

The Ecology of Sequoia sempervirens

By James A. Snyder, December, 1992

Abstract

The ecology of coast redwood (*Sequoia sempervirens*) is examined with an emphasis on the climatic, physiographic, edaphic, and hydrologic factors responsible for its present distribution. Adaptations to fire and flood-interrupted environments, as well as resistance to depredations by mammals, invertebrates, and fungal pathogens, are recognized as important adjuncts to its regeneration and dominance throughout its range. A review of paleo-sequoian distributions for coast redwood, dawn redwood and giant sequoia is also provided.

Detailed appendices include a botanical comparison of the three redwood species, and an annotated register of the tallest coast redwoods. The etymology of *Sequoia sempervirens* is also discussed.

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Introduction

Discovery

The superlative redwood groves of the central California coast had been known to Native Americans for nearly 11,000 years before the arrival of Don Gaspar de Portola in 1769 (Greenlee, 1983). Although redwoods may have been chanced upon by former explorations of the coast (Dewitt, 1985; Dolezal, 1974; Hewes, 1981; Weaver, 1975), the chronicle of Portola's expedition overland provides the first written description of the trees (Carranco, 1982). On October 10, 1769, a Franciscan missionary, Fray Juan Crespi, described the Spanish transit north of the Pajaro River, "...over plains and low hills, well forested with very high trees of a red color, not known to us. They have a very different leaf from cedars, and although the wood resembles cedar somewhat in color, it is very different and has not the same odor; moreover, the wood of the trees that we found is very brittle. In this region, there is great abundance of these trees and because none of the expedition recognizes them, they are named redwood from their color (Appendix I)."

The first botanist to examine the coast redwood, or "palo colorado (Jepson, 1910)," attended Alejandro Malaspina's landfall on Monterey Bay in September of 1791 (Thomas, 1961). The expedition fielded two botanists, Louis Née and Thaddeus Haenke, but only Haenke collected ashore where Malaspina had seen "the red pine, a tree much taller than the rest (Eastwood, 1939)." It is curious that neither scholar attempted to name the dominant conifer, since Née later described the coast live oak (*Quercus agrifolia*) and valley oak (*Q. lobata*) from specimens brought to him by ship's officers. Apparently, one redwood is known to still be growing in Spain from seed collected during the expedition (Baker, 1965).

Whereas Haenke might be considered the "botanical discoverer" of coast redwoods (Jepson,

1910), a more appropriate candidate would be Archibald Menzies, a Scottish botanist and surgeon with the Vancouver Expedition of 1790-1795 (Baker, 1965; Jepson, 1923; Roy, 1966). In 1794, Menzies obtained a sample of the tree near Santa Cruz which was to become the basis for its botanical description by Aylmer Bourke Lambert in 1824 (Jepson, 1910; Hastings, 1928). There is some doubt, however, that Menzies personally collected the type specimen, since Vancouver was known to deny him landfalls (Eastwood, 1939) and Menzies' "journal does not show that he himself was ever at Santa Cruz though other members of the expedition were (Shirley, 1937)."

Delayed Description

Upon Vancouver's return to London in 1795, Menzies' herbarium collection was cached in the British Museum (Natural History) for more than a quarter century before coming to the attention of Lambert. Inasmuch as Menzies only collected in California during the late fall and early winter (Eastwood, 1939), the unsatisfactory condition of his redwood specimen may have been responsible for the delay in its description. Indeed, Eastwood (1939) discovered many of Menzies' California specimens still unnamed.

But Lambert acknowledged while "having only a single imperfect specimen of this species for examination, it is not without some hesitation, that I have referred it to *Taxodium*... leaving to future observations to determine, whether or not the place I have assigned to it be correct (Jepson, 1910)." Although Lambert recognized that the redwood appeared to be intermediate between *Taxodium* and *Cupressus*, and that a colleague, "the late Mr. Salisbury considered it as forming a new genus, and had applied to it the name *Condylocarpus* (Jepson, 1910)," he chose *Taxodium* because of the specimen's close resemblance to the bald cypress (*Taxodium distichum*). But the evergreen nature of the redwood was very much unlike the deciduous cypress, so he christened the species *Taxodium sempervirens* to differentiate between

the two habits (Jepson, 1923). The propriety of “sempervirens,” meaning “ever-living (Hewes, 1981)” or “always-alive (Coombes, 1987),” was incidental to the tree’s extraordinary longevity (Baker, 1965).

Lambert’s binomial survived intact for only 23 years before yielding to the adoption of *Sequoia sempervirens* by Stephen Endlicher in 1847 (Chaney, 1951). In his manuscript, *Synopsis Coniferarum*, Endlicher redescribed the coast redwood with good reason to segregate it from *Taxodium* (Hartesveldt et al., 1975). But Endlicher’s publication failed to intimate the origin of the word “sequoia (Hastings, 1928);” and his untimely death in 1849 left the etymology of the new genus regrettably shrouded in mystery.

Origin of Sequoia Name

Punctilious scrutiny of Endlicher’s papers by the eminent American botanist, Asa Gray, could not betray the origin of *Sequoia* (Hartesveldt et al., 1975), which has most often been associated with the remarkable Cherokee Indian scholar, Sequoyah, or Sikwayi (Farquhar, 1947). Though lacking formal education (Shirley, 1937), Sequoyah devised an 85-character syllabary for the Cherokee Nation in 1821 to facilitate reading and writing in their native language (Hartesveldt et al., 1975). His ignoble death in San Fernando, Mexico in 1843 (Sargent, 1947) may have prompted Endlicher, a known philologist, to honor Sequoyah’s passing.

But “no one has ever found mention in his writings of Sequoyah’s name (Hartesveldt et al., 1975)” or the Cherokee syllabary. Rather, Gray believed that the stem of the word was a derivation from the Latin “sequi” or “sequor,” meaning “sequence (Hastings, 1928)” or “following (Harvey, 1978),” and alluded to the fact that redwoods were remnants or followers of numerous fossil ancestors. Another proposal of an obscure origin in one of California’s Indian dialects remains unsubstantiated (Hartesveldt et al., 1975), and in Cherokee, “sequoyah” means “opossum (Dolezal, 1974).” Yet the la-

bors of the gifted Sequoyah are certainly deserving of such lasting tribute, regardless of Endlicher’s intention. Hartesveldt et al. (1975) concur that “perplexity and doubt notwithstanding, let it so remain.”

Species Associated with Sequoia

Sequoia sempervirens belongs to the redwood (Jepson, 1910) or deciduous cypress family (Hewes, 1981), Taxodiaceae, representing 15 species and ten largely monotypic genera. Included are two species closely related to the coast redwood: the giant sequoia (*Sequoiadendron giganteum*) and the dawn redwood (*Metasequoia glyptostroboides*) (Stebbins, 1948).

The giant sequoia, largest of all living things with more than 630,000 board feet in the General Sherman Tree (Harvey et al., 1981), is widely dispersed among 75 groves and 35,607 acres along the western Sierra Nevada in California (Hartesveldt et al., 1975). The range of the smaller and uniquely deciduous dawn redwood is limited to the central China provinces of Sichuan and Hubei where they were discovered by Professor T. Kan in 1941 (Hu, 1948).

While the coast redwood may be regarded as the giant sequoia’s nearest living relative geographically, only recently segregated by genus (Buchholz, 1939), the dawn and coast redwoods are more closely related (Harvey, 1978). *Sequoia sempervirens* may even be descendant “from hybrids between an early Tertiary or Mesozoic species of *Metasequoia* and some probably extinct type of taxodiaceous plant (Stebbins, 1948).” Further comparison between the three species may be found on pages 90-92 (Appendix II).

Mesozoic Origins

The redwoods are considered to be relicts of a Mesozoic group of conifers that were once richly developed and coherent, and widespread throughout the northern hemisphere (Florin, 1963). Progenitors of Taxodiaceae might have evolved as early as 200 million years ago (Engbeck, 1976), when the cycadeoids, ginkgos, and

other conifers dominated the Mesozoic forests of the dinosaurs (Simpson, 1983).

The proliferation of the sequoia line was favored by a remarkably stable climate that was generally warmer, humid and more equable than at present (Florin, 1963). This was especially true during the Cretaceous period (Appendix III), 135 to 65 million years ago, when the average temperature of high-latitude North America was 59° to 77° F warmer with perhaps 25 percent more annual precipitation (Rigby, 1987). Mild conditions persisted even in northern extremes where Florin (1963) found no evidence of Mesozoic glaciation in the arctic islands regarded by Berry (1920) as the center of sequoian evolution.

Although Engbeck (1976) preferred a more southern origin in west-central North America, the paleontological record is far from conclusive. And the oldest known sequoias are found in southern Manchuria from late Jurassic deposits (Chaney, 1951). However, by the end of the Mesozoic era, representatives of each extant genera had become established throughout the northern continents (Fig. 1).

Widest Distribution

Sequoias achieved their widest and northernmost limits of distribution during the Paleocene and Eocene epochs, 65 to 38 million years ago (Florin, 1963), when the general cooling trend in Tertiary climates was often interrupted by warmer periods (Tidwell, 1975). Ancient relatives of the giant sequoia occupied parts of central and eastern North America, Greenland, Spitzbergen and Europe; those of the coast redwood became established in central and western North America, Greenland, Spitzbergen, Europe and Japan (Florin, 1963). Early *Metasequoia* forests were even more widespread, colonizing eastern Asia, Japan, Greenland, Spitzbergen, northern Siberia, and Ellesmere Island.

Although plate tectonic theory was not discussed by Chaney or Florin, Chaney (1948) attributed the success of *Metasequoia* in ex-

treme latitudes to its deciduous habit which enabled it to endure prolonged winters without sunshine in a dormant condition. From the late Mesozoic until Miocene time, *Metasequoia* was also the most abundant and widely distributed genus of *Taxodiaceae* in North America (Chaney, 1951).

Incomplete Fossil Record

It should be kept in mind that such broad paleodistributions are biased by an incomplete fossil record spanning millions of years and do not imply that the northern hemisphere was simultaneously covered by temperate sequoian forests through 40° of latitude (Cain, 1944). The sequoias were only part of an exceptional diversity of species and taxa characteristic to subalpine and mixed conifer forests of the period, and were regularly admixed in communities far richer than any surviving today (Raven and Axelrod, 1978). Examination of the communities associated with each ancestral sequoia indicates that they inhabited environments similar to conditions occupied by their modern counterparts (Hartesveldt et al., 1975), with latitudinal distributions that fluctuated with oscillations in global climate.

For example, Tertiary *Sequoia* forests were spread mainly over a belt bounded by latitudes 34 and 58, yet northern outposts existed for a time in western Spitzbergen during the Paleocene or Eocene at latitude 79 (Florin, 1963). Whereas some sequoian species inhabited ranges that overlapped (Chaney, 1979), others remained as mutually exclusive as the absence of contemporary fossils of *Sequoia* and *Sequoiadendron* have shown in western North America (Mason, 1947; Raven and Axelrod, 1978). However, Florin (1963) noted that the reconstruction of past *Sequoiadendron* distributions has been much less satisfactory than those of *Sequoia* because of "difficulties involved in the identification of fossil remains (Florin, 1963)."

Species Recognized

The number of species recognized by paleontologists has also been subject to considerable

debate and revision. By 1910, more than 40 species of sequoia had been described from fragmentary remains, but there was by no means agreement as to the validity of the species (Jepson, 1910). And Seward (1919) determined that many impressions of vegetative shoots and cones described as *Sequoia* from the Jurassic and early Cretaceous did not bear close scrutiny. The twelve species of fossil redwood reported by Shirley (1937), Hewes (1981) and others most likely refers to Jepson's (1910) account of the number recognized by Schimpfer in 1903.

The collection of the first living specimens of *Metasequoia* in 1944, only three years after Shigeru Miki described the genus from Pliocene fossils in Japan, led to an important contribution in the revision of paleo-sequoian nomenclature by Chaney in 1951 (Florin, 1963). Chaney (1951) reassigned Tertiary fossils of several North American taxa, including 11 species of *Sequoia*, into new combinations of *Metasequoia occidentalis* and *Sequoia affinis*. Both were recognized as ancestral to their extant species to the extent of being very nearly conspecific. The immediate ancestor of the giant sequoia, *Sequoiadendron chaneyi*, was later described by Axelrod (1956) from Mio-Pliocene floras in Nevada.

Impact of Cooler, Drier Climate

In contrast to the conditions which encouraged periods of northern expansion, a progressively cooler and drier climate throughout the remainder of the Tertiary precipitated a gradual retreat of the sequoias to the relict areas they now occupy (Engbeck, 1976). As early as the late Oligocene, 26 million years ago, *Sequoiadendron*-like conifers had vanished from the floras of eastern North America, Greenland, Spitzbergen and Europe (Fig. 2), while *Metasequoia* had retreated to latitudes bounded by 40° and 49° in western North America, and 47° and 58° in western Siberia (Florin, 1963). Although the Oligocene range of *Metasequoia* was expanded across central Asia, from the Pacific Ocean to the Aral Sea, it was

to perish altogether from North America by the end of the Miocene, 20 million years later. And by the close of the Tertiary, 2.5 million years ago, *Metasequoia* had become extinct in central Asia, Siberia, Kamchatka and Japan (Fig. 3).

