

Silvics of Giant Sequoia¹

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Abstract: Ecological relationships—including habitat and life history—of giant sequoia (*Sequoiadendron giganteum* [Lindl.] Buchholz) in natural stands are summarized. Such silvical information provides an important foundation for sound management of the species.

Silvics is defined by the Society of American Foresters (Ford-Robertson 1971, p. 240) as "the study of the life history and general characteristics of forest trees and stands, with particular reference to locality factors, as a basis for the practice of silviculture." Silvics deals primarily with ecological relationships of trees in natural stands. Consequently, the degree to which some specific subject areas of silvics apply directly to management of a species depends on the type of management—i.e., how far the management practice departs from natural stand processes.

Management of giant sequoia (*Sequoiadendron giganteum* [Lindl.] Buchholz) covers a wide spectrum. Because the species has broad public appeal and a restricted natural range, most groves of giant sequoia have been accorded protected status. In these groves, which generally are managed to maintain the functioning of natural processes, the silvical characteristics summarized in this paper are in large part directly applicable to management. Elsewhere, both within and outside the natural range of the species, giant sequoia is managed for other purposes, such as timber production. Where intensive timber management is practiced, for example, a manager might have limited interest in the characteristics of older trees, associated vegetation occurring in natural stands, and some aspects of natural regeneration (if regeneration is to be achieved through planting). Nevertheless, many aspects of the silvics of giant sequoia comprise an essential foundation for any form of sound management of the species and, as a bonus, tell the ecological story of a fascinating species.

HABITAT

Native Range

The natural range of giant sequoia is restricted to about 75 groves scattered over a 260-mi (420-km) belt, nowhere more

than about 15 mi (24 km) wide, extending along the west slope of the Sierra Nevada in central California (Hartesveldt and others 1975). The northern two-thirds of the range, from the American River in Placer County southward to the Kings River, takes in only eight widely disjunct groves. The remaining groves, including all the large ones, are concentrated between the Kings River and the Deer Creek Grove in southern Tulare County (Rundel 1971). Varying in size from 1 to 4000 acres (less than 1 to 1619 ha), the groves occupy a total area of 35,607 acres (14,410 ha) (Harvey and others 1980).

Climate

Giant sequoia is found in a humid climate characterized by dry summers. Mean annual precipitation in the groves varies from about 35 to 55 inches (900 to 1400 mm), with high year-to-year variation. Less than 1.2 inches (30 mm) usually falls between June 1 and September 30. Most of the precipitation falls in the form of snow, between October and April. Mean annual snowfall ranges from 144 to 197 inches (367 to 500 cm), and snow depths of 6.6 ft (2 m) or greater are common in midwinter (Rundel 1969).

Mean daily maximum temperatures for July for typical groves are 75 to 84 ° F (24 to 29 ° C). Mean minimum temperatures for January vary from 34 to 21 ° F (+1 to -6 ° C). Extremes are about -12 and 104 ° F (-24 and 40 ° C) (Rundel 1969, Stark 1968a).

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 (Rundel 1972).

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 (Hartesveldt and others 1975, Schubert and Beetham 1962).

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; and fine-loamy, mixed, mesic Ultic Haploxeralfs. 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 (Mallory 1981).

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

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habitats within a grove. Total acreage of these productive sites is small, however. Relatively shallow and rocky soils support vigorous individuals, some quite large, wherever the trees can become established and where underground water is available to maintain them (Hartesveldt and others 1975, Rundel 1969).

Soil pH ranges mostly from 5.5 to 7.5, with an average of about 6.5 (Mallory 1981). Long-term site occupancy by giant sequoia appears to develop a soil of high fertility, good base status, and low bulk density (Zinke and Crocker 1962).

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 (Schubert and Beetham 1962). One study has shown more available soil moisture within a grove, possibly associated with subterranean flow from higher elevations, than in adjacent forested areas (Rundel 1972). 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 (Hartesveldt and others 1975).

Elevations of the groves generally range from 4600 to 6600 ft (1400 to 2000 m) in the north, and 5600 to 7050 ft (1700 to 2150 m) in the south. The lowest natural occurrence of the species is 2720 ft (830 m) and the highest is 8860 ft (2700 m). The eight northern groves are all on slopes of a generally southern aspect. Between the Kings 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 (Rundel 1969).

