Pinus lambertiana Dougl. Sugar Pine

Pinaceae Pine family

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Called "the most princely of the genus" by its discoverer, David Douglas, sugar pine *(Pinus lambertiana)* is the tallest and largest of all pines, commonly reaching heights of 53 to 61 m (175 to 200 ft) and d.b.h. of 91 to 152 cm (36 to 60 in). Old trees occasionally exceed 500 years and, among associated species, are second only to giant sequoia in volume. For products requiring large, clear pieces or high dimensional stability, sugar pine's soft, even-grained, satin-textured wood is unsurpassed in quality and value. The huge, asymmetrical branches high in the crowns of veteran trees, bent at their tips with long, pendulous cones, easily identify sugar pine, which "more than any other tree gives beauty and distinction to the Sierran forest" (25).

Habitat

Native Range

Sugar pine (fig. 1) extends from the west slope of the Cascade Range in north central Oregon to the Sierra San Pedro Martir in Baja California (approximate latitude 30" 30' to 45" 10' N.). Its distribution is almost continuous through the Klamath and Siskiyou Mountains and on west slopes of the Cascade Range and Sierra Nevada, but smaller and more disjunct populations are found in the Coast Ranges of southern Oregon and California, Transverse and Peninsula Ranges of southern California, and east of the Cascade and Sierra Nevada crests. Its southern extremity is an isolated population high on a plateau in the Sierra San Pedro Martir in Baja California. Over 80 percent of the growing stock is in California *(49)* where the most extensive and dense populations are found in mixed conifer forests on the west slope of the Sierra Nevada.

In elevation, sugar pine ranges from near sea level in the Coast Ranges to more than 3000 m (10,000 ft) in the Transverse Range.

Elevational limits increase with decreasing latitude, with typical ranges as follows:

Cascade Range	335 to 1645 m (1,100 to 5,400 ft)
Sierra Nevada	610 to 2285 m (2,000 to 7,500 ft)
Transverse and Peninsula Ranges	1220 to 3000 m (4,000 to 10,000 ft)
Sierra San Pedro Martir	2150 to 2775 m (7,056 to 9,100 ft)

Climate

Temperature and precipitation vary widely throughout the range of sugar pine. For equivalent latitudes, temperature decreases and precipitation increases with elevation, and for equivalent elevations, temperature increases and precipitation decreases from north to south. Patterns unifying this variability are relatively warm, dry summers and cool, wet winters. Precipitation during July and August is usually less than 25 mm (1 in) per month, and summertime relative humidities are low. Although water stored in snowpacks and soils delays the onset and shortens the duration of summer drought, evaporative stress often becomes great enough to arrest growth in the middle of the season *(15)*. Most precipitation occurs between November and April, as much as two-thirds of it in the form of snow at middle and upper elevations (26). Within its natural range, precipitation varies from about 840 to 1750 mm (33 to 69 in). Because winter temperatures are relatively mild and seldom below freezing during the day, considerable photosynthesis and assimilation are possible during the dormant season, at least partially offsetting the effects of summer drought *(15)*.

Soils and Topography

Sugar pine grows naturally over a wide range of soil conditions typically associated with conifer–hardwood forests. Soil parent materials include rocks of volcanic, granitic, and sedimentary origin and their metamorphic equivalents and are usually not of critical importance. Soils formed on ultrabasic intrusive igneous rocks such as peridotite and serpentinite, however, have low calcium-to-magnesium ratios and usually support open conifer stands of inferior growth and quality Nevertheless, sugar pine is often the dominant conifer on the more mesic of these sites *(39,40)*.

Because site productivity is a function of several environmental variables-edaphic, climatic, and biotic-it is difficult to relate parent material groups or particular soil series with specific productivity