Florin (1963) reconstructed similar patterns of retreat from high latitudes for *Sequoia*, accompanied by a lowering in its altitudinal distribution in the mountains. The northernmost limits of its range appear to have been latitude 60 during the Oligocene (western Siberia), 56 during the Miocene (Denmark), and 51 during the Pliocene (the Netherlands). There was also an Oligocene expansion of its area across central Asia, comparable to that of *Metasequoia*, which prefaced its southernmost record of distribution in southwestern China during the Pliocene at latitude 26 .

Yet the Eurasian migrations of *Sequoia* terminated at the end of the Pliocene, when it disappeared completely from Europe, Japan and Asia. In North America, its survival was aided by the equability of the climate along the Oregon and California coast (Raven and Axelrod, 1978) where the abundant rainfall and prolonged maintenance of narrow fluctuations in seasonal temperature provided refuge from an increasingly hostile continental interior (Li, 1953).

Sequoia forests were further isolated from the westward advance of xerothermic conditions by the onset of coastal orogenic movements during the late Pliocene (Raven and Axelrod, 1978). Although subsequent Quaternary migrations extended as far south as the Santa Ynez Mountains near Santa Barbara (Chaney and Mason, 1933; Putnam, 1942), the distribution of *Sequoia* by the end of the Tertiary was similar to its present range, with representatives persisting only as far inland as 35 miles southeast of Santa Rosa (Axelrod, 1976, 1977).

Present Range

The last and present stronghold of *Sequoia sempervirens* adjoins the Pacific along a nar-

row and discontinuous belt from southwestern Oregon to Monterey County in California (Fig. 4). Roughly 5 to 35 miles wide and 450 miles long (Roy, 1966), 1,971,000 acres of virgin redwood forest awaited Portola's discovery in 1769 (USDI, 1964). However, since the construction of the first water-powered sawmill in 1834 (Carranco, 1982), the redwood lumber industry has not only harvested more than 95 percent of the timber (Kelly and Braasch, 1988), but diminished its range by 100,000 acres (Stone, 1965). In California, just 68,035 acres of old-growth redwood, 3.5 percent of the original forest, have been preserved within 21 state and two national parks (Appendix IV).

Northernmost

Of the six principal redwood groves in Oregon surveyed by the U.S. Forest Service in 1964, the northernmost is bounded by two clear-cut logging sites in the Little Redwood Creek drainage of the Chetco River (Becking, 1971). Other stands are scattered along downstream tributaries to within six miles of the Chetco River mouth (Sudworth, 1927), to the east along Wheeler Creek, and throughout the Winchuck River and Bear Creek watersheds into California (Becking, 1971).

Interior Redwoods

Ranging southward to Sonoma County, the "redwood belt (Jepson, 1910)" is continuous except for a transverse break along the Kings Peak Range and headwaters of the Mattole River (Roy, 1966). Another hiatus occurs among the hills of southern Sonoma and northern Marin Counties, where "coastal" redwood stands have been displaced eastward into Napa County (Griffin and Critchfield, 1976). Only isolated colonies lie east of Napa, achieving their farthest distribution inland some 42 miles from the sea. However, to the north near Angwin and the Pope Valley, a more "interior" locality of redwood may be found upon the eastern flank of Howell Mountain (Sudworth, 1967), 36.8 miles from the coast (Zinke, 1977). "This is a most remarkable sta-

tion, for not elsewhere does the Redwood occur on the waters of the Sacramento or any other interior stream (Jepson, 1910)." Three other colonies have subsequently been found to face the Sacramento Valley drainage: at Swartz Creek, Ink Grade and i.Aetna Springs; (Griffin and Critchfield, 1976).

Southern Balance

The southern balance of the redwood belt occurs in detached and irregular areas most prominently among the canyons of Marin County, the Oakland Hills, and Santa Cruz Mountains (Jepson, 1923). Only scattered remnants are found south of Monterey, confined to coastal arroyos where "stringers of redwood (Zinke, 1977)" seldom extend more than 175 feet from main stream channels (Borchert et al., 1988). In the Soda Springs Creek drainage (Borchert, 1990; personal communication), 1.5 miles north of Salmon Creek (Griffin and Critchfield, 1976), a small windswept clump marks the southernmost limit of redwood distribution, surrounded by coastal sage scrub a few hundred meters inshore (Zinke, 1977). The often published "claim that Salmon Creek Canyon is the southern limit of the redwoods is erroneous (Havlik and Ketcham, 1968)."

Restricted by Salt Spray

Recognized as a typical lowland species (Becking, 1982) ranging in elevation from 3200 feet (Borchert et al., 1988) to near sea-level (Jepson, 1910), redwoods do not inhabit coastal margins where the influx of marine air is excessive (Zinke, 1977). Prevailing winds and ocean fogs, high in salt spray aerosols, not only contribute unsuitable amounts of sodium and magnesium to ocean terrace soils, but directly inhibit redwood growth through foliage salt burn (Zinke, 1964).

Insufficient rainfall on the immediate coast also establishes the western redwood boundary (Baker, 1965), especially in areas exposed to desiccating offshore winds (Daniel, 1942). Redwoods grow best beyond the reach of salt spray fallout atop moist, sheltered plains and

valleys opening toward the sea, along river deltas and the protected flats and benches of larger streams, and upon moderate western slopes (Sudworth, 1967) between 100 and 2500 feet in elevation (Person, 1937). As one progresses inland, the influx of marine air and the occurrence of summer fog have a significant impact upon local factors which tend to favor or mitigate against the presence of redwood forest (Zinke, 1977).

Climate

Cool, wet winters and warm summer droughts exemplify the Mediterranean-type climate of the redwood region (Bakker, 1984). Maritime fog and stratus regimes ameliorate conditions throughout most of the dry season (Byers, 1953), which Thorntwaite (1941) classified as dry subhumid to superhumid. The amount of annual precipitation increases northward along the coast from 20 to 120 inches (McMinn and Maino, 1980), primarily falling as winter rain although snow sometimes accumulates upon the highest ridgetops (Sudworth, 1967).

Exceptional years have recorded as much as 153.54 inches at Monumental Station in Del Norte County (Sprague, 1941). Severe winter storms, like the 1989 blizzard which left 14 inches of snow at Prairie Creek Redwood State Park, are rare (Wilkinson et al., 1989). Eighty percent of the total precipitation falls between November 1 and April 30 (Twight, 1973), with January normally the wettest month, and August the driest (Fowells, 1965).

Summertime droughts increase southward along the coast from two to five months in duration (Kuser, 1976), aggravating the protracted moisture requirements of redwood during its growing season from mid-March until September (Roy, 1966). Kuser (1976) found that supplemental moisture from high water tables and fog was critical during this period, contributing an equivalent of 16 to 30 inches of water to the 40 to 80 inches of annual precipitation needed for optimal redwood growth.

Summer Fogs

The redwood belt has long been causally linked to frequent summer fogs (Cooper, 1917) which "seem to be more important than the amount of precipitation in delineating the redwood type (Fowells, 1965)." From early spring until September, advection fogs intermittently blanket the coast when the moist marine air borne by prevailing north-westerly winds cools upon contact with coastal upwellings of deep-sea currents, 10 to 15° F colder than the surface (Gilliam, 1962). The winds and onshore pressure gradients respond to low pressure areas above the Central Valley, driving the fogs inland (Patton, 1956), pervading mountains, river valley gaps and canyons while sliding beneath the warmer air of the interior to form a temperature inversion (Gilliam, 1962).

The boundary between the two layers remains intact as the volume of fog and cool marine air increases over land, pushing the ceiling of warm air upward. Additional condensation occurs along this plane of contact to create stratus, or high fog. Seldom found below 300 feet, the stratus layer commonly penetrates the coast at 800 to 1200 feet above the inland valleys, capped by 1000 to 3000-foot ceilings which average around 1500 feet (Byers, 1953). Diurnal temperatures above and below the layer can differ by as much as 65° F (Borchert et al., 1988). Although the fog/stratus layer normally lasts from late evening until morning, it may also perdure for several days with the more coastal sites hesitant to dissipate in the afternoon warmth (Azevedo and Morgan, 1974). The predominance of fog/stratus penetration along the coast ebbs and flows in cycles, and achieves a maximum width of 100 miles over land and sea in August (Gilliam, 1962).

The precipitative importance of summer fog drip has received considerable attention since Cannon (1901) first compared the redwood's "fern-like" boughs to filters "by which water may be 'combed' out from fog (Cannon, 1901)." Redwoods require prodigious amounts of moisture during the growing season, which

Golte (1974) attributed to the low efficiency of their vascular conducting system. Transpiration rates of 500 gallons per day have been reported by Hewes (1981), whereas more drought-resistant associates, such as old-growth Douglas-fir (*Pseudotsuga menziesii*), transpire 140 gallons daily (Kline et al., 1976).

Azevedo and Morgan (1974) determined that fog drip affects both water balances and nutrient cycling within such coastal ecosystems. They recorded as much as 3.15 inches of fog precipitation beneath one Humboldt County redwood in 48 hours. And in the mountains east of Half Moon Bay, an astounding 58.8 inches of fog drip was collected by Oberlander (1956) under an exposed, 20-foot high tanoak (*Lithocarpus densiflora*) in 39 days! The extent of forest cover, position and shape of the tree, wind velocity and temporal character of the fog affect the spatial distribution of fog drip upon the ground (Azevedo and Morgan, 1974), which Parsons (1960) construed as mainly a hillcrest phenomenon where sufficient exposure, elevation and temperature combine to intercept stratus below the maximum 49 F required for drip formation (Freeman, 1971). Because dense, wet surface fogs seldom penetrate the major redwood groves (Byers, 1953), “the more extravagant claims advanced for water income from this source should be treated with reserve (Kerfoot, 1968).”

The redwood’s marked mesophytic reaction to low humidities (Daniel, 1942) led Freeman (1971) to conclude that reduced insolation and the high relative humidity of fog/stratus events were more important than fog drip in reducing summer water losses. Inasmuch as the energy expended in the evaporation of leaf surface moisture is the same for dissipating transpirational water, intercepted mists that do not reach the soil would be just as significant to the foliage as moisture gained from fog drip (White, 1958). “Moreover, some of the condensed water is actually absorbed and redistributed within the plant (White, 1958).”

Fog-laden air may even increase photosynthesis as a result of its high carbon dioxide con-

tent (Wilson, 1948; Wiant, 1964), or by contributing to the reduction in leaf water deficits which limit CO_2 assimilation (Hodges, 1967). It has also been suggested that the level of diffuse radiation on the forest floor might conceivably be higher on thin foggy days than when days are clear, particularly during the late afternoon (Black, 1963). The “summer fog blanket (Cooper, 1917)” not only relieves evapotranspirational stress by altering net radiation, temperature and humidity (Marotz and Lahey, 1975), but may sharply delimit redwood distribution in areas where its influence is overcome by inland heating of the land (Zinke, 1977).

One such example is the Mattole River basin where grassland persists though redwood forest might be expected (Bakker, 1984). Desiccating offshore winds and downdrafts peculiar to the inner face of the Kings Peak Range appear to be responsible for this anomaly, generated by large back eddies in the summertime wind pattern (Zinke, 1977). Redwoods are conspicuously absent from the basin despite the fact that its overall annual precipitation of 120 inches (Cooper, 1965) is the highest in the redwood region (Zinke, 1977). The trees, however, are not strictly circumscribed by the limits of fog/stratus penetration (McBride and Jacobs, 1977), and may persist in some relatively fog-free localities (Adams, 1969; Cooper, 1965) while failing establishment in others subject to heavy summer fogs (Baker, 1962; Cooper, 1965; Zinke, 1964).

Indeed, along the California coast, the Point Reyes Peninsula weathers the greatest number of days with fog (Sprague, 1941), yet supports only Douglas-fir and Bishop pine (*Pinus muricata*) forests (Evens, 1988). Since the frequency range of early morning and early season stratus within the redwood belt is substantial, fog/stratus events may not serve as a dominant factor in redwood distribution (Marotz and Lahey, 1975). At least, no causal relationship between coastal fogs and redwood has been clearly established (Black, 1963; Simmons and Vale, 1975).

Temperature

Redwoods require a temperate, maritime regime of temperatures where monthly means do not fall below 36 F, nor exceed 84° F (Kuser, 1976). Mean annual temperatures throughout the region vary between 50 and 60 F, with daily extremes rarely falling below 15 F or rising above 100 F (Roy, 1966). The range in mean annual maximum and mean annual minimum temperatures increases with elevation and distance inland (Zinke, 1977), from 10 or 15° F along the coast to 30 F for the easternmost colonies (Person, 1937). Position relative to the ameliorating influence of the sea controls the gradient of increasing temperature extremes, compounded by local topographical factors (Zinke, 1977). Climate, therefore, tends to be more severe in the leeward valleys exposed to broad ranges of temperature and low humidity (Franklin and Waring, 1980).

Frost Intolerance

The sensitivity of redwood seedlings and young foliage to persistent frost also restricts the northern portion of its range (Daniel, 1942; Kuser, 1976; MacGinitie, 1933) to the warmer ridgetops, saddles and upper slopes below 1500 feet in elevation (Becking, 1971), where snowfall might not exceed five inches per year (Becking, 1967).

