Sequoiadendron giganteum (Lindl.) Buchholz **Giant Sequoia**

Taxodiaceae **Redwood family**

C. Phillip Weatherspoon

Since its discovery in the mid-nineteenth century, giant sequoia ***(Sequoiadendron giganteum),*** also called sequoia, bigtree, and Sierra redwood, has been noted for its enormous size and age, and its rugged, awe-inspiring beauty. Because the species has broad public appeal and a restricted natural range, most groves of giant sequoia have been accorded protected status. Outside its natural range, both in the United States and in many other countries, giant sequoia is highly regarded as an ornamental and shows promise as a major timber-producing species.

Habitat

Native Range

The natural range of giant sequoia (fig.1) is restricted to about 75 groves scattered over a 420-km (260-mi) belt, nowhere more than about 24 km (15 mi) wide, extending along the west slope of the Sierra Nevada in central California (16). The northern two-thirds of the range, from the American River in Placer County southward to the Rings River, takes in only eight widely disjunct groves. The remaining groves, including all the large ones, are concentrated between the Rings River and the Deer Creek Grove in southern Tulare County (33). Varying in size from less than 1 to 1619 ha (1 to 4,000 acres), the groves occupy a total area of 14 410 ha (35,607 acres> *(17).*

Climate

Giant sequoia is found in a humid climate characterized by dry summers. Mean annual precipitation in the groves varies from about 900 to 1400 mm (35 to 55 in), with high year-to-year variation. Less than 30 mm (1.2 in) usually falls between June 1 and September 30. Most of the precipitation comes in the form of snow between October and April. Mean annual snowfall ranges from 366 to 500 cm (144 to 197 in), and snow depths of 2.0 m (6.6 ft) or greater are common in midwinter (32).

Mean daily maximum temperatures for July for typical groves are 24” to 29” C (75” to 84” F). Mean minimum temperatures for January vary from 1° to -6” C (34” to 21” F). Extremes are about -24” and 40” C (-12” and 104” F) *(32,37).*

Low temperatures seem to be a limiting factor for giant sequoia at the upper elevational limits of its range, as well as in areas with severe winters where the species has been introduced. Distribution of the species at low elevations is limited mainly by deficient soil moisture during the growing season (34).

Soils and Topography

Soils are derived from a variety of rock types. Most groves are on granitic-based residual and alluvial soils, and three are on glacial outwash from granite. Schistose, dioritic, and andesitic rocks also are common parent materials *(16,361.*

Typical soil series are Dome, Shaver, Holland, and Chaix. Characteristic soil families are coarse-loamy, mixed, mesic Dystric Xerochrepts; coarse-loamy, mixed, mesic Entic (and Typic) Xerumbrepts of the order Inceptisols; and fine-loamy, mixed, mesic Ultic Haploxeralfs of the order Alfisols. The natural range of the species lies mostly within the mesic temperature regime, extending only a short distance into the frigid regime, and wholly within the xeric moisture regime (22).

Giant sequoia grows best in deep, well-drained sandy loams. Its density also is much greater in the more mesic sites, such as drainage bottoms and meadow edges, than in other habitats within a grove. Total acreage of these productive sites is small, however. Relatively shallow and rocky soils support vigorous individuals, some large, wherever the trees can become established and where underground water is available to maintain them *(16,32).*

Soil pH ranges mostly from 5.5 to 7.5, with an average of about 6.5 (22). Long-term site occupancy by giant sequoia appears to develop a soil of high fertility, good base status, and low bulk density *(40).*

Adequate soil moisture throughout the dry growing season is critical for successful establishment of giant sequoia regeneration, although seedlings do not survive in wet soils (36). One study has shown more available soil moisture within a grove, possibly associated with subterranean flow from higher elevations, than in adjacent forested areas (34). Except for its moisture content, soil apparently plays only a minor role in influencing the distribution of the species, as evidenced by the considerable variability in parent material among groves and the fact that giant sequoia grows vigorously when planted in diverse soils around the world *(16).*