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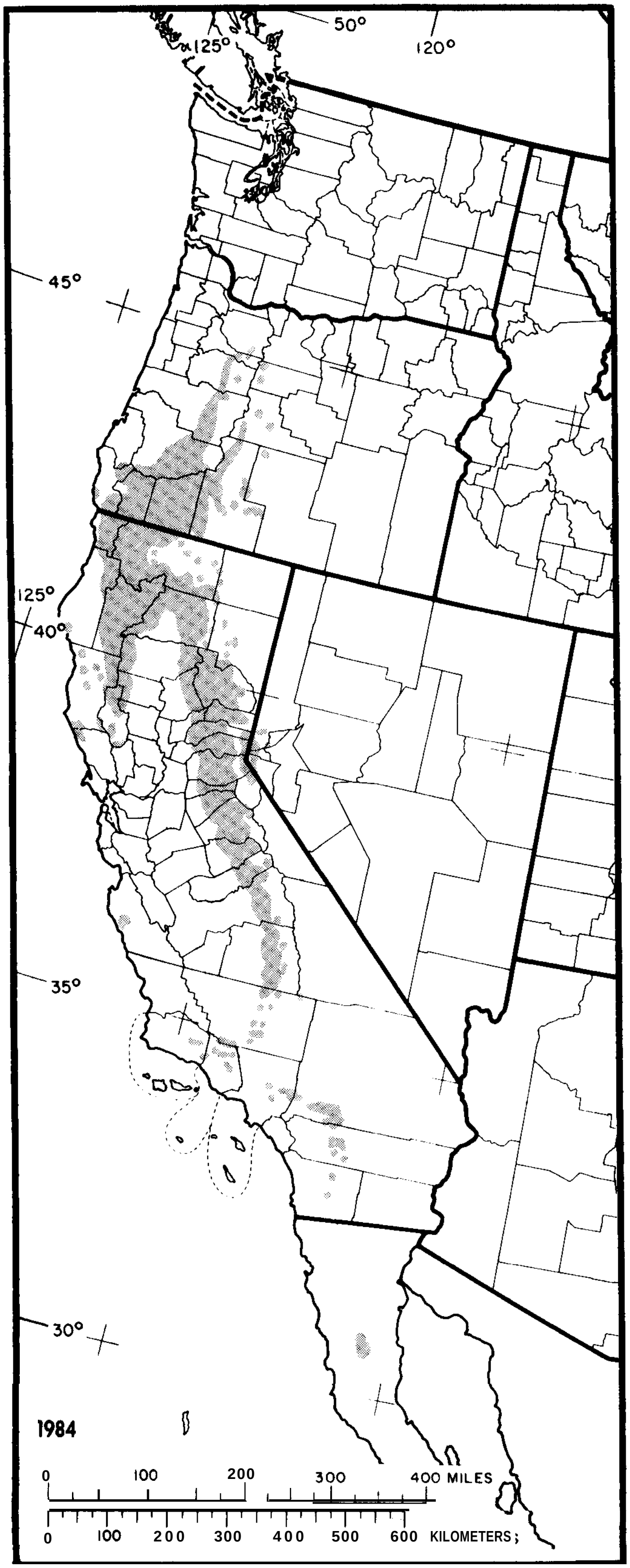

Figure 1-*The native range of sugar pine.*

classes, especially when they span wide ranges of elevation and latitude. Other factors being equal, the main edaphic influences on conifer growth are soil depth and texture, permeability, chemical characteristics, and drainage and runoff properties *(5)*.

The most extensive soils supporting sugar pine are well drained, moderately to rapidly permeable, and acid in reaction. Soils derived from ultrabasic rocks are very slightly acid to neutral (pH 7.0). In general, acidity increases with soil depth. Several edaphic properties are influenced by the degree of soil profile development. Soil porosity, permeability, and infiltration rate decrease with more developed profiles, while water-holding capacity, rate of run-off, and vulnerability to compaction increase.

Sugar pine reaches its best development and highest density on mesic soils of medium textures (sandy loam to clay loams) but ranges into the lower reaches of frigid soils when other climatic variables are suitable. These soils are found most commonly in the order Ultisols and Alfisols. The best stands in the Sierra Nevada grow on deep, sandy loam soils developed from granitic rock. In the southern Cascade Range the best stands are on deep clay loams developed on basalt and rhyolite. In the Coast Range and Siskiyou Mountains in California and Oregon, the best stands are on soils derived from sandstone and shale.

Much of the terrain occupied by sugar pine is steep and rugged. Sugar pines are equally distributed on all aspects at lower elevations but grow best on warm exposures (southern and western) as elevation increases. Optimal growth occurs on gentle terrain at middle elevations.

