Sequoia *sempervirens* (D. Don) Endl.

Redwood

Taxodiaceae Redwood family

David F. Olson, Jr., Douglass F. Roy, and Gerald A. Walters

Redwood (Sequoia *sempervirens*), also called coast redwood and California redwood, is native to the central and northern California coast, a region of moderate to heavy winter rain and summer fog so vital to this tree. It is one of three important North American trees of the family Taxodiaceae. Close relatives are the giant sequoia (Sequoiadendron giganteum) of the Sierra Nevada in California and the baldcypress (Taxodium distichum) of the southeastern states.

Habitat

Native Range

The range of redwood (fig. 1) extends southward from two groves on the Chetco River in the extreme southwest corner of Oregon (lat. 42" 09' N.), to Salmon Creek Canyon in the Santa Lucia Mountains of southern Monterey County, CA (lat. 35" 41' N.). This redwood belt is an irregular coastal strip about 724 km (450 mi) long and generally 8 to 56 km (5 to 35 mi) wide (39). Within this region, redwood trees grow now, or could grow, on an estimated 647 500 ha (1.6 million acres). Of this area, 260 200 ha (643,000 acres) comprise the commercial coast redwood forest type (more than 50 percent redwood stocking). The remainder of the area contains parks, other forest types containing redwood, and recently logged redwood type (12). The old-growth redwood, much of which is in State and National Parks, occupies less than 80 940 ha (200,000 acres) (36). The old-growth in commercial forests will be harvested within the next few decades. A major discontinuity splits the type in southern Humboldt County, CA. South of Sonoma County, CA, redwoods grow in detached and irregular areas to the southern extremity of the range (38,391.

Climate

The mild climate of the redwood forest region can be classed broadly as super-humid or humid. Mean annual temperatures vary between 10" and 16" C (50° and 60" F). Differences between mean annual maximum and mean annual minimum temperatures

The authors are Supervisory Research Forester (retired) and Research Forester (deceased), and Research Forester, Pacific Southwest Forest and Range Experiment Station, Berkeley, CA.

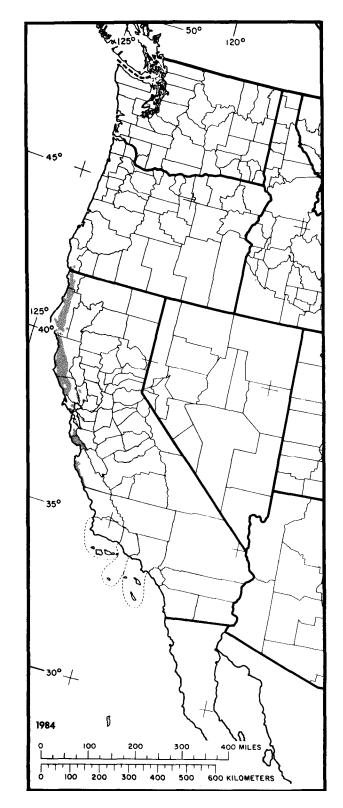


Figure 1-l'he native range of redwood.

vary from -12" C (10° F) for coastal points to -1" C (30° F) for the eastern edge of the redwood type. Temperatures rarely drop below -9" C (15° F) or rise above 38" C (100° F). The frost-free period varies from 6 to 11 months (34).

Annual precipitation varies between 640 and 3100 mm (25 and 122 in) and is mostly winter rain, although snow sometimes covers the highest ridges. Generally, January is the wettest month and July is the driest. With substantial precipitation in all months except summer, only slight summer drought on deep soils, and mild winters, the climate is productive, and some of the world's grandest forests are indigenous to it (34).

The frequent summer fogs that blanket the redwood region seem to be more significant than the amount of precipitation in delineating the redwood type. The major effect of fog is to decrease water loss from evaporation and transpiration. An additional effect of condensation and fog drip from tree crowns is an increased soil moisture supply during the dry summers (1). The natural range of redwood is limited to areas where heavy summer fogs from the ocean provide a humid atmosphere, although its successful growth in plantations or amenity plantings is not as limited. Redwood is among the most successful trees in the Central Valley of California, and at low elevations in the Sierra Nevada. It grows well at considerable distance from the ocean in New Zealand, France, Spain, and elsewhere (26,27).

Soils and Topography

The parent rock material of the redwood region is largely massive marine sandstone formed in the Tertiary and Upper Mesozoic periods. Considerable shale and lesser amounts of Mesozoic limestones and Franciscan slates, cherts, limestones, and sandstones also are present, and schists are fairly common in some localities.

High-site soils for redwood consist of Xerochrepts, Haploxerults, and Haplohumults of the Hugo, Josephine, Melbourne, Empire, Sites, and Larabee series (orders Inceptisols and Ultisols) and associated alluvial soils. The high-site residual soils have been derived from either consolidated or soft sedimentary rocks. In the Coastal Forest Practice Act District of California, which encompasses the natural range of redwood, the Hugo soil series predominates. In current soil taxonomic terms, the Hugo series is a Typic Distrochrept of the order Inceptisols (45,46). It is a member of a loamy-skeletal, mixed, mesic family, typically pale brown, moderately acid, gravelly (sandy> clay loam A horizons, and pale brown, strongly acid gravelly (sandy> clay loam B horizons. Limits of redwood forests sometimes are determined by soil types. For example, redwood does not grow on soils having high amounts of magnesium and sodium.

Fertility of soils under redwood stands has been studied by measuring the replaceable calcium concentration, expressed in equivalents, present in a square meter (10.76 ft²) to a depth of 30 cm (12 in). This measure indicates fertility best because it separates nutritional properties from other environmental effects. Equivalents ranged from 4 to more than 80, with 63 appearing to be optimum (49).