Redwood frost intolerance may be aggravated by the unusually high water content of its tissues: as much as 70 pounds, or 8.4 gallons, per one-inch by one-foot by twenty-foot board (Kuser, 1976). In growth chamber studies of redwood seedlings, Hellmers (1964) noted a marked restriction in growth at nocturnal temperatures below 59 F which might explain why the tallest redwoods grow so near their northern limit of distribution. Optimum seedling growth was achieved under 66 F day and 59 F night conditions with little evidence of the salient thermoperiod characteristic of other conifers (Hellmers, 1966). This result is consistent with those of Kuser (1976), who found the highest site index or potential pro-

ductivity of coast redwood at a mean summer temperature of 64° F.

Impact of Winds

The deleterious impact of ocean winds, high in salt spray aerosols and frequency, not only precludes redwood establishment along the proximate coast, but along interior wind gaps such as those between Bodega Bay and Petaluma, the Golden Gate, and the Salinas Valley (Zinke, 1977). The severity of exposure increases southward along the Santa Lucia Mountains where less than two percent of the annual precipitation falls from June to September (Borchert et al., 1988). Wind desiccation and foliage salt burn severely stunt the growth of southern redwoods near canyon mouths and ridgetops (Becking, 1971), repeatedly killing the tops of unprotected trees (Daniel, 1942). The redwood's considerable sensitivity to transpirational water loss may result from the inability of their stomatal guard cells to close properly (Kuser, 1976).

Wind-dwarfed redwoods may even suffer a net reduction in diameter due to the cumulative desiccation of their tissues over a period of years (Haasis, 1933). Hence, the southernmost colonies persist only upon western and northern exposures that are at least moderately sheltered from ocean gales (Roy, 1966). "The conditions are, on the whole, so unfavorable that... mature trees with very long branches, broad or irregular crowns, or with a flat crown like a broad, flat hat are a feature of this country (Jepson, 1910)."

Examples of wind-intensified evapotranspirational stress can be seen throughout the redwood belt in the severe dieback of many mature Sequoia crowns reduced to naked spires (Kuser, 1976; Stone, 1965; Zinke, 1964). Commonly known as "spike-tops (Fritz, 1931)," the condition is familiar among old-growth stands (Cooper, 1965) where wind speeds exceed the tolerance of redwood to drying effects on the canopy (Zinke, 1964).

Older, larger redwoods are more vulnerable because their ability to conduct water through the sapwood decreases with age (Waring and Schlesinger, 1985), and the time required to transfer water from the roots to the leaves is too great in larger trees to permit roots to contribute much to daily water deficits (Waring and Running, 1976). Noxious moisture stress may also result from fire damage to the basal cambium, diminishing the active water conducting area of the sapwood (Fritz, 1931). Wiant (1964) further proposed that since the lower limbs of older redwoods might require a greater portion of the photosynthates used in respiration, stress for both moisture and carbohydrates may contribute to the spike-top death of upper limbs and branches.

Windfirm

Although redwoods do not have tap roots (Fritz, 1978), they remain remarkably windfirm under most conditions (McCollum, 1957).

Their extensive, shallow root systems, four to six feet deep and up to 50 feet in lateral spread (Shirley, 1937), frequently interlock (Becking, 1982), allowing individual trees of great height and massive crown to resist windthrow, especially among groves with uniform stand density (Sturgeon, 1964). The susceptibility to windfall, therefore, is largely focused upon redwoods growing along the margins of virgin stands, roads and logging sites (Cooper, 1965). A combination of strong wind and saturated soil is necessary for significant windfall damage, compounded by the depth of soil, condition and size of the root system, crown size and shape, trunk strength, and collision with other falling trees (Boe, 1966).

In the aftermath of the Columbus Day hurricane of 1962, Boe (1966) surveyed the timber lost on several experimental cutting sites hammered by winds gusting to 120 knots for three to five hours. Eighty-three percent of redwood casualties was attributed to uprooting, while breakage accounted for the rest. Bole rot was not considered to be a major factor since 59 percent of the broken trees

showed no signs of disease. Redwoods with the smallest and largest diameters emerged the most windfirm; and losses were proportionately lowest at the shelterwood cutting site where windfall was minimized in all diameter classes.

In the protected forests of Jedediah Smith Redwoods State Park, the damage to virgin redwood was minimal, yet poignant, for “95 percent of the old-growth trees that fell were Douglas-fir. Of the relatively few redwood trees that went down, the majority fell because Douglas-fir trees fell into them (Sturgeon, 1964).” It is important to appreciate that storms of this magnitude are exceedingly rare within the redwood belt (Decker et al., 1962; Fujimori, 1972); and that from 1960 to 1962, just three winter storms accounted for nearly all of the windfall damage discovered by Boe (1966) on the experimental cutting sites.

Topography

Characteristic of the topography that dominates much of the redwood forest is the rugged, broken landscape of the Coast Range Mountains (Person, 1937), deeply etched by rivers and streams that often parallel the coastline and the San Andreas Fault (Zinke, 1977). Interior valleys accordingly trend southeast to northwest, although many individual ranges cut obliquely across the belt and terminate at the sea (Howard, 1979). The precipitous rise of peaks along the coast can be impressive, but the total relief is considered small for a mountainous country (Person, 1937) where the average summit commands an altitude of 2000 to 4000 feet (Howard, 1979). Roughly 40 to 90 miles in width, the Coast Ranges trend about 30 west of north which tends to accentuate the interior climatic aspects of river valleys that drain to the northwest (Zinke, 1977).

By reinforcing the summer influx of marine air from the prevailing northwesterly winds, redwood distribution in areas like the Eel River Valley extends further inland. When river valleys broaden to form alluvial flats and benches, redwood stands of almost unbelievable volume

occur, but they constitute only a small percentage of the total (Person, 1937). The hewn topography of the Coast Range Mountains is principally forged by long, narrow watersheds with steep slopes and considerable movement of soil (Black, 1963) punctuated by numerous linear lowlands such as the Petaluma Valley and by a few irregular basins such as Clear Lake (Howard, 1979).

Geology

The predominant rock is sedimentary (Zinke, 1977), a marbled coalition of coastal and Franciscan sandstones from the late Jurassic and Cretaceous, redoubled by Tertiary marine deposits and cleaved by an eastern belt of weakly metamorphosed Franciscan material (Irwin, 1960). The Franciscan Formation differs from the coastal series by the almost complete absence of potassium feldspar in the dominant rock, graywacke (Waring and Major, 1964), and by its characteristic assemblages of greenstone, chert, slate and minor limestones (Irwin, 1960).

In addition, marine and coastal sandstones generally lack the clay that is abundant in the matrix of Franciscan sandstone (Thomas, 1961). Significant amounts of shale and conglomerate are found in all formations (Irwin, 1960), with serpentine and schist locally abundant (Person, 1937). And in the north Coast Ranges, the absence of granitic intrusions distinguishes the area geologically from the Klamath Mountains in the east (Waring and Major, 1964), and from the Santa Cruz (Thomas, 1961) and Santa Lucia Mountains in the south (Borchert et al., 1988).

Geological Types

The geological types trend in a manner similar to the topography of the region, thereby reinforcing the edaphic and topographical controls on the distribution of flora (Zinke, 1977). Intrusions of basalt are commonly shot through the thin-bedded sandstones of the Franciscan Formation, cemented by clays and silicious elements that readily erode into good forest soils (Baker, 1962). But site quality and timber types vary with the character of the binding

cement and the amount of basalt in soil deposits, both of which affect porosity.

Younger, less consolidated sandstones near the coast generally produce deeper soils with greater water-holding capacities than those older and harder and farther inland (Zinke, 1977). However, coastal terraces adjacent to the sea often have ancient surfaces covered with old, infertile soils and hardpans which restrict drainage and soil aeration, promoting depauperate vegetation of pygmy forest types such as *Cupressus pygmaea* and *Pinus contorta* ssp. *bolanderi* in Mendocino County (Westman and Whittaker, 1975).

And where local outcrops of serpentine and peridotite give rise to shallow soils that are extremely high in magnesium (Baker, 1962) and low in potassium, calcium and phosphorous (Zinke, 1977), redwood distribution abruptly ends (Becking, 1971; Zinke, 1964). Similar barriers occur upon glades or grassland openings where high-pH, heavy clay soils are derived from rocks richer in basic elements than those of adjoining forests (Zinke, 1977).

Grassland prairies further dominate the heavy clay soils that arise from metamorphic rocks like glaucophane schist. The exclusion of redwoods from these grassland areas might even be advanced by the unfavorable influence of humus and grass-root remains upon the sod (Zinke, 1964).

Soils

A wide range of soil types occur within the redwood region (Black, 1963), marked by considerable variation in texture: from thin rocky loams on some of the steepest slopes to deep, fine sandy loams on alluvial flats and benches (Person, 1937). Among the most productive are the Mendocino (Zinke, 1964), Empire (Roy, 1966), Hugo, Larabee, Melbourne, Josephine (Black, 1963), Gamboa (Borchert et al., 1988) and Ferndale series (Waring and Major, 1964).

Conifers typically do best upon medium textured, deep soils with more than four feet to bedrock, where permeable, well-drained pro-

files are moderately acidic increasing with depth (Storie and Wieslander, 1952), which, for coast redwood, ranges in pH from 5.0 to 7.5, with an optimum pH of 6.5 (Zinke, 1964). These conditions are roughly analogous to the upland forest soils of the Hugo series whose gravelly to clay loams (Lenihan, 1990) support nearly 80 percent of redwood stands in central Humboldt County (Waring and Major, 1964; Zinke, 1964).

The sovereignty of the Hugo series is maintained by the youthful topography of the region (Zinke, 1964), subject to frequent earthquakes and relatively rapid uplift (Black, 1963), facilitating an equilibrium between soil erosion and weathering rates (Zinke, 1964). Both the Hugo and its more inland counterpart, the Josephine series (Storie and Wieslander, 1952), are developed on Franciscan sandstone, and normally possess 15 to 20 percent gravel with sufficient clays to qualify as loams (Black, 1963). Although Waring and Major (1964) found the Hugo to be the most variable of those studied, the series may be broadly classified as a gray-brown podzolic soil (Black, 1963; Zinke, 1964) or, on occasion, a fine, loamy, mixed mesic dystric xerochrept (Lenihan, 1990)!

Subsoil Development

Debris avalanche is a dominant hillslope erosion process in the Coast Range Mountains (Borchert et al., 1988), yet pockets of colluvium may remain stable for as long as 17,000 years to permit significant pedogenesis (Marron, 1982). Subsoil development may even be advanced by slope creep, superimposing one subsurface layer upon another to form a double B horizon, and possibly improving site quality (Zinke, 1964). Within the maritime province of northern redwood forests, upland soils weather to produce loams that are comparable to the Melbourne and Larabee series, with deeply developed horizons on subsoil clay formations that often support almost pure stands of redwood (Black, 1963). The gravelly to clay loams of the Larabee arise from weakly consolidated

conglomerates, gray-brown to pale brown in color (Waring and Major, 1964), with common clay contents of 20 to 25 percent (Black, 1963). Larabee deposits may also exhibit a semi-permeable horizon of clays, three or more feet below the surface, which affects subsurface water drainage. Residual soils of the Melbourne have contrastingly darker profiles, with dark brown to brown clay loams and gleyed subsurface horizons that are chiefly derived from graywacke sandstones, shales and conglomerates (Lenihan, 1990).

A more complex assemblage of parent rock material fosters the most productive, albeit weakly developed, series for redwood in the Santa Lucia Mountains (Borchert et al., 1988). Known as the Gamboa series, these gravelly to very gravelly loams generally develop on debris slide colluviums of Franciscan shales and sandstones, abundantly admixed with granitic-metamorphic deposits of gneiss, schist, marble, quartz, diorite and tonalite. Borchert et al. (1988) concluded that the severity in slope topography was largely responsible for the weak pedogenesis of southern subsoils, since the period of pocket development is probably longer and the duration of stability shorter than in most northern colluviums.

Water-holding Capacity

Perhaps the most fundamental requisite common to all redwood soils is a high water-holding capacity (Cooper, 1965; McBride and Jacobs, 1977), to wit, "the redwood requires little of the soil except that it be moist (Fisher, 1903)." Prosaic simplism notwithstanding, redwoods are very exacting in their soil moisture requirements (Sudworth, 1967), especially during the summer growing season when 69 to 90 percent of potential evapotranspiration occurs (Becking, 1967). In terms of minimum available moisture in the soil, Waring and Major (1964) discovered that redwood distribution is limited by moisture regimes of 18 to 86 percent of storage capacity, with an ecological optimum or highest population density of 62 percent during the driest month of the year.

But the ecological optimum does not necessarily depict where the largest or most vigorous specimens are found, and the better redwood sites are closer to 80 percent of storage capacity (Zinke, 1964). The high soil moisture requirement is partly due to the relative inefficiency of the root system (Becking, 1967; Stone, 1965), notably lacking root hairs (Canon, 1926) which diminishes the surface area available for water absorption. Redwoods must depend upon the prodigious volumes of water stored within their trunks to alleviate periods of moisture stress (Stone, 1965).