Associated Forest Cover

Giant sequoia groves lie wholly within the Sierra Nevada mixed conifer type---SAF (Society of American Foresters) forest cover type 243 (Eyre 1980). 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 (Rundel 1971). Nowhere does giant sequoia grow in a pure stand, although in a few small areas it approaches this condition (Hartesveldt and others 1975).

Based on density or canopy coverage, groves typically are dominated strongly by California white fir (*Abies concolor* var. *lowiana* [Gord.] Lemm.), despite the presence of emergent individuals of giant sequoia that overtop the canopy. Sugar pine (*Pinus lambertiana* Dougl.) is a characteristic associate. Incense-cedar (*Libocedrus decurrens* Torr.) at low elevations and California red fir (*Abies magnifica* A. Murr.) at high elevations may rival California white fir for dominance. Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and California black oak (*Quercus kelloggii* Newb.) often occupy drier sites within the grove boundaries. Trees less commonly associated with giant sequoia include Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), Pacific yew (*Taxus brevifolia* Nutt.), Pacific dogwood (*Cornus nuttallii* Audubon), California hazel (*Corylus cornuta* var. *californica* [A. DC.] Sharp),

white alder (*Alnus rhombifolia* Nutt.), Scouler willow (*Salix scoulerana* Barratt ex Hook.), bigleaf maple (*Acer macrophyllum* Pursh), bitter cherry (*Prunus emarginata* Dougl. ex Eaton), and canyon live oak (*Quercus chrysolepis* Liebm.).

Shrub species most often found in giant sequoia groves are bush chinquapin (*Castanopsis sempervirens* [Kell.] Dudl.), mountain misery (*Chamaebatia foliolosa* Benth.), mountain whitethorn (*Ceanothus cordulatus* Kell.), littleleaf ceanothus (*C. parvifolius* [Wats.] Trel.), deerbrush (*C. integerrimus* H. & A.), snowbrush (*C. velutinus* Dougl. ex Hook.), greenleaf manzanita (*Arctostaphylos patula* Greene), western azalea (*Rhododendron occidentale* [T. & G.] Gray), *Ribes* spp., *Rosa* spp., and *Rubus* spp. (Hartesveldt and others 1975, Harvey and others 1980, Rundel 1971, Schubert and Beetham 1962).

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 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 (Rundel 1971).

LIFE HISTORY

Reproduction and Early Growth

Flowering and Fruiting

Male and female cone buds form on the same tree 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 as the 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, 2 to 3.5 inches (5 to 9 cm) in length, yield an average of 200 seeds each (Hartesveldt and others 1975, Harvey and others 1980, Schubert and Beetham 1962).

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 (Hartesveldt and others 1975, Schubert and Beetham 1962).

Giant sequoias have serotinous cones which, at maturity, may remain attached to the stems without commencing seed dissemination. For 20 years or more, cones may retain viable

seeds and continue to photosynthesize and grow, their peduncles producing annual rings which can be used to determine cone age (Hartesveldt and others 1975, Schubert and Beetham 1962).

A typical mature giant sequoia produces an average of 1500 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 (Hartesveldt and others 1975, Harvey and others 1980).

Estimates of percent germination of seeds removed from green cones range from about 20 to 40 percent (Fins 1981, Harvey and others 1980, Stark 1968b). 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 (Hartesveldt and others 1975). Artificial stratification of seeds for 60 days or more resulted in faster germination, but not in higher germination percent (Fins 1981).

Browning of 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* LeConte, 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 will open several scales at a time, beginning during late summer and fall, and continuing for 6 months to 1 year. Cone and seed insects other than *Phymatodes* have only a minor impact on seed production (Harvey and others 1980).

The second animal having a significant role in giant sequoia regeneration is the chickaree or Douglas squirrel (*Tamiasciurus douglasii*). 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 (Harvey and others 1980).

The chickaree prefers cones 2 to 5 years old, whereas *Phymatodes* is most 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 400,000 seeds per acre (1,000,000/ ha) per year (Harvey and others 1980).

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, 8,000,000 per acre (20,000,000/ ha) (Harvey and others 1980). This increased seedfall coincides both spatially and temporally with fire-related seedbed conditions favorable for seed germination and seedling survival.