Soil nutrient levels that were observed to change during harvest of old-growth or second-growth redwood recovered to nearly original values during regrowth. In the one-meter soil profile, carbon, nitrogen, phosphorus, and exchangeable potassium and sodium increased in amount, while calcium decreased (52). Soil organic matter showed a small decline and recovery after logging (18).

The lowest amount of soil moisture available during the year has been related to minimum basal area growth of redwood stands. Basal area is used as an index of stand development. This minimum available soil moisture, expressed as a percentage of storage capacity, ranged between 18 and 86, with 62 correlated with maximum basal area (49).

The redwood region, generally, is characterized by irregular ridges oriented northwest to southeast with deep narrow valleys. Consequently, the principal streams drain to the northwest. Much of the terrain is rough, steep, and extremely dissected both by major streams and smaller drainages. Redwoods grow from sea level to about 915 m (3,000 ft) elevation, but most are found between 30 and 760 m (100 and 2,500 ft). The best stands have developed on flats and benches along the larger streams, on moist coastal plains, river deltas, moderate westerly slopes, and valleys opening toward the sea.

Although most redwood stands are close to the ocean, redwood does not tolerate ocean winds, and considerable evidence suggests that it is sensitive to ocean salts carried inland during storms. Usually redwoods do not grow on hillsides that face the ocean. The absence of redwood near the ocean also may be caused by the absence of forest soils of sufficient depth and fertility to support redwood.

Redwoods are smaller and give way to other species as altitude, dryness, and slope increase. In the north, redwoods clothe all exposures and reach their maximum development as forest trees. In the southern part of the range, redwoods are restricted to western or northern exposures, and at the extreme southern extension they are restricted almost entirely to the bottoms of narrow canyons that cut through steep foothills abutting the ocean. Trees near the mouths of these canyons often are exposed to onshore winds and frequently have flat tops with dead limbs on the windward side. This effect has been attributed to the trees' inability to replace moisture lost through desiccation by winds.

On alluvial flats, where redwoods reach their maximum development, soils have been built up by deposits of sediment from successive floods. In one area the ground level has been raised 3.4 m (11 ft) in 700 years. In another, repeated flooding in the past 1,000 years deposited nearly 9.1 m (30 ft) of silt and gravel around the bases of many large redwood trees. Deposits from a single flood have been as deep as 76 cm (30 in). Redwoods adapt to the new ground levels by originating new and higher root systems (43,51). This flooding generally kills competing species and thereby allows redwood to maintain nearly pure stands on such plains.

Associated Forest Cover

Redwood is a principal species in only one forest cover type, Redwood (Society of American Foresters Type 232) (42), but is found in three other Pacific Coast types, Pacific Douglas-Fir (Type 229), Port-Orford-Cedar (Type 231), and Douglas-Fir-Tanoak-Pacific Madrone (Type 234).

Pure stands of redwood are found only on some of the best sites, usually the moist river flats and gentle slopes below 305 m (1,000 ft). Although redwood is a dominant tree throughout its range, generally it is mixed with other conifers and broad-leaf trees.

Douglas-fir **(Pseudotsuga menziesii)** is well distributed throughout most of the redwood type. Distributions of other conifer associates are more limited. Significant species on the coastal side of the redwood type are grand fir (*Abies grandis*) and western hemlock (*Tsuga heterophylla*) north from northern Sonoma County, CA, and Sitka spruce (*Picea sitchensis*) north from the vicinity of Humboldt Bay, CA.

Conifers associated less commonly on the coastal side of the redwood type are Port-Orford-cedar (Chamaecyparis lawsoniana), Pacific yew (Taxus brevifolia), western redcedar (Thuja plicata), and California torreya (Torreya californica). Other conifers found with redwood include Gowen cypress (Cupressus goveniana) and several species of pine, including bishop pine (Pinus muricata), knobcone pine (P. attenuata), lodgepole pine (P. contorta), Monterey pine (P. radiata), and sugar pine (P. lambertiana).

The two hardwoods most abundant and generally distributed in the redwood region are tanoak

(Lithocarpus densiflorus) and Pacific madrone (Arbutus menziesii). Other hardwoods found with redwood include vine maple (Acer circinatum), bigleaf maple (A. macrophyllum), red alder (Alnus rubra), giant chinkapin (Castanopsis chrysophylla), Oregon ash (Fraxinus latifolia), Pacific bayberry (Myrica californica), Oregon white oak (Quercus garryana), cascara buckthorn (Rhamnus purshiana), willows (Salix spp.), and California-laurel (Umbellularia californica).

Of the great variety of lesser vegetation found in association with redwood, these species are especially common: bracken (*Pteridium aquilinum* var. *lanuginosum*), sword fern (*Polystichum munitum*), salal (*Gaultheria shallon*), blueblossom (*Ceanothus thyrsiflorus*), California huckleberry (*Vaccinium ovatum*), Pacific rhododendron (*Rhododendron macrophyllum*), salmonberry (*Rubus spectabilis*), coyotebrush (*Baccharis pilularis*), and snowbrush (*Ceanothus velutinus*).

