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The ecology of Sequoia sempervirens : an addendum to "On the edge : nature's last stand for coast redwoods"

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San Jose State University, 1992

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THE ECOLOGY OF Sequoia sempervirens:
AN ADDENDUM TO
"ON THE EDGE: NATURE'S LAST STAND FOR COAST REDWOODS"

A Thesis
Presented to
The Faculty of the Department of Biological Sciences
San Jose State University

In Partial Fulfillment
of the Requirements for the Degree
Master of Arts

by
James A. Snyder
December, 1992

APPROVED FOR THE DEPARTMENT OF BIOLOGICAL SCIENCES

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ABSTRACT

THE ECOLOGY OF *Sequoia sempervirens*: AN ADDENDUM TO "ON THE EDGE: NATURE'S LAST STAND FOR COAST REDWOODS"

by James A. Snyder

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 adjuvants 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.

This manuscript is presented as an addendum to my video documentary, "On the edge: nature's last stand for coast redwoods," written for the California Department of Parks and Recreation, the Sempervirens Fund, and James Daniels Productions.

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I would also like to extend a special note of appreciation to Hjordis Madsen and the staff of the Inter-Library Loan office at San Jose State University, whose indefatigable efforts to retrieve many of the documents cited herein were truly blessed events.

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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 Nee 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 Nee later described the coast live oak (<u>Quercus agrifolia</u>) and valley oak (<u>Q. lobata</u>) 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).

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.

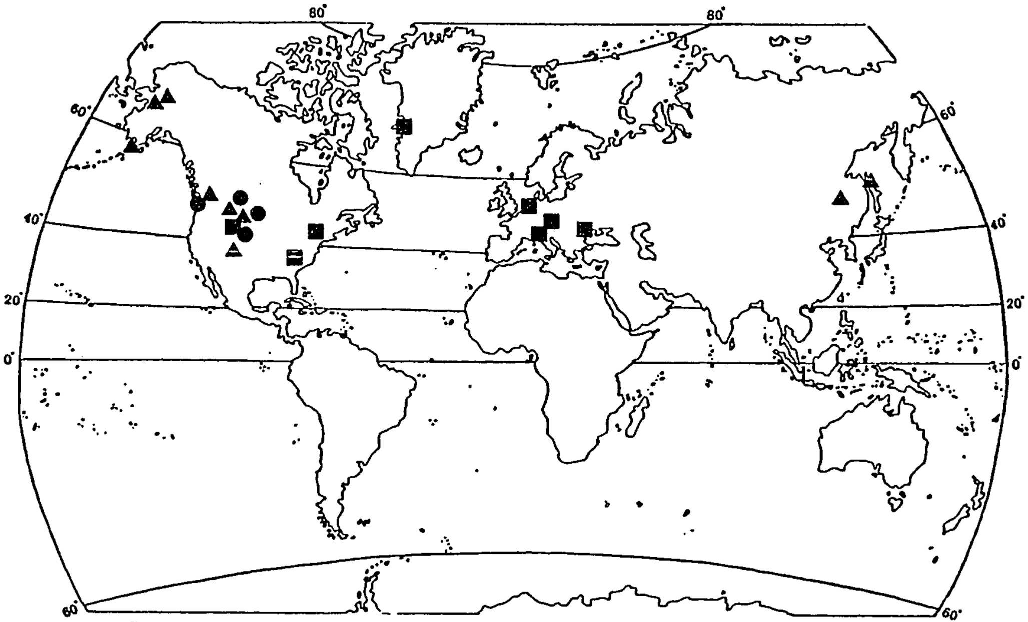
Punctilious scrutiny of Endlicher's papers by the eminent American botanist, Asa Gray, could not betray the origin of *Sequoia* (Hartesveldt et al., 1975), which has most often been associated with the remarkable Cherokee Indian scholar, Sequoyah, or Sikwayi (Farquhar, 1947). Though lacking formal education (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 labors 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."

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

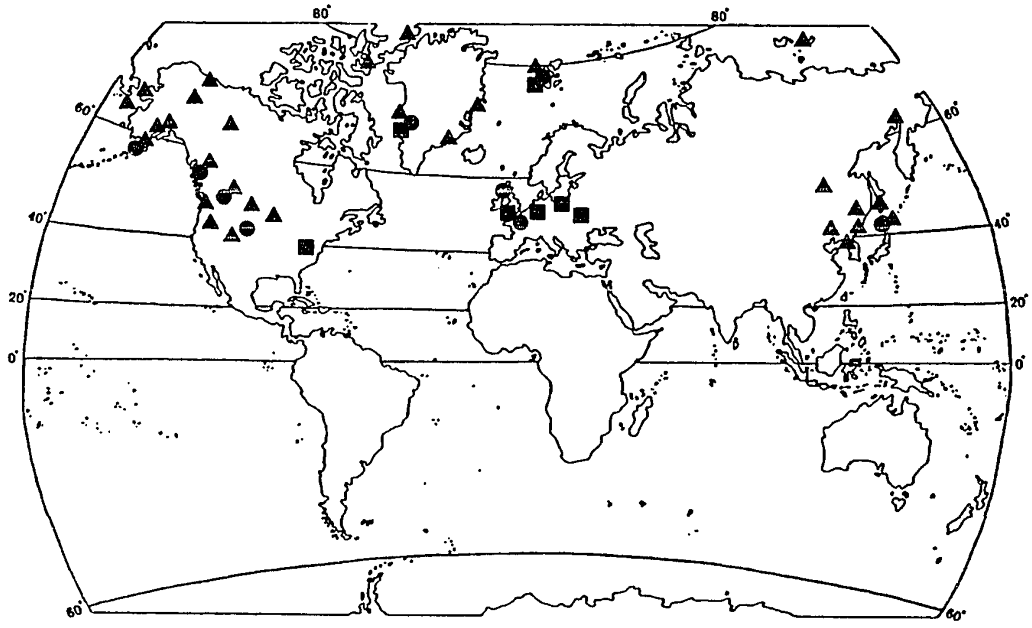
Mesozoic species of Metasequoia and some probably extinct type of taxodiaceous plant" (Stebbins, 1948). Further comparison between the three species may be found on pages 90-92 (Appendix II).

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^{o} to 77^{o} 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).

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



Cretaceous distribution of *Sequoia* ●, *Metasequoia* ▲, and *Sequoiadendron* ■.



Paleo-Eocene distribution of *Sequoia* ⊖, *Metasequoia* ▲, and *Sequoiadendron* ▤.

Figure 1. Distribution of fossil sequoias
135 to 38 million years ago (After Florin, 1963).

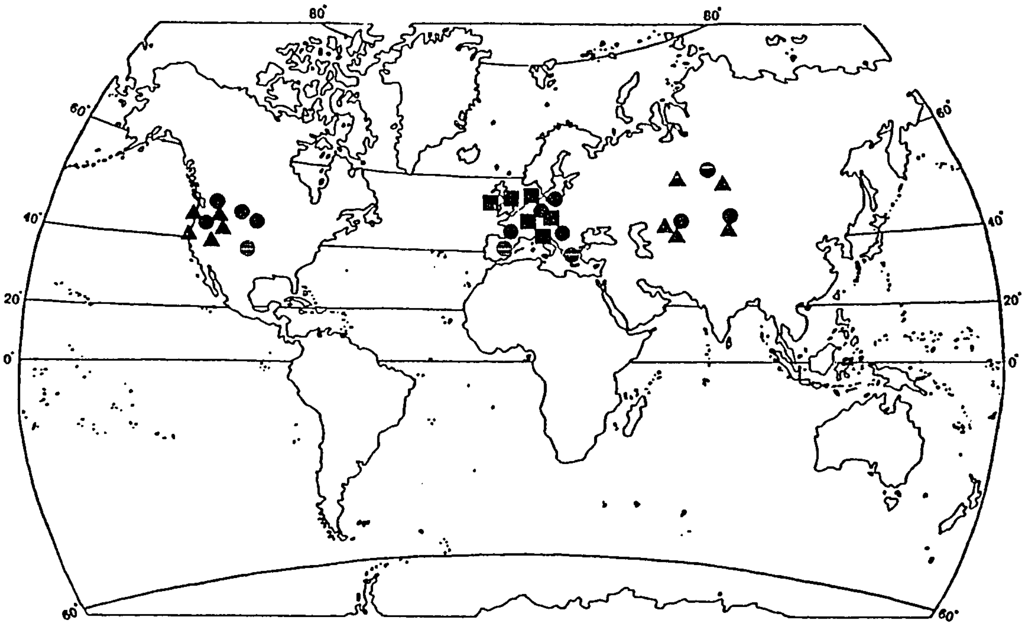
climates was often interrupted by warmer periods (Tidwell, 1975). Ancient relatives of the giant sequoia occupied parts of central and eastern North America, Greenland, Spitzbergen and Europe; those of the coast redwood became established in central and western North America, Greenland, Spitzbergen, 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 extreme 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).

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^{o} 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^{o} and 58^{o}, 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).

