning gives better growth responses in Douglas-fir than either fertilizer or thinning alone *(41).*

Damaging Agents-From seed to maturity, Douglas-fir is subject to serious damage from a variety of agents. Douglas-fir is host to hundreds of fungi, but relatively few of these cause serious problems. Various species of *Pythium, Rhizoctonia, Phytophthora, Fusarium,* and *Botrytis* may cause significant losses of seedlings in nurseries *(58,60),* whereas *Rhizina undulata,* shoestring root rot *(Armillaria mellea),* and laminated root rot *(Phellinus weirii)* have caused significant damage in plantations. In fact, the latter two fungi represent a serious threat to management of young-growth stands of Douglas-fir, especially west of the summit of the Cascades. Trees die or are so weakened that they are blown over. Effective control measures are not available. Of the many heart rot fungi (more than 300) attacking Douglas-fir, the most damaging and widespread is red ring rot *(Phellinus pini).* Knots and scars resulting from fire, lightning, and falling trees are the main courts of infection. Losses from this heart rot far exceed those from any other decay. Other important heart rot fungi in the Pacific Northwest are *Fomitopsis officinalis, F. cajanderi,* and *Phaeolus schweinitzii* (28). In the Southwest, *Echinodontium tinctorium, Fomitopsis cajanderi,* and *F. pinicola* are important.

Several needle diseases occur on Douglas-fir. The most conspicuous, a needlecast, is caused by *Rhabdocline pseudotsugae.* It is mainly a disease of younger trees, reaching damaging proportions only after prolonged periods of rain while the new needles are appearing. The interior variety is particularly susceptible to the disease but is less often exposed to long periods of rain during the spring growth period.

The most damaging stem disease of Douglas-fir is *Arceuthobium douglasii.* This dwarf mistletoe occurs throughout most of the range of Douglas-fir (26).

Over 60 species of insects are indigenous to Douglas-fir cones, but only a few species damage a significant proportion of the seed crop. Damage by insects is frequently more pronounced during the years of light or medium seed crops that may follow good or heavy crops.

The most destructive insects include: (a) the Douglas-fir seed chalcid *(Megastigmus spermotrophus),* which matures in the developing seed and gives no external sign of its presence; (b) the Douglas-fir cone moth *(Barbara colfaxiana)* and the fir cone worm *(Dioryctria abietivorella)* whose larvae bore indiscriminately through the developing cones and may leave external particles of frass; and (c) the Douglas-fir cone gall midge *(Contarinia oregonensis)* and cone scale midge *(C. washingtonensis),* which destroy some seed but prevent harvest of many more by causing galls that prevent normal opening of cones. The Douglas-fir cone moth is perhaps a more serious pest in the drier, interior portions of the Douglas-fir range and the *Contarinia* spp. in the wetter regions. Any of these insects, however, may effectively destroy a cone crop in a given location (27).

Insects are generally not a severe problem for Douglas-fir regeneration, although both the strawberry root weevil *(Otiorhynchus oratus)* and cranberry girdler *(Chrysoteuchia topiaria)* may cause significant damage to seedlings in nurseries; damage to plantations by rain beetles *(Pleocoma* spp.) and weevils *(Steremnius carinatus)*—the latter particularly damaging to container-grown-plants-has been reported.

The Douglas-fir tussock moth *(Orgyia pseudotsugata)* and the western spruce budworm *(Choristoneura fumiferana)* are the most important insect enemies of Douglas-fir. Both insects attack trees of all ages at periodic intervals throughout the range of interior Douglas-fir, often resulting in severe defoliation of stands. The Douglas-fir beetle *(Dendroctonus pseudotsugae)* is a destructive insect pest in old-growth stands of coastal and interior Douglas-fir. Its impact is diminishing, however, with the change to second-growth management and rotations of less than 100 years *(24)*.