Life History

Reproduction and Early Growth

Flowering and Fruiting-Redwood is monoecious; inconspicuous male and female flowers are borne separately on different branches of the same tree. The ovulate conelets grow into broadly oblong cones (10). Redwood female strobili become receptive and pollen sheds between late November and early March, although flowering usually is over by the end of January Weather conditions during pollination may directly affect seed quality Continuous rains during flowering wash pollen from the male strobili and little pollen may reach the receptive female strobili. Dry periods during pollination permit better pollen dispersal and improve seed viability

Redwood cones are terminal and are 13 to 29 mm (0.5 to 1.1 in) long. They mature in autumn of the first year after flowering and are open from early September until late December. Although cones persist for several months, they open and shed seeds soon after ripening.

Seed Production and Dissemination-Redwoods start to bear seeds when 5 to 15 years old (8). One study showed that seed viability increased with the age of parent trees (38,391. Maximum seed viability was reached when trees were more than 250 years old. Seeds produced by trees younger than 20 years generally were less than 1 percent viable, and seeds from trees more than 1,200 years old were not more than 3 percent viable. Redwoods produce abundant seeds almost every year. Even trees in the intermediate crown class often produce seed crops. Fair to abundant crops were produced in 5 consecutive years in north coastal California (8). Cones often are rare, however, or nonexistent on large areas for many years in stands in Mendocino County, CA (central part of the range). Large mature stands on Maui, HI, have few or no cones or pollen (27).

Trees with new, narrow crowns resulting from sprouting of dormant buds after fire has killed the crown produce few cones during the first 4 years after the fire. About one-half such narrow-crowned trees, locally called fire-columns, bear cones in the fifth year, and almost all produce cones by the seventh or eighth year.

The germination rate of redwood seeds is usually low. Poor germination often results from a low percentage of sound seeds (less than 15 percent) rather than from dormancy. When obviously defective seeds are removed, germination rarely is below 80 percent, and is sometimes 100 percent (27). Identification of defective seeds often is difficult, however, because many seeds appearing sound are filled with tannin. In one seed study, soundness varied significantly with seed size. Seeds passing 12, 10, and 8 mesh screens were 2, 8, and 15 percent sound, respectively. Seeds from seven populations were photographed by X-ray. The distribution in categories was as follows: seeds empty or tannin filled, 58 to 97 percent; seeds from embryos damaged by fungi, 0 to 11 percent; and sound seeds, 1 to 32 percent (38,39).

Although only scant evidence is recorded on storage of redwood seeds, they do not seem to store well. One seed lot was stored successfully for 3 years but lost its viability completely after 5 years (19).

Redwood cones dry readily under conditions of low humidity and quickly release their seeds with slight shaking. But because weather conditions at cone ripening in nature usually are unfavorable for rapid drying, seed dispersal may be spread over periods that vary considerably in length. Rains, however, may hasten seed dissemination. One observer found in many instances that redwood seeds remained in the open cones until a drenching rain dissolved the tannic crystals in the cones (38,39). Seed dissemination during the winter months seems characteristic of redwood in the northern stands. More than fourfifths of the sound seeds in one study were shed during December and January.

Redwood seeds are small and light, number about 265,000/kg (120,000/lb), but lack efficient wings to slow them in falling (10). They fall at rates between 1.5 and 6.2 m/s (4.9 and 20.5 ft/s), averaging 2.6 m/s (8.6 ft/s). These rates are faster than for most other wind-disseminated forest seeds and limit seed dispersal considerably.

Timbered edges of clearcut units have effective seeding distances of only 61 m (200 ft) uphill and 122 m (400 ft) downhill under average redwood stand conditions. A recent study in Del Norte County, CA, showed that the largest clearcut units should not be more than 12 to 16 ha (30 to 40 acres) if regeneration will be completed by natural seeding (38,39). No silvicultural reasons exist for restricting the size of clearcuts, if areas are regenerated by artificial methods. Maximum size of clearcuttings is specified in Forest Practice Rules, based on erosion hazard, or other criteria.

Seedling Development-Redwood seeds, generally, are ready to germinate soon after they fall to the ground if seedbeds are moist and the weather is warm enough. Redwood seeds do not require pretreatment to germinate, but germination speed is increased by an overnight soak in aerated water (27). Mineral soil is the best seedbed, but seeds will germinate readily in duff, on logs, in debris, or under other vegetation, and in either shade or full sunlight if adequate soil moisture is available. Redwood seed germination is epigeal.

New redwood seedlings require a greater supply of soil moisture for survival than that needed by seedlings of most associated trees (19). Late spring and early fall rains can be critical survival factors. Apparently, redwoods have no root hairs. Consequently, redwood roots do not seem to function efficiently in extracting soil moisture. This fact may limit natural distribution to sites where favorable water relations result from high rainfall, humid air, moist soil, or low summer temperatures, or from various combinations of these conditions. Redwood seedlings on fully exposed soil can withstand considerable surface heat if their roots have reached a permanent moisture supply. Otherwise, they die before soil surface temperatures reach 60" C (140" F). Redwood seedlings are extremely vulnerable to infection by damping-off and Botrytis fungi during their first year (22).

In its early stages, redwood grows rapidly in height. Seedlings often grow about 46 cm (18 in) in the first season and trees 4 to 10 years old sometimes grow 0.6 to 2.0 m (2 to 6.5 ft) in a year. In many instances, however, rapid height growth of trees that originate from seed does not commence until the trees are more than 10 years old.

Juvenile growth of redwood is best in full sunlight. Although redwood seedlings can endure heavy shade, growth there is slow. Photosynthetic capacity in redwood is remarkably high at low light intensities and keeps increasing as light intensity increases, much like more intolerant species. Redwood grew vigorously in much weaker light than 12 other tree species studied (38,39). For example, it increased its size 8.8 times in 10 percent of full sunlight in a g-month period, more than twice the growth of any of the other species in the test. For appreciable growth, Engelmann spruce (*Picea engelmannii*) and Douglas-fir require twice as much light as redwood. Pine requires three to four times as much.