Even upon habitually well-watered sites, Stone (1965) observed that large redwoods may suffer a net reduction of 25 percent in their bole reservoirs from June to September. Thus, it is not surprising that the most superlative redwood groves flank major rivers and streams upon alluviums (Zinke, 1977) allied to the Ferndale series, whose gravelly to pure silt loams are complimented by an abundant supply of subsurface water (Waring and Major, 1964).

Timber Yields

The biomass accumulations of old-growth redwood atop alluvial flats are legendary, and are without equal, the largest stands of timber in the world (Harlow and Harrar, 1958). Per-acre yields of 125,000 to 150,000 board feet are not uncommon (Harlow and Harrar, 1958; Jepson, 1910, 1923), while harvests of more than one million board feet have been scaled from a single acre of felled logs (Browne, 1914; Fritz, 1957b; Sudworth, 1967).

Nineteenth-century loggers achieved unimaginable yields. As much as 7.15 billion board feet were once milled from a 36,000-acre tract near Big River on the Mendocino coast (Andrews, 1958), or at the rate of 198,611 board feet per acre. "And, in one instance, a single acre contained 2,500,000 feet B.M. (board measure) of standing redwood, and yielded 1,500,000 feet of cut lumber. Of course, such quantities are exceptional (Soule, 1899)," but no less unexpected considering the size of individual trees. A record 480,000 board feet of first-class lum-

ber was reportedly milled from a single redwood (Jepson, 1910; Peattie, 1980; Soule, 1899), and "many other trees have yielded 400,000 (Soule, 1899)." The famous Captain Elam Tree in Humboldt County (Appendix II) was 308 feet high and over 20 feet in diameter at five feet above the ground, scaling 361,366 board feet, enough to build 22 five-room bungalows (Peattie, 1980; Roy, 1966; Shirley, 1937; Tiemann, 1935).

Moreover, Humboldt County redwoods have produced the greatest accumulations of stem biomass ever recorded (Franklin and Waring, 1980) at nearly 1401 tons per acre (Fujimori, 1977), or better than eight times the maximum total above ground biomass found in mature tropical rain forests (Art and Marks, 1971). According to Fujimori (1972), the addition of redwood branch, leaf and root biomass would likely increase the estimate of standing crop to an extraordinary 1831 tons per acre! Correspondingly high values have also been tallied for the mass of fallen logs at Prairie Creek Redwoods State Park: as much as 66 tons of decaying redwood logs per acre of upland old-growth forest (Bingham and Sawyer, 1988).

Height

The overwhelming ambiance of gigantism which ennobles the redwood forest is matched by a peerless supremacy in height (Appendix V). They are the tallest trees in the world (Dewitt, 1985; Huxley, 1985; Peattie, 1980; Shirley, 1937; Tiemann, 1935; Zahl, 1964). "Not just occasionally taller, in individual specimens growing under unprecedentedly favorable conditions, but taller as a whole, as a race, a titan race (Peattie, 1980)." Average large redwoods range from 190 to 280 feet high with eight to 15-foot diameters (Sudworth, 1967), and crowns in excess of 300 feet are familiar to alluvial flats and benches (Fritz, 1957b).

Exceptional trees are 325 to 350 feet high, and may scale 18 or 20 feet in diameter at nearly 12 feet above the ground (Sudworth, 1967). Such extremes are usually rare in occurrence and scattered over the entire range (Fritz, 1957b);

yet in Redwood National Park, the fabled Tall Trees Grove on Redwood Creek boasts the first, second, third and sixth tallest living things on earth in 1963 (Zahl, 1964). At 367.8 feet high, the champion Tall Tree was discovered by Zahl (1964) to barely eclipse the crowns of nearby rivals topping 367.4, 364.3 and 352.3 feet in height. However, in the aftermath of the winter floods of 1964, siltation around the base of the Tall Tree had reduced its standing height to 366.6 feet (Becking, 1967). Becking (1968) also found two additional redwoods exceeding 353 feet in the Redwood Creek Valley. Since the crown of the Tall Tree is spike-topped (Carranco, 1982), it would appear that there may still be some prospecting to be done for the world's loftiest tree (Zinke, 1965). At least, existing registers of the tallest redwoods are encumbered by the lack of recent investigation and may not accurately rank the current champions.

Historical Measurements

Historical measurements of tall trees long ago felled or destroyed are often unreliable (Tiemann, 1935), but the frequency of record citations in excess of 367.8 feet for redwood, Douglas-fir and mountain ash (*Eucalyptus regnans*) is notable and merits further attention. According to Carranco (1982), a phenomenal 424-foot redwood was felled in 1886 by the Elk River Mill and Lumber Company, yielding 79,736 board feet from 21 logs cut in lengths of four at 16 feet, 12 at 20 feet, and five at 24 feet long! This record only just surpasses a massive Douglas-fir in the Seymour Valley near Vancouver, British Columbia (Appendix VI). At 417 feet high, the tree had a base diameter of 25 feet and was reportedly free of limbs for 300 feet when logged in 1895 (Tiemann, 1935).

Other Large Tree Species

Another former Douglas-fir, 15 feet in diameter, once stood 385 feet tall near Mineral, Washington (Harlow and Harrar, 1958). Among the many dubious, early accounts of Australian eucalypts is one notorious 464-foot claim that

was later discounted by government surveyors to be less than 220 feet high (Tiemann, 1935), and another poorly documented 1872 record by the Inspector-General of Forests, Victoria, of a giant mountain ash 433 feet long to the point where the crown broke off in felling (Penfold and Willis, 1961). The tallest eucalypt of reliable authority was probably a mountain ash from Gippsland, Victoria, which topped 375 feet when felled and measured by theodolite in 1880 (Hardy, 1918; Huxley, 1985; Penfold and Willis, 1961; Tiemann, 1935). Maximum heights are comparatively modest for living *Pseudotsuga* and *Eucalyptus*, with a 324-foot Douglas-fir at Ryderwood, Washington (Tiemann, 1935; Zahl, 1964), and a 322-foot mountain ash in the Styx River Valley of Tasmania (Hartesveldt et al., 1975; Penfold and Willis, 1961) recognized as the tallest known survivors of their species (Zahl, 1964).

Longevity

The remarkable stature and large biomass accumulations of redwood and Douglas-fir are not only a consequence of their genetic potential for sustained height growth, but for longevity (Franklin and Waring, 1980; Westman and Whittaker, 1975). Douglas-firs may typically live for 750 years, and exceptionally 1375 (Appendix VII), while the greatest age yet recorded for coast redwood is just over 2200 years (Fritz, 1957b, 1958; Hartesveldt et al., 1975), lamentably ascribed to an ancient *Sequoia* 12 feet in diameter when felled in the Avenue of the Giants, Humboldt County, in 1934 (Weaver, 1975). However, such patriarchs are very much in the minority, as are redwoods of great diameter, and the majority of trees are perhaps less than 600 years old (Fritz, 1929b). Indeed, according to Fritz (1964), there has been a popular misconception that all redwoods "are immense in size and hoary with age. The fact is, a tree 1,800 years old or older is a great rarity and so is a redwood exceeding 15 feet in diameter at the standard point of measurement - breast height (Fritz, 1964)."

Age and Size Classes

The classic virgin redwood stand contains a wide representation of age and size classes (Wiant, 1964), with no correlation between the two (Fritz, 1957b). Nineteen-inch diameter redwoods have been found to be more than 400 years old (Fritz, 1938), which is commensurate with the estimated age of the Tall Tree (Dolezal, 1974). On a 30-acre tract of average redwood timber logged in Humboldt County, Fritz (1929b) compiled diameter and age profile data for the harvested forest. Of 1263 trees and stumps that measured over 12 inches in diameter at breast height, 18.9 percent were more than 61 inches in diameter, 34.5 percent were 31 to 60 inches, and 51.6 percent were 12 to 30 inches. The corresponding age profile was obtained from 567 stumps over 18 inches in diameter:

Table 1 Age Class Distribution on 30 acres of Old-Growth Redwood Forest

Age (years)	Number of Trees
0 to 200	unknown
201 to 300	108
301 to 400	89
401 to 500	81
501 to 600	102
601 to 700	67
701 to 800	38
801 to 900	34
901 to 1000	31
1001 and older	17

(After Fritz, 1929b).

The two oldest redwoods were 1380 and 1246 years of age; and those believed younger than 200 years were omitted from the tally because

only a few trees under 18 inches in diameter were cut. Otherwise, more than a thousand redwoods might have been included in the 0- to 200-year age class. Fritz (1929b) also did not obtain ages for many trees with incomplete ring chronologies due to burned-out centers, rot and other factors.

A similar investigation of redwood stumps was conducted by Cooper (1965) on several logging sites in Humboldt and Del Norte Counties (Appendix VIII). From 1601 stumps greater than three feet in diameter, only 14, or less than one percent, exceeded 650 years of age. The age profile data from both of these studies appears to be representative of the typical old-growth forest. However, an interesting variation occurs in redwood groves atop alluvial flats and benches. Zinke (1965) discovered that for areas subjected to periodic flooding, new age classes tend to arise from waves of redwood seedlings that become established after each flooding event, thereby producing waves of younger trees from sediment layers of comparable age.

Longevity of Other Species

Although the individual lifespan of 22 centuries for coast redwood is impressive, it is hardly a contender for record longevity (Hartesveldt et al., 1975). Giant sequoias are known to live for as long as 3126 years (Fry and White, 1931), and mountain junipers (*Juniperus occidentalis* ssp. *australis*) (Vasek and Thorne, 1988) for 3250 (Glock, 1937), while the i. Alaska yellow-cedar; (*Chamaecyparis nootkatensis*) may persist for nearly 3500 years (Franklin and Dyrness, 1988). A 4900-year old bristlecone pine (*Pinus aristata*) on Wheeler Peak in the eastern Great Basin of Nevada is widely regarded as the world's oldest living tree (Currey, 1965).

Yet these records pale in comparison to the estimated physiological age of the creosote bush (*Larrea tridentata*) in the Mojave Desert of California, where rings of creosote bush clones develop by irregular radial growth, stem segmentation and the production of new stems at the outer edge of stem segments (Vasek,

1980). Based on established growth rates for creosote bush rings over long periods of time, the extrapolated age of the largest known clone approaches 11,700 years!

Cloning

The potential for cloning species to attain great physiological age is an attribute shared by coast redwood, whose capacity to regenerate from basal sprouts following stem collapse (Lang and McBride, 1979) may ultimately foster a circle or “fairy ring (Cannon, 1908)” of venerable redwood clones up to 80 feet in diameter (Fritz, 1936), “the latest incarnations of a genetic individual of incalculable age (Wallace, 1984).”

Sucker development is rare among gymnosperms (Coulter, 1901); and just two conifers associated with redwood, the California nutmeg (*Torreya californica*) and Pacific yew (*Taxus brevifolia*), commonly sprout from stumps, although vigorously only in the former (Jepson, 1910). Redwoods are unique among commercial conifers in their ability to sprout profusely in response to disturbances such as fire, cutting, mechanical injury or change in light intensity (Cole, 1983).

As many as 300 suckers may ring a single stump (Fritz, 1929a), and though few can be expected to survive, each successive generation of sprouts continues to enlarge the ring of survivors until it may finally lose its identity among the surrounding trees (Stone and Vasey, 1968). Thus, the physiological age of many redwoods, cloned from innumerable generations of suckers, must be tremendous (Wiant, 1964) and would efficaciously discount 2200 years of age to merely “the tip of an iceberg of genetic invariability (Wallace, 1984).”

Dormant Buds

Although sprouts may occasionally stem from adventitious buds within the callus tissue wounds (Kramer and Kozlowski, 1960) of the trunk, roots, side of the stump, or cambium zone on top of the stump (Davidson, 1971;

Metcalf, 1924; Peirce, 1901; Roy, 1966; Sturgeon, 1964; Wiant, 1964), most if not all originate from numerous dormant buds (Boe, 1965) concentrated just above the root crown (Stone and Vasey, 1968). The buds begin to form when the tree is very young (Cannon, 1926), massing in large numbers on seedlings as young as one year (Stone, 1965), and soon encircle the stem in massive root collar burls or lignotubers as the tree develops (Barbour et al., 1987; Becking, 1967, 1982; Daubenmire, 1978).

But the rate of attrition is high as many of the buds are killed by failure to keep abreast of diameter growth (Stone and Vasey, 1968), or by severe fires and other causes (Powers and Wiant, 1970). Those that survive generally remain dormant, suppressed in part by the constant flow of growth regulators moving down the tree from the crown (Stone, 1965). When the flow is interrupted by an injury to the crown or stem, the buds are permitted to break and send up shoots, sprouting vigorously for many years thereafter (Sturgeon, 1964). Observations by Cole (1983) indicate that root collar burls may continue to sprout on redwood stumps for at least 20 years after logging. And in one instance, stumps that had been repeatedly pruned for 40 or 50 years persisted in generating suckers (Stone, 1965). Redwoods may even sprout along the length of fallen stems (Lang and McBride, 1979) only to perish without the support of roots (Jepson, 1910).

Basal sprout production appears to be a function of large numbers of viable buds and high physiological vigor (Powers and Wiant, 1970), and tends to vary inversely with stump diameter and age (Boe, 1965). The most prolific sprouting occurs among redwoods in the 200- to 400-year age classes with a rapid decrease in sprouting intensity beyond these ages (Powers and Wiant, 1970). The peak in viable seed production is also from trees in this range, reaching a maximum sometime after 250 years (Lott, 1923; Metcalf, 1924). But the difference between initial growth rates for seedling and sprout is considerable, and after five years, seedlings may reach one to four feet in height

while contemporary suckers stand 15 feet tall (Boe, 1965).