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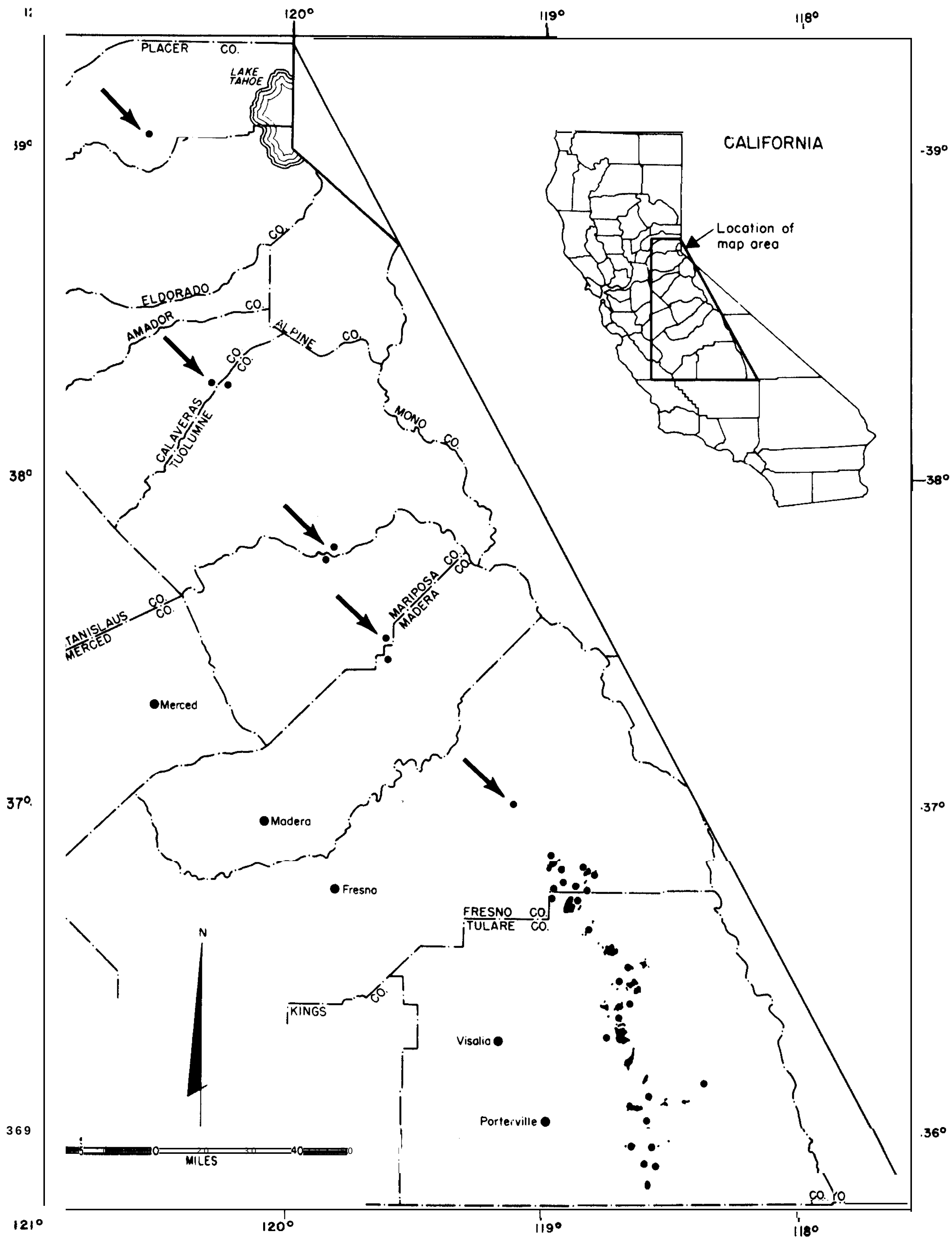

Figure 1-The *native* range *of giant sequoia.*

Elevations of the groves generally range from 1400 to 2000 m (4,590 to 6,560 ft) in the north, and 1700 to 2150 m (5,580 to 7,050 ft) in the south. The lowest natural occurrence of the species is 830 m (2,720 ft) and the highest is 2700 m (8,860 ft). The eight northern groves are all on slopes of a generally southern aspect. Between the Rings River and the southern boundary of Sequoia National Park, groves appear on north and south slopes with about equal frequency. Farther south, aspects are predominantly northerly *(32).*

Associated Forest Cover

Giant sequoia groves lie wholly within the Sierra Nevada Mixed Conifer type-SAF (Society of American Foresters) forest cover type 243 (8). A grove is distinguished from similar mesic habitats in this type only by the presence of giant sequoia itself: no other species is restricted to the groves (33). Nowhere does giant sequoia grow in a pure stand, although in a few small areas it approaches this condition *(16).*