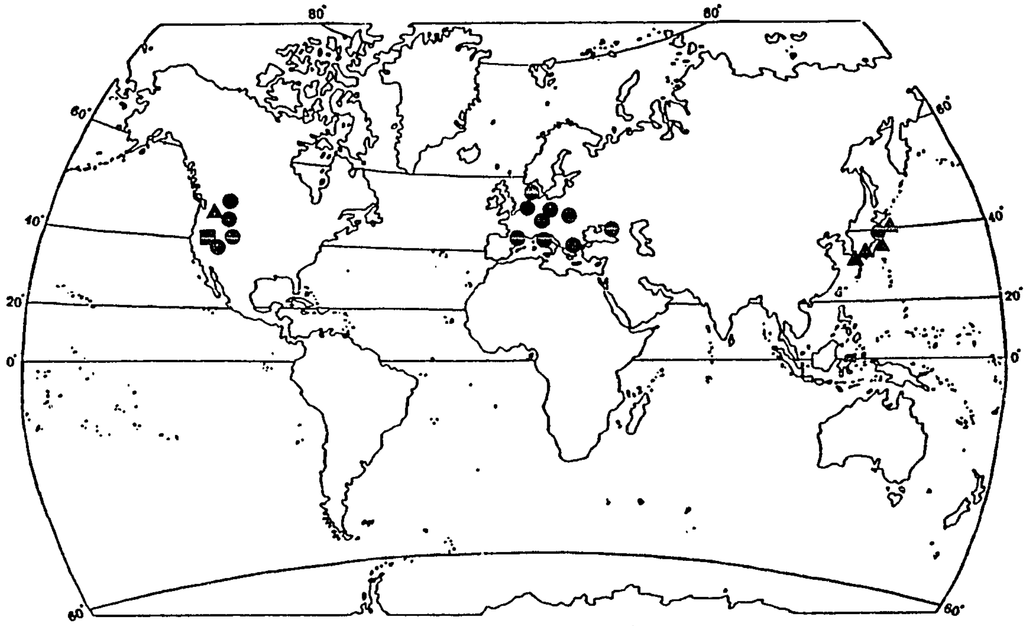
The number of species recognized by paleontologists has also been subject to considerable debate and revision. By 1910, more than 40 species of sequoia had been described from fragmentary remains, but there was "by no means agreement as to the validity of the species" (Jepson, 1910). And Seward (1919) 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.

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

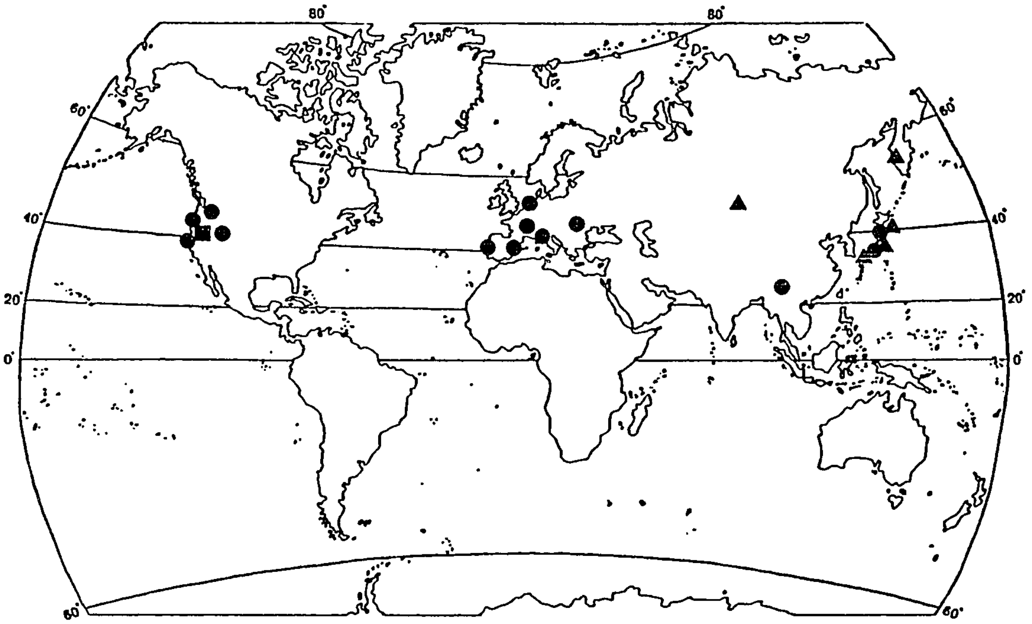


Oligocene distribution of Sequoia ●, Metasequoia ▲, and Sequoiadendron ■.

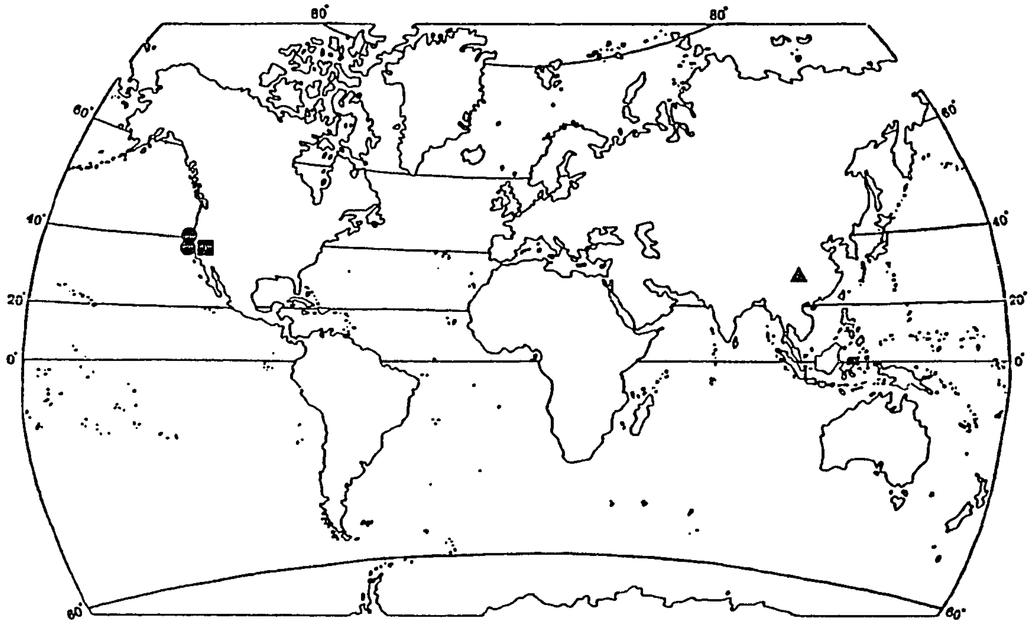


Miocene distribution of Sequoia ●, Metasequoia ▲, and Sequoiadendron ■.

Figure 2. Distribution of fossil sequoias 38 to six million years ago (After Florin, 1963).



Pliocene distribution of Sequoia ●, Metasequoia ▲, and Sequoiadendron ■.



Present distribution of Sequoia ●, Metasequoia ▲, and Sequoiadendron ■.

Figure 3. Distribution of fossil and living sequoias
six million years ago to the present (After Florin, 1963).

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).

The last and present stronghold of Sequoia sempervirens adjoins the Pacific along a narrow 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).

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).

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 station, 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 Aetna Springs (Griffin and Critchfield, 1976).

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

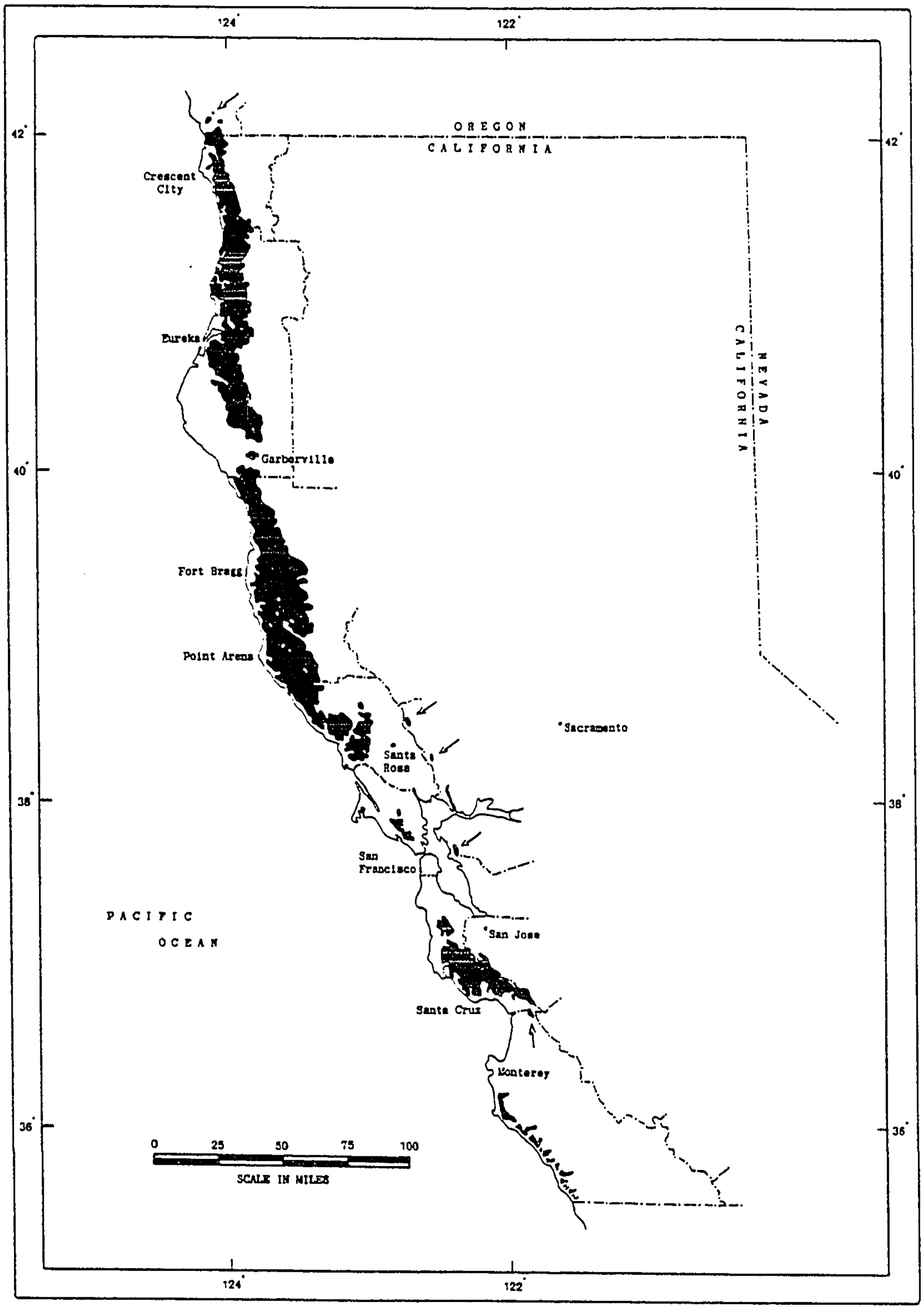


Figure 4. Present distribution of Sequoia sempervirens (After Becking, 1971; Griffin and Critchfield, 1976; Roy, 1966).