Exceptional sprouts may grow eight to ten feet high in the first year (Wiant, 1964), and after 50, produce trees up to 150 feet in height and 30 inches in diameter (Fritz, 1936). Although seedling growth will eventually match the rate of suckers (Boe, 1965), it is not unlikely that sprouting has been the principal means of redwood reproduction (Wiant, 1964). Indeed, according to Stone (1965), without the rapid ability of the tree to sprout and the vigorous growth of its suckers, coast redwood as a species might well have vanished.

Seedling Regeneration

The importance of seedling regeneration, however, cannot be ignored since all existing genotypes must have had a seedling origin sometime in the past (Wiant, 1964). Not only can an acre of redwoods produce more than 6.9 million sound seeds per year with an average viability of 85 percent (Boe, 1961, 1968), the survival of just a few redwood seedlings would be sufficient to maintain the long-lived and sprouting species (Lang and McBride, 1979; Muelder and Hansen, 1961a; Wiant, 1964). On selectively logged sites of redwood, Douglas-fir and white fir (*Abies concolor*), Person and Hallin (1942) found eight times as many redwood seedlings produced from only twice as many seed trees than its associates after five years.

Restocking from redwood sprouts was considered to be inadequate; and unless supplemented by seed, reproduction by sprouting may result in insufficiently and irregularly stocked stands (Metcalf, 1924; Show, 1932). In addition, the mere proximity of secondary-growth close to an old-growth stump may not necessarily indicate sprout origin (Becking, 1967) as seedlings are frequently found at the base of stumps that fail to generate suckers (Davidson, 1971). Becking (1967) further noted that the position of a seedling next to the stump would have great ecological significance and may be primarily responsible for its ultimate survival (Appendix IX).

Flowering

The flowering season for coast redwood extends from mid-October (Becking, 1971) to early March (Metcalf, 1924; USDA, 1948), when tiny, inconspicuous male and female flowers are borne separately and terminally on different branches (Becking, 1971; Boe, 1974a). Whereas some male strobili may persist in dispersing pollen as late as April, the pollination of most female conelets is achieved by the end of January (Becking, 1967). In comparison to other conifers, redwoods are relatively poor producers of pollen, dispersing less than 1/1000 the amount of pollen released by Douglas-fir, grand fir (*Abies grandis*) or Sitka spruce (*Picea sitchensis*) (Becking, 1971). Redwood pollen grains also lack the characteristic air sacs common to most wind pollinators such as *Pinus* and *Alnus* (Becking, 1967).

Redwood pollination can be further impaired by prolonged periods of inclement weather when rainfall may wash much of the pollen away before it reaches the female strobili (Becking, 1967, 1971; McBride and Jacobs, 1977). Yet intervals of dry, windy weather occur with sufficient frequency (Boe, 1970) to permit the optimum midwinter dispersal of pollen required for seed crops of high viability (Lott, 1923).

Fertilization of the conelets usually does not occur until early summer, from mid-May to early July; and in the cooler, wetter regions of redwood distribution, it may possibly be delayed until the end of July (Davidson, 1971). The maturation of cone and seed is completed by August or late September (Lott, 1923), and throughout the winter months until early summer (Davidson, 1971), seeds are opportunistically shed whenever weather conditions of low humidity permit the ripened cones to dry and open (Roy, 1966).

Seed Dispersal

Thus, the rate of seed dissemination is affected by local precipitation patterns, altitude and exposure, and can vary greatly depending upon

the dryness of the site. Although remarkably small and light at 59,000 to 300,000 seeds per pound (Lott, 1923), dispersal is limited by their narrow, inefficient wings (Roy, 1966) that are seldom as broad as the body of the seed (Buchholz, 1939; Sargent, 1947). The seeds fall to the ground at an average speed of 8.6 feet per second (Siggins, 1933), which is faster than most other conifers (Becking, 1967) and may restrict effective seeding distances to only 200 feet uphill or 400 feet downhill from the margins of clearcut redwood logging sites (Person and Hallin, 1942).

Seed dispersal is also limited by the tendency of viable seeds to sink in water (Chaney, 1924, 1930). Among northern redwood forests, more than 85 percent of the total seed may fall between November and February, including the majority of sound seed containing both endosperm and embryo (Boe, 1968). This would be a favorable period for the regeneration of redwood logging sites, as winter rains, optimum seedfalls and maximum viability coincide to provide ideal conditions for germination on exposed mineral soils when temperatures are suitable (Boe, 1965, 1968). Virtually no sound seed was recovered by Boe (1968) in late spring or summer.

Cones and Seeds

Redwoods are prolific producers of cones and seeds (Harlow and Harrar, 1958), capable of bearing thousands of cones per tree each year (Becking, 1982) with an average yield of 60 (Lott, 1923) to 120 seeds per cone (Becking, 1967). On experimental redwood cutting sites, annual crops of more than of 24.5 million seeds have been collected by Boe (1968) from just three residual seed trees. But individual and stand productivity varies tremendously in accordance with regional, local and physiological factors not clearly understood (McBride and Jacobs, 1977).

While dominant and codominant redwoods typically produce more cones than those in the overtopped classes (Boe, 1968), intermediate

crown-class trees can frequently generate good crops even before logging (Fritz, 1951).

In addition, entire stands have been found to produce little or no seed for extended periods (Muelder and Hansen, 1961b). Fritz (1951) confirmed that some redwoods apparently never produce seed, a condition that might be determined by permanent features of the root environment where impairment of the root system by disturbances such as road-cuts, soil compaction or flooding is required to stimulate cone production (Becking, 1968; Muelder and Hansen, 1961b).

There is also some indication that periodic, low-intensity fires may serve to invigorate seed production immediately after burning (Becking, 1967, 1982). In general, redwoods produce fair to abundant seed over most of its range with regularity, though poor and sporadic crops occur with increasing frequency southward (Boe, 1974a; Muelder and Hansen, 1961b), accompanied by a gradual decrease in the average size of the seed (USDA, 1948).

Seed Production

Redwoods begin to bear seed at five to 15 years of age (Boe, 1974a), achieving good viable seed production after 20 years (Fritz, 1951) and optimum yields at ages 60 to 250 (Metcalf, 1924). According to Becking (1967), maximum cone production may not occur until much later, from 300 to 700 years, with trees older than 1200 years having only a reduced cone crop. But the viability of seed produced by such patriarchs is either low or absent (Lott, 1923). An exceptional cone-bearing record of a plantation seedling scarcely three years old and 12 inches high was reported by Merriam (Anon, 1927b), while many seedling trees up to 80 years of age have been observed to be largely barren (Becking, 1967).

Germination Rate

Metcalf (1924) and Lott (1923) found that redwood forests of medium crown closure normally generate the highest caliber crops, with

60- to 100-year old individuals producing the largest seeds. Good seed quality was not obtained in very dense or very open stands. The ability of redwoods to produce abundant seed is tempered by crops of low germinative capacity (Davidson, 1971). Whereas Boe (1968) recorded sound seed germination rates of 75 to 94 percent, the corresponding viability of the total seedfall was only 2.5 to 12 percent. Comparable levels of viability were reported by Davidson (1971) for 10,762 seeds examined by X-ray photography and germinated in lots of 200:

Table 2 Germination rates of redwood seeds classified by radiography

Seed Classification	Total Germination
Sound (filled and healthy)	13% 84%
Dubious (filled, with some defect)	12% 67%
Shriveled (collapsed or decayed)	62% 0%
Empty	13% 0%
All seed classes	100% 19%

(After Davidson, 1971)

A remarkable germination capacity of 20 to 40 percent was obtained by Fritz (1950) from crops of squirrel-cut cones, which are often felled in large quantities (Metcalf, 1924) when green and unopened by the Douglas' squirrel, or redwood chickaree, (*Tamiasciurus douglasii*) (Nowak and Paradiso, 1983; Roy, 1966). Hansen and Muelder (1963) also recorded crops of 40 percent maximum viability, although, in some of the samples tested, 99 percent of the seed lacked discernible embryos. The percentage of viable seed produced by redwoods younger than 20 years is usually less than one percent, and no more than three percent for 1200 to 1500-year old trees (Lott, 1923; Metcalf, 1924).

The average germinative capacity of the seed is about ten percent (USDA, 1948) which, under normal field conditions, may be completely lost at the conclusion of the first growing season (Becking, 1971).

Low Viability

Low viability is attributed to not only a high percentage of aborted embryos, commonly tannin-filled or empty, but to frequent cone invasions by fungal pathogens and insects (Davidson, 1971; Hansen and Muelder, 1963; Keen, 1952). More than 120 fungi have been isolated from developing seeds and cones, initiating decay from pollination to maturity (Davidson, 1970, 1971). Davidson (1971) discovered that all redwood cones were infected as early as late June, including 31 percent of the seed. And by mid-August, 93 percent of the cones and 59 percent of the scales bore symptoms of disease, while 91 percent of the seeds and all of the scales were infected.

Further damage was caused by larvae of the cone moth (*Commophila fuscodorsana*), which mined up to 100 percent of the seeds in 38 percent of the cones. The roundheaded borer (*Phymatodes nitidus*) has also been observed to feed on redwood cones (Keen, 1952), but with questionable frequency and impact (DeLeon, 1952). The beetle was not detected in Davidson's (1971) study. Nonetheless, it is probable that cone disease and larval feeding destroy as much as 60 percent of potential seed crops since the early death of cone scales would likely prevent the maturation of seeds regardless of seed infection (Davidson, 1971).

In deference to the great inherent variability of redwood germination (Becking, 1971), most seeds will germinate immediately (Becking, 1967) after falling on exposed mineral soils, duff, litter or rock crevices under any light intensity if temperature and moisture regimes are suitable (Boe, 1965; Cooper, 1965; Fritz, 1950, 1951, 1958). Germination can even occur on moist logs and stumps (Fritz, 1951) with such vigor that seedling roots may eventually

straddle the trunk and reach the soil to carry the tree to maturity (Dallimore, 1931).

Cooper (1965) found the accumulation of five to eight inches of rain at temperatures above 58 F conducive to good germinating success, usually within 20 to 35 days. However, in the samples tested by Boe (1968), the range in the number of days required for germination was significantly greater: from five to 45 days, with a germination peak at seven to 12 days. It is also interesting to note that the germination of sound seed by Davidson (1971) occurred within 23 days in contrast to the 31 days required for dubious seed (Table 2), and that 75 percent of "the germinants that failed to complete germination or were unlikely to survive were in the dubious class (Davidson, 1971)."

Reasons for Germination Failure

The reasons for germination failure are many. Most deleterious is the inadequate retention of moisture (Fritz, 1958) in the seeds (Becking, 1968) and in the top half or full inch of the seedbed during periods of drought (Fritz, 1950). Soil dessication is lethal to germinating seeds, imprisoning still partly bent hypocotyls beneath the hardened surface, while reducing seedling tolerances to high surface temperatures that are correspondingly more severe (Baker, 1929; Fritz, 1958). The risks are compounded by late dispersal and seeding, where seedlings germinating after the end of March may not have adequate time to extend their roots into moist soil areas before the onset of summer droughts (Becking, 1968; Fritz, 1950; Stone and Vasey, 1968).

The advantage of early seeding, however, is not without hazard, as heavy winter rains may wash away seeds or bury them too deeply for proper germination (Fritz, 1950). Moreover, mid-winter conditions that favor germination also promote the pre-emergence damping-off of seeds by fungal pathogens (Davidson, 1971; Hansen and Muelder, 1963). Davidson (1971) found humus and seedcoat mycroflora sufficiently virulent to destroy 75 to 100 percent of

sound seeds sown in damp, decomposing litter at 41 to 48 F.

There is also evidence that predation by rodents and invertebrates, such as the grey millipede (*Spirabolida californica*), contributes to germination failure (Davidson, 1971; Fritz, 1950), but with equivocal impact on the effectiveness of redwood seedfall (Boe, 1961; Roy, 1966). Seed consumption has been noted by McBride and Jacobs (1977) for the western grey squirrel (*Sciurus griseus*), Douglas' squirrel, and Townsend or redwood chipmunk (*Tamias ochrogenys*) (Jameson and Peeters, 1988); while the ubiquitous deer mouse (*Peromyscus maniculatus*) (Ingles, 1965) has been reported to feed extensively on redwood seeds (Davidson, 1971; Lauck, 1964; McBride and Jacobs, 1977), consuming as much as 63 percent of the supplemented seedfalls examined by Davidson (1971).

Critical Factors

Among the factors critical to the establishment and growth of redwood seedlings are the availability of soil moisture and the intensity of solar radiation (Becking, 1967; Lang and McBride, 1979). Becking (1968) observed that seedlings seem to exhibit a retardation in foliage and height development during the first year of growth, focusing major growth activities on the establishment of root systems. The risk of seedling dessication due to its high transpiration rate (Daniel, 1942) underscores the importance of rapid root elongation and penetration into well-watered soils, particularly before the summer retreat of moisture from the surface (Becking, 1968; Stone and Vasey, 1968). Effulgent sunlight is required for the expeditious growth of roots (Baker, 1945; Lang and McBride, 1979) that are most vigorous and abundantly branched in soils loosened to a depth of eight inches (Cooper, 1965; Fritz, 1950), and may penetrate more than four feet deep after ten weeks (Florence, 1965).