Associated Forest Cover

Sugar pine is a major timber species at middle elevations in the Klamath and Siskiyou Mountains, Cascade, Sierra Nevada, Transverse, and Peninsula Ranges. Rarely forming pure stands, it grows singly or in small groups of trees. It is the main component in the forest cover type Sierra Nevada Mixed Conifer (Society of American Foresters Type 243) *(10)* generally comprising 5 to 25 percent of the stocking. It is a minor component in 10 other types:

207 Red Fir
211 White Fir
229 Pacific Douglas-Fir
231 Port-Orford-Cedar
232 Redwood
234 Douglas-Fir-Tanoak-Pacific Madrone
244 Pacific Ponderosa Pine-Douglas-Fir
246 California Black Oak
247 Jeffrey Pine

249 Canyon Live Oak

In the northern part of its range, sugar pine is commonly associated with Douglas-fir *(Pseudotsuga* ***menziesii),*** ponderosa pine *(Pinus* ***ponderosa),*** grand fir ***(Abies grandis),*** incense-cedar ***(Calocedrus*** *decurrens)*, western hemlock *(Tsuga* ***heterophylla),*** western redcedar ***(Thuja*** *plicata*), Port-Orford-cedar ***(Chamaecyparis lawsoniana),*** tanoak ***(Lithocarpus*** *densiflorus)*, and Pacific madrone ***(Arbutus*** *menziesii).* In the central part it is associated with ponderosa pine, Jeffrey pine ***(Pinus jeffreyi),*** white fir ***(Abies concolor),*** incense-cedar, California red fir ***(A. magnifica),*** giant sequoia ***(Sequoiadendron*** *giganteum)*, and California black oak *(Quercus* ***kelloggii).*** Farther south, the usual associates are Jeffrey pine, ponderosa pine, Coulter pine *(Pinus* ***coulteri),*** incense-cedar, white fir, and bigcone Douglas-fir *(Pseudotsuga* ***macrocarpa).*** At upper elevations Jeffrey pine, western white pine *(Pinus* ***monticola),*** California red fir, and lodgepole pine ***(P. contorta)*** grow with sugar pine. In the Sierra San Pedro Martir, Jeffrey pine and white fir are the main associates.

Common brush species beneath sugar pine include greenleaf manzanita ***(Arctostaphylos patula),*** deerbrush ***(Ceanothus integerrimus),*** snowbrush (C. ***velutinus),*** mountain whitethorn *(C.* ***cordulatus),*** squawcarpet (C. ***prostratus),*** bearclover ***(Chamaebatia foliolosa),*** bush chinkapin *(Castanopsis* ***sempervirens),*** bitter cherry *(Prunus* ***emarginata),*** salal ***(Gaultheria shallon),*** coast rhododendron ***(Rhododendron californicum),*** and gooseberries and currants in the genus ***Ribes (11).*** From a silvicultural standpoint, ***Ribes*** spp. are especially important because they are alternate hosts to the white pine blister rust fungus ***(Cronartium*** *ribicola).* At least 19 different species grow in the Mixed Conifer Type, of which the Sierra gooseberry *(Ribes roezlii)* is most prevalent on more xeric, upland sites, and the Sierra currant ***(R. nevadense)*** on more mesic sites (35).

Life History

Reproduction and Early Growth

Flowering and Fruiting-Sugar pine is monoecious. Reproductive buds are set in July and August but are not discernible until late in the next spring. Time of pollination ranges from late May to early August, depending on elevation, and to a lesser extent on latitude.

Female strobili are 2.5 to 5.0 cm (1 to 2 in) long at time of pollination and double in size by the end of the growing season. Fertilization of eggs by male gametes takes place late the following spring, about 12 months after pollination. By this time, the seed is at its final size with a fully developed coat. Conelet elongation continues during the second season until maturation in late summer. Mature sugar pine cones (fig. 2) are among the largest of all conifers, averaging 30 cm (12 in) and ranging up to 56 cm (22 in) long. Dates of cone opening range from mid-August at low elevations to early October at high elevations *(12,19,32).*