Consumption of Douglas-fir seeds by small forest mammals such as white-footed deer mice, creeping voles, chipmunks, and shrews, and birds such as juncos, varied thrush, blue and ruffed grouse, and song sparrows further reduces seed quantity. A single deer mouse may devour 350 Douglas-fir seeds in a single night. Mouse populations of 7 to 12/ha (3 to 5/acre) are not uncommon. Most seedfall occurs at least 150 days before the germination period, so this single rodent species has the capacity to destroy the great majority of natural seedfall. Spot seeding studies in the Western United States have clearly demonstrated that forest mammals destroy virtually all unprotected seed.

Browsing and clipping by hares, brush rabbits, mountain beaver, pocket gophers, deer, and elk often injure seedlings and saplings. Recent reports have indicated that such damage in western Oregon and Washington may strongly affect seedling survival in many plantations *(7,61)*. In drier areas, domestic livestock have caused considerable damage to variety *glauca* plantations by grazing and trampling seedlings. In pole-sized timber, bears sometimes deform and even kill young trees by stripping off the bark and cambium.

High winds following heavy rains occasionally cause heavy losses from blowdown in the Pacific Northwest. Heavy snow and ice storms periodically break the tops of scattered trees in dense young stands. Crown fires, when they occur, destroy stands of all ages. The thick bark of older Douglas-firs, however, makes them fairly resistant to ground fires.

Special Uses

Douglas-fir is grown as a Christmas tree on rotations ranging from 4 to 7 years. Trees are sheared each year to obtain a pyramid-shaped crown. Attempts to grow Douglas-fir as a Christmas tree in North America outside its native range have failed. Coastal Douglas-fir is usually killed by frost, and the interior variety suffers too much from the needle cast disease ***Phaeocryptopus gaeumanni.***

Genetics

The genus ***Pseudotsuga*** includes two species ***(P. menziesii*** and ***l? macrocarpa)*** indigenous to North America and five species native to Asia. All except *P. menziesii* have a karyotype of 2N=24, the number of chromosomes characteristic of Pinaceae. But the Douglas-fir karyotype is 2N=26, a probable reason for the general failure of hybridization trials with this species (56).

Population Differences

Pseudotsuga menziesii has two widely recognized varieties: ***menziesii,*** the green variety indigenous to the area west of the summit of the Cascade Range in Washington and Oregon and of the Sierra Nevada in California; and ***glauca,*** the blue Douglas-fir native to the interior mountains of the Pacific Northwest and the Rocky Mountains in the United States, and to Mexico. The division between the two varieties is not as clearly defined in Canada, although ***menziesii*** is commonly considered indigenous to the area west of the crest of the mainland Coast and Cascade Ranges.

The varieties differ in both growth rate and size at maturity, ***menziesii*** being more rapid growing and much larger. In habit, ***glauca*** is more shade tolerant, has a more pronounced tap root, is more susceptible to ***Rhabdocline pseudotsugae*** when grown in a moist environment, and is significantly more cold hardy. The coastal and interior varieties also differ in botanical and morphological characteristics. Because of variation within the two recognized varieties, it has been suggested that variety glauca be replaced with several varieties, and many forms have been reported. Chemical and cytological investigations have shown differences both between and within the two varieties, but such work has not led to further differentiation *(38,48)*.

Races

Douglas-fir has one of the broadest ranges of any North American conifer, much of it over extremely dissected terrain, and the species exhibits a great deal of genetic differentiation. Much of this variation is strongly associated with geographic or topographic features (47). Thus, clinal patterns of variation in growth and phenological traits have been observed over north-south, east-west, and elevational transects despite the appreciable gene flow expected in this species. Adaptive patterns of genetic variation also occur among Douglas-fir populations within local regions. For example, evidence exists for "aspect races" in variety ***menziesii:*** Seedlings grown from seed collected on the more xeric southern aspects grow slower, set buds earlier, and form larger roots in relation to shoots than seedlings grown from seeds collected on adjacent north-facing slopes. Seedlings from seed sources on the south aspect have characteristics consistent with adaptation to the shorter growing seasons and drier soil conditions generally found on south-facing slopes and may be better able to survive under drought stress than seedlings from north-aspect seed sources (33). Topoclinal variation in response to microenvironmental heterogeneity has also been found in the central part of the Oregon Cascades *(11)*.

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