Radial growth of redwood in Mendocino County, CA, at points 6, 14, and 32 km (4, 9, and 20 mi) from the coast did not vary markedly in growth pattern. Radial growth began after mid-March, increased to a maximum in late May, and then declined at a fairly uniform rate to a minimum at the end of September. Radial growth was negligible from October 1 to March 15.

Vegetative Reproduction-Redwood can be propagated by cuttings, but few large-scale attempts of this kind have been reported. In an early study in California, 40 percent of the cuttings from the tops of fast-growing seedlings that had been pushed into forest nursery soil with no special treatment developed root systems (38,39). Currently, rooting in excess of 90 percent is obtained routinely, with mist in a favorable medium, using juvenile cuttings from seedlings (27). Cuttings from older trees are more difficult to root.

Studies in the past 10 years have improved the cutting procedure by hedging-a technique that seems to maintain the juvenility of the donor tree. A single seedling and its clonal descendants can produce about 1 million cuttings in 3 years by repeated hedging of seedlings and their descendants (29).

Modern methods of plant tissue culture also have propagated redwood successfully (3). Tissues from outstanding mature trees may be cultured in nutrient medium, becoming undifferentiated masses of cells or callus. In different nutrient media, fragments of the callus can be induced to differentiate into small plants. When these plants become large enough, juvenile cuttings can be taken from them (30). In France, scientists have found that shoots of redwood 10 to 20 mm (0.4 to 0.8 in) long are the best reactive material for producing explants, with fragments of the annual shoots being more reactive than the annual sprouts of 2-year-old shoots (13). Tissue cultured plantlets are generally twice the size of seedlings of the same age (2).

Redwood can sprout from stumps and root crowns anytime of the year (fig. 2). Numerous and vigorous sprouts originate from both dormant and adventitious buds within 2 to 3 weeks after logging. Sprouting capacity is related to variables associated with tree size or age. Stumps of small young trees



Figure 2—Redwood sprouting in an area cut 2 or 3 years earlier. New sprouts around a stump are shown in foreground; center background is filled with a cluster Of young trees from sprouts.

sprout more readily than those of large old trees (35). Stumps often are circled by more than 100 sprouts. Many sprouts may be necessary to sustain a healthy stump-root system (4,15). Powers and Wiant (37) found that sprout vigor was related to sprout density. Sprout vigor was reduced at densities less than one sprout per 2 feet of stump circumference. Each sprout soon develops its own root system, and in a remarkably short time the dominant sprouts create circles of new trees around the old stumps.

Depending on the intensity of thinning or partial cutting in redwood, sprouts grow and develop successfully in openings (11,31). A recent study showed that more than 90 percent of all redwood stumps sprouted in a 40-year-old redwood stand thinned to 25, 50, and 75 percent of the initial basal area. Consequently, all thinned stands contained several

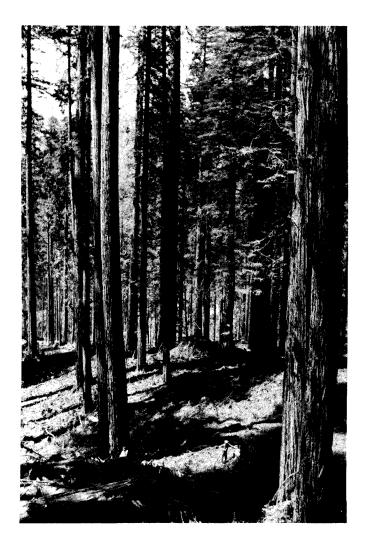


Figure 3—Redwoods in an experimental forest.

hundred redwood sprout clumps per acre, and several thousand individual sprouts. The heavier the thinning, the more sprouts developed into vigorous young crop trees (*31*).

Sprouting by redwood is principally from root crowns, but sprouts sometimes grow from the sides and tops of stumps. These high sprouts are less desirable because they are mechanically weak and not as vigorous as root-crown sprouts. Sprouts originating from the sides and top of stumps often are destroyed by strong wind.

Sprouts are commonly about 60 to 90 cm (24 to 36 in) tall at the end of the first year but may be more than 1.8 m (6 ft) tall. In one instance, a fire killed all sprouts around a stump. About 300 new sprouts appeared within a few days, and at the end of one growing season many reached 2.1 m (7 ft). Sprouts grow more rapidly than seedlings and the initial im-

petus lasts many years. However, the best phenotypes at age 40 to 80 in stands originating from both sprouts and seedlings often are found to be of seedling origin (27).

Early estimates of stocking from root crown sprouts varied from 20 to 35 percent of full stocking. A later study showed that redwood sprouts on old growth cutover redwood land in Mendocino and Humboldt Counties, CA, provided only 8 percent of full stocking. This finding is low compared to more recent stand examinations where the majority of redwood stems in 163 moderately to fully stocked young growth stands originated from sprouts (33).

Redwood can also sprout along almost the entire length of its trunk. If the crown of a tree is destroyed by fire or mechanically damaged, or the stem is suddenly exposed to light, numerous dormant buds along the trunk are stimulated and produce new foliage. Most of the trunk is then covered by feathery foliage extending 0.6 to 0.9 m (2 to 3 ft) from the trunk. Eventually, normal crowns develop again.