Based on density or canopy coverage, groves typically are dominated strongly by California white fir *(Abies concolor* var. *lowiana),* despite the presence of emergent individuals of giant sequoia that overtop the canopy. Sugar pine *(Pinus Zambertiana)* is a characteristic associate. Incense-cedar *(Libocedrus decurrens)* at low elevations and California red fir *(Abies magnifica)* at high elevations may rival California white fir for dominance. Ponderosa pine *(Pinus ponderosa)* and California black oak *(Quercus kelloggii)* often occupy drier sites within the grove boundaries. Trees less commonly associated with giant sequoia include Jeffrey pine *(Pinus jeffreyi),* Douglas-fir *(Pseudotsuga menziesii),* Pacific yew *(Taxus brevifolia),* Pacific dogwood *(Cornus nuttallii),* California hazel *(Corylus cornuta* var. *californica),* white alder *(Alnus rhombifolia),* Scouler willow *(Salix scoulerana),* bigleaf maple *(Acer macrophyllum),* bitter cherry *(Prunus emarginata),* and canyon live oak *(Quercus chrysolepis).*

Shrub species most often found in giant sequoia groves are bush chinkapin *(Castanopsis sempervirens),* mountain misery *(Chamaebatia foliolosa),* mountain whitethorn *(Ceanothus cordulatus),* littleleaf ceanothus *(C. parvifolius),* deerbrush *(C. integerrimus),* snowbrush *(C. velutinus),* greenleaf manzanita *(Arctostaphylos patula),* western azalea *(Rhododendron occidentale), Ribes* spp., *Rosa* spp., and *Rubus* spp. *(16,17,33,36).*

Stand structure and species frequency vary substantially with elevation, latitude, exposure, soil moisture, and time since fire or other disturbance. In general, protection of groves from fire has resulted in increased prevalence of California white fir, reduced regeneration of giant sequoia and pines, and reduced density of shrubs. The age-class distribution of giant sequoia also varies widely among groves. Most groves today, however, appear to lack sufficient young giant sequoias to maintain the present density of mature trees in the future. In these groves, giant sequoia regeneration evidently has been declining over a period of 100 to 500 years or more (33).

Life History

Reproduction and Early Growth

Flowering and Fruiting-Giant sequoia is monoecious; male and female cone buds form during late summer. Pollination takes place between the middle of April and the middle of May when the female conelets are only two or three times as large in diameter as the twigs bearing them. Fertilization usually occurs in August, by which time cones are almost full-size. Embryos develop rapidly during the next summer and reach maturity at the end of the second growing season. The egg-shaped mature cones, 5 to 9 cm (2.0 to 3.5 in) in length, yield an average of 200 seeds each *(16,17,36).*

Seed Production and Dissemination-Cones bearing fertile seeds have been observed on trees as young as 10 years of age, but the large cone crops associated with reproductive maturity usually do not appear before about 150 or 200 years. Unlike most other organisms, giant sequoia seems to continue its reproductive ability unabated into old age. The largest specimens (not necessarily the oldest) bear heavy crops of cones containing viable seeds *(16,36).*

Giant sequoias have serotinous cones which, at maturity, may remain attached to the stems without opening to release seeds. For 20 years or more, cones may retain viable seeds and continue to photosynthesize and grow, their peduncles producing annual rings that can be used to determine cone age *(16,36).*

A typical mature giant sequoia produces an average of 1,500 new cones each year, although variability among trees and from year to year is great. Cones produced during years with ample soil moisture are more numerous (more than 20,000 cones on one large tree in an exceptional year) and yield seeds of greater viability than those produced in dry years. The upper third of the crown generally bears at least two-thirds of the cone crop. Because of extended cone retention, a mature tree may have 10,000 to 30,000 cones at any given time, two-thirds of which may be green and closed, and the remainder opened, brown, and largely seedless *(16,17)*.

Estimates of percent germination of seeds removed from green cones range from about 20 to 40 percent *(11,17,38)*. A number of variables, however, account for departures from these average values. Trees growing on rocky sites yield seeds with substantially higher germinability than those on bottom lands with deeper soils. Larger seeds germinate in higher percentages than small ones. In tests of cone age, germination increased from 20 percent for seeds from 2-year-old cones to 52 percent for 5-year-old cones, then dropped to 27 percent for cones 8 years of age. Germinability also varies with cone location in the crown, seed position within the cones, and among groves ***(16).*** Artificial stratification of seeds for 60 days or more resulted in faster germination, but not in higher germination percent *(11)*.