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).

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).

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 Thornthwaite (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.

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 content (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).

Redwoods require a temperate, maritime regime of temperatures where monthly means do not fall below 36^{o} F, nor exceed 84^{o} F (Kuser, 1976). Mean annual temperatures throughout the region vary between 50^{o} and 60^{o} F, with daily extremes rarely falling below 15^{o} F or rising above 100^{o} 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^{o} F along the coast to 30^{o} 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). 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^{o} F which might explain why the tallest redwoods grow so near their northern limit of distribution. Optimum seedling growth was achieved under 66^{o} F day and 59^{o} 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 productivity of coast redwood at a mean summer temperature of 64° F.

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 dessication 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 dessication 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). Nocuous 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.

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 susceptibilty 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.

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^{0} 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).

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).

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).

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 profiles 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)!

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.

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 (Cannon, 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).

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 lumber 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).

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 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 (<u>Eucalyptus regnans</u>) 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). 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).

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).

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 (After Fritz, 1929b).

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

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.

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 Alaska yellow-cedar (*Chamaecyparis nootkatenis*) 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 comparision 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!

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).

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.

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).

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). 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.

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).

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). 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 (After Davidson, 1971).

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

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 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^{o} 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).

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 comsumption 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).

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 evaporation 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.

Canopy shading also affects the temperature of redwood soils, which Hellmers (1961) found to be most propitious for laboratory seedlings at 64^{0} F when compared to 46^{0} and 82^{0} seedbeds. Though redwood seedlings have been observed to withstand considerable surface heat, as high as 140^{0} F barring concurrent dessication (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).

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). 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). 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 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.

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 Harrrar, 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). 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).

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).

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 excercised 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 remarkable vitality when assailed by dyadic catastrophes.

No less remarkable is the redwood's celebrated resistance to attack by insects (Fritz, 1957b). Of the 54 species (Table 3) reported to find

Table 3. Associated mites and insects injurious to coast redwood (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).

Order	Species	
Acari	*Oligonychus ununguis*	
Isoptera	*Kalotermes minor*	*R. tibialis*
	Reticulitermes hesperus	*Zootermopsis angusticollis*
Homoptera	*Amphorophora morrisoni*	*Dysmicoccus ryani*
	Aonidia shastae	*Lindingaspis rossi*
	Aspidiotus hederae	*Pseudococcus citri*
	Carulaspis minima	*Puto cupressi*
	C. visci	*Spilococcus sequoiae*
Coleoptera	*Anoplodera crassipes*	*Ips latidens*
	A. impura (a)	*Leptura obliterata*
	A. mathewsii	*Monarthrum scutellare*
	Anthaxia aeneogaster	*Phloeosinus cristatus*
	Atimia confusa dorsalis	*P. cupressi*
	Callidium pallidum (*)	*P. sequoiae*
	C. sempervirens (*)	*Phymatodes decussatus* (b)
	Ceruchus striatus	*P. nitidus*
	Ctenicera sp.	*Platypus wilsoni*
	Dicentrus bluethneri	*Prionus californicus*
	Dichelonyx valida	*Ptilinus basalis*
	Dromaeolus nitens	*Semanotus ligneus sequoiae* (*)
	Ergates spiculatus	*Serropalpus barbatus*
	Glyptoscelis sequoiae	*S. substriatus*
	Gnathotrichus retusus	*Taenioglyptes pubescens*
	G. sulcatus	*Trypodendron lineatum*
	Hemicoelus gibbicollis	
Lepidoptera	*Argyresthia cupressella*	*Cydia cupressana*
	Commophila fuscodorsana	*Vespamima sequoiae* (c)
Hymenoptera	*Camponotus* sp.	*Xylocopa tabaniformis*
	Sirex areolatus	

(*) 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.

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

Location	Species
Cones and seeds	Roundheaded borer (*Phymatodes nitidus*)
	Cone moth (*Commophila fuscodorsana*)
Foliage	Spider mite (*Oligonychus ununguis*)
	Aphid (*Amphorophora morrisoni*)
	Redwood scale (*Aonidia shastae*)
	Black araucaria (*Lindingaspis rossi*)
	Redwood mealybug (*Spilococcus sequoiae*)
	Green chafer (*Dichelonyx valida*)
	Redwood leaf beetle (*Glyptoscelis sequoiae*)
Buds and shoots	Tip moth (*Argyresthia cupressella*)
Twigs and small branches	Cypress puto (*Puto cupressi*)
(in bark)	Anthaxia (*Anthaxia aeneogaster*)
(under bark)	Anthaxia (*Anthaxia aeneogaster*)
	Cypress twig borer (*Phloeosinus cristatus*)
	Redwood bark beetle (*P. sequoiae*)
	Bark beetle (*Taenioglyptes pubescens*)
(in wood)	Black-horned borer (*Callidium sempervirens*)
	Roundheaded borer (*Dicentrus bluethneri*)
	Roundheaded borer (*Phymatodes nitidus*)
Trunk and large branches	Cypress puto (*Puto cupressi*)
(in bark)	Click beetle (*Ctenicera* sp.)
	Bark moth (*Cydia cupressana*)
(under bark)	Roundheaded borer (*Anoplodera mathewsii*)
	Small cedar borer (*Atimia confusa dorsalis*)
	Click beetle (*Ctenicera* sp.)
	Redwood bark beetle (*Phloeosinus sequoiae*)
	Large cedar borer (*Semanotus ligneus sequoiae*)
(in wood)	Dampwood termite (*Zootermopsis angusticollis*)
	Black-horned borer (*Callidium pallidium*)
	Spined woodborer (*Ergates spiculatus*)
	Hemlock wood stainer (*Gnathotrichus sulcatus*)
	Powderpost beetle (*Hemicoelus gibbicollis*)
	Roundheaded borer (*Leptura obliterata*)
	California prionus (*Prionus californicus*)
	Sapwood borer (*Serropalpus substriatus*)
	Carpenter ants (*Camponotus* sp.)
	Western horntail (*Sirex areolatus*)
Logs and finished lumber	Common drywood termite (*Kalotermes minor*)
	Subterranean termite (*Reticulitermes hesperus*)
	Dampwood termite (*Zootermopsis angusticollis*)
	California prionus (*Prionus californicus*)
	Mountain carpenter bee (*Xylocopa tabaniformis*)

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). 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-suseptible sapwood make second-growth lumber less desirable than the old-growth resource it is rapidly replacing (Mockus-Lubin, 1986).

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

Table 5. Projected old-growth redwood volumes and producing areas, 1953-2003 (After American Forest Products Industries Inc., 1965; Simmons and Vale, 1975).

Year	Area (acres)	Volume (board feet)	Percent (*)
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	-	-	-

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

yields that will not be rivaled for a millenium (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).

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 politics were balanced by "a strong respect for the rights of private property and the needs of industry, an adversion 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 ardous 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... butressed with great lynx-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 occurence 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).

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APPENDIX I

Additional notes on the Spanish discovery of coast redwood.

The exact location of Portola's discovery appears to have been Pinto Lake in Santa Cruz County (Bolton, 1927; Griffin and Critchfield, 1976). Crespi's journal recounts heading "northwest. We could not make the march as long as intended, because the sick men were worse, and each day their number increased, so we must have traveled but little more than a league" (Bolton, 1927) from their camp upon the Pajaro River (near Watsonville) before reaching the first sequoias "...near a lagoon which has much pasture about it and a heavy growth of the redwoods" (Bolton, 1927). The quotation embraced by the text is from Bolton (1927).

The earliest recorded measurement of coast redwood was conducted by another Franciscan missionary, Fray Pedro Font, who chronicled d'Anza's expedition to San Francisco Bay in 1776 (Shirley, 1937). On March 26, the expedition crossed "the arroyo of San Francisco" (Bolton, 1933) where Font noted "a few spruce trees which they call redwood, a tree that is certainly beautiful; and I believe that it is very useful for its timber, for it is very straight and tall, as I shall show later on" (Bolton, 1933). The party continued northward, reaching the tip of the San Francisco Peninsula within two days, whereupon Font proclaimed, "The port of San Francisco... is a marvel of nature, and might well be called the harbor of harbors" (Bolton, 1933). On March 29, their return journey brought them to a small promontory near Dolores Creek overlooking "a very high redwood, which stands on the bank of the arroyo of San Francisco, visible from a long distance, rising like a great tower... and whose height I afterward measured" (Bolton, 1933). The following day, Font "found it to be, according to the calculation which I made, some fifty varas high (137.5 feet), a little more or less. The trunk at the foot was five and a half varas in circumference (15.125 feet), and the soldiers said that they had seen even larger ones in the sierras. The method by which I measured the tree was as follows: I set up the graphometer thirty-six varas from the foot of the tree (99 feet) and a vara and a half above the ground (4.125 feet), and, pointing at its top through the sights of the alidade, it showed 52.5 degrees. Then, with the graduated semicircle, forming the triangle of those degrees, and adding to it the height of the base of the graphometer, which was a vara and a half, it gave as a result the altitude stated. Present at all this performance were the Indians who live in the village here. They came to see us and were very attentive and quiet, and appeared surprised to see what I was doing" (Bolton, 1933). One vara is equal to 33 inches (Shirley, 1937).

The trade in redwood lumber began only two months later, when Don Diego Choquet arrived at Monterey Bay to procure building materials for Fray Junipero Serra and his Mission San Diego de Alcala (Carranco, 1982; Cox, 1974). Between May 21 and June 30, 1776, Choquet took aboard a cargo of pit-sawn timbers before returning south on the ship that had earlier supported Portola's expedition, the San Antonio.

Font's tall tree, or "palo alto," still stands on San Francisquito Creek within the city of Palo Alto (Bolton, 1933; Campbell, 1946), and is prominently featured on the seal of Stanford University (Peattie, 1980).