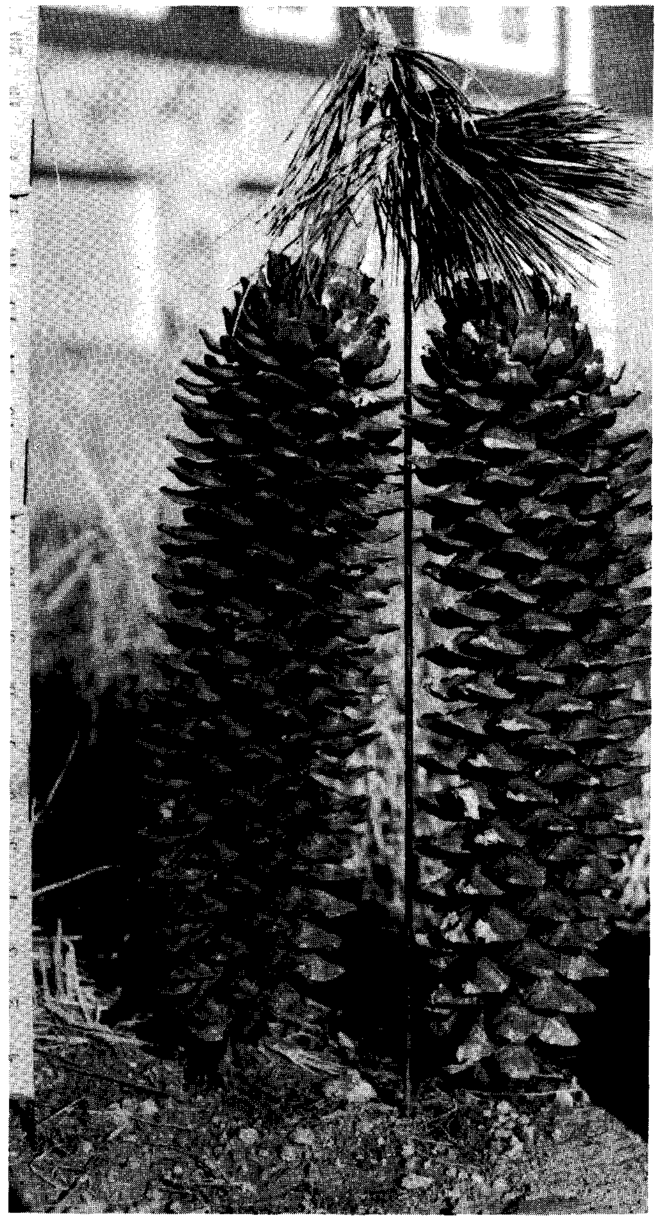

Figure 2—*Sugar pine cones.*

Cone production starts later and is less prolific in sugar pine than in its associates. During a 16-year study in the central Sierra, fewer than 5 percent of sugar pines less than 20 cm (8 in) in d.b.h., and 50 percent less than 31 cm (12 in) in d.b.h., produced cones. Of trees 51 cm (20 in) or more, 80 percent produced cones, and dominant trees produced 98 percent of the total. Intervals between heavy cone crops averaged 4 years and ranged from 2 to 7 *(12)*.

Loss of sugar pine cones is heavy; the probability of a pollinated conelet developing to maturity is only 40 to 50 percent. Predation by the sugar pine cone beetle ***(Conophthorus Zambertianae)*** can cause up to 93 percent loss. Douglas squirrels and white-headed woodpeckers also take a heavy toll *(7,11,17)*.

Spontaneous abortion of first-year conelets is high. Observations of control-pollinated trees in the Klamath Mountains showed that 19 percent of female strobili were lost 5 to 12 weeks after bagging, with no obvious signs of insect or pathogen-caused damage *(41)*. The amount of abortion varied from 15 to 85 percent among trees, for both bagged and unbagged strobili. Since this pattern was consistent in successive years, a genetic cause was suggested.

Seed Production and Dissemination-Mature trees produce large amounts of sound seeds. In a study of 210 trees in 13 stands in the central and northern Sierra Nevada, the average number of sound seeds per cone was 150, with individual trees ranging from 34 to 257. Higher numbers of seeds per cone (209 to 219) have been reported, but whether the count was based on sound or total seeds was not specified. In good crop years, the proportion of sound seeds is usually high (67 to 99 percent) but in light crop years can fall as low as 28 percent *(7,12)*.

Cones are ripe and start to open when their color turns light brown and specific gravity (fresh weight basis) drops to about 0.62. Seed shed may begin in late August at low elevations and at higher elevations is usually complete by the end of October *(11)*.

Seeds are large and heavy, averaging 4,630 seeds per kilogram (2,100/lb). Since their wings are relatively small for their size, seeds are not often dispersed great distances by wind, and 80 percent fall within 30 m (100 ft) of the parent tree. Birds and small mammals may be an important secondary mechanism of dispersal, even though they consume most of the seeds they cache. In good seed years, large amounts of seed fall, with estimates ranging from 86,500 to more than 444,800/ha (35,000 to 180,000/acre) in central Sierra Nevada stands *(11,32)*.

Seedling Development—Sugar pine seeds show dormancy, which can be readily broken by stratification for 60 to 90 days or by removal of the seed coat and inner papery membrane surrounding the seed. Germination of fresh seed is uniformly rapid and high, exceeding 90 percent if adequately ripened, cleaned, and stratified. Viability may decline rapidly with time in storage at temperatures above freezing, but deep-frozen seed maintains viability much longer *(1,32,47)*.