Browning or drying of cones, with subsequent shrinkage of scales and dispersal of seeds, is brought about largely by three agents, two of which are animals. The more effective of the two is ***Phymatodes nitidus,*** a long-horned wood-boring beetle. The larvae of the beetle mine the fleshy cone scales and cone shafts, damaging occasional seeds only incidentally. As vascular connections are severed, scales successively dry and shrink, allowing the seeds to fall. Cones damaged during the summer open several scales at a time, beginning during late summer and fall, and continuing for 6 months to 1 year ***(17).***

The second animal having a significant role in giant sequoia regeneration is the chickaree, or Douglas squirrel ***(Tamiasciurus douglasi).*** The fleshy green scales of younger sequoia cones are a major food source for the squirrel. The seeds, too small to have much food value, are dislodged as the scales are eaten. During years of high squirrel densities, the animals tend to cut large numbers of cones and store and eat them at caches. When squirrels are few, most of the cone consumption is in tree crowns-a habit more conducive to effective seed dispersal. The squirrels are active all year ***(17).***

The chickaree prefers cones 2 to 5 years old, whereas ***Phymatodes*** is more prevalent in cones at least 4 years old. The combined activities of these animals help to ensure that seeds of all age classes are shed, and that rate of seedfall is roughly constant throughout the year and from year to year, despite variability in new cone production. An average rate is about 1 million seeds per hectare (400,000/acre) per year ***(17).***

The third and perhaps most important agent of seed release is fire. Hot air produced by locally intense fire and convected high into the canopy can dry cones, resulting in release of enormous quantities of seed over small areas-for example, 20 million/ha (8 million/acre) *(17)*. This increased seedfall coincides both spatially and temporally with fire-related seedbed conditions favorable for seed germination and seedling survival (fig. 2).

Figure 2—*Young sequoias which came in after a fire burned slash and humus (California).*

Giant sequoia seeds are well adapted for wind dispersal. They are light (average 200,000/kg [91,000/lb]), winged, and fall in still air at a rate of 1.2 to 1.8 m (4 to 6 ft) per second. Winds common in late summer and winter storms in the Sierra Nevada can disperse seeds more than 0.4 km (0.25 mi) from the tall crowns of mature trees *(16,36)*.

Cone and seed insects other than ***Phymatodes*** have only a minor impact on seed production ***(17).***

Birds and mammals exert a negligible effect on giant sequoia seeds on the ground. Sequoia seeds consistently rank at or near the bottom in food preference tests that include seeds of associated species, primarily because they are small and contain little energy *(17,38)*.

Seedling Development-Natural reproduction in giant sequoia is an unusually tenuous process. Of the enormous numbers of seeds shed each year, extremely few encounter the combination of conditions necessary to become successfully established seedlings.

In contrast with most coniferous seeds, a large majority of seeds of giant sequoia die from desiccation and solar radiation soon after reaching the forest floor, especially during the summer. In one study, viability of seeds removed from fresh cones and placed on the ground dropped from 45 percent to 0 in 20 days. Seeds collected from the forest floor showed an average viability of 1 percent *(17).*

Seed dormancy is not evident in giant sequoia, so surviving seeds germinate as soon as conditions are favorable (17). Germination is epigeal. The most significant requirement for germination is an adequate supply of moisture and protection of the seed from desiccation. This is best provided by moist, friable mineral soil that covers the seed to a depth of 1 cm (0.4 in), and that is partially shaded to reduce surface drying. A wide range of temperatures is acceptable for germination. The generally sandy soils of the groves normally provide the additional requirement of adequate aeration and the optimum pH range of 6 to 7 (38). Because of rapid percolation, however, adequate moisture retention for germination and initial root development is often marginal.

Seeds dropped just before the first snow or just as the snow melts may have the best chance of germinating and becoming successfully established. Seedlings that produce roots early in the season during favorable soil moisture conditions are more likely to survive the dry summer. The first stage of germination-extension of the radicle-sometimes takes place beneath the snow *(16).*

Thick litter usually dries too quickly for seeds to germinate, and virtually all seedlings that do get started die before their roots can penetrate to mineral soil *(17,36).* Only in exceptionally wet years do significant numbers of seedlings become established on undisturbed forest floor. The role of damping-off fungi in the mortality of natural giant sequoia seedlings is not well known, but they are almost certainly a greater problem on thick litter than on mineral soil *(2,25).* After seedlings are established on more favorable seedbeds, a light covering of litter can moderate soil surface temperatures and retard drying (37).

Seedlings rarely become established in dense grass cover, probably because moisture is depleted in the surface soil early in the season (36).

Soil disturbance and increased availability of light and moisture resulting from past logging in some of the groves have led to establishment of several fine young-growth stands dominated by giant sequoia. Mechanical seedbed preparation is currently a legitimate regeneration option in some groves, although such treatment is inconsistent with management direction in most of the natural range of the species.