APPENDIX II

Comparison of the giant sequoia, coast redwood and dawn redwood (After Boe, 1974a, 1974b; Buchholz, 1939; Chu and Cooper, 1950; Davidson, 1971; Elias, 1989; Harlow and Harrar, 1958; Hartesveldt et al., 1975; Harvey, 1978; Johnson, 1974; Li, 1957; Munz and Keck, 1973; Ouden and Boom, 1978; Rehder, 1940; Shirley, 1937; Sterling, 1949; USDA, 1948).

In the literature reviewed for this appendix, examples of albinism (Davis and Holderman, 1980; Peirce, 1901) and fasciation (Becking, 1970; Peirce, 1901; Roy, 1966) were reported for coast redwood, but not for giant sequoia or dawn redwood.

Characteristic	Giant Sequoia	Coast Redwood	Dawn Redwood
Discovery (leading to botanical description)	by Augustus Dowd in Calaveras North Grove, Calaveras County, 1852	by Archibald Menzies in Santa Cruz County, 1794	by Tsang Wang near Mo-tao-hsi, Sichuan Province, China, 1944
Early Names	known as "wawona" or big tree to Mokelumne Tribe	known as "palo colorado" or redwood to Spanish-Americans	known as "shui-hsa" or water-fir to Chinese
Distribution	western Sierra Nevada in California	Pacific coast ranges of California and southwestern Oregon	Shui-hsa and Wangjiaying valleys, Hubei and adjacent Sichuan mountains, China
	usually found in mixed stands with other conifers; young trees not tolerant of shade	often found in nearly pure stands, or in mixed stands; young trees moderately tolerant of shade	widely scattered in mixed stands; most abundant in shady ravines(a); young trees tolerant of shade
	drought resistant	high moisture requirement	high moisture requirement
Altitudinal Range	2800-8900 feet	near sea level-3200 feet	2300-4400 feet
Max. Height	310 feet(b)	367.8 feet(c)	164 feet(d)
Max. Diameter	40.3 feet(e) at base; 25-30 feet near base	30.5 feet(f) at base; 12-18 feet near base	10.9 feet(d) at base; 5-8 feet near base
Max. Circumference	112 feet(g) at base	95.7 feet(f) at base	
Max. Bole Volume	52,500 cubic feet(h), or 630,000 board feet	30,114 cubic feet(i), or 361,366 board feet	

(a) The California Academy-Lingnan Dawn-Redwood Expedition discovered only 1219 trees remaining in Sichuan and Hubei in 1948. Most were found growing in an "apparent state of semicultivation," planted around farmhouses, or in straight rows along the edges of rice fields bordering streams. "There can hardly be said to be any <u>Metasequoia</u> forests or even moderate natural stands. Most of the trees are in rows following up side streams. There are rarely as many as 50 along a single branch stream" (Gressitt, 1953).

(b) The "California Tree," Grant Grove, Kings Canyon National Park (Shirley, 1937). In nearby Redwood Mountain Grove, Fry and White (1931) measured one prostrate giant sequoia 347 feet long.

(c) The "Tall Tree," Tall Trees Grove, Redwood National Park (Zahl, 1964). Also known as the "Howard A. Libbey Tree" for the founding president of the Arcata Redwood Company (Carranco, 1982). In the aftermath of winter floods in 1964, siltation around the base reduced its standing height to 366.6 feet (Becking, 1967).

(d) An isolated tree near Wangjiaying, Hubei Province (Chu and Cooper, 1950). Estimated to stand "about 50 meters" (Chu and Cooper, 1950) in 1948, the tree was reported by Gressitt (1953) to be 115 feet high with a diameter of 8.5 feet at six feet above the ground.

(e) The "General Grant Tree," Grant Grove, Kings Canyon National Park (Harvey et al., 1981). Standing 267.4 feet high, the tree had a ground circumference of 107.6 feet and bole volume of 47,450 cubic feet (569,400 board feet) in 1976. Its bole volume scaled 43,038 cubic feet (516,456 board feet) in 1931 (Jourdan, 1932).

(f) The "Reed Tree," North Fork of the Mad River, Humboldt County (Zinke, 1965). Standing 302 feet high, the tree had a breast height diameter of 26.9 feet in 1966 (Becking, 1968). Although spared by loggers cutting the proximate forest, it has since been toppled by winds (Zinke, 1990; personal communication). The largest standing circumference would be the "Big Tree," Circle Trail, Prairie Creek Redwoods State Park (Shirley, 1937). In 1937, the tree stood 300 feet high with a ground circumference of 90 feet and breast height diameter of 17.7 feet.

(g) The "Boole Tree," Converse Basin Grove, Sequoia National Forest (Shirley, 1937). Standing 268.8 feet high, the tree had a mean diameter of restored base of 33.2 feet and bole volume of 39,974 cubic feet (479,688 board feet) in 1931 (Jourdan, 1932).

(h) The "General Sherman Tree," Giant Forest, Sequoia National Park (Harvey et al., 1981). Standing 274.9 feet high, the tree had a ground circumference of 102.6 feet and base diameter of 36.5 feet in 1976. Its bole volume scaled 49,660 cubic feet (595,920 board feet) in 1931 (Jourdan, 1932).

(i) The "Captain Elam Tree," Maple Creek drainage, Humboldt County (Peattie, 1980; Roy, 1966; Tiemann, 1935). Standing 308 feet high, the tree had a 20-foot diameter at five feet above the ground, and a 12-foot diameter at 230 feet, scaling 14 logs from 12 to 17 feet in length. However, the largest coast redwood was likely felled before 1900. According to Soule (1899), "one of these giant redwood trunks, near Bucksport, yielded, a few years since, 480,000 feet B.M. (board measure) of first-class lumber, and many other trees have yielded 400,000." Bucksport is located near the mouth of the Elk River on Humboldt Bay within Eureka city limits.

Characteristic	Giant Sequoia	Coast Redwood	Dawn Redwood
Max. Age	3126 years(j)	2200 years(k)	300-600 years(l)
Wood	brittle, light, soft(m); coarse-grained; heartwood red; tending to fracture transversely when felled	tough, light, soft(m); close-grained; heartwood red; tending to fracture lengthwise when felled	brittle, light, soft(n)
Bark	fibrous, deeply furrowed into large ridges, 1-2 feet thick at base; rich cinnamon-brown color	fibrous, furrowed into small ridges; 0.5-1.0 feet thick at base; red-brown to dull grey-red color	fibrous, fissured, deeply fluted and tressed at base; thin; red-brown to dark grey color
Burls	few; when cut from tree will not grow leaves	common(p); when cut from tree will grow new leaves	
Roots	to 150 feet from base, 6-8 feet below surface	to 50 feet from base, 4-6 feet below surface	
Buds	naked	naked and scaly(q)	scaly
Leaves	small, awl-shaped appressed around stem; sessile; blue-green color	two kinds: awl-shaped appressed around stem; and flat needle-like, alternate in two rows; sessile; dark yellow-green color	flat needle-like, opposite in two rows; with small stalks; blue-green color
	evergreen, falling with branchlets in 2-5 years	evergreen, falling with branchlets in 2-5 years (maximum 7 years)	deciduous
Long Branchlets	bear short shoots in alternate array	bear short shoots in alternate array	bear short shoots in opposite pairs
Short Branchlets	leaves in spirals; deciduous	leaves in spirals and in two rows, except at tip; deciduous	leaves opposite in two rows; deciduous
Reproduction	only by seeds	by seeds, and by root collar or crown sprouts(r)	only by seeds
Pollen Cones (staminate)	sessile; 0.16-0.31 inches long; scales arranged in spirals	stipitate; 0.06 inches long; scales arranged in spirals	stipitate; 0.16-0.24 inches long; scales opposite

(j) Measuring 26.5 feet in diameter at six feet above the ground, the tree was felled by loggers in the Millwood Grove near Grant Grove, Kings Canyon National Park (Fry and White, 1931). In 1925, A.E. Douglass traced the ring chronology of a giant sequoia stump near Springville to 1120 B.C. (Douglass, 1945). The age of the General Sherman Tree is less than 2500 years (Hartesveldt et al., 1975).

(k) Measuring 12 feet in diameter, the tree was felled by loggers in the Avenue of the Giants, Humboldt County, in 1934 (Weaver, 1975).

(l) "According to Chaney (personal communication) increment cores suggest for the largest trees an age of at least 300 years" (Chu and Cooper, 1950). Hu (1948) preferred a maximum age of about 600 years.

(m) The wood of giant sequoia has a dry weight of 18 lb/ft^3; and coast redwood, 26 lb/ft^3 (Peattie, 1980).

(n) Ouden and Boom (1978) projected that *Metasequoia* may "become one of the most valuable timber trees, since careful investigations have shown that the quality of wood equals that of *Abies alba* (European silver fir)." Although its pulping characteristics are similar to and its fibers stronger than southern pines (Johnson, 1974), the U.S. Forest Products Laboratory regarded *Metasequoia* as "too light in weight, too weak, limber and soft to have economic value as a solid wood product" (Wyman, 1968). The wood has not been considered valuable in China (Gressitt, 1953).

(p) Exceptional burls include a seven-ton growth that was nine feet in diameter at 150 feet above the ground (Pioneer Western Lumberman, 1917), and another that nearly encircled a trunk for a distance of 60 feet (Fritz, 1928). But the greatest burl on record once extended 1.5 feet into the ground, massed like a giant boulder, 105 feet in circumference and nine feet high at the crown (Anon, 1945). Seven redwoods up to six feet in diameter grew out of this giant burl near Big Lagoon in Humboldt County, which required four men and 30 days to harvest its extraordinary yield of 60 tons of sound veneer stock in 1944.

(q) In contrast to scaly buds found on the lower, two-ranked foliage, Davidson (1971) reported that bud leaves of the many-ranked tip foliage "become, in effect, naked since the so-called bud 'scales' remain alive and green for about five years... indistinguishable from ordinary leaves except that they are usually shorter."