On unprepared seed beds, seed-to-seedling ratios are high (244 to 483). Soil scarification reduced the ratio to 70 in one case, and scarification with rodent poisoning dropped it to 38 in another *(12)*.

Seedling losses are continual and only 20 to 25 percent of the initial germinants may survive as long as 10 years. Drought may kill up to half of the first-year seedlings. Cutworms and rodents, which eat seeds still attached to seedling cotyledons, also take their toll *(11,12)*. Seedlings infected by blister rust rarely survive more than a few years.

Germination is epigeal(32). Seedlings rapidly grow a deep taproot when seeds germinate on bare mineral soil. In one comparison, taproots penetrated to an average depth of 43 cm (17 in) on a bare sandy soil, but only half as deep when the soil was overlain with duff *(11)*. Lateral roots develop near and parallel to the soil surface, often growing downward some distance from the stem. In heavier, more shallow soils, laterals are often larger than taproots. During the second season, laterals commonly originate on the lower taproot and occupy a cone of soil which has its base at the tip of the taproot. After 2 years on three different soil types in Oregon, the taproots of natural sugar pine seedlings ranged from 56 to 102 cm (22 to 40 in), were significantly deeper than those of Douglas-fir and grand fir, but shorter than those of ponderosa pine and incense-cedar. Lengths of main lateral roots showed the same species differences. Top-to-root ratios for sugar pine ranged from 0.17 to 0.28 (length) and from 1.33 to 1.60 (dry weight) (46).

Seasonal shoot growth starts later and terminates earlier in sugar pine than in its usual conifer associates, except white fir. At middle elevations in the central Sierra Nevada, shoot elongation begins in late May, about 2 weeks after ponderosa pine and a month before white fir, and lasts about 7 weeks. Radial growth begins about 6 weeks earlier than shoot growth and extends throughout the summer *(11)*.

Planting of sugar pine has not been so easy or successful as for some of the yellow pines. Although reasons for the many recorded failures are often complex, lower drought tolerance may be one of the factors. During natural regeneration, the ability of sugar pine seedlings to avoid summer drought by rapidly growing a deep taproot largely compensates for the relative intolerance of tissues to moisture stress (38).

To survive the first summer after planting, seedlings must have the capacity to regenerate vigorous new root systems. For other western conifers, root growth capacity is conditioned by particular combinations of nursery environment and time in cold storage after lifting; these requirements are species and seed-source specific *(22,24,38).* Although patterns of root growth capacity have not been worked out for sugar pine, it is clear that amounts of root growth are substantially less for sugar pine than for its associates (23).

Early top growth of sugar pine is not so rapid as that of western yellow pines, and l-year stock is too small for planting when seed is sown in May, for years the tradition in California nurseries. Root diseases, to which young sugar pines are unusually vulnerable, can compound the problem by weakening seedlings that survive, thus reducing their chances of establishment on the site. Sowing stratified seed in February or March extended the growing season and produced healthy seedlings of plantable size in one season (23). A more expensive alternative to bareroot stock that holds some promise is containerized seedlings grown under accelerated growth regimes (28).

Vegetative Reproduction-Sugar pine does not sprout, but young trees can be rooted from cuttings. The degree of success is apparently under strong genetic control. In one trial the proportion of cuttings that rooted from different ortets from 3 to 6 years old ranged from 0 to 100 percent (27). As for most conifers, rootability diminishes rapidly with age of donor tree. Grafts, however, can be made from donors of all ages, with success rates from 70 to 80 percent common. Problems of incompatibility, frequent in some species such as Douglas-fir, are rare in sugar pine.

Sapling and Pole Stages to Maturity

Growth and Yield-Veteran sugar pines (fig. 3) often reach great size. Large trees have commonly scaled 114 to 142 m^3 (20,000 to 25,000 fbm, Scribner log rule), with a record of 232 m^3 (40,710 fbm). A "champion," located on the North Fork of the Stanislaus River in California, measured 65.8 m (216 ft) tall and 310 cm (122 in) in d.b.h., but trees up to 76 m (250 ft) tall have been reported *(11,36).* These and previous champions of this century are dwarfed by the first sugar pine measured by David Douglas and described in his diary (37): "Three feet from the

Figure *3-Mature sugar pine. (Courtesy of Western Wood Products Assoc., Portland, OR.)*

ground, 57 feet 9 inches in circumference; 134 feet from the ground, 17 feet 5 inches; extreme length 215 feet."