Of the various types of natural disturbances that may remove litter and bare mineral soil, fire is undoubtedly the most significant. Locally intense or highly consumptive fires are more effective than light surface fires or physical disturbance in promoting germination and subsequent seedling survival and early growth (17). The resulting short-lived friable soil condition facilitates seed penetration beneath the surface and root penetration following germination. Increased wettability in the surface soil layers resulting from high temperatures appears to improve water penetration and retention in the zones important for seeds and young seedlings. Fire also may kill some understory trees, thereby providing more light to speed the development (especially root penetration) of the shade-intolerant giant sequoia seedlings. Additional benefits include providing a surge of available nutrients, reducing populations of fungi potentially pathogenic to seedlings, and killing seeds and rootstocks of competing vegetation ***(17).***

On the other hand, the dark surface and possibly increased insolation resulting from fire may cause more desiccation and heat killing of giant sequoia seeds and seedlings at the surface. Also, populations of endomycorrhizal fungi may be severely reduced temporarily ***(17).*** And low-consumption fires, rather than reducing competing vegetation, may instead greatly stimulate germination and sprouting of shrubs. Partially burned litter, in terms of its suitability for successful seedling establishment, ranks between undisturbed forest floor and areas subjected to hot fires (38).

First-year giant sequoia seedlings established on treated-bulldozed or burned or both-areas were 30 to 150 times more numerous than those on undisturbed forest floor ***(17).*** Mortality of first-year seedlings during the 3 summer months on one treated area averaged 39 percent, with an additional 25 percent dying during the next 9 months. Desiccation was the primary cause of mortality in the summer. During a year of increased seasonal precipitation, mortality attributable to desiccation decreased, whereas that caused by insects increased to 25 percent of total mortality. Heat canker, damage by birds and mammals, and fungal attacks were of minor importance.

In the same study, direct mortality of first-year seedlings from insect predation ranged from 3 to 18 percent of all seedlings present. Some of the significant additional insect damage probably caused delayed mortality Largest seedling losses were in areas recently disturbed, especially by fire, probably because alternative food sources were reduced temporarily. Insects responsible for the damage were early instars of ***Pristocauthophilus pacificus***, a camel cricket, and larvae of the geometrids ***Sabulodes caberata*** and ***Pero behrensaria.***

Survival of sequoia seedlings for a 7- to 9-year period was 27 percent on areas subjected to a hot burn as opposed to 3.5 percent on other treated substrates. No seedlings survived in undisturbed areas. In another instance, only 1.4 percent of seedlings established following light surface burning were alive after two summers. Mortality slows substantially after the first 2 or 3 years. At the end of 3 years, surviving seedlings usually have root systems that penetrate the soil to depths that supply adequate moisture through the summer, or to about 36 cm (14 in).

Height growth of giant sequoia seedlings in the groves is relatively slow during the first few years, presumably because of competition for light and moisture from the larger trees. Seedlings 7 to 10 years old had grown at an average rate of about 4 cm (1.6 in) per year. Periodic annual height increment from 10 to 20 years was only 5 cm (2 in). Seedlings grew significantly faster on areas subjected to hot burns than they did elsewhere (17).

In contrast, giant sequoia seedlings in the open grow rapidly and, given an even start, can outgrow any associated tree species (fig. 3). Height growth up to 60 cm (24 in) per year is not uncommon *(9).*

Up to 2 or 3 years of age, seedlings growing in dense shade (less than 25 percent of full sunlight) survive about as well as others, but grow poorly and develop abnormally (37). At higher light levels, one study found moderate reduction in height growth compared with seedlings in full sunlight *(37),* whereas another study found no significant effect of reduced light on height growth ***(17).*** The adverse effects of shade on older giant sequoias are more conspicuous with respect to both mortality and growth reduction.

Vegetative Reproduction-Giant sequoias up to about 20 years of age may produce stump sprouts subsequent to injury (19). Unlike redwood ***(Sequoia sempervirens),*** older trees normally do not sprout from stumps or roots. A recent report *(30),* however, noted sprouts on two small stumps from suppressed trees about 85 years old. Giant sequoias of all ages may sprout from the bole when old branches are lost by fire or breakage *(17,36).*

Cuttings from juvenile donors root quickly and in high percentages (up to 94 percent) *(3,10,12).* Limited success has been achieved in rooting cuttings from older (30- or 40-year-old) trees *(3,10).* Differences in vegetative regeneration capacities between juvenile and older donors may be reduced if cuttings are taken at the time of budbreak, instead of during the dormant period *(24).*