Giant sequoia seeds are well adapted for wind dispersal. They are light (average 91,000/lb [200,000/kgD and winged, and fall in still air at a rate of 4 to 6 ft (1.2 to 1.8 m) per second. Winds common in late summer and winter storms in the Sierra Nevada can disperse seeds more than 0.25 mi (0.4 km) from the tall crowns of mature trees (Hartesveldt and others 1975, Schubert and Beetham 1962).

Birds and mammals exert a negligible effect on giant sequoia seeds on the ground. Because they are small and contain little energy, sequoia seeds consistently rank at or near the bottom in food preference tests that include seeds of associated species (Harvey and others 1980, Stark 1968b).

Seedling Development

Natural reproduction in giant sequoia is an unusually tenuous process. Of the enormous numbers of seeds shed each year, few encounter the combination of conditions necessary for seedling establishment.

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 zero in 20 days. Seeds collected from the forest floor showed an average viability of 1 percent (Harvey and others 1980).

Seed dormancy is not evident in giant sequoia, so surviving seeds germinate as soon as conditions are favorable (Harvey and others 1980). 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 about 0.4 inch (1 cm), 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 (Stark 1968b). Because of rapid percolation, however, 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 germi-

nation -extension of the radicle -sometimes takes place beneath the snow (Hartesveldt and others 1975).

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 (Harvey and others 1980, Schubert and Beetham 1962). 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 (Bega 1981), but they are almost certainly a greater problem on thick litter than on mineral soil. After seedlings are established on more favorable seedbeds, a light covering of litter can moderate soil surface temperatures and retard drying (Stark 1968a).

Seedlings rarely become established in dense grass cover, probably because moisture is depleted in the surface soil early in the season (Schubert and Beetham 1962).

Soil disturbance, along with increased availability of light and moisture, resulting from early logging in some of the groves has 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 (Harvey and others 1980). The resulting short-lived friable soil condition facilitates seed penetration beneath the surface and root penetration after 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 (Harvey and others 1980).

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 (Harvey and others 1980). 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 (Stark 1968b).

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

(Harvey and others 1980). 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 due to 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 *Pristocaulophilus pacificus* Thomas, a camel cricket, and larvae of the geometrids *Sabulodes caberata* Gn. and *Pero behrensaria* Packard.

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 14 inches (36 cm).

Height growth of giant sequoia seedlings in the groves is relatively slow during the first few years, presumably due to competition for light and moisture from the larger trees. Seedlings 7 to 10 years old grew at an average rate of about 1.6 inches (4 cm) per year. Periodic annual height increment from 10 to 20 years was only 2 inches (5 cm). Seedlings grew significantly faster on areas subjected to hot burns than they did elsewhere (Harvey and others 1980). In contrast, giant sequoia seedlings in the open grow rapidly, and, given an even start, can outgrow any associated tree species. Height growth up to 24 inches (60 cm) per year is not uncommon (Fins 1979).

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 (Stark 1968a). At higher light levels, one study found moderate reduction in height growth compared with seedlings in full sunlight (Stark 1968a), whereas another study found no significant effect of reduced light on height growth (Harvey and others 1980). 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 after injury (Libby 1981). Unlike redwood (*Sequoia sempervirens* [D. Don] Endl.), older trees normally do not sprout from stumps or roots. Piirto and others (1986), however, reported 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 (Harvey and others 1980, Schubert and Beetham 1962).

Cuttings from juvenile donors root quickly and in high percentages (94 percent average) (Fins 1982).

Sapling and Pole Stage to Maturity

Growth and Yield

One tree species has a greater diameter than giant sequoia, three grow taller, and one lives longer (Hartesveldt and others 1975). In terms of volume, however, the giant sequoia is undisputedly the world's largest tree. The most massive specimen, the General Sherman tree, located in Sequoia National Park, has an estimated bole volume of 52,500 ft³ (1490 M³) (Flint 1981). The greatest known height for the species is 310 ft (94.5 m), and the greatest mean diameter at breast height (d.b.h.)---for the General Grant tree, in Kings Canyon National Park---is 28.9 ft (8.8 m). 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 27.0 ft (8.2 m) (Flint 1981). Mature specimens commonly reach a diameter of 10 to 20 ft (3 to 6 m) above the butt swell and average about 250 ft (76 m) in height (Hartesveldt and others 1975).

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 Nevada conifer (Hartesveldt and others 1975). In contrast, young open-grown giant sequoias taper markedly.