Early growth of sugar pine is slow compared with ponderosa pine, but growth rates accelerate in the pole stage and are sustained for longer periods than those of common associates. Consequently, sugar pines are usually the largest trees, except for giant sequoia, in mature and old-growth stands. On better sites annual growth increments in basal area of 2.5 percent and more can be sustained up to stem diameters of 76 to 127 cm (30 to 50 in) or for 100 to 150 years *(11).* Growth of sugar pine is best between 1370 and 1830 m (4,500 and 6,000 ft) in the central Sierra Nevada, between the American and San Joaquin Rivers.

In young mixed conifer stands, sugar pine often constitutes a relatively small proportion of the total basal area but contributes disproportionately to growth increment. On the El Dorado National Forest in the western Sierra Nevada, in stands ranging in age from 50 to 247 years, the sugar pine component was only 6 to 7 percent (range: 3 to 14 percent) of the average basal area, but its average annual basal area growth was 11.3 percent (range: 2 to 35 percent) of the stand total. A similar relationship was found on the Plumas National Forest in the northern Sierra Nevada: in stands from 58 to 95 years old, average basal area of sugar pine was 7 percent (3 to 16), but lo-year growth was more than 12 percent (6 to 19). Ten-year volume increment in mixed conifer stands from 40 to 80 years old was greater for sugar pine than for Douglas-fir, white fir, ponderosa pine, and incense-cedar in each of five basal area categories *(9).* Mean increment for sugar pine was 4.1 percent, compared to 3.1 percent for all others.

Yields of sugar pine are difficult to predict, because it grows in mixes of varying proportion with other species. In the old-growth forest, the board foot volume of sugar pine was 40 percent of total in stands dominated by ponderosa pine and sugar pine. In exceptional cases on very small areas, yields were 2688 m^3/ha (192,000 fbm/acre) *(11).* Yield tables for young growth are based on averages for all commercial conifers and assume full stocking (8). The data base is limited, so the tables are at best a rough guide. Realistically, yields may reach 644 m^3/ha (46,000 fbm/acre) in 120 years on medium sites, and up to 1190 m^3/ha (85,000 fbm/acre) in 100 years on the best sites, with intensive management *(11).*

Rooting Habit-Sugar pine develops a deep taproot at an early age.

Reaction to Competition-Sugar pine tolerates shade better than ponderosa pine but is slightly less tolerant than incense-cedar and Douglas-fir and much less so than white fir *(14).* A seral species, it becomes less tolerant with age, and overtopped trees decline unless released *(11).* Thus, dominant sugar pines in old-growth stands were probably dominant from the start, or released by natural causes early in life. White fir would usually be the climax species in mixed conifer forests in the absence of any natural disturbance; however, fire, insects, disease, and other agents are natural and pervasive features of these forests. Such disturbances frequently cause gaps, in which the relatively tolerant sugar pine is adapted to grow *(14).* For these reasons, sugar pine is often adapted to regenerate in a shelterwood silvicultural system (33).

Competition from brush severely retards seedling establishment and growth. Only 18 percent of seedlings starting under brush survived over a period of 18 to 24 years, and after 10 years the tallest seedlings measured were only 29 cm (11.4 in). Given an even start with brush, however, seedlings can compete successfully *(11).*

Light shelterwoods can protect seedlings of sugar pine and white fir against frost, which seldom affects ponderosa and Jeffrey pines, and provide them with a competitive advantage because of their greater tolerance to shade *(13,43,44).* On the other hand, young sugar pines stagnate beneath an overstory and in competition with root systems of established trees or brush. But because they respond well to release, the basal area increment of sugar pines is often double that of companion species after heavy thinnings (33). Thus, skill in the amount and timing of overstory removal is a key factor in successful silvicultural management of sugar pine.

Sugar pine does not self-prune early, even in dense stands, and mechanical pruning is necessary to ensure clear lumber of high quality.

Damaging Agents-The pathology of sugar pine is dominated by white pine blister rust, caused by ***Cronartium ribicola,*** a disease serious enough to severely limit natural regeneration in areas of high hazard, and thereby alter successional trends. Among commercially important North American white pines, sugar pine is the most susceptible. Infected seedlings and young trees are inevitably killed by cankers girdling the main stem.