Yet seedling survival is favored by partial shade or canopy cover of 60 to 80 percent (Becking, 1967) which significantly reduces the evapora-

tion of surface moisture (Fritz, 1950). Bates and Roeser (1928) found that redwood seedlings have a remarkable efficiency for photosynthesis at low light intensities, with the capacity to increase their size 8.8 times in ten percent of full sunlight after nine months, a rate that was more than twice that of the other trees tested. Even with only one percent of full sunlight, Shirley (1929) discovered that redwood seedlings may survive as long as six months.

Although the exact relationship between soil moisture and light intensity has yet to be determined (Becking, 1967), Lang and McBride (1979) suggested that the rapid root development associated with high levels of solar radiation may compensate for the corresponding moisture loss in upper soil layers, in addition to reducing seedling vulnerability to pathogenic infections.

Soil Temperature

Canopy shading also affects the temperature of redwood soils, which Hellmers (1961) found to be most propitious for laboratory seedlings at 64 F when compared to 46 and 82 seedbeds. Though redwood seedlings have been observed to withstand considerable surface heat, as high as 140° F barring concurrent desiccation (Fritz, 1950, 1958), they are easily killed when internal stem temperatures top 131 degrees (Baker, 1929). According to Wiant (1964), heat injury to litter-borne seedlings where the ability to dissipate heat is limited “probably accounts to some extent for the scarcity of redwood seedlings of any appreciable age on undisturbed forest floors (Wiant, 1964).” And despite their marked sensitivity to freezing temperatures (Daniel, 1942; Kuser, 1976; MacGinitie, 1933), the impact of low temperature soils on seedling regeneration is relatively minor since frost-heaving occurs infrequently within its natural range, and rarely on other than north-facing slopes (Fritz, 1950).

First Three Months

The critical period for seedling establishment is during the first three months of growth

(Cooper, 1965), when fungal pathogens and predation by animals (Bega, 1964; Davidson, 1971; Muelder and Hansen, 1961a; Pelton, 1962) can be expected to destroy more than 99 percent of seedlings emerging on undisturbed forest floors (Cooper, 1965). Long-term incorporation of redwood litter into the soil not only limits microbial decomposition and the process of nutrient mineralization (Florence, 1965), but supports high populations of post-emergence damping-off and root rot pathogens (Davidson, 1971).

Impact of Fungi

More than 80 fungi have been isolated from redwood seedling roots, effectively eliminating regeneration on litter covered areas (Muelder and Hansen, 1961a) where the inoculum potential of the top five inches of mineral soil may be high enough to cause a level of post-emergence damping-off comparable to humus (Davidson, 1971).

Nematodes and Other Attacks

Seedlings roots are also attacked by parasitic nematodes, severely damaging cortical tissues (Cid del Prado Vera and Lownsbery, 1984) to subsequently inhibit the height of seedling growth by nearly 64 percent (Maggenti and Viglierchio, 1975). Additional agents of destruction include the grey millipede, which has been reported by Davidson (1971) to eat emerging seedlings in a manner usually attributed to cutworms, and the omnipresent .i.banana slug; (*Ariolimax columbianus*) (Lauck, 1964), which has been implicated by Pelton (1962), confirmed by Larson (1963), suspected by Fritz (1950), and questioned by Becking (1968) and Roy (1966).

Redwood seedlings may also be consumed by brush rabbits (*Sylvilagus bachmani*) (Fritz, 1950; Roy, 1966), deer mice (McBride and Jacobs, 1977), and possibly meadow voles (*Microtus* sp.) (Roy, 1966), while black-tailed deer (*Odocoileus hemionus columbianus*) can cause considerable browsing damage to the tips of developing shoots (Browning and Lauppe,

1964; McBride and Jacobs, 1977; Roy, 1966; Stone, 1965), particularly when the seedlings are over one foot tall (Fritz, 1950). Becking (1968) observed that seedlings suffering the loss of more than 75 percent of their foliage will inevitably die within a few months.

Mineral Soil

The comparative freedom of exposed mineral soil seedbeds from intolerable levels of fungal pathogens and understory plants competing for moisture and light has led many authors to recognize the importance of disturbed forest soils to seedling survival (Bakker, 1984; Becking, 1982; Boe, 1965, 1968; Cooper, 1961, 1965; Davidson, 1971; Dolezal, 1974; Florence, 1965; Fritz, 1931, 1950, 1951, 1958; Harlow and Harrar, 1958; Helms, 1980; Hewes, 1981; Lang and McBride, 1979; Metcalf, 1924; Muelder and Hansen, 1961a; Person and Hallin, 1942; Stone, 1965; Stone and Vasey, 1968; USDA, 1948; Wiant, 1964).

A broken soil surface that will help retain moisture throughout the first two dry seasons would be favorable (Fritz, 1958), and exposed mineral soils have a more stable moisture regime than forest litter or humus (Lang and McBride, 1979; Wiant, 1964). From ten years of laboratory study on redwood seedlings, Cooper (1965) found "that excellent establishment was obtained if the following conditions were met:

1. Seeds must fall on mineral soil, exposed at least six to eight inches in depth to remove or materially reduce various diseases and fungi that attack the seedlings;
2. Or the areas must be broadcast-burned. Burning apparently has a sterilizing effect on these organisms, and seedlings develop normally;
3. Or the soil must be sterilized artificially;
4. Where the chemical composition of the soil was below:
 - a) Nitrogen content of 0.2 percent
 - b) Phosphorous content of 11 (0.11) percent (citric acid soluble)

- c) Organic matter content of ten percent (from Walkley-Black wet-digestion method for carbon)

These conditions are most extensively created when there has been considerable disturbance in the forest, such as logging (Cooper, 1965)." Davidson (1971) noted that Cooper's (1965) requisites roughly correspond to the "removal of the upper A layer or the top six to eight inches of soil. Since in natural soils some pathogens may be found at all depths, these levels probably indicate also the soil nutrient requirements for maintaining a sufficient pathogenic population to cause significant damping-off (Davidson, 1971)," suggesting the development of some incompatibility in the relationship between coast redwood and its site (Florence, 1965).

Fire and Flood

According to Muelder and Hansen (1961a), “the sites where redwood seedlings do survive have one common condition: root rot is excluded for a while or strongly reduced in its aggressiveness. This is brought about naturally in stream bottom stands when floods deposit fresh silt, by blowdown and slides which expose subsoil material, and possibly by hot fires (Muelder and Hansen, 1961a).” Moreover, the unique capacity of redwood to take advantage of fire- and flood-interrupted environments has been integral to its establishment, survival and domination within such habitats (Barbour et al., 1987; Stone et al., 1972).

Fire

Although wildfire is uncommon to the redwood forest type (McBride and Jacobs, 1977), it can be an important facilitator of seedling regeneration (Cooper, 1965). Periodic, low intensity fires not only consume forest litter and debris to expose and temporarily sterilize mineral soils (McBride and Jacobs, 1977), but destroy understory vegetation to reduce competition for moisture and light (Fritz, 1950; Lang and McBride, 1979).

However, the difficulties of seedling establishment are compounded by greater fire frequency and intensity (Veirs, 1980a). Hot, sustained fires create undesirable seedbeds (Boe, 1965) by severely burning humus to leave soils hard and dense and difficult for roots to penetrate (Fritz, 1950), in addition to favoring the establishment of shade-intolerant species such as Douglas-fir by opening the redwood canopy (Norse, 1990).

Wildfires can also gravely damage trees less than 20 years of age because of their thin and unprotective bark (Roy, 1966). The impact of fire upon seedling regeneration is dependent upon fire intensity, temperature, flame length, duration, and time of day and season (USDI, 1985), and is most conducive to redwood stand

development when its frequency and intensity is low (Veirs, 1980a).

Within the redwood forest, the presence of countless charred trees and snags (Jacobs et al., 1985), of ancient heartwood fire scars (Simmons and Vale, 1975), of hollowed-out bases or “goose pens (Fritz, 1929b),” of stratigraphically-embedded charcoal in alluvial soil deposits (Zinke, 1964, 1977), and the development of fairy rings (Stone and Vasey, 1968) and spike-tops (Fritz, 1931) attest to fire as part of the natural environment, yet its ecological relationship to redwood stand dynamics is poorly understood (Jacobs et al., 1985; USDI, 1985; Veirs, 1980a, 1985).

Whereas old-growth forests may require periodic fires to maintain their open character or even dominance of a site (Jacobs et al., 1985), investigations by Veirs (1980a) suggest that northern redwoods maintain their dominant status with or without the influence of fire. Indeed, fire has been characterized by Fritz (1929b, 1931) and Roy (1966) as the “redwood’s worst enemy throughout life (Roy, 1966).”

It should be noted, however, that “in no observed case has a natural redwood stand been decimated by fire (Veirs, 1980b)” in the northern part of its range. And since other forest species are favored by fire suppression, the net result in its absence “would be the establishment of an understory of shade-tolerant trees beneath the redwoods. Although these trees would complete several life cycles while the redwood was completing but one, they would be present and ready to occupy the space vacated in the forest canopy any time an old redwood should lose its foothold and crash to the ground. Some re-establishment of redwood could be expected to occur on these exposed areas of mineral soil... But with the completion of each succeeding life cycle, the percentage of redwood would decrease and eventually they would disappear (Stone et al., 1972).” Thus, the impact of fire suppression would ultimately be expressed through changes in the composition, density and vegetation structure of redwood forest species (USDI, 1985).

Status of Old-Growth Redwood

The status of old-growth redwood in the presence of fire has been a matter of considerable conjecture. Redwood stands have been described as disaster climax forests (Bakker, 1984), as fire-dependent, sub-climaxes (Cooper, 1965; Stone and Vasey, 1968; Stone et al., 1972), and as a climax species (Cornelius, 1969; Daubenmire, 1978; Fisher, 1903; Fritz, 1957b; Roy, 1966; Veirs, 1980a, 1980b; Weaver and Clements, 1938; Wiant, 1964) to which fire is an integral part of the environment, but nonessential to stand maintenance (USDI, 1985).

According to McBride and Jacobs (1977), evidence to support these contradictory views has been fairly presented, but a consummate understanding of the successional position of the redwood forest is complicated by the tree's unusual longevity. Inasmuch as the concepts of plant succession and climax were developed for environments where significant vegetation changes occur within a few decades to several hundred years, they "may not be directly applicable to an area in which the life span of a single species is in excess of 2000 years. Furthermore, the common tree associates of redwood seldom live more than 500 years. This difference in life expectancy puts the associated trees into a category where the concepts of plant succession and climax may be useful in understanding their ecology.

Redwood, on the other hand, has a life expectancy of such length that its dynamics may need to be examined in the context of vegetation change over time periods longer than those normally associated with succession... Examination of such a forest would suggest a climax status for the associated species and a sub-climax status for redwood if the average time period associated with plant succession were applied. Using a longer time period, both redwood and certain of its associates must be viewed as climax species, but not members of the same climax type (McBride and Jacobs, 1977)." *Sequoia sempervirens* is nevertheless a seral species, dependent upon periodic disturbance by flood or fire in order to maintain its

vigor, reproduction and dominance (Barbour et al., 1987).

Further appreciation of the role of fire in old-growth redwood has been handicapped by limited data on fire regimes throughout the broad, latitudinal range of redwood forest types (USDI, 1985), characterized by variations in associated species (Appendix X) and fire frequency (USDI, 1985). Near Muir Woods National Monument, a relationship between fire and fog occurrence was supported by Jacobs et al. (1985), who found an average fire interval of 27 years at a more coastal site and 22 years at a more inland site.

Fire hazard and therefore fire frequency might be expected to increase along climatic west to east and north to south gradients, coincident with declines in relative humidity and precipitation (Veirs, 1985). But since the historical frequency and intensity of redwood fires are not easily determined (USDI, 1985) and may vary locally relative to fog-induced temperatures and humidity, caution must be exercised when making generalizations about the frequency of fire in the redwood community (Jacobs et al., 1985).

Similarly, attempts to distinguish between fires of human and natural origin are frustrated by the ancient, widespread utilization of fire by indigenous tribes to manage their environment and resources (Lewis, 1973). Mean fire intervals were probably much longer in the pre-human era of lightning-initiated burns, resulting in greater densities of vegetation and accumulations of dead biomass, hot, crowning fires notwithstanding (Greenlee, 1983).

The marked variability of fire regimes throughout the redwood region has been demonstrated by several studies. In addition to the four to five fires per century reported by Jacobs et al. (1985) near Muir Woods National Monument, Greenlee (1983) estimated a mean fire interval of 70.9 years over a 900-year period from 400 sites in Big Basin Redwoods State Park, only 75 miles to the south (Jacobs et al., 1985). And in Redwood National Park, 250 miles north of Muir Woods, Veirs (1980a,

1980b) reported fire intervals of greater than 500 years for the more mesic redwood sites, 150 to 200 years for typical upland sites, and 33 to 50 years for high elevation interior sites where redwood loses its dominance to Douglas-fir.