(r) Two conifers associated with coast redwood also sprout from stumps: the California nutmeg or torreya (*Torreya californica*) and the Pacific yew (*Taxus brevifolia*) (Jepson, 1910; Roy, 1966). Sprouting is vigorous in the former and weak in the latter. Although neither has been regarded as commercially important, there has been much recent interest in the bark of Pacific yew, provenance of the cancer-fighting drug taxol (Daly, 1992).

Characteristic	Giant Sequoia	Coast Redwood	Dawn Redwood
Seed Cones	ellipsoid, 2-3.5 inches long; mature second season; persistent and may remain growing for over 20 years	ovoid, 0.5-1.125 inches long; mature first season; persistent and shed seeds during 2nd winter season	globose or ovoid, 0.80 inches across; mature and shed seeds first season in late December-early January
	25-40 scales arranged in spirals; 3-9 seeds per scale	14-24 scales(t) arranged in spirals; 2-5 seeds per scale	16-26 scales opposite; 5-8 seeds per scale
Seeds	with broad lateral wings; 0.25 inches long; in two rows on each scale	with narrow lateral wings; 0.0625 inches long; in one or two rows(u) on each scale	with minute lateral wings; 0.23 inches long; in one row on each scale
	average 230 seeds per cone or 81,000 per pound(v)	average 60 seeds(w) per cone or 120,000 per pound(x)	
Chromosomes	22 per diploid cell	66 per diploid cell (y)	22 per diploid cell

(t) 18-35 scales were reported by Becking (1982).

(u) Cone scales of the coast redwood may bear 1-14 ovules in one or two rows, not solely in one row as previously reported (Davidson, 1971).

(v) Average number obtained from 21 samples (Boe, 1974b). The number of cleaned seeds per pound ranged between 62,000 and 100,000.

(w) Davidson (1971) found this figure to be about half the average number of ovules that he obtained per cone, "which calls into question" what might be considered a seed. 90-150 seeds per cone were reported by Becking (1982).

(x) Average number obtained from 157 samples (Boe, 1974a). The number of cleaned seeds per pound ranged between 59,000 and 300,000.

(y) All other known wild conifers have between 20 and 24 chromosomes (Libby and McCutchan, 1978).

All three species are remarkably resistant to depredations by insects and fungi, and have been extensively used as an ornamental in temperate and sub-temperate latitudes.

APPENDIX III

Geologic time scale (After Florin, 1963; Simpson, 1983).

Dates are posted in years before the present.

Eras	Periods	Epochs	Major Events
Cenozoic		Holocene (Recent)	
	Quaternary	10,000	Many extinctions of large mammals
		Pleistocene	Ice Ages; Sequoia established near Santa Barbara
		2,500,000	Sequoia restricted to western North America, Metasequoia to China
		Pliocene	Southernmost record of Sequoia distribution at 26° (China)
	Tertiary	6,000,000	Early hominids (human family)
		Miocene	Metasequoia extinct in North America
		26,000,000	Sequoiadendron restricted to west-central North America
		Oligocene	Retreat of sequoias southward; central Asia expansion of Metasequoia and Sequoia; Metasequoia most abundant and widely distributed sequoia in North America
		38,000,000	
		Eocene	Increasing specialization and modernization of mammals
		55,000,000	Northernmost sequoia distribution: 83° for Metasequoia (Ellesmere Island); 79° for Sequoia and Sequoiadendron (Spitzbergen)
		Paleocene	Great spread of primitive and archaic mammals
		65,000,000	Extinction of dinosaurs
Mesozoic	Cretaceous		Sequoia, Sequoiadendron and Metasequoia forests widespread First primates, and many other animals; spread of flowering plants
		135,000,000	
	Jurassic		First birds; earliest sequoia fossils (Manchuria)
		190,000,000	First mammals
	Triassic		First dinosaurs
		225,000,000	
Paleozoic	Permian		Many extinctions of invertebrates
		280,000,000	
	Carboniferous		First reptiles
		345,000,000	
	Devonian		First amphibians; spread of fishes
		395,000,000	First forests
	Silurian		First air-breathing animals
		430,000,000	First land plants
	Ordovician		
		500,000,000	First vertebrates
	Cambrian		Great spread of marine invertebrates
		570,000,000	
Precambrian		700,000,000	First animals
		3,400,000,000	Possible bacteria and blue-green algae; possible first organisms
		4,600,000,000	Origin of earth

APPENDIX IV

Estimated old-growth redwood forest within California state and national parks (After Dolezal, 1974; Lang and McBride, 1979; National Park Service, 1964; Sempervirens Fund, 1989, 1990).

Name of Park	County	Total Acreage	Old-growth Acreage
Admiral William H. Standley SRA	Mendocino	45.2	40
Armstrong Redwoods SR	Sonoma	440.0	120
Big Basin Redwoods SP	Santa Cruz	15,180.4	2,000
Butano SP	San Mateo	2,176.8	1,500
Del Norte Coast Redwoods SP	Del Norte	5,932.0	2,600
Grizzly Creek Redwoods SP	Humboldt	149.5	120
Hendy Woods SP	Mendocino	604.7	60
Henry W. Cowell Redwoods SP	Santa Cruz	1,736.8	600
Humboldt Redwoods SP and Holbrook-Whittemore Groves	Humboldt	37,762.8	20,333
Jedediah Smith Redwoods SP	Del Norte	9,539.5	9,450
Julia Pfeiffer Burns SP	Monterey	1,700.0	100
Mailliard Redwoods SR	Mendocino	242.0	200
Montgomery Woods SR	Mendocino	647.1	400
Mount Tamalpais SP	Marin	2,404.3	300
Muir Woods NM	Marin	510.0	17
Pfeiffer-Big Sur SP	Monterey	820.5	30
Portola SP	San Mateo	1,740.3	1,400
Prairie Creek Redwoods SP	Humboldt	10,288.7	8,240
Redwood NP	Humboldt/Del Norte	76,205.0	19,650
Richardson Grove SP	Humboldt	790.5	250
Samuel P. Taylor SP	Marin	2,576.3	600
Smithe Redwoods SR	Mendocino	459.0	15
Standish-Hickey SRA	Mendocino	635.2	10
Totals	8 counties	172,586.6	68,035

NM - National Monument
NP - National Park
SP - State Park
SRA - State Recreation Area
SR - State Reserve

Cooper (1965) reported that from a total of 1,918,000 acres of commercial redwood forest in California, "615,000 acres or 32% lie in Humboldt County; 143,000 acres or 7.5% in Del Norte County; 771,000 acres or 40% in Mendocino County, 180,000 acres or 9.5% in Sonoma County, 120,000 acres or 6% in Santa Cruz County; 55,000 acres or 3% in San Mateo County; and the remainder in Marin (15,000), Santa Clara (10,000), and Monterey (9,000) Counties."

The total area in California dominated by redwood forest might even be higher, as much as 2,320,254 acres (Barbour and Major, 1988). Agee (1980) reported the preservation of nearly 77,000 acres of old-growth forest among 223,000 acres of redwood parkland, but his sources were not clearly documented.

Nevertheless, it is lamentable that no redwood parkland was established along the Mad River in Humboldt County where the "Reed Tree" once stood (Appendix II). When compared by early lumbermen to the Eel River Valley, the Mad River, "while not as important a stream, is perhaps the most celebrated, for on its banks, and those of its tributaries, are found the finest bodies of redwood timber in the entire belt" (Redwood Lumber Manufacturers Association, 1897).

APPENDIX V

Register of the largest known coast redwoods ranked according to height (After Becking, 1967, 1968; Bowers, 1965; Shirley, 1937; Zahl, 1964).

Measurements taken by different surveyors have not always been in agreement, and their records are noted with appropriate citations. The register is also limited to California redwoods, and to data published before 1969 which may no longer rank the current champions in proper order. All measurements are posted in feet; and for redwoods not identified by name, vegetation plot numbers have been included according to Becking (1968).

Name of Tree and Location	Height	Breast Height Diameter	Diameter Circumference	Citation
"Tall Tree," Tall Trees Grove, Redwood Creek RNP	367.8		44.0	(zt,op)
also known as "Howard A. Libbey Tree"	366.6	14.0	28.0	(br)
"Harry W. Cole Tree," Tall Trees Grove, Redwood Creek RNP	367.4			(zt,op)
	367.0	15.3		(br)
"National Geographic Society Tree," Tall Trees Grove, Redwood Creek RNP	364.3			(zt,op)
	364.0	13.0		(br)
"Ram's Head Burl Tree," Upper Loop Grove Trail MW	363.0	16.5	51.9	(br)
	360.0			(bt)
"Rockefeller Tree," Bull Creek Flats HR	359.1	13.2	41.3	(bt)
	359.3	13.4	42.0	(op)
	356.5			(zt)
Redwood #102, Cow Creek Grove HR	353.8	9.6	30.0	(br)
Unnamed (plot #660611), Grove 5, Redwood Creek RNP	353.5	14.1		(br)
"Hill-Davis Tree," Tall Trees Grove, Redwood Creek RNP	352.3			(zt,op)
Unnamed (plot #660823), Ferrell Grove JSR	350.2	18.6		(br)
Unnamed (plot #650617), Grove 3, Redwood Creek RNP	349.0	11.2		(br)
Unnamed (plot #660620), Grove 1, Redwood Creek RNP	347.8	15.0		(br)
"Founders Tree," Founders Grove, Dyerville Flats HR	346.3	12.7	40.1	(bt)
	346.1	12.7	40.0	(op)
	352.6			(zt)
	364.0	15.0 (base)	47.0 (base)	(cs)
"Big Tree," Big Tree Area, Bull Creek HR	345.0	16.5	72.0 (base)	(cs)
Unnamed (plot #660823), Stout Grove, Smith River JSR	342.0	13.6		(bt,br)
Redwood BC #7, Bull Creek Flats HR	338.8	10.2		(bt)
Redwood #103, Cow Creek Grove HR	336.2	11.1	35.0	(br)
Unnamed (plot #660636), Emerald Creek RNP	336.0	12.0	37.8	(br)
Redwood FG #2, Founders' Grove HR	334.0	12.0	37.6	(bt)
	328.0			(br)
Redwood TT #2, Rockefeller Forest HR	332.2	12.0	37.6	(bt)
	327			(br)
Redwood #104, Cow Creek Grove HR	327.5	15.1	47.3	(br)
"Stout Tree," Stout Grove, Smith River JSR	326.0	16.2	51.8	(br)
	323.0	16.5	63.1 (base)	(br)
	340.0	16.5	62.3 (base)	(cs)
	340.0	20.0	62.3 (base)	(op)
Unnamed (plot #660611), Grove 5, Redwood Creek RNP	326.0	9.2		(br)
Redwood #95, Rockefeller Forest HR	325.9	10.3	32.5	(br)
Unnamed (plot #660636), Emerald Creek RNP	309.2	12.6	39.5	(bt)
"Mother of the Forest," Redwood Loop Trail BBR	300.6	14.8	46.4	(bt)
	329.0	15.3	70.0 (base)	(cs,op)
"Big Tree," Circle Trail PCR	300.0	17.6	90.0 (base)	(cs)