Blister rust was introduced into western North America shortly after the turn of the century at a single point on Vancouver Island and has since spread eastward throughout the Inland Empire and south through the Cascade, Klamath, North Coast, and Sierra Nevada Ranges. It has not yet been found in the Transverse or Peninsular Ranges of southern California, even though alternate host species are abundant there. Within the range of sugar pine, conditions for infection are not nearly so uniform as for western white pine in the Inland Empire. Incidence and intensity of infection on sugar pine are highest in Oregon and northern California and become progressively less to the south, as climate becomes warmer and drier. Within any area, however, hazard varies widely and depends on local site conditions. These are complex, but two of the most important factors are the duration of moisture retention on foliage following rain, fog, or dew, and the distribution and density of the alternate hosts, currant and gooseberry bushes (*Ribes* spp.). Thus, cool north slopes are more hazardous than warm south slopes, and relatively humid stream bottoms and lakesides are more hazardous than upland sites. In the Cascade Range and Sierra Nevada of northern California, infection averaged two to three times higher near stream bottoms than on adjacent slopes (4).

Attempts to control blister rust by chemical therapy or eradicating alternate hosts have been abandoned as impractical and ineffective. Except on highly hazardous sites, sugar pine in natural stands can be effectively managed by judiciously selecting leave trees with cankers relatively far from the bole and by pruning cankers in the lower crown (4).

Plantations are a much more serious problem. The microenvironmental changes on a site following clearcutting-including dew formation on foliage and the rapid regeneration of alternate host *Ribes* spp.—greatly augment the probability of rust intensification and spread on both hosts. Uniform age and stocking make sugar pine plantations vulnerable to nearly total destruction for 20 years or longer. Genetically resistant sugar pines in mixture with other conifers offer the most promising solution.

Dwarf mistletoe (*Arceuthobium californicum*) may seriously damage infected trees by reducing growth in height, diameter, and crown size, and predisposing weakened trees to attack by bark beetles. Extending throughout the range of sugar pine, except for isolated stands in Nevada, the south Coast Ranges of California, and Baja California, this mistletoe was found in only 22 percent of the stands examined and on only 10 percent of the trees in those stands. Spread is slow and can be controlled by sanitation cutting *(20,42)*.

A needle cast caused by *Lophodermella arcuata* is occasionally and locally damaging. Root diseases caused by *Armillaria mellea, Heterobasidion annosum,* and *Verticicladiella wageneri* are capable of killing trees of all ages and sizes but, though widespread, are usually at endemic levels. Several trunk and butt rots attack sugar pine but are usually confined to mature and overmature trees *(2,21)*.

Several root and damping-off pathogens cause severe damage to sugar pine in nurseries, with annual losses up to 50 percent *(45)*. In approximate order of importance, these are *Fusarium oxysporum, Macrophomina phaseoli,* and species of *Pythium, Phytophthora,* and *Rhizoctonia.* In addition to causing direct losses in the nursery, these diseases may reduce field survival of planted seedlings in more stressful environments by causing stunting and chlorosis. Nursery fumigation controls most of the organisms involved but is least effective on *Fusarium.* A simple and promising alternative control method is early sowing of stratified seed. Soil temperatures in late winter and early spring permit seed germination and root development but are still cool enough to inhibit fungal growth.

Sugar pine hosts many different insects, but the mountain pine beetle *(Dendroctonus ponderosae)* is of overwhelming importance. This insect can cause widespread mortality, often killing large groups of trees (48). Several other bark-feeding insects contribute directly or indirectly to mortality in sugar pines, particularly after periods of drought. Death results from predisposing trees to mountain pine beetle. The red turpentine beetle *(Dendroctonus valens)* is usually restricted to small areas near the root crown but during drought may extend two or more meters up the bole, destroying the entire cambium. The California flatheaded borer *(Melanophila californica)* usually attacks decadent and unhealthy trees, but trees under heavy moisture stress are also vulnerable. The California fivespined ips *(Ips paraconfusus)* is only capable of penetrating thin bark in sugar pine. Small trees are often killed, but large trees only top-killed *(16)*.

The sugar pine cone beetle *(Conophthorus lambertianae)* can be extremely destructive to developing second-year cones, destroying up to 75 percent of the crop in some years. Since stunted cones are apparent by mid-June, the extent of the crop loss can be assessed well before cone collection. The sugar pine scale *(Matsucoccus paucicicatrices)* occasionally kills foliage and branches, predisposing trees to bark beetle attack. The dead "flags" resulting from heavy attack mimic advanced symptoms of white pine blister rust. Occasionally, the black pineleaf scale *(Nuculaspis californica)* defoliates sugar pine at midcrown, weakening the tree. These scale attacks are often associated with industrial air pollution or heavy dust deposits on foliage *(16)*.