Fires of greater frequency occur in southern Humboldt County, where Stuart (1987) found mean pre-settlement (pre-1875) fire intervals of 24.6 to 31.0 years for the Bull Creek watershed in Humboldt Redwoods State Park. This is consistent with nearly 1000 years of charcoal deposition recovered by Zinke (1964, 1977) from each sediment layer in Bull Creek Flat alluviums, establishing a fire-flood sequence every 30 to 60 years. And on a 30-acre logging site to the east of Weott (Stuart, 1987), Fritz (1929b, 1931) conservatively reported the occurrence of 45 severe fires within the past 1100 years, an average of four major fires per century.

In the presence of fire, redwood is favored over other species by its tough, dense, fibrous, essentially fire-resistant bark (Becking, 1982; Stone et al., 1972) that may be one foot thick at the base (Isenberg, 1943) and shallow to deeply furrowed into straight, spiraled or reticulated ridges (Luxford, 1930a). Although redwood bark will burn (USDI, 1985), it does so slowly and reluctantly (Jepson, 1910), containing mere traces of resins and volatile oils (Anderson, 1961; Okamoto et al., 1981).

The bark is also a poor conductor of heat (Fritz, 1957b), protecting the cambium from excessive thermal damage by fire (Jacobs et al., 1985) while forming an additional insulating barrier of carbon during combustion (Anderson, 1961). Even when hot, prolonged fires succeed in breaching the bark to burn the heartwood from within, resistance to catastrophe is high.

Not only can the trunk of a 200-foot tall, five-foot diameter redwood hold as much as 34,000 pounds of water (Luxford, 1930b) to slow the rate of burning (Weaver, 1975), large trees can quickly regenerate crowns from adventitious buds along the stems and branches (Stone and

Vasey, 1968) despite recurring fires that may penetrate and burn and tunnel through heartwoods like chimneys (Fritz, 1936; Jepson, 1910). And while heavy burning and partial debarking may depress the production of suckers (Boe, 1965), the redwood's capacity to sprout from root collar burls following injury to the stem favors regeneration even if the bole is completely destroyed (Stone et al., 1972).

Paradoxically, the frequent burning of cavernous heartwood fire scars (McBride and Jacobs, 1977), of which one was reportedly 33 feet in diameter (!) (Carranco, 1982), encourages redwood survival by increasing its susceptibility to heart-rot (Stone et al., 1972). The scars, in themselves, are not critical but serve as points of entry for heart-rot fungi (Stone and Vasey, 1968) that may also gain entrance through dead or broken crowns (Kimmey and Lightle, 1955). Of the 20 fungi known to initiate decay in the redwood's bark and heartwood (Bega, 1964; Bonar, 1971), only two are responsible for causing extensive damage and gross volume culls as high as 23 percent (Kimmey and Lightle, 1955).

A brown cubical pocket rot common throughout the redwood region is caused by *Poria sequoia*, while a white ring rot attributed to *P. albipellucida* is most severe among northern stands. Neither heart-rot is fatal, but the combined action of repeated fires and advancing decay weaken the tree mechanically, hastening its loss to windthrow (Fritz and Bonar, 1931). And since redwoods can only produce basal sprouts when their root crowns remain intact, anything that would increase the percentage of root crowns left in the ground upon felling "increases the number of trees that can replace themselves by sprouting; and heart-rot does just this. Heavily infected trees generally break off above the ground when they fall and fail to pull up their root crowns in the process. Uninfected trees, on the other hand, almost invariably pull up their root crowns when they fall (Stone et al., 1972)." Because fire predisposes 90 to 100 percent of basal heart-rots (Fritz, 1931), the profusion of fairy rings throughout the redwood region evinces re-

markable vitality when assailed by dyadic catastrophes.

Table 3 Associated Mites and Insects Injurious to Coast Redwood

Order	Species	Species
Acari	Oligonychus ununguis	
Isoptera	Kalotermes minor Reticulitermes hesperus	R. tibialis Zootermopsis angusticollis
Homoptera	Amphorophora morrisoni Aonidia shastae Aspidiotus hederæ Carulaspis minima C. visci	Dysmicoccus ryani Lindin-gaspis rossi Pseudococcus citri Puto cupressi SPilococcus sequoiae
Coleoptera	Anoplodera crasipes A. impura (a) A. mathewsii Anthaxia aeneogaster Atimia confusa dorsalis Callidium pallidum (*) C. sempervirens (*) Cercuchus striatus Ctenicera sp. Dicentrus bluthneri Dichelonyx valida Dromaeolus nitens Ergates spiculatus Glyptosceli	Ips latidens Lep-tura obliterata Monarthrum scutellare Phloeosinus cristatus P. cupressi P. sequoiae Phymatodes decussatus (b) P. nitidus Platypus wilsoni Prionus californicus Ptilinus basalis Semanotus ligneus sequoiae (*) Serropalpus barbatus S. substria
Lepidoptera	Argyresthia cupressella Comophila fuscodorsana	Cydia cupressana Vespa mima sequoiae (c)
Hymenoptera	Camponotus-sp. Sirex areolatus	Xylocopa tabaniformis

(After Chamberlin, 1939, 1958; Coleman, 1901; Davidson, 1971; DeLeon, 1952; Doane et al., 1936; Essig, 1915, 1926; Furniss and Carolin, 1977; Hopkins, 1903; Keen, 1952; Lauck, 1964; McKenzie, 1956; Powell and Hogue, 1979; Roy, 1966).

(*) Species/subspecies recorded only from coast redwood (DeLeon, 1952).

(a) Commonly known as the redwood borer, but DeLeon (1952) found no authenticated record of it feeding in this host.

(b) Recorded by Hopkins (1903), but may have been incorrectly identified (DeLeon, 1952).

(c) According to Dolezal (1974), severe infestations of sequoia pitch moths may cause the death of young redwoods, but Furniss and Carolin (1977) reported they do not feed in this host.

Resistance to Insect Attack

No less remarkable is the redwood's celebrated resistance to attack by insects (Fritz, 1957b). Of the 54 species (Table 3) reported to find redwood a congenial host, most are incidental associates (Lauck, 1964) and none are capable of singularly killing mature trees (Fritz, 1957b), a record not matched by any other timber tree in North America (Lauck, 1964). Douglas-firs, by comparison within the same range, are known to be attacked by 30 species of bark beetle, while redwoods suffer but four. And where Douglas-fir cones may be mined by 28 species of insects (Bringuel, 1967; Dewey, 1970; Koerber, 1960, 1963), merely two invade cones of coast redwood (Table 4).

Activities of even the most common redwood borer, the redwood bark beetle (*Phloeosinus sequoiae*), are confined to weakened or recently felled trees and to injured or broken branches (DeLeon, 1952). The reasons for this general unpalatability are not clear, since redwoods possess very little resin (Anderson, 1961) to discourage dendrophagous insects (Barbosa and Wagner, 1989).

It is likely that redwoods have developed allelochemicals that are either toxic or repellant to

most indigenous insects and their larvae, or incapable of attracting many species, or a combination of both (Lauck, 1964). What is most astounding is how such a long-lived conifer could have evolved resistance to short-lived enemies like microbes and insects when the potential rate of spread of a favorable gene in the enemy population would be many hundreds, perhaps thousands of times faster than the annual rate of increase of a comparably fa-

vorable gene in the redwood population (Gill, 1986). The mystery remains one of the major unsolved questions in coevolutionary theory, and an important adjuvant to redwood dominance in environments where trees weakened and stressed by fire become more susceptible to disease and insect entry (Barbosa and Wagner, 1989; Barbour et al., 1987; Kilgore, 1972).

Table 4 Principal areas of infestation by some associated insects & mites

Cones and seeds	Roundheaded borer (<i>Phymatodes nitidus</i>) Cone moth (<i>Commophila fuscodorsana</i>)
Foliage	Spider mite (<i>Oligonychus ununguis</i>) Aphid (<i>Amphorophora morrisoni</i>) Redwood scale (<i>Aonidia shastae</i>) Black araucaria (<i>Lindingaspis rossi</i>) Redwood mealybug (<i>Spilococcus sequoiae</i>) Green chafer (<i>Dichelonyx valid</i>) Redwood leaf beetle (<i>Glyptoscelis sequoiae</i>)
Buds and shoots	Tip moth (<i>Argyresthia cupressella</i>)
Twigs and small branches (in bark) (under bark) (in wood)	Cypress puto (<i>Puto cupressi</i>) Anthaxia (<i>Anthaxia aeneogaster</i>) Anthaxia (<i>Anthaxia aeneogaster</i>) Cypress twig borer (<i>Phloeosinus cristatus</i>) Redwood bark beetle (<i>P. sequoiae</i>) Bark beetle (<i>Taenioglyptes pubescens</i>) Black-horned borer (<i>Callidium sempervirens</i>) Roundheaded borer (<i>Dicentrus bluethneri</i>) Roundheaded borer (<i>Phymatodes nitidus</i>)

Trunk and large branches (in bark) (under bark) (in wood)	<p>Cypress puto (<i>Puto cupressi</i>) Click beetle (<i>Ctenicera</i> sp.) Bark moth (<i>Cydia cupressana</i>) Roundheaded borer (<i>Anoplodera mathewsii</i>) Small cedar borer (<i>Atimia confusa dorsalis</i>) Click beetle (<i>Ctenicera</i> sp.) Redwood bark beetle (<i>Phloeosinus sequoiae</i>) Large cedarborer (<i>Semanotus ligneus sequoiae</i>) Dampwood termite (<i>Zootermopsis angusticollis</i>) Black-horned borer (<i>Callidium pallidum</i>) Spined woodborer (<i>Ergates spiculatus</i>) Hemlock wood stainer (<i>Gnathotrichus sulcatus</i>) Powderpost beetle (<i>Elemicoelus gibbicollis</i>) Roundheaded borer (<i>Leptura obliterata</i>) California prionus (<i>Prionus californicus</i>) Sapwood borer (<i>Serropalpus substriatus</i>) Carpenter ants (<i>Camponotus</i> sp.) Western horntail (<i>Sirex areolatus</i>)</p>
Logs and finished lumber	<p>Common drywood termite (<i>Kaloterme minor</i>) Subterranean termite (<i>Reticulitermes hesperus</i>) Dampwood termite (<i>Zootermopsis angusticollis</i>) California prionus (<i>Prionus californicus</i>) Mountain carpenter bee (<i>Xylocopa tabaniformis</i>)</p>

(After DeLeon, 1952; Doane et al., 1936; Furniss and Carolin, 1977; Lauck, 1964; McKenzie, 1956; Powell and Hogue, 1979).

Redwood Allelochemicals

Although the chemistry of redwood allelochemicals is still incompletely known (Clark and Scheffer, 1983), redwood durability has long been attributed to its extractive components (Hawley et al., 1924; Sherrard and Kurth, 1933), principally hydrolyzable tannins and other phenolic compounds, and condensed tannins (Anderson, 1961; Institute of Paper Chemistry, 1946; Wilcox and Piirto, 1976) or phlobatannins (Buchanan et al., 1944).

The distribution of these allelochemicals is highest in the outermost heartwood of the bole, and lowest in the innermost (Clark and

Scheffer, 1983; Sherrard and Kurth, 1933), with darker, denser woods of old-growth trees possessing the greatest concentrations (Mockus-Lubin et al., 1986; Wilcox and Piirto, 1976) and resistance to decay (Clark and Scheffer, 1983). According to Balogh and Anderson (1965), the specific constituents that make the wood unpalatable to both insects and fungi may be the same phenolic compounds that cause chemical stains in seasoned lumber: sequirins A, B and C.

But the lability and hygroscopic nature of redwood extractives (Anderson et al., 1960) make it difficult to ascribe the toxic entity to any one

compound (Anderson, 1961). And since the effects of these allelochemicals may act in concert with physical and nutritional characteristics of the tree and affect a wide variety of organisms, they cannot be considered in isolation (Barbosa and Wagner, 1989).

Decay resistance, for example, has been demonstrated to decline precipitously after hot water extraction, yet the extract itself may or may not exhibit fungicidal properties (Anderson, 1961; Sherrard and Kurth, 1933). Multiple bonding between tannins and collagen proteins is also well-known (Fuller, 1989), forming the basis of the tanning process in leather manufacture (Anon, 1927a; Haslam, 1966).

It is likely that redwood tannins interfere with the availability of nutrients to dendrophagous insects by complexing with proteins or digestive enzymes (Barbour et al., 1987; Reese, 1977) just as oak leaf tannins (*Quercus robur*) reduce the growth of winter moth larvae (*Operophtera brumata*) (Feeny, 1968).

There is also the possibility of induced resistance, since the increased concentration of phenolics and other phytoalexins after fungal attack has been well-documented in other plants (Barbour et al., 1987; Raven et al., 1987; Waiss et al., 1977). Zucker (1983) suggested that hydrolyzable tannins may be most effective against herbivorous slugs and insects, while condensed tannins may inhibit the ability of fungi and bacteria to hydrolyze cellulose (Raven et al., 1987). Condensed tannins can also be expected to degrade more slowly in time, thus impeding the decomposition of dead biomass (Zucker, 1983).