BBR - Big Basin Redwoods State Park
HR - Humboldt Redwoods State Park
JSR - Jedediah Smith Redwoods State Park
MW - Montgomery Woods State Reserve
PCR - Prairie Creek Redwoods State Park
RNP - Redwood National Park

(br) Data from Becking (1968) with height measurement performed by relascope.
(bt) Data from Becking (1968) with height measurement performed by transit.
(cs) Data from California State Division of Parks, September 4, 1937 (Bowers, 1965; Shirley, 1937).
(op) Data posted on official plaques in front of the tree (Becking, 1968).
(zt) Data from Zahl (1964) with height measurement performed by transit.

Name of Tree and Location	Height	Breast Height Diameter	Diameter Circumference	Citation
"Parson Jones Tree," Pioneer Trail AR	292.0	12.1		(br)
	310.0	11.7		(op)
Unnamed (plot #660731), Waddell Creek BBR	284.0	12.5	39.2	(br)
"Colonel Armstrong Tree," Pioneer Trail AR	282.0	11.8		(br)
	308.0	14.5		(op)
"Giant Tree," Redwood Grove Loop Trail HCR	281.0	16.3	51.3	(br)
"General Sherman Tree," Redwood Grove Loop Trail HCR	264.0	15.5	48.6	(br)
"Father of the Forest," Redwood Loop Trail BBR	260.6	17.1	53.7	(bt)
	250.0	16.8	66.8 (base)	(cs,op)
"Santa Clara Tree," Opal Creek BBR	240.0	17.8	65.5 (base)	(cs)
	240.5	16.0	65.5 (base)	(op)
Measurements for the Dyerville Giant, toppled by storms on 24 March 1991, are noted in memorial:				
"Dyerville Giant," Founders Grove, Dyerville Flats HR	358.8	16.1	50.8	(bt,op)
	358.0		63.8 (base)	(br)

AR - Armstrong Redwoods State Reserve
BBR - Big Basin Redwoods State Park
HCR - Henry Cowell Redwoods State Park
HR - Humboldt Redwoods State Park

(br) Data from Becking (1968) with height measurement performed by relascope.
(bt) Data from Becking (1968) with height measurement performed by transit.
(cs) Data from California State Division of Parks, September 4, 1937 (Bowers, 1965; Shirley, 1937).
(op) Data posted on official plaques in front of the tree (Becking, 1968).

Height measurements for redwoods in Oregon were not available for this register; but in 1964, the U.S. Forest Service recognized Bear Creek as the site of the largest trees, ranging 9 to 15 feet in diameter (Becking, 1971).

In the 1930's, the California Park Board commissioned E.P. French, Superintendent of the Northwest District and experienced timber cruiser, to compile one of the first registers of large redwoods (Bowers, 1965; Shirley, 1937). In addition to his measurements cited above (cs), French estimated the bole volumes for several well-known trees listed below in board feet:

Name of Tree and Location	Stand	Mill Cut
"Big Tree," Big Tree Area, Bull Creek HR	235,000	154,000
"Santa Clara Tree," Opal Creek BBR	200,000	145,000
"Father of the Forest," Redwood Loop Trail BBR	177,000	133,000
"Stout Tree," Stout Grove, Smith River JSR	-	130,800
"Big Tree," Circle Trail PCR	-	128,000
"Founders Tree," Founders Grove, Dyerville Flats HR	-	125,000
"Mother of the Forest," Redwood Loop Trail BBR	141,345	101,960

BBR - Big Basin Redwoods State Park
HR - Humboldt Redwoods State Park
JSR - Jedediah Smith Redwoods State Park
PCR - Prairie Creek Redwoods State Park

Investigation of record Douglas-fir in the Seymour Valley, British Columbia (After Tiemann, 1935).

"I have investigated the basis of this information and am convinced that the data is well substantiated from a number of different sources, although it has been much questioned. The available information gives the height as 417 feet; diameter at the butt 25 feet (this diameter is substantiated by a photograph of the felled butt in which there are a number of people); thickness of bark, 16 inches. At a height of 207 feet the diameter was 9 feet. The trunk was free from limbs for a height of 300 feet! This was a remarkable tree if the information is correct, and it establishes the Douglas fir in former times as one of the tallest trees in the world!

"Unfortunately, direct information about this tree has been peculiarly difficult to obtain. Mr. Carey, who felled the tree, and who was apparently a long time resident of Vancouver, from whom the data was obtained, is no longer living, and a Mr. Mullett, formerly a scaler in the British Columbia Forestry Service, who was present at the felling, cannot be located. The alleged photograph of the stump was published in the British Columbia Lumberman, March, 1927.

"Mr. H. Steere-Clark, Safety Director of the B.C. Loggers Association, in a letter to Mr. Newton B. Drury dated June 17, 1931, after quoting the dimensions stated above, continues: 'These dimensions are in no way exaggerated, but were taken by the head feller and his crew at the time of felling. Mr. Carey, who actually felled the tree, has been dead for some years, but the record left behind him is authentic.' And in a letter to me of March 3, 1931, he says: 'This is also confirmed by Mr. O. Mullett, who was employed in the Forest Service at that time, as a scaler. The photograph which I exhibited at the National Safety Congress would not actually give the true perspective as to the size of the butt, owing to the position from which the picture was taken, but that it was actually 25 feet through is confirmed by several residents of that district. I am very sure that the statement that I made is based on fact, for this particular tree was quite historical in the annals of British Columbia logging. The statement made by the B.C. Lumberman was obtained from the same source as my own.'

"Mr. R.M. Essie, Editor of the British Columbia Lumberman, writes (Sept. 30, 1930): 'At the time this picture was given to me I also was very doubtful as to its authenticity, but Mr. O.L. Mullett, late of the B.C. Forest Service, who lent me the picture, assured me that the photograph was absolutely genuine, and that he had heard several people talking about this wonder tree.' ...In another letter from Mr. R.M. Essie to Mr. Donald Bruce, dated Oct. 23, 1930, he says: 'There is not the slightest doubt that the tree was felled in the vicinity of Vancouver. Several of the people in the picture can be identified as residents of this district.' And finally, in a letter to Prof. Emanuel Fritz, Mr. Essie, November 19, 1934, states: 'Some years ago the picture was brought to us (with the dimensions) by a member of the Forest Service of B.C. (Mr. Mullett). We cannot vouch for the measurements of the log, but as you will see from the picture it is an exceptionally large one. The only clue we have of the size of the tree is the evidence of Mr. M. Lavell, since deceased, who in a letter dated February 24, 1926, states that he was one of the people who were taken in the picture and that the tree was felled in the Lynn Creek Valley on the north shore of Barrard Inlet, Vancouver. I have no reason to doubt the statement of Mr. Mullett regarding the size of this tree, but we have no actual signed affidavit or anything like that concerning the matter.'

"The evidence of the letter from Mr. Lavell is important, since if true it establishes the photograph as authentic and not that of a California redwood as some have inferred. And if the photograph is really that of the butt of a Douglas fir, there seems no reason to doubt the dimensions given, for it was indeed a huge tree, larger than any now living" (Tiemann, 1935).

APPENDIX VII

Typical and maximum ages and dimensions attained by selected species of forest trees on better sites in the Pacific Northwest (After Franklin and Dyrness, 1988; Franklin and Waring, 1980).

Species	Typical			Maximum		Corr.
	Age (years)	Diameter (cm)	Height (m)	Age (years)	Diameter (cm)	Height (m)
Silver fir (*Abies amabilis*)	400+	90-110	45-55	590	210	63
Grand fir (*) (*Abies grandis*)	300+	75-125	40-60	-	217	53
Noble fir (*Abies procera*)	400+	100-150	45-70	600+	275	85
Incense-cedar (*) (*Calocedrus decurrens*)	500+	90-120	45	542+	374	46
Port Oxford cedar (*) (*Chamaecyparis lawsoniana*)	500+	120-180	60	-	488 (c)	69
Alaska yellow-cedar (*Chamaecyparis nootkatenis*)	1000+	100-150	30-40	3500	310	34
Western larch (*Larix occidentalis*)	700+	140	50	915	243 (c)	54
Engelmann spruce (*Picea engelmannii*)	500+	30-100 (b)	45-50	660 (c)	235	55
Sitka spruce (*) (*Picea sitchensis*)	700+	180-230	70-75	800 (c)	534	76
Knobcone pine (*) (*Pinus attenuata*)	150+ (c)	30-60 (c)	3-15 (b)	-	100	30
Lodgepole pine (*) (*Pinus contorta*)	250+	50-100 (b)	25-35	600 (b)	206	34
Sugar pine (*) (*Pinus lambertiana*)	400+	100-125	45-55	623 (c)	311	66
Western white pine (*Pinus monticola*)	400+	110	30-50 (b)	615	243 (c)	63
Ponderosa pine (*Pinus ponderosa*)	600+	75-125	30-50	726	271	49
Douglas-fir (*) (*Pseudotsuga menziesii*)	750+	150-220	70-80	1375 (c)	518 (c)	67
Coast redwood (*Sequoia sempervirens*)	1250+	150-380	75-100	2200	820 (a)	92
Pacific yew (*) (*Taxus brevifolia*)	300+ (c)	30-60 (b)	10-18 (b)	-	142	18
Western redcedar (*) (*Thuja plicata*)	1000+	150-300	30-50 (b)	1200+	641	37
Western hemlock (*) (*Tsuga heterophylla*)	400+	90-120	50-65	500+	274 (c)	79
Mountain hemlock (*Tsuga mertensiana*)	400+	75-100	25-35	800+	224	34
Bigleaf maple (*) (*Acer macrophyllum*	300+	50	15	-	250	30
Red alder (*) (*Alnus oregona*)	100	55-75	30-40	-	152 (c)	-
Pacific madrone (*) (*Arbutus menziesii*)	-	60-120 (b)	9-40 (b)	225 (b)	299	24
Tanoak (*) (*Lithocarpus densiflorus*)	180	25-125	15-30	350 (b)	278	30

Maximum breast-height diameters and their corresponding heights are from Pardo and Provost (1973).