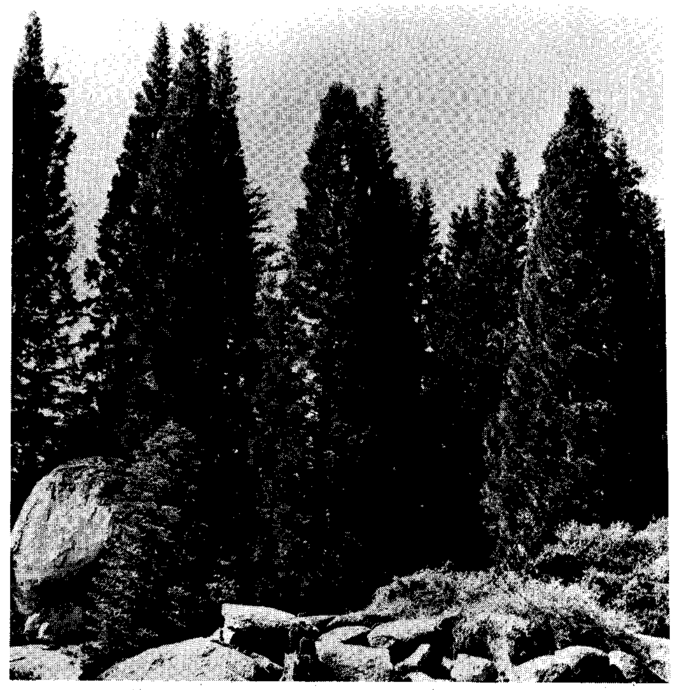

Figure *3-Young sequoias with characteristic conical crowns (Courtesy National Park Service).*

Sapling and Pole Stages to Maturity

Growth and Yield-One tree species has a greater diameter than giant sequoia, three grow taller, and one lives longer ***(16).*** In terms of volume, however, the giant sequoia is undisputedly the world's largest tree (fig. 4). The most massive specimen, the General Sherman tree, located in Sequoia National Park, has an estimated bole volume of 1486 m^3 (52,500 ft^3) ***(13).*** The greatest known height for the species is 94.5 m (310 ft), and the greatest mean d.b.h.-for the General Grant tree, in Kings Canyon National Park-is 881 cm (347 in). The indicated mean d.b.h. includes a large abnormal buttress; excluding this abnormality gives a more realistic estimate of the maximum mean d.b.h. for the species-approximately 823 cm (324 in) (13). Mature specimens commonly reach a diameter of 305 to 610 cm (120 to 240 in) above the butt swell and average about 76 m (250 ft) in height *(16).*

A notable characteristic of mature giant sequoias that contributes substantially to their great volume is the slight taper of the bole-a feature more prominent in this species than in any other Sierra

Figure *4-The General Grant tree (Courtesy National* **Park** *Service).*

Nevada conifer *(16).* In contrast, young open-grown giant sequoias taper markedly.

The greatest known age of a giant sequoia is 3,200 years, determined from a stump count of rings *(16).* Calculations based on increment borings yield age estimates of 2,000 to 3,000 years for many living trees.

Beyond the seedling stage, giant sequoia unhindered by an overstory continues to grow at least as well as associated species of the same age. In both clearcuts and group selection cuts on a high site in the central Sierra Nevada, it has outgrown other conifers in plantations up to 18 years of age. Furthermore, giant sequoia appears less susceptible than associated conifers to growth reductions caused by shrub competition *(18).* In a survey of California plantations up to 50 years of age in which giant sequoia had been planted, it outgrew other conifers (mostly ponderosa pine) in most instances in which species differed significantly in height or diameter growth. In the best plantations, giant sequoia averaged 0.5 to 0.7 m (1.6 to 2.3 ft) per year in height growth, and 1.3 to 2.0 cm (0.5 to 0.8 in) in diameter growth per year (9).

Yields of second-growth stands dominated by giant sequoia were found to equal or slightly exceed those of second-growth mixed-conifer stands on the same high sites (site index 53 m [175 ft] at base age 300 years) (6). Volumes at selected stand ages were as follows:

Stand age	Total volume	
yr	*m³/ha*	*fbm/acre (Scribner)*
18	2.6	188
31	83.1	5,938
63	339.3	24,237
86	757.1	54,077

In cubic measure, mean annual increment at age 86 was approximately 9 m^3/ha (126 ft^3/acre).

In contrast to the brittleness and low tensile strength of the wood of old-growth giant sequoia, young-growth trees have wood properties comparable to those of young-growth redwood *(5,28).* Because most groves have protected status, the potential of the species for fiber production within its natural range is limited. It has been planted widely and often successfully in many parts of the world, however. As in California plantations, on the proper sites it outperforms most other species *(7).* An 80-year-old giant sequoia plantation in Belgium, for example, grew at an average annual rate of 36 to 49 m^3/ha (514 to 700 ft^3/acre) *(20).* Many foresters see considerable potential for giant sequoia as a major timber-producing species of the world.