The greatest known age of a giant sequoia is 3200 years, determined from a stump count of rings (Hartesveldt and others 1975). Calculations based on increment borings yield age estimates of 2000 to 3000 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 a survey of California plantations up to 50 years old 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 1.6 to 2.3 ft (0.5 to 0.7 m) per year in height growth, and 0.5 to 0.8 inch (1.3 to 2.0 cm) in diameter growth per year (Fins 1979).

The growth and yield and wood properties of young-growth giant sequoia are discussed in detail in other papers in these proceedings (Dulitz 1986, Piirto 1986). Suffice it to say here that the species has been planted widely and often successfully in many parts of the world. Not only is it highly regarded as an ornamental, but many foresters see considerable potential for giant sequoia as a major timber-producing species of the world (Libby 1982).

In old-growth groves, rapid height growth continues on better sites for at least 100 years, producing dense conical crowns. At 400 years, trees range in height from about 110 to 240 ft (34 to 73 m). The rate of height growth declines beyond

400 years, and the typical tree levels off near 250 ft (76 m) at an age of 800 years to 1500 years (Harvey and others 1980).

Analysis of a large old-growth population showed average d. b. h. of 1.6 ft (0.5 m) at 100 years, 4.3 ft (1.3 m) at 400 years, 7.2 ft (2.2 m) at 800 years, and 14.0 ft (4.3 m) at 2000 years (Harvey and others 1980).

Although radial growth gradually decreases with age, volume increment generally is sustained into old age. The General Sherman tree, at an approximate age of 2500 years, has a current radial growth rate at breast height of about 0.04 inch (1 mm) per year (Hartesveldt and others 1975). Average volume increment for this tree since 1931 has been estimated by different methods at 40 ft³ (1.13 m³) per year (Hartesveldt and others 1975) and 51 ft³ (1.44 m³) per year (Flint 1981). Therefore, the world's largest tree also may be, in terms of volume increment, the world's 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 (Hartesveldt and others 1975).

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 (Schubert and Beetham 1962). The ratio of root length to shoot height during this period is about 2 to 2.5, with drier sites having higher ratios (Harvey and others 1980). After 6 to 8 years, lateral root growth predominates, and elongation of the taproot practically stops (Schubert and Beetham 1962).

Roots of a mature tree commonly extend 100 ft (30 m) or more from the bole in well-drained soils, and occupy an area of 0.7 acre (0.3 ha) or more. Along drainage bottoms or edges of meadows, the radial extent of the root system may be no more than 40 to 50 ft (12 to 15 m). The largest lateral roots are usually no more than 1 ft (0.3 m) in diameter. Few roots extend deeper than 3 ft (1 m) and even less in areas with a high water table. Most of the abundant feeder roots are within the upper 2 ft (0.6 m) of soil. Concentrations of feeder roots often are high at the mineral soil surface (Hartesveldt and others 1975).

Immature trees, both in the groves and in older plantings, are notably windfirm (Libby 1982). Considering the shallowness of the root system and the great above-ground mass of large mature giant sequoias, however, it is remarkable that so many of them---especially leaners---remain standing for so long (Hartesveldt and others 1975).

Root grafting is common in giant sequoia (Hartesveldt and others 1975, Schubert and Beetham 1962).

Reaction to Competition

Giant sequoia is shade-intolerant throughout its life. Of its common coniferous associates, ponderosa pine also is intolerant, sugar pine is intermediate in tolerance, incense-cedar is intermediate to tolerant, and California white fir is tolerant (Harvey and others 1980).

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 (Harvey and others 1980). Also, young seedlings cannot tolerate low soil moisture, including that induced by competing vegetation.

Once established and with adequate light, young giant sequoias maintain dominance over competitors through rapid growth, and at maturity are the tallest trees in the forest. In dense thickets, however, young trees stagnate and recover slowly if released (Schubert and Beetham 1962).

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 undisturbed 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 (Hartesveldt and others 1975).

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 (Bonnicksen and Stone 1981). Since the advent of fire suppression, density of California white fir has in fact increased markedly, while densities of early successional stage species have decreased (Parsons and DeBenedetti 1979).

Damaging Agents

Fire is the most universal and probably most serious damaging agent of giant sequoia in its natural range (Schubert and Beetham 1962). 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 are associated species. Nevertheless, repeated fires over the centuries sear through the bark at 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 much of the basal circumference (Hartesveldt and others 1975). 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 heartrot (Piirto and others 1984). Decayed wood, in turn, is more easily consumed by subsequent fires. The net result is further structural weaken-

ing of the tree. In addition, fire scars have been cited as the main cause of dead tops, so common in older trees (Rundel 1973).