(a) Data from Becking (1968).
(b) Data from Elias (1989).
(c) Data from Harlow and Harrar (1958).

(*) Species associated with coast redwood according to Becking (1982) and Roy (1966).

APPENDIX VIII

Summary of age class diameters for redwood stumps in Humboldt and Del Norte Counties (After Cooper, 1965).

The number of redwoods logged after they had died are indicated by parentheses ( ).

Age Class (years)	Diameter (feet)							Total Trees
	3-5	5-7	7-9	9-11	11-13	13-14	14-15	
100-150	15	0	2 (1)	0	0	0	0	17 (1)
151-200	1	2	0	0 (1)	0	0	0	3 (1)
201-250	2 (1)	1	0 (1)	0 (1)	0	0	0	3 (3)
251-300	17 (1)	20 (1)	61	0	0 (1)	0	0	98 (3)
301-350	66 (1)	35	6 (1)	1 (1)	0	1	0	109 (3)
351-400	0	0	2 (4)	0	0 (1)	0	1	3 (5)
401-450	5 (7)	60 (23)	2 (1)	1 (1)	1	0	0	69 (32)
451-500	108 (13)	135 (48)	68 (36)	4 (5)	0	0	0	315 (102)
501-550	113 (18)	132 (29)	159 (33)	22 (4)	1 (1)	0	2	429 (85)
551-600	0 (1)	48 (41)	31 (15)	0 (1)	0	0	1	80 (58)
601-650	32 (1)	69 (2)	63 (1)	0	0	0	0	164 (4)
651-700	0	1 (2)	0 (1)	0	0	0	0	1 (3)
701-750	0	2	1	1	1	0	1	6
751-800	0	0	0	0	0	0	0	0
801-850	0	0	0	0 (1)	0	1	0	1 (1)
851-900	0	0	0	0	0	0	0	0
901-950	0	0	0	0 (1)	0	0	0	0 (1)
951-1400	0	0	0	0	0	0	0	0
1401-1500	0	0	1	0	0	0	0	1
Totals	359 (43)	505 (146)	396 (94)	29 (16)	3 (3)	2	5	1299 (302)
Combined	402	651	490	45	6	2	5	1601

APPENDIX IX

Comparison of sprout and seedling regeneration by coast redwood after logging (After Becking, 1967).

Sprouting Characteristics	Seedling Characteristics
Sprouts develop immediately after the cutting of the stump, creating a great imbalance between the shoot and root ratio of the cut tree. This inevitably results in massive root dieback with a general weakening of the root system of the live stump. A new root system will have to develop itself with numerous new lateral roots replacing old and dying roots.	Seedlings develop a much better balanced ratio between shoot and root systems. While shoot growth may be retarded initially, root growth expands rapidly in depth and numerous well-branched lateral roots develop. The roots extend in a more symmetrical manner around the tree bole providing it with better support and wind firmness.
Sprouts can occupy the site only at the same spacing distances as previously occupied by the old-growth stumps. Since there are comparatively few trees at an average stand age of 1500 to 2000 years, such spacing cannot fully occupy the site for the incoming stand. Further disadvantages are that: -sprouts are generally densely grouped around the same stump creating severe competition among themselves, -clonal sprout clumps limit the important genetic variability of future trees, and its gene pool, -sprouts initially derive their nutrients from the same major root system, -sprouts develop very asymmetrical crowns with heavy branches on one side of the tree bole and asymmetrical growth rings, -sprouts depend greatly upon each other for wind firmness and support.	Seedlings normally distribute themselves more evenly and densely over the entire logging site which results in: -a more favorable equilateral spacing pattern, -a greater number of seedlings per acre in accordance with normal stand development, -a greater selection among trees of different genetic potentials and growth superiority, -a lesser chance of growth stagnation among seedlings, -a greater wind firmness with a symmetrical bole and crown development inducive to higher timber quality, and an independent root system.
Initial height growth of the sprouts is very rapid, often exceeeding four to five feet per year during the first few growing seasons. The sprouts will develop long internodes with heavy branch whorls that are prone to wind damage.	Initial height growth of the seedling is retarded, particularly if the seedling lacks the benefit of shade and forest shelter. The average five-year old seedling is about one foot in height.
As the root-shoot imbalance becomes more acute, the stump root system will begin to dieback partly. Subsequent height growth will be impaired, resulting in reduced internodal length and reduced sprout vigor until, after many years, a new, more balanced and independent root system has regenerated itself. The sprout may then become overtopped by other, more vigorous trees.	Root development is initially greatly favored, and a better balanced root-shoot ratio is maintained. As the root system penetrates deeper soil layers, it provides a more continuous moisture supply during periods of drought, and its shoot development will accelerate greatly.
Normally, the sprout will decline rapidly in vigor after its five-year impetus, and often start to produce cones within twenty years, long before its normal maturity. Seed quality of such sprout growth is generally inferior to seed from normal seedlings maturing at 100 to 150 years of age.	Generally, after six to fifteen years of age, the average leader growth exceeds two to three feet per year, sometimes seven feet per year. Rapid height growth, however, is maintained to about 50 to 80 years of age when the trees may reach heights of over 200 feet depending upon site conditions and sexual maturity.
Timber quality is impaired by the wide growth rings in the center of the bole.	Timber quality is not so much impaired because of the denser rings in the center of the bole.
Great differences in age have been observed among sprouts of the same stump, and between sprout age and year of logging. Sprouts often differ more than ten to twenty-five years from the logging date, indicating great mortality and regrowth of new sprouts which delays restocking of the site and consequently wood production.	Seedling age is generally in closer agreement with the age of logging activities, although age differences of five to ten years between seedling establishment and and logging date are not uncommon. Generally, only one dominant age class of seedlings prevails. Restocking with redwood after the failure of its first regeneration wave becomes increasingly difficult the more advanced the age of regeneration.

According to Becking (1967), the best and most successful manner of regenerating redwoods on cutover forest lands is natural regeneration by means of seedlings.

APPENDIX X

Plants associated with coast redwood (After Becking, 1982; Borchert et al., 1988; Cooney-Lazaneo et al., 1981; Jepson, 1984; Munz and Kenk, 1973; Person, 1937; Roy, 1966; Shreve, 1927; Thomas, 1961).

While no one associate has a range completely coincidental with the distribution of coast redwood (Langenheim and Thimann, 1982), the more frequently associated trees are indicated by asterisk (*).

Associated Conifers

- Santa Lucia fir (*Abies bracteata*)
- Grand fir (*A. grandis*) (*)
- Incense-cedar (*Calocedrus decurrens*)
- Port Oxford cedar (*Chamaecyparis lawsoniana*)
- Gowen cypress (*Cupressus goveniana*)
- Sitka spruce (*Picea sitchensis*) (*)
- Knobcone pine (*Pinus attenuata*)
- Lodgepole pine (*P. contorta*)
- Sugar pine (*P. lambertiana*)
- Bishop pine (*P. muricata*)
- Douglas-fir (*Pseudotsuga menziesii*) (*)
- Pacific yew (*Taxus brevifolia*) (*)
- Western redcedar (*Thuja plicata*)
- California nutmeg (*Torreya californica*) (*)
- Western hemlock (*Tsuga heterophylla*) (*)

Associated Hardwoods

- Vine maple (*Acer circinatum*)
- Bigleaf maple (*A. macrophyllum*) (*)
- California buckeye (*Aesculus californica*)
- Red alder (*Alnus oregona*) (*)
- White alder (*A. rhombifolia*) (*)
- Pacific madrone (*Arbutus menziesii*) (*)
- Golden chinquapin (*Castanopsis chrysophylla*)
- Pacific dogwood (*Cornus nuttallii*)
- Oregon ash (*Fraxinus latifolia*)
- Tanoak (*Lithocarpus densiflora*) (*)
- Pacific wax myrtle (*Myrica californica*) (*)
- Western sycamore (*Platanus racemosa*)
- Black cottonwood (*Populus trichocarpa*)
- Coast live oak (*Quercus agrifolia*)
- Canyon live oak (*Q. chrysolepis*)
- Oregon white oak (*Q. garryana*)
- California black oak (*Q. kelloggii*)
- Interior live oak (*Q. wislizeni*)
- Cascara sagrada (*Rhamnus purshiana*)
- Pacific willow (*Salix lasiandra*)
- Arroyo willow (*S. lasiolepis*)
- Sitka willow (*S. sitchensis*)
- California bay (*Umbellularia californica*) (*)