In old-growth groves, rapid height growth continues on the better sites for at least 100 years, producing dense conical crowns. At 400 years, trees range in height from about 34 to 73 m (110 to 240 ft). The rate of height growth declines beyond 400 years, and the typical tree levels off near 76 m (250 ft) at an age of 800 to 1,500 years *(17).*

Analysis of a large old-growth population showed an average d.b.h. of 48 cm (18.9 in) at 100 years, 132 cm (52.0 in) at 400 years, 219 cm (86.1 in) at 800 years, and 427 cm (168.0 in) at 2,000 years *(17).*

Although radial growth gradually decreases with age, volume increment generally is sustained into old age. The General Sherman tree, at an approximate age of 2,500 years, has a current radial growth rate at breast height of about 1 mm (0.04 in) per year *(16).* Average volume increment for this tree since 1931 has been estimated by different methods at 1.13 m^3 (40 ft^3) per year *(16)* and 1.44 m^3 (51 ft^3) per year *(13).* Therefore, the world's largest tree also may be, in terms of volume increment, the worlds fastest-growing tree. A related conclusion can be applied to the species: the enormous size attained by giant sequoia results not only from its longevity, but also—despite the apparent decadence of most veterans—from its continued rapid growth into old age *(16).*

Lower branches of giant sequoia die fairly readily from shading, but trees less than 100 years old retain most of their dead branches. Boles of mature trees generally are free of branches to a height of 30 to 45 m (98 to 148 ft) (36).

Rooting Habit-During the first few years, the root system of giant sequoia seedlings consists of a taproot with few laterals-a habit that facilitates survival during dry summers (36). The ratio of root length to shoot height during this period is about 2 to 2.5, with drier sites having higher ratios *(17).* After 6 to 8 years, lateral root growth predominates, and elongation of the taproot practically stops (36).

Roots of a mature tree commonly extend 30 m (100 ft) or more from the bole in well-drained soils, and occupy an area of 0.3 ha (0.7 acre) or more. Along drainage bottoms or edges of meadows, the radial extent of the root system may be no more than 12 to 15 m (40 to 50 ft). The largest lateral roots are usually no more than 0.3 m (1 ft) in diameter. Few roots extend deeper than 1 m (3 ft), and even less in areas with a high water table. Most of the abundant feeder roots are within the upper 0.6 m (2 ft) of soil. Concentrations of feeder roots often are high at the mineral soil surface *(16).*

Immature trees, both in the groves and in older plantings, are notably windfirm *(20).* Considering the shallowness of the root system and the great aboveground mass of large giant sequoias, it is remarkable that so many of these giants, especially leaners, remain standing for so long *(16).*

Root grafting is common in giant sequoia *(16,36).*

Reaction to Competition-Giant sequoia is shade intolerant throughout its life. Of its common coniferous associates, ponderosa pine is also intolerant, sugar pine is intermediate in tolerance, incerise-cedar is intermediate to tolerant, and California white fir is tolerant *(17).*

Fires or other disturbances that bare mineral soil and open the canopy characteristically benefit intolerant species, including giant sequoia, and move plant communities to earlier successional stages. In contrast, successful regeneration of giant sequoia in shade and in the absence of disturbance is less likely than that of any associated conifer *(17).*

Once established, and with adequate light, young giant sequoias maintain dominance over competitors through rapid growth. In dense thickets, however, trees stagnate and recover slowly if released (36). At maturity, giant sequoias are the tallest trees in the forest.

Although conspicuous in late successional communities dominated by California white fir, giant sequoia is not a true climax-stage species, because it fails to reproduce itself successfully in an undisturbecl forest. Instead, mature trees are successional relicts because they live for many centuries while continuing to meet their light requirements by virtue of their emergent crowns *(16).*

If various natural agents of disturbance—especially fire-operated freely, giant sequoia groves would consist of a roughly steady-state mosaic of even-aged groups of trees and shrubs in various stages of succession. The patchy nature of vegetational units would correspond to the pattern of disturbances. In the absence of disturbance, however, successional pathways converge toward a multilayered climax forest of pure California white fir (4). In fact, since the advent of fire suppression, density of California white fir has increased markedly, while densities of early successional stage species have decreased (26).