Sapling and Pole Stages to Maturity

Growth and Yield-Redwood (fig. 3) is long lived, grows taller than any other tree species in the world, and is exceeded in bulk only by the giant sequoia. Redwoods are sexually mature at 10 years or less but continue to increase in volume for centuries. The oldest redwood found so far, determined by growth ring counts, is nearly 2,200 years old. Old-growth redwood forests sometimes are incorrectly called even-aged and over-mature when, in fact, few forests in the world can match many redwood stands in range of ages and mixture of vigorously growing and decadent trees.

Redwood probably is best known for its great size, although the average redwood is smaller than commonly believed. Trees larger than 30 cm (12 in) in d.b.h. on a 12-ha (30-acre) old-growth tract in Humboldt County, CA, fell approximately into these divisions: 30 to 77 cm (12 to 30 in) in d.b.h., 50 percent; 78 to 153 cm (31 to 60 in), 32 percent; 155 cm (61 in) and larger, 18 percent. Redwoods 366 to 488 cm (144 to 192 in) in d.b.h., found scattered over the entire range, are considered large. Trees 610 cm (240 in) or more in diameter at a point 1.5 m (5 ft) above the ground are rare.

Redwoods more than 61 m (200 ft) tall are common, and many trees growing on riverside benches, where soils are deep and moist, are taller than 91 m (300 ft). The tallest measured redwood was 112.1 m (367.8 ft) in 1964 (50).

Large trees and dense stocking combine to produce high yields. More than 81 percent of the commercial



Figure 4-A young redwood stand with some Douglas-fir on an area from which almost all trees and snags have been removed.

redwood forest land is classified as highly productive, and only 2 percent is poor for growing trees. Flats along rivers have yielded approximately 10 500 to 14 000 m³/ha (about 750,000 to 1,000,000 fbm/acre) in scaled logs. Harvest cuttings in Del Norte County, CA, on units of 5.3 ha (13 acres) and larger, produced gross volumes ranging from 1330 to 3921 m³/ha (95,000 to 280,000 fbm/acre, Scribner).

Biomass accumulates to record levels. A redwood stand in Humboldt State Park in California provides the greatest biomass ever recorded, with a stem biomass of 3461 t/ha (1,544 tons/acre) (20).

Economical conversion of old-growth redwood to young managed stands by shelterwood or selection cutting is difficult because net growth is negative during the decade after logging. Windthrow, slow growth of residual trees, and damage to established reproduction when residual trees are removed contribute to economic losses. Considering effect on growth, small clearcuttings seem to be a good method for converting old-growth redwood to young managed stands (9) (fig. 4).

Young-growth redwood is often nearly as spectacular in size and yield as old growth. Dominant young-growth trees on good sites are 30.5 to 45.7 m (100 to 150 ft) tall at 50 years, and 50.3 to 67.1 m (165 to 220 ft) at 100 years. Height growth is most rapid up to the 35th year. On the best sites, however, height growth continues to be rapid well past 100 years (24,33).

Diameter growth of individual young trees can be rapid or extremely slow. In dense stands where competition is severe, annual diameter increment is commonly less than 1 mm (0.03 in>. Occasionally, 40 or more rings per centimeter (more than 100/in) can be counted. At the other extreme, diameter growth sometimes exceeds 2.5 cm (1 in) a year. One redwood growing with little competition was 213 cm (84 in) in d.b.h. when 108 years old.

The yield of young-growth redwood stands at 100 years is expected to range from 742 m³/ha (10,600 ft³/acre) on low sites to 3576 m³/ha (51,080 ft³/acre) on high sites (32). The same stands yield 781 to 4998 m³/ha (55,760 to 357,000 fbm/acre International quarter-inch rule), and yields of more than 2800 m³/ha (about 200,000 fbm/acre International quarter-inch rule) are common in young-growth redwood stands. At earlier ages, however, the greatest yields are in stands that contain a mixture of redwood and Douglas-fir (25).

Natural pruning in young redwood stands often is not good. Although live crowns may be limited to the upper third of the trunk, dead limbs are persistent. Branch stubs, although decayed, may remain more than 50 years. In old trees, some branch stubs have affected the quality of the timber over a 200-year period. Trees in the intermediate crown class, however, often prune well naturally, and some trees in a heavily stocked stand have clean trunks for 23 to 30 m (75 to 100 ft) at 85 years.

Rooting Habit-Redwoods have no taproots, but lateral roots are large and wide-spreading. Small trees have better-than-average windfirmness, and large redwoods are windfirm under most conditions.

A study in extreme northwestern California indicated that a combination of wet soil and strong winds is necessary for significant windfall damage. Consequently, windfall is caused by only a few of the many winter storms. Storms that cause windfall come mainly from the south, Uprooting accounted for 80 percent of the redwood windfall in this study (7).

Reaction to Competition-The redwood forest is a climax type. When growing with other species, redwood usually is a dominant tree. Douglas-fir can keep pace with redwood on many sites and occupy dominant and codominant crown positions along with redwood. Redwood has been classed as tolerant or very tolerant, the two highest categories in a scale of five shade tolerance classes. It is probably most accurately classed as very tolerant of shade in most situations.

Redwood stands are dense. At 60 years, redwood may have a basal area of more than 126 m^2/ha (550 ft²/acre) on the best sites (32). Heavy stocking is desirable because the relatively high tolerance permits land to support a large number of dominant and codominant trees per unit area.

Under some conditions, redwood can endure suppression almost indefinitely. A 25-cm (10-in) sup-

pressed tree might be more than 100 years old. Small trees may be suppressed for more than 400 years but still maintain a remarkable capacity to accelerate growth rates when released if they have not been crowded too closely and are not injured seriously during logging or slash burning. Large trees also can accelerate growth when released from competition.