Among its coniferous associates, sugar pine is the most tolerant to oxidant air pollution *(34)*, while intermediate in fire tolerance (39) and frost tolerance *(43,44)*. It is less tolerant of drought than most companion species with which it has been critically compared, including knobcone *(Pinus attenuata)* and Coulter pines *(50,51)*, ponderosa pine, Douglas-fir, incense-cedar, and grand fir *(40)*.

Special Uses

Upper grades of old-growth sugar pine command premium prices for specialty uses where high dimensional stability, workability, and affinity for glue are essential. The wood is light (specific gravity, 0.34 ± 0.03) *(3)*, resists shrinkage, warp, and twist, and is preferred for finely carved pattern stock for machinery and foundry casting. Uniformly soft, thin-celled spring and summer wood and straight grain account for the ease with which it cuts parallel to or across the grain, and for its satin-textured, lustrous finish when milled. Its easy working qualities favor it for molding, window and door frames, window sashes, doors, and other special products such as piano keys and organ pipes. Wood properties of young growth are not so well known. Pruning would undoubtedly be required to produce clear lumber during short rotations.

Genetics

Sugar pine is one of the more genetically variable members of the genus. Average heterozygosity of specific genes coding for seed proteins (isozymes) was 26 percent, a value near the upper range (0 to 36 percent) of pines studied so far (6). How adaptive variation is distributed over the range of environments encountered in over 14” of latitude and 2000 m (6,560 ft) of elevation is largely unknown, however, because of a lack of field data from provenance or progeny tests.

In a 3-year nursery trial, pronounced differences in height and diameter growth were found among seedlings of five seed sources sampled along an elevational transect on the west slope of the Sierra Nevada *(18)*. The fastest growing seedlings were from the lower-middle elevation (1100 m or 3,595 ft) and were twice the height of those from the highest elevation (2195 m or 7,200 ft). Except for the source from the lowest elevation (770 m or 2,525 ft), which ranked second, growth varied inversely with elevation. Elevation of the seed source accounted for 52 percent of the total variance among seedlings, and the component of variance for families within stands was a substantial 16 percent. More comprehensive nursery trials, of families from seed parents ranging from southern California to southern Oregon, showed similar trends (27). Greatest growth was expressed in seedlings from intermediate elevations in the central Sierra Nevada, a result consistent with observations in natural stands. Thus, genetic adaptation to climatic variables associated with elevation is clearly evident in sugar pine, requiring a close match between seed source and planting site in artificial regeneration. The degree of variability expressed among progenies of different seed parents within seed collection zones indicates that selection for rapid early growth should be effective.

Resistance to white pine blister rust is strongly inherited, and three different kinds have been recognized (29). A rapid, hypersensitive reaction to invading mycelium is conditioned by a dominant gene. This gene, which occurs at variable but relatively low frequencies throughout the range of sugar pine, is highly effective against most sources of inoculum. A race of blister rust capable of overcoming this gene was discovered in a plantation in the Klamath Mountains *(30)*, but evidently had not spread from this site 10 years after it was found *(31)*. In certain families, another kind of resistance is expressed by slower rates of infection and mortality, fewer infections per tree, and by a higher rate of abortion of incipient infections. This “slow rusting” is apparently inherited quantitatively and, while less dramatic than single gene resistance, may be more stable to variation in the pathogen in the long term. Probably two or more generations of selection and breeding will be necessary to accumulate enough genes in parental stock to make this kind of resistance usable in commercial silviculture. A third kind of resistance is age-dependent. In common garden tests, infection among grafted clones from mature trees ranged from 0 to 100 percent, yet offspring from the apparently resistant clones were fully susceptible. Although not understood, the mechanisms and inheritance of mature tree resistance are very strong and could play a significant role in stabilizing resistance over a rotation. Since all three kinds of resistance are inherited independently, there is a real promise for an enduring and well-buffered genetic control of this most destructive disease.

Hybrids

Barriers to crossing with other white pines are very strong in sugar pine (7). No natural hybrids are known and repeated attempts to cross sugar pine with other North American white pines have failed. Small numbers of F_1 hybrids were made with two Asiatic white pines, however: Korean pine *(Pinus koraiensis)* and Armand pine *(P. armandii)*. These species are of silvicultural interest because of their relative resistance to blister rust. Mass production of F_1 seed is probably impractical because of low seed set, but backcrosses of *P. lambertiana x armandii* to sugar pine have yielded abundant sound seed. In limited field tests, the backcross progenies were more resistant than intraspecific crosses of the same sugar pine parents. By using a broader genetic base of *P. armandii,* resistance in the backcross could be improved.

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