Prostrate redwoods decay very slowly (Becking, 1982), a quality not unnoticed by loggers (Redwood Lumber Manufacturers Association, 1897). Though long and fervidly heralded by the lumber industry (Eddy, 1987; Redwood Lumber Manufacturers Association, 1897), no testimonial to redwood durability could be more prophetic than Fray Junipero Serra's request to be interred in a redwood coffin (Hyde and Leydet, 1963). "And in this he was buried in 1784 at Mission San Carlos Borromeo at

Carmel. When the roof of this abandoned mission fell in 1852, the burial place of the good Father could not be found in the ruins, but in 1882, or 98 years after the burial, it was rediscovered, the redwood coffin in perfectly sound condition (Peattie, 1980)."

It should be noted, however, that resistance to decay is a function of age, with very resistant heartwoods about five times as prevalent in old-growth redwood as in 180 year-old trees (Clark and Scheffer, 1983). Not only do heartwoods of young trees contain lesser amounts of allelochemicals (Mockus-Lubin, 1986), but the redwood's vigorous ability to respond to release (Wiant, 1964), particularly on logging sites, produces wood that is lighter, softer and coarser grained than timber grown with deliberation (Fritz, 1938).

Growth Rates

Accelerated growth rates from 30 to six rings per inch have been noted on a redwood only partially freed from competition by highway right-of-way cutting (Fritz, 1951), while another grew an extraordinary seven feet in diameter in 108 years (Fritz, 1957b)! Record annual second-growth yields of 5074 board feet per acre have also been reported (Fritz, 1945), but the reduced durability and increased volume of decay-susceptible sapwood make second-growth lumber less desirable than the old-growth resource it is rapidly replacing (Mockus-Lubin, 1986).

Table 5 Projected old-growth redwood volumes & producing areas

Year	Area (acres)	Volume (board feet)	% (*)
1953	1,099,595	24,790,891,000	56%
1963	783,307	16,823,904,000	40%
1973	449,722	10,128,244,000	23%
1983	200,151	4,534,402,400	10%
1993	988	42,377,593	0.05%
2003	—	—	—

(After American Forest Products Industries Inc., 1965; Simmons and Vale, 1975).

- (*) Based upon 1,971,000 acres of original virgin growth (USDI, 1964).

Old-Growth Logging

Moreover, the sharply diminished availability of old-growth lumber is poignantly mindful of how quickly the virgin redwood forest has been felled (May, 1953, 1957; Simmons and Vale, 1975), largely within the last few decades (Table 5). Nineteenth-century loggers attained per acre yields that will not be rivaled for a millennium (Andrews, 1958; Soule, 1899), yet their annual rate of production was modest compared to recent harvests, with 90 to 100 sawmills cutting 107 to 224 million board feet per year from 1866 to 1880 (May, 1957).

The introduction of railroads and steam-powered winches, or Dolbeer donkeys (Carranco, 1982), increased the rate of production to 361 million board feet by 1899 (May, 1953); and from 1904 to 1929, roughly 500 million board feet of redwood lumber was milled each year (May, 1957). Even during the worst of the Great Depression, annual production never fell below 136 million board feet, returning to pre-Depression era levels by the 1940's. When the post-war logging boom (Agee, 1980) more than tripled the number of mills along the redwood

coast, from 117 in 1945 to 398 in 1948 (Hyde and Leydet, 1963), more than half of the original forest remained intact (May, 1953, 1957).

But from 1953 to 1976, the stands were decimated by sustained production levels of over one billion board feet per year (Agee, 1980; Hewes, 1981)! The commercial old-growth forest that Rhodes (1923) had predicted would last 140 years was all but exhausted in less than 65. By 1988, more than 95 percent of the original redwood forest had been cut down (Kelly and Braasch, 1988).

Ninety-five percent! It is both remarkable and sobering to tally the cost of America's growth this past century. And had it not been for the indefatigable crusades of early conservationists (De Vries, 1978; Dewitt, 1985; Engbeck, 1980; Hyde and Leydet, 1963; Schrepfer, 1983), many more redwoods would have fallen (Drury, 1957).

Move to Preserve Ancient Redwoods

The movement to preserve the ancient redwood forest has been unique in the history of conservation not only because of the rare magnificence of the trees themselves (Dewitt, 1985) and their enrichment of the human experience (Drury, 1957), but because of its unprecedented resistance to political conservatism that long permitted the massive deterioration of the nation's landscapes to go unchecked (Schrepfer, 1983). Indeed, the federal government did not move to appropriate funds for the purchase and preservation of old-growth redwood until 1968, when 50 years of struggle and controversy culminated in the establishment of Redwood National Park (Agee, 1980; Carranco, 1982; Dewitt, 1985).

Prior to this landmark acquisition, the only other redwood parkland under federal control was Muir Woods National Monument, a gift to the nation from Congressman William Kent that was three times offered and twice refused (Weaver, 1975)!

What little remains of the virgin redwood forest is chiefly the legacy of an inspired coalition of private citizens (Engbeck, 1980), whose poli-

tics were balanced by “a strong respect for the rights of private property and the needs of industry, an aversion to disruptive social action, a distrust of concentrations of power, and a strict attention to the means as well as the goals of reform (Schrepfer, 1983).”

They were not militant, striving to avoid the use of economic boycott, eminent domain, and publicity adverse to the timbermen, while fighting for efficient, centralized, professional land planning and management of redwood parks in order to improve the future. As Dr. John C. Merriam, co-founder of the Save-the-Redwoods League, succinctly put in 1931, “The state of civilization of a people may be measured by its care and forethought for the welfare of generations to come (Engbeck, 1980).”

Though subsequent efforts would become increasingly more militant as loggers rushed to fell the old-growth, the fate of the redwoods indicates that even militancy and popular enthusiasm have been limited in their effectiveness to preserve an economically valuable resource (Schrepfer, 1983). Nevertheless, the 68,035 acres of virgin forest held inviolate by California’s state and national redwood parks (Appendix IV) salute their long and arduous struggle: an inestimable gift of providence that saved many acres of alluvial flats (Drury, 1957) upon which the redwoods achieve their greatest development (Jepson, 1910) and affinity for wonder.

Although comprising only a small part (less than 32,000 acres) of the total redwood forest (Sudworth, 1967), the superlative stands of pure redwood that dominate alluvial soils have inspired much eulogy and reverence from those who have walked among them. “Like stepping into a cloister, one infinitely more spacious and lofty than any ever raised by man, ...the goose honking of a car, the calling of a child, fade into the immensity of silence... But this solemnity is not like that of a church or tomb; it is enlivened by the soft dispute of a stream with its bed, or the swirling, blurred whistle of the black-throated gray warbler... And now and then, the treetops utter a slow,

distant sea-hush, a sigh that passes, and then comes again, as if it were the breathing of a life beside which our lives are as a single day. At any time... the mist may roll silently through the forest aisles. It may rest on the forest floor, drenching the beds of oxalis and moss; it may wander, like the incense smoke in a temple, among the trees; it may move through their crowns, leaving the forest floor quite dry. But always the strong sun comes piercing through the fogs in beams of smoky light, slant shafts that fall with unerring drama upon... the great trees... mighty past telling. Their enormously swelled bases... buttressed with greatly bear-like claws, as if the trees gripped the earth to keep their balance. The ruddy shafts rise up, unlike almost all other trees, with scarcely any discernible taper... til they disappear in the high canopy of branches (Peattie, 1980).”

The effect of gigantism, the ponderous strength of the columns, and “an almost infinite variety in expression of light and shade and color... compose a scene such as canvas has yet to receive (Merriam, 1978).” For the redwoods, as John Steinbeck recalled, “are not like any trees we know, they are ambassadors from another time (Appendix XI).”

The evolution of such stands of pure, old-growth redwood is supported by the tree’s physiological capacity to exploit flood-interrupted environments where excessive siltation and saturation of the soil preclude lengthy tenure by other species (Stone and Vasey, 1968). Not only can redwoods endure flooding for many months without apparent injury, they can also withstand episodic silt depositions of three feet or more (Becking, 1967) by negative geotropic root growth in which new roots grow upward and into the silt from old roots buried beneath it (Stone and Vasey, 1968).

Thus, when the roots of other trees are fatally smothered by siltation (Daubenmire, 1978), redwoods keep pace with the rise in soil by the initial establishment of aerotropic roots (McBride and Jacobs, 1977), and the subsequent development of new, lateral root systems

adventitiously generated from their buried stems (Stone and Vasey, 1968). As many as seven successive root systems have been identified on a fallen redwood, each grown in response to the periodic floods and heavy sedimentation that precipitated an 11-foot rise in ground level during its 1229-year life span (Fritz, 1978).

And on Bull Creek Flat alluviums, excavations have shown redwoods older than 1000 years to be survivors of nearly 30 feet of accumulated sediments (Zinke, 1964, 1977). According to Stone (1965), this is a remarkable adaptation unique among plants, and one that is often accompanied by an accelerated growth of the bole (Zinke, 1964). It is likely that the inorganic sediments of fine silt loams are nutritionally important to continued good redwood growth (Simmons and Vale, 1975), while the deposition of alluviums high in organic matter and debris are deleterious, reducing redwood vigor and resistance to insects (Becking, 1967; Zinke, 1964).

Although redwoods can survive periods marked by extremely low quantities of oxygen (Stone, 1965), they are sensitive to the prolonged lack of aeration in sedimentary deposits, especially in alluviums that fail to crack upon drying (Becking, 1968, 1982). Yet the capacity of redwood seedlings to tolerate saturated soils is much greater than that of its associates, notably Douglas-fir (Vasey, 1970); and when conjoined with the advantages of recent mineral soils (Muelder and Hansen, 1961a) and reductions in species competition (Becking, 1967), the regeneration and dominance of redwood in flood-interrupted environments is strongly favored (Stone et al., 1972).

In addition to this dynamic regime of river flooding, sediment deposition and soil build-up (Zinke, 1977), periodic fires (Stone et al., 1972) redouble the characteristic openness, lack of understory plants, and homogeneity of redwood groves atop alluvial flats (Becking, 1967) by introducing fire-flood sequences (Zinke, 1964, 1977) that are hostile to seedlings and

young trees of its principal associates (Stone et al., 1972).

For example, upon Eel River Valley alluviums, only tanoak, Douglas-fir, grand fir, and California bay (*Umbellularia californica*) are potential redwood competitors, all abundantly represented on adjacent slopes with the capacity to disperse large amounts of seed onto the alluviums (Stone and Vasey, 1968). Fire is lethal to seedlings and young trees of the latter three, "but not tanoak, which sprouts vigorously after fire.

Flooding, if accompanied by heavy silting, kills seedlings, young trees, and even old trees of Douglas-fir, grand fir and tanoak. Thus, two of the species that are potential competitors of redwood on the alluvial flats are killed either by fire or flooding, one is killed only by fire, and one is killed only by flooding. Unlike redwood, none of these four potential competitors can withstand a combination of fire and flooding (Stone and Vasey, 1968)" with a frequency of recurrence every 30 to 60 years (Zinke, 1964, 1977).

Despite astonishingly shallow root systems (Shirley, 1937) and the difficult footing afforded by alluvial flat environments (Stone and Vasey, 1968), redwoods are capable of resisting the force of the most catastrophic flooding events (Becking, 1967).

As Becking (1967) reported in the aftermath of the 1964 Eel River floods which obliterated the community of Pepperwood, a "single row of planted redwood trees some 50 to 60 feet in height... held against itself logging debris and some 15 houses and structures that upon recession of the floods covered some five to six acres. Many of these houses were completely crushed by the force of the current, yet there is no apparent damage to this row of trees.

On the other hand, the current has at flood stage destroyed or flattened extensive alder (*Alnus oregona*) and cottonwood (*Populus trichocarpa*) stands and killed practically every Douglas-fir, grand fir, or tanoak tree in its flood plain... Whenever there was a solitary

redwood or group of redwoods in such a forest, they withstood the same flood impact remarkably well, and remained standing (Becking, 1967).”

Although redwoods are vulnerable to flood-induced toppling, its occurrence is primarily limited to exposed trees growing along the margins of alluvial stands where erosion can severely undermine stream banks and root systems (Sturgeon, 1964). Such was the fate of 525 large Bull Creek Flat redwoods felled by the floods of 1955-56 (Lowdermilk, 1961), an aberrant disaster that was aggravated by logging and repeated burning of the upper watershed which had seriously reduced its water retention capacity (Sturgeon, 1964).

The force of raging floods may also result in initiating lean (Dolezal, 1974), but redwoods can subsequently restore their balance by buttressing their undersides with an accelerated growth of cellulose (Stone, 1965) or compression wood (Raven et al., 1987). It is not unusual for every redwood atop an alluvial flat to display some degree of buttressing, with exceptional individuals or “flatiron” trees growing eccentrically 17 feet in diameter in the direction of the lean (Stone and Vasey, 1968). Buttressing may also be common among redwoods tilted by slopes with unstable soils, particularly near active faults, where movements due to earthquakes may be recorded by heartwood fractures, changes in radial growth rates and compression wood development (LaMarche and Wallace, 1972).

It has been the objective of this paper to not only celebrate the ecology of an extraordinary conifer, but to facilitate additional investigation through substantial citation. Attention, therefore, is directed to the annotated bibliographies compiled by Fritz (1957a), and Jacobs and McBride (1977).