Damaging Agents-Fire is the principal damaging agent in both young-growth and old-growth stands. The above-ground portions of young stands may be killed outright by a single ground fire, but the stands sprout and reoccupy the site. Fires are especially damaging to trees less than 20 years old because their thin bark does not protect them. Also, more flammable litter lies on the ground, and the microclimate is drier than under old-growth forest.

Old-growth redwood stands show evidence of three or more severe fires each century (23,44). In many instances, fires may only reduce the thickness of the protective bark, which may be more than 30 cm (12 in) thick. In other instances, fires cause basal wounds through which heart rots enter. The combination of recurring fires and advancing decay produces large basal cavities called "goose pens." In extreme instances, mature trees may be so weakened mechanically that they fall.

In its northern range, in and around Redwood National Park, CA, fire has a moderate ecological role in redwood stands. Light ground fires that do not open the canopy favor western hemlock regeneration but usually eliminate older hemlock from the stand. Douglas-fir establishment is infrequent and unsuccessful under a full overstory canopy, even following light ground fires on mesic sites. Relatively hot fires appear essential for the establishment of Douglas-fir trees in discrete age classes. Redwood, grand fir, and tanoak maintain their status in redwood stands with and without the influence of fire (47,48).

Frequency distributions of fires indicate a natural pattern of several short intervals between fires followed by one or more long interval. This suggests that prescribed burning to maintain ecosystems should also be done on a short-short-long interval pattern (23).

Redwood has no tree-killing diseases other than seedling diseases previously listed, but heart rots cause extensive cull. Most common heart rot in the southern part of the range of redwood is a brown cubical rot, caused by *Poria sequoiae*. Most significant farther north is a white ring rot caused by *P. albipellucida* (5,22).

A twig branch canker (*Coryneum* spp.) has been observed on sprouts and plantation trees of seedling and sapling size. This canker, which girdles stems and branches, could become damaging in plantations (5,22).

Several insects are found on redwood but none cause significant damage. These include a flatheaded twig borer and girdler (*Anthaxia aeneogaster*), two redwood bark beetles (*Phloeosinus sequoiae* and 1? *cristatus*), and the sequoia pitch moth (*Vespamima sequoiae*) (21).

Bark stripping by the American black bear has caused serious damage in some parts of the redwood region. Wide strips of bark are ripped from the tree, often from the top to the ground, during April to August. Trees 10 to 30 years old and 15 to 25 cm (6 to 10 in) in diameter are damaged most and many may be girdled. Woodrats often injure planted trees on cutover land and occasionally attack sprouts and larger trees.

In a few instances, redwood is deformed by fasciation, a flattening of the normally cylindrical stem by formation of a row of linked meristems. The causes of most fasciations are unknown (40).

Special Uses

Redwood is used where decay resistance is important. Clark and Scheffer (14) found that decay resistance varied among trees or within the heartwood of individual trees. Decay resistance decreased from outer to inner hardwood. Wood classified as very decay resistant was about five times more prevalent in old-growth than in young-growth trees.

A prominent special feature of the redwood is its production of burls from which beautifully figured table tops, veneers, bowls, and other turned products are cut. These burls are found on any part of the trunk and in sizes varying from an inch to many feet in diameter. Their cause is unknown. Small burls containing hundreds of dormant buds often are cut and placed in shallow containers, kept moist, and allowed to sprout. These live burls serve as attractive house plants.

Another feature of redwood is its extremely tough and fibrous bark. The bark must be removed before logs reach the head saws so that sawing uniform lumber will be possible. The bark is used as hog fuel, insulation, or garden mulch.

Genetics

Sequoia is unique within Coniferales, being of a hexaploid nature (41). It was thought that redwood originated as an allopolyploid from hybrids between early Tertiary or Mesozoic species of *Metasequoia* and some extinct Taxodiaceous plant such as the

modern giant sequoia. However, the types and numbers of marker chromosomes found in *Metasequoia* and *Taxodium distichum* are different than those present in *Sequoia*, making it unlikely that these species contributed to the polyploidy of *Sequoia*. Comparisons between the marker chromosomes in *Sequoia* and those in *Sequoiadendron* indicate that genomic contribution by *Sequoiadendron* to *Sequoia* is not probable (41).

Races of redwood are not known, but the following cultivars (cultivated varieties) have been recognized (16):

- cv. 'Adpressa' Tips of shoots creamy white. Awl-like leaves.
- cv. 'Glauca' Leaves 6 mm (0.25 in) long, glaucous, bluish. cv. 'Nana

Pendula' Leaves glaucous, branches pendulous.

- cv. 'Pendula' Branches pendulous.
- cv. 'Prostrata' Prostrate at first; leaves green, glaucous beneath.

Four varieties of redwood now available in nurseries show a range of growth habits, texture, color, and form. They are named Aptos Blue, Los Altos, Soquel, and Santa Cruz (6).

An uncommon form of redwood, the albino redwood, has been described in a few locations within the redwood region (17). These albinos result from a genetic disorder and exist by attachment to a normal green tree, generally at the roots. The tallest albino observed was 19.8 m (65 ft) tall. Albinism is often a useful trait in genetics research to determine mutation rate, and for other purposes.

Preliminary results from studies of self and related outcross families indicate that, compared with outcrosses, selfing produced no additional cone abortion or variable effects on germination. Under stress conditions in nurseries and outplantings, some inbreeding depression becomes evident, and restricting inbreeding in redwood seed-orchards seems prudent (30).