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 (Hartesveldt and others 1975).

Old giant sequoias most commonly die by toppling. Weakening of the roots and lower bole by fire and decay is primarily responsible (Hartesveldt and others 1975, Piirto and others 1984). 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 (Hartesveldt and others 1975).

Disease and insect relationships are discussed by Parmeter (1986).

Of various types of human impact on giant sequoia in the groves (Hartesveldt and others 1975, Harvey and others 1980, Piirto and others 1984), the most significant has been fire exclusion. The damage caused by fire is outweighed by its benefits in perpetuating the species. As indicated earlier, fire is necessary to create and maintain conditions favorable for regeneration (Harvey and others 1980). Furthermore, the infrequency of 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 have programs designed to reintroduce fire into giant sequoia ecosystems. An important part of these proceedings consists of descriptions by agency representatives of such fire management activities and other aspects of their overall management strategy for giant sequoia (Benson 1986, Harrison 1986, Heald 1986, Parsons and Nichols 1986, Rogers 1986).

REFERENCES

- Bega, Robert V. Pacific Southwest Forest and Range Experiment Station, Berkeley, CA. [Telephone conversation with C. Phillip Weatherspoon]. January 1981.
- Benson, Norman J. Management of giant sequoia on Mountain Home Demonstration State Forest. In: Weatherspoon, C. Phillip; Iwamoto, Y. Robert; Piirto, Douglas D., tech. coords. Proceedings of the workshop on management of giant sequoia; May 24-25, 1985; Reedley, California. Gen. Tech. Rep. PSW-95. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 1986:30-31.
- Bonnicksen, Thomas M.; Stone, Edward C. The giant sequoia-mixed conifer forest community characterized through pattern analysis as a mosaic of aggregations. *Forest Ecol. and Manage.* 3: 307-328; 1981.
- Dulitz, David. Growth and yield of giant sequoia. In: Weatherspoon, C. Phillip; Iwamoto, Y. Robert; Piirto, Douglas D., tech. coords. Proceedings of the workshop on management of giant sequoia; May 24-25, 1985; Reedley, California. Gen. Tech. Rep. PSW 95. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 1986: 14-16.
- Eyre, F. H., ed. Forest cover types of the United States and Canada. Washington, DC: Society of American Foresters; 1980. 148 p.
- Fins, Lauren. Genetic architecture of giant sequoia. Berkeley: University of California; 1979. 237 p. Ph.D. Dissertation.