Damaging Agents-Fire is the most universal and probably most serious damaging agent of giant sequoia in its natural range (36). Seedlings and saplings of giant sequoia, like those of most other tree species, are highly susceptible to mortality or serious injury by fire. However, in those locations most favorable for successful establishment and early growth-that is, mineral soil seedbeds and well-lighted openings-fuels tend to be sparser and to accumulate more slowly than in adjacent forested areas. The more vigorous seedlings and saplings thus may be large enough to survive a light fire by the time one occurs.

Larger giant sequoias, because of their thick nonresinous bark and elevated crowns, are more resistant to fire damage than associated species. Nevertheless, repeated fires over the centuries sear through the bark of a tree's base, kill the cambium, and produce an ever-enlarging scar. Almost all of the larger trees have fire scars, many of which encompass a large percentage of the basal circumference *(16).* Few veterans have been killed by fire alone, but consequent reduction in supporting wood predisposes a tree to falling. Furthermore, fire scars provide entry for fungi responsible for root disease and heart rot (29). Decayed wood, in turn, is more easily consumed by subsequent fires. The net result is further structural weakening of the tree. In addition, fire scars have been cited as the main cause of dead tops, so common in older trees (35).

Lightning strikes, besides starting ground fires, sometimes knock out large portions of crowns or ignite dead tops. Mature trees seldom are killed by lightning, however *(16).*

Old giant sequoias most commonly die by toppling. Weakening of the roots and lower bole by fire and decay is primarily responsible *(16,29)*. The extreme weight of the trees, coupled with their shallow roots, increases the effects of this weakening, especially in leaning trees. Other causative factors include wind, water-softened soils, undercutting by streams, and heavy snow loads *(16)*.

Although diseases are less troublesome for giant sequoia in its natural range than for most other trees, the species is not as immune to disease as once assumed *(1)*. Heartwood of downed sequoia logs is extremely durable, sometimes remaining largely intact for thousands of years. The heartwood of living trees, however, is less resistant to decay *(2)*. At least nine fungi have been found associated with decayed giant sequoia wood. Of these, *Heterobasidion annosum*, *Armillaria mellea*, *Poria incrassata*, and *P. albipellucida* probably are most significant (29). The first two species also are serious root pathogens. Diseases generally do not kill trees past the seedling stage directly, but rather by contributing to root or stem failure. No other types of diseases, including seedling diseases, are known to be significant problems within the natural range of giant sequoia *(2)*. In nurseries and when planted outside its natural range, however, giant sequoia is highly susceptible to, and sometimes rapidly killed by, a number of organisms that may attack it at any stage from seedlings to mature trees *(1,25,39)*.

Insect depredations do not seriously harm giant sequoias older than about 2 years, although sometimes they may reduce vigor *(17)*. Carpenter ant *(Camponotus* spp.) galleries in decayed wood of tree bases evidently are not a direct cause of tree failure. Carpenter ants and other insects may facilitate the entry and spread of decay fungi, although the importance of such a role is not well known (29). Like disease injury, damage by insects is more significant outside the tree's natural range.

Of various types of human impact on giant sequoia in the groves *(16,17,29)*, the most significant has been fire exclusion. The damage caused by fire is outweighed by its benefits in perpetuating the species. Fire is necessary to create and maintain conditions favorable for regeneration *(17)*. Furthermore, the elimination of frequent fires has permitted a large buildup of both dead and live fuels, and an associated increase in the potential for catastrophic crown fires. Agencies responsible for managing most of the groves currently have programs designed to reintroduce fire into giant sequoia ecosystems *(15,27,31)*.

Special Uses

Within its natural range, giant sequoia is valued primarily for esthetic and scientific purposes. Outside this range, it is highly regarded as an ornamental in several parts of the United States and in numerous other countries *(16)*. Some interest has been expressed for utilizing it in Christmas tree plantations.

Genetics

Population Differences

Isolation of the groves, or populations, of giant sequoia has existed sufficiently long for a number of population differences to become discernible. A recent study *(12)* found differences among populations on the basis of isozyme analyses, percent germination, and frequency distribution of cotyledon numbers. Levels of heterozygosity differed between the northern and southern parts of the range. Provenance tests in West Germany showed differences in cold hardiness and early growth among populations *(14,20,23)*. Bark pattern of mature trees varies among groves (16). Somewhat surprisingly, however, genetic variability of giant sequoia is distinctly subdued when compared with that of other Sierra Nevada conifers and other trees in general *(21)*.

Races and Hybrids

No races of giant sequoia exist (36). Fourteen horticultural forms are known, only two of which are common *(16)*.

Hybridization of giant sequoia with redwood has been reported in the Soviet Union but is unconfirmed in the western literature *(19)*.

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