The tissue culture techniques described earlier also allow genetic manipulation of redwood at the cellular level. Possibilities being explored include the production of dihaploid redwood from female gametophyte cultures (2).

Hybrids

In Russia, hybridization of redwood with giant sequoia, bald cypress, and Japanese cryptomeria (*Cryp*tomeria japonica) has been reported (38,39).

Other attempts to develop a hybrid between coast redwood and giant sequoia by normal controlled-pollination crosses have failed (28). Cell fusion in culture may be used to create interspecific hybrids with giant sequoia or other species (28).

Literature Cited

- 1. Azevedo, J., and D. L. Morgan. 1974. Fog precipitation in coastal California forests. Ecology 55:1135–1141.
- Ball, E. A. 1980. Personal communication. University of California, Division of Natural Sciences, Santa Cruz.
- 3. Ball, Ernest A., Dawn M. Morris, and James A. Rydelius. 1978. Cloning of *Sequoia semperuirens* from mature trees through tissue culture. *In* Proceedings, Table Ronde: Multiplication "In vitro" d'Espèces Ligneuses. Gembloux, Belgique; 6-8 June, 1978. p. 181-226. Royaume de Belgique, Centre de Recherches Agronomiques de l'Etat, Administration de la Recherche Agronomique, Ministère de l'Agriculture.
- Barrette, B. R. 1966. Redwood sprouts on Jackson State Forest. California Division of Forestry. State For. Note 29, 8 p.
- Bega, Robert V., tech. coord. 1978. Diseases of Pacific Coast conifers. U. S. Department of Agriculture, Agriculture Handbook 521. Washington, DC. 206 p.
- Blythe, Gene. 1984. Cutting propagation of Sequoia semperuirens cultivars. Proc. International Plant Propagators Society 34:204–211.
- Boe, Kenneth N. 1966. Windfall after experimental cuttings in old-growth redwood. *In* Proceedings, Society of American Foresters National Meeting; Oct. 24-28, 1965, Detroit, MI. p. 59-63. Washington, DC.
- Boe, Kenneth N. 1968. Cone production, seed dispersal, germination, in old-growth redwood cut and uncut stands. USDA Forest Service, Research Note PSW-184. Pacific Southwest Forest and Range Experiment Station, Berkeley, CA. 7 p.
- Boe, Kenneth N. 1974. Growth and mortality after regeneration cuttings in old-growth redwood. USDA Forest Service, Research Paper PSW-104. Pacific Southwest Forest and Range Experiment Station, Berkeley, CA. 13 p.
- Boe, Kenneth N. 1974. Sequoia semperuirens (D. Don) Endl. redwood. In Seeds of woody plants in the United States. p. 764-766. C. S. Schopmeyer, tech. coord. U.S. Department of Agriculture, Agriculture Handbook 450. Washington, DC.
- 11. Boe, Kenneth N. 1975. Natural seedlings and sprouts after regeneration cuttings in old-growth redwood. USDA Forest Service, Research Paper PSW-111. Pacific Southwest Forest and Range Experiment Station, Berkeley, CA. 17 p.
- Bolsinger, Charles L. 1980. California forests: trends, problems, and opportunities. USDA Forest Service, Resource Bulletin PNW-89. Pacific Northwest Forest and Range Experiment Station, Portland, OR. 138 p.
- Boulay, M. 1979. Multiplication et clonage rapide du Sequoia sempervirens per la culture "in vitro." p. 49-55. In Etudes et Recherches, Association Foret-Cellulose, Domaine de l'Etancon, Nangis, France.
- Clark, Joe W., and Theodore C. Scheffer. 1983. Natural decay resistance of heartwood of coast redwood Sequoia semperuirens (D. Don) Endl. Forest Products Journal 33(5):15-20.
- 15. Cole, Dana W. 1983. Redwood sprout growth three decades after thinning. Journal of Forestry 81(3):148–150, 157.

- Dallimore, W., and A. Bruce Jackson. 1967. A handbook of Coniferae and Ginkgoaceae. 4th ed. Revised by S. G. Harrison. St. Martin's Press, New York. 729 p.
- 17. Davis, Douglas F., and Dale F. Holderman. 1980. The white redwoods: ghosts of the forest. Naturegraph Publishers, Happy Camp, CA. 45 p.
- Durgin, Philip B. 1981. Organic matter content of soil after logging of fir and redwood forests. USDA Forest Service, Research Note PSW-346. Pacific Southwest Forest and Range Experiment Station, Berkeley, CA. 4 p.
- Fritz, Emanuel, and James A. Rydelius. 1966. Redwood reforestation problems: an experimental approach to their solution. Foundation for American Resource Management, San Francisco, CA. 130 p.
- Fujimori, Takao. 1977. Stem biomass and structure of a mature *Sequoia sempervirens* stand on the Pacific Coast of northern California. Journal of the Japanese Forestry Society 59(12):435–441.
- Furniss, R. L., and V. M. Carolin. 1977. Western forest insects. U.S. Department of Agriculture, Miscellaneous Publication 1339. Washington, DC. 654 p.
- Hepting, George H. 1971. Diseases of forest and shade trees of the United States. U.S. Department of Agriculture, Agriculture Handbook 386. Washington, DC. 658 p.
- Jacobs, Diana F., Dana W. Cole, and Joe R. McBride. 1985. Fire history and perpetuation of natural coast redwood ecosystems. Journal of Forestry 83(8):494–497.
- 24. Krumland, B., and L. C. Wensel. 1977. Height growth patterns and fifty-year base age site index curves for young growth coastal redwood. Cooperative Redwood Yield Research Note 4. University of California, Department of Forestry and Resource Management, Berkeley. 11 p.
- 25. Krumland, B., and L. C. Wensel. 1980. Illustrative yield tables for coastal conifers in California. Cooperative Redwood Yield Research Note 18. University of California, Department of Forestry and Resource Management, Berkeley. 25 p.
- Kuser, John E. 1976. Potential site index of redwood as a function of climate. Thesis (MS.), Rutgers University, New Brunswick, NJ. 98 p.
- Libby, W. J. 1981. Personal communication. University of California, Department of Forestry and Conservation, Berkeley. 25 p.
- Libby, William J. 1982. Cloning coast redwoods. California Agriculture 36(8):34–35.
- 29. Libby, W. J., and B. G. McCutchan. 1978. Taming the redwood. American Forests 84(8):18–23, 37–39.
- Libby, W. J., B. G. McCutchan, and C. I. Millar. 1981. Inbreeding depression in selfs of redwood. Silvae Genetica 30:15–25.
- Lindquist, James L. 1979. Sprout regeneration of young-growth redwood: sampling methods compared. USDA Forest Service, Research Note PSW-337. Pacific Southwest Forest and Range Experiment Station, Berkeley, CA. 8 p.
- Lindquist, James L., and Marshall N. Palley. 1963. Empirical yield tables for young-growth redwood. California Agricultural Experiment Station, Bulletin 796. Berkeley. 47 p.
- Lindquist, James L., and Marshall N. Palley. 1967. Prediction of stand growth of young redwood. California Agricultural Experiment Station, Bulletin 831. Berkeley. 47 p.