- Fins, Lauren. Seed germination of giant sequoia. *Tree Planters' Notes* 32(2): 3-8; 1981.
- Fins, L.; Libby, W. J. Population variation in *Sequoiadendron*: seed and seedling studies, vegetative propagation, and isozyme variation. *Silvae Genetica* 31(4): 102-110; 1982.
- Flint, Wendell D. [Letter to C. Phillip Weatherspoon]. 1981 March 9. 1 leaf. Located at: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station, Redding, CA.
- Ford-Robertson, F. C., ed. Terminology of forest science, technology, practice and products. Washington, DC: Society of American Foresters; 1971. 349 p.
- Harrison, Wayne. Management of giant sequoia at Calaveras Big Trees State Park. In: Weatherspoon, C. Phillip; Iwamoto, Y. Robert; Piirto, Douglas D., tech. coords. Proceedings of the workshop on management of giant sequoia; May 24-25, 1985; Reedley, California. Gen. Tech. Rep. PSW-95. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 1986: 40-42.
- Hartesveldt, Richard J.; Harvey, H. Thomas; Shellhammer, Howard S.; Stecker, Ronald E. The giant sequoia of the Sierra Nevada. Washington, DC: U.S. Department of the Interior, National Park Service; 1975. 180 p.
- Harvey, H. Thomas; Shellhammer, Howard S.; Stecker, Ronald E. Giant sequoia ecology. *Sci. Monogr. Series* 12. Washington, DC: U.S. Department of the Interior, National Park Service; 1980. 182 p.
- Heald, Robert C. Management of giant sequoia at Blodgett Forest Research Station. In: Weatherspoon, C. Phillip; Iwamoto, Y. Robert; Piirto, Douglas D., tech. coords. Proceedings of the workshop on management of giant sequoia; May 24-25, 1985; Reedley, California. Gen. Tech. Rep. PSW-95. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 1986: 37-39.
- Libby, W. J. Some observations on *Sequoiadendron* and *Calocedrus* in Europe. *California Forestry and Forest Products* 49. Berkeley: University of California, Forest Products Laboratory; 1982. 12 p.
- Libby, William J., University of California, Berkeley. [Telephone conversation with C. Phillip Weatherspoon]. February 1981.
- Mallory, James I., California State Cooperative Soil-Vegetation Survey, Redding, CA. [Telephone conversation with C. Phillip Weatherspoon]. February 1981.
- Parmeter, John R., Jr. Diseases and insects of giant sequoia. In: Weatherspoon, C. Phillip; Iwamoto, Y. Robert; Piirto, Douglas D., tech. coords. Proceedings of the workshop on management of giant sequoia; May 24-25, 1985; Reedley, California. Gen. Tech. Rep. PSW-95. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 1986: 11-13.
- Parsons, David J.; DeBenedetti, Steven H. Impact of fire suppression on a mixed-conifer forest. *Forest Ecol. and Manage.* 2: 21-33; 1979.
- Parsons, David J.; Nichols, H. Thomas. Management of giant sequoia in the National Parks of the Sierra Nevada, California. In: Weatherspoon, C. Phillip; Iwamoto, Y. Robert; Piirto, Douglas D., tech. coords. Proceedings of the workshop on management of giant sequoia; May 24-25, 1985; Reedley, California. Gen. Tech. Rep. PSW-95. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 1986: 26-29.
- Piirto, Douglas D. Wood of giant sequoia: properties and unique characteristics. In: Weatherspoon, C. Phillip; Iwamoto, Y. Robert; Piirto, Douglas D., tech. coords. Proceedings of the workshop on management of giant sequoia; May 24-25, 1985; Reedley, California. Gen. Tech. Rep. PSW-95. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 1986: 19-23.
- Piirto, Douglas D.; Hawksworth, W. John; Hawksworth, Marjorie M. Giant sequoia sprouts. *J. For.* 84 (9): 24-25; 1986.
- Piirto, Douglas D.; Wilcox, W. Wayne; Parmeter, John R.; Wood, David L. Causes of uprooting and breakage of specimen giant sequoia trees. *Bull.* 1909. Berkeley: Division of Agriculture and Natural Resources, University of California; 1984. 14 p.
- Rogers, Robert R. Management of giant sequoia in the National Forests of the Sierra Nevada, California. In: Weatherspoon, C. Phillip; Iwamoto, Y. Robert; Piirto, Douglas D., tech. coords. Proceedings of the workshop on management of giant sequoia; May 24-25, 1985; Reedley, California. Gen. Tech. Rep. PSW-95. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 1986:32-36.
- Rundel, Philip W. The distribution and ecology of the giant sequoia ecosystem in the Sierra Nevada, California. Durham, NC: Duke University; 1969. 204 p. Ph.D. Dissertation.
- Rundel, Philip W. Community structure and stability in the giant sequoia groves of the Sierra Nevada, California. *Am. Midland Nat.* 85(2):478-492; 1971.
- Rundel, Philip W. Habitat restriction in giant sequoia: the environmental control of grove boundaries. *Am. Midland Nat.* 87(1): 81-99; 1972.
- Rundel, Philip W. The relationship between basal fire scars and crown damage in giant sequoia. *Ecology* 54(1): 210-213; 1973.
- Schubert, Gilbert H. (revised by N. M. Beetham). Silvical characteristics of giant sequoia. Tech. Pap. 20. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 1962. 16 p.
- Stark, N. The environmental tolerance of the seedling stage of *Sequoiadendron giganteum*. *Am. Midland Nat.* 80(1): 84-95; 1968a.
- Stark, N. Seed ecology of *Sequoiadendron giganteum*. *Madrone* 19(7): 267-277; 1968b.
- Weatherspoon, C. Phillip. Giant sequoia (*Sequoiadendron giganteum* [Lindl.] Buchholz). In: *Silvics of North America*. Washington, DC: U.S. Department of Agriculture; [In press].
- Zinke, Paul J.; Crocker, Robert L. The influence of giant sequoia on soil properties. *Forest Sci.* 8(1): 2-11; 1962.