- Major, Jack. 1977. California climate in relation to vegetation. *In* Terrestrial vegetation of California. p. 11-74. Michael G. Barbour and Jack Major, eds. John Wiley, New York.
- 35. Neal, Robert L., Jr. 1967. Sprouting of old-growth redwood stumps-first year after logging. USDA Forest Service, Research Note PSW-137. Pacific Southwest Forest and Range Experiment Station, Berkeley, CA. 8 p.
- Olson, David F., Jr., and John Fiske. 1983. Redwood. *In* Silvicultural systems for the major forest types of the United States. p. 37-40. Russell M. Burns, tech. compiler. USDA Forest Service, Agricultural Handbook 445.
- Powers, R. F., and H. V. Wiant, Jr. 1970. Sprouting of old-growth coastal redwood stumps. Forest Science 16:339–341.
- Roy, Douglass F. 1965. Redwood (Sequoia sempervirens [D. Don] Endl.). In Silvics of forest trees of the United States. p. 663-670. H. A. Fowells, comp. U.S. Department of Agriculture, Agriculture Handbook 271. Washington, DC.
- Roy, Douglass F. 1966. Silvical characteristics of redwood (Sequoia sempervirens [D. Don] Endl.). USDA Forest Service, Research Paper PSW-28. Pacific Southwest Forest and Range Experiment Station, Berkeley, CA. 20 p.
- 40. Roy, Douglass F. 1972. Fasciation in redwood. Madroño 21(7):462.
- Sclarbaum, S. E., and T. Tsuchiya. 1984. A chromosome study of coast redwood, *Sequoia sempervirens* (D. Don) Endl. Silvae Genetica 3(2/3):56–62.
- Society of American Foresters. 1980. Forest cover types of the United States and Canada. F. H. Eyre, ed. Washington, DC. 148 p.
- 43. Stone, Edward C., and Richard B. Vasey. 1968. Preservation of coast redwood on alluvial flats. Science 159(3811):157-161.
- Stuart, John D. 1987. Fire history of an old-growth forest of Sequoia sempervirens (Taxodiaceae) forest in Humboldt Redwoods State Park, CA. Madroño 34(2):128–141.
- 45. U.S. Department of Agriculture, Soil Conservation Service. 1975. Soil taxonomy: a basic system of soil classification for making and interpreting soil surveys. Soil Survey Staff, coords. U.S. Department of Agriculture, Agriculture Handbook 436. Washington, DC. 754 p.
- 46. University of California. 1979. California forest soils: a guide for professional foresters and resource managers and planners. Robert J. Laacke, coord. University of California, Division of Agricultural Sciences, Berkeley. 181 p.
- Veirs, Stephen D., Jr. 1980. The role of fire in northern coast redwood forest dynamics. *In* Proceedings, Conference on Scientific Research in the National Parks. vol. 10, Fire Ecology. Nov. 26–30, 1979, San Francisco, CA. p. 190-209. National Park Service, Washington, DC. 403 p.
- Veirs, Stephen D., Jr. 1980. The influence of fire in coast redwood forests. *In* Proceedings, Fire History Workshop, Oct. 20-24, 1980, Tucson, AZ. p. 93-95. USDA Forest Service, General Technical Report RM-81. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.
- Waring, R. H., and J. Major. 1964. Some vegetation of the California coastal redwood region in relation to gradients of moisture, nutrients, light, and temperature. Ecological Monographs 34(2):167–215.
- Zahl, Paul A. 1964. Finding the Mt. Everest of all living things. National Geographic 126(1):10–51.

- Zinke, Paul J. 1977. The redwood forest and associated north coast forests. *In* Terrestrial vegetation of California. p. 679-698. Michael G. Barbour and Jack Major, eds. John Wiley, New York.
- 52. Zinke, Paul J. 1984. Forest soil properties related to nutrient storage and their change in the harvest of old-growth, and the regrowth and harvest of second-growth redwood forests. *In* Proceedings of Convention of Society of American Foresters. 1983. Washington, DC. p. 210–215.