Associated Shrubs

- Lady bloom (*Ceanothus parryi*)
- Blue-blossom (*C. thyrsiflorus*)
- Creek dogwood (*Cornus californica*)
- Smooth dogwood (*C. glabrata*)
- California hazel (*Corylus cornuta* var. *californica*)
- Western burning bush (*Euonymus occidentalis*)
- Quinine bush (*Garrya elliptica*)
- Salal (*Gaultheria shallon*)
- Ocean spray (*Holodiscus discolor*)
- Wild honeysuckle (*Lonicera hispidula*)
- Mock azalea (*Menziesia ferruginea*)
- Oso berry (*Osmaronia cerasiformis*)
- Pacific ninebark (*Physocarpus capitatus*)
- Coffee berry (*Rhamnus californica*)
- California rhododendron (*Rhododendron macrophyllum*)
- Western azalea (*R. occidentale*)
- Poison oak (*Rhus diversiloba*)
- Stink currant (*Ribes bracteosum*)
- Straggly gooseberry (*R. divaricatum*)
- Canyon gooseberry (*R. menziesii*)
- Blood currant (*R. sanguineum*)
- California rose (*Rosa californica*)
- Wood rose (*R. gymnocarpa*)
- Nootka rose (*R. nutkana*)
- Western raspberry (*Rubus leucodermis*)
- Thimbleberry (*R. parviflorus* var. *velutinus*)
- Salmonberry (*R. spectabilis*)
- Pacific blackberry (*R. ursinus*)
- Coast red elderberry (*Sambucus callicarpa*)
- California huckleberry (*Vaccinium ovatum*)
- Red huckleberry (*V. parvifolium*)

Associated Herbs

- Deer-foot (*Achlys triphylla*)
- Western red baneberry (*Actaea rubra* ssp. *arguta*)
- Trail plant (*Adenocaulon bicolor*)
- Glade anemone (*Anemone deltoidea*)
- Windflower (*A. quinquefolia* var. *grayi*)
- Crimson columbine (*Aquilegia formosa* var. *truncata*)
- Elk clover (*Aralia californica*)
- Wild ginger (*Asarum caudatum*)
- Oregon grape (*Berberis nervosa*)
- Small ground cone (*Boschniakia hookeri*)
- Brook foam (*Boykinia elata*)
- White globe lily (*Calochortus albus*)
- Calypso (*Calypso bulbosa*)
- California harebell (*Campanula prenanthoides*)
- Round-fruited carex (*Carex globosa*)
- California hedge parsley (*Caucalis microcarpa*)
- Enchanter's nightshade (*Circaea alpina* var. *pacifica*)
- Red clintonia (*Clintonia andrewsiana*)
- Spotted coral root (*Corallorhiza maculata*)
- Striped coral root (*C. striata*)
- Western hound's tongue (*Cynoglossum grande*)
- Toothwort (*Dentaria californica* var. *californica*)
- Pacific bleeding heart (*Dicentra formosa*)
- Hooker's fairy bells (*Disporum hookeri*)
- Fairy lantern (*D. smithii*)
- Common fireweed (*Epilobium angustifolium*)
- Stream orchid (*Epipactis gigantea*)
- Common scouring rush (*Equisetum hyemale*)
- Giant horsetail (*E. telmateia* var. *braunii*)
- California strawberry (*Fragaria californica*)
- Checker lily (*Fritillaria lanceolata*)
- Goose grass (*Galium aparine*)
- California bedstraw (*G. californicum*)
- Rattlesnake orchid (*Goodyera oblongifolia*)
- Rein orchid (*Habenaria unalascensis*)
- Gnome plant (*Hemitomes congestum*)
- Cow parsnip (*Heracleum lanatum*)
- Alum root (*Heuchera micrantha*)
- White-flowered hawkweed (*Hieracium albiflorum*)
- Pacific waterleaf (*Hydrophyllum tenuipes* var. *viride*)
- Mountain iris (*Iris douglasiana*)
- Common Pacific pea (*Lathyrus vestitus*)
- Tiger lily (*Lilium columbianum*)
- Kellogg's tiger lily (*L. kelloggii*)
- Leopard lily (*L. pardalinum*)
- Redwood lily (*L. rubescens*)

Associated Herbs (continued)

Heart-leaved twayblade (Listera cordata)
Stipulate lotus (Lotus stipularis)
Club moss (Lycopodium clavatum)
Skunk cabbage (Lysichiton americanum)
Woodland madia (Madia madioides)
Solomon's seal (Maianthemum dilatatum)
Common manroot (Marah fabaceus)
Coastal manroot (M. oreganus)
Scarlet monkey flower (Mimulus cardinalis)
Tooth-leaved monkey flower (M. dentatus)
Large monkey flower (M. guttatus ssp. arvensis)
Star-shaped miterwort (Mitella caulescens)
Common miterwort (M. ovalis)
Moneses (Moneses uniflora var. reticulata)
Indian pipe (Monotropa uniflora)
Indian lettuce (Montia parvifolia)
Miner's lettuce (M. sibirica)
Wood forget-me-not (Myosotis latifolia)
Small-flowered nemophila (Nemophila parviflora)
Pacific oenanthe (Oenanthe sarmentosa)
Evening primrose (Oenothera hookeri ssp. wolfii)
Wood cicely (Osmorhiza chilensis)
Sweet cicely (O. purpurea)
Redwood sorrel (Oxalis oregana)
Western coltsfoot (Petasites palmatus)
Fringed pinesap (Pleuricospora fimbriolata)
California milkwort (Polygala californica)
Oregon wintergreen (Pyrola asarifolia var. bracteata)
White-veined wintergreen (P. picta)
Buttercup (Ranunculus orthorhynchus)
Little buttercup (R. uncinatus)
Pacific sanicle (Sanicula crassicaulis)
Yerba buena (Satureja douglasii)
Saxifrage (Saxifraga sp.)
Slink pod (Scoliopus bigelovii)
Coast figwort (Scrophularia californica)
Spike moss (Selaginella oregana)
Fat solomon (Smilacina racemosa var. amplexicaulis)
Slim solomon (S. stellata var. sessilifolia)
California hedge nettle (Stachys bullata)
Emerson's hedge nettle (S. mexicana)
Twisted stalk (Streptopus amplexifolius)
Snow queen (Synthyris reniformis)
Fringe cups (Tellima grandiflora)
Meadow rue (Thalictrum polycarpum)
Sugar-scoop (Tiarella unifoliata)
Thousand mothers (Tolmiea menziesii)
Starflower (Trientalis borealis)
Pacific starflower (T. latifolia)
Giant wake robin (Trillium chloropetalum)
Western wake robin (T. ovatum)
Stinging nettle (Urtica holosericea)
Lyall's nettle (U. lyallii)
Inside-out flower (Vancouveria hexandra)
Evergreen vancouveria (V. planipetala)
Common vetch (Vicia angustifolia)
Stream violet (Viola glabella)
Western heart's ease (V. ocellata)
Redwood violet (V. sempervirens)
Yerba de Selva (Whipplea modesta)

Associated Ferns

California maidenhair (Adiantum jordanii)
Five-finger fern (A. pedatum var. aleuticum)
Western lady fern (Athyrium filix-femina)
Deer fern (Blechnum spicant)
Brittle fern (Cystopteris fragilis)
Coastal wood fern (Dryopteris arguta)
Spreading wood fern (D. dilatata)
Goldenback fern (Pityrogramma triangularis)
California polypody (Polypodium californicum)
Licorice fern (P. glycyrrhiza)
Leather fern (P. scouleri)
Dudley's shield fern (Polystichum dudleyi)
Western sword fern (P. munitum)
Bracken (Pteridium aquilinum var. pubescens)
Western chain fern (Woodwardia fimbriata)

Associated Grasses

Narrow-flowered brome grass (Bromus vulgaris)
Reed grass (Calamagrostis rubescens)
Western fescue (Festuca occidentalis)
California vanilla grass (Hierochloe occidentalis)
Geyer's onion grass (Melica geyeri)
Tall trisetum (Trisetum canescens)

Transcript of the video documentary, "On the edge: nature's last stand for coast redwoods."

In all the world, can there be a more grand and ancient forest? Sown on the edge of the New World, coast redwoods stand as nature's tabernacle, loftier and more exalted than any built by man.

As the great American author, John Steinbeck, wrote, "The redwoods, once seen, leave a mark, or create a vision that stays with you always... They are not like any trees we know, they are ambassadors from another time."

I'm Jim Snyder and for the next two quarters of an hour, we shall probe the edge of coastal fogs to find these redwood ambassadors. And we shall see, that from a geological standpoint, nature has not only poised the coast redwood on the edge of California, but on the edge of survival.

At first encounter, many people are impressed by the redwood's size. Standing more than 350 feet high, coast redwoods can grow 20 feet in diameter and can yield 360,000 board feet of lumber; enough board feet to build 22 average-sized houses!

Yet to others, a redwood sojourn might summon a more primeval scene, when dinosaurs roamed the ancient redwood forests of North America. One hundred and thirty million years ago, gazelle-like hypsilophodontids nested in colonies along the forest's edge. Elsewhere, herds of Diplodocus reared their 85-foot long bodies to browse on uppermost cones and needles or repell attacks from allosaurs. By the end of the Age of Reptiles, nocturnal predators were common and Dromiceiomimus stalked ancestral redwoods in search of lizards and small mammals.

When the long reign of dinosaurs collapsed, 65 million years ago, the world was ravaged by a great dying of all land animals larger than 55 pounds. Yet for ancient redwoods, the thread of life was not extinguished and they endured for 650,000 centuries more.

Their prehistoric ranges can be traced to nearly all the northern continents. From 12 or more ancestral species of redwood, three persist into the present. The uniquely deciduous dawn redwood was only recently known to science when relict stands were discovered in central China in 1944. Forebears of the giant sequoia, largest of all living things, appear to have been restricted to Greenland, Europe and North America; while those of the coast redwood were more widespread.

We know the range of these ancient forests from the fossils they left behind, and from those rare and magnificent occasions when the trees were preserved beneath ash, mud and volcanic debris from some primal eruption. These petrified monarchs are found near California's Napa Valley. Three million years ago, a volcanic eruption leveled and buried this redwood forest to preserve even the soft, fibrous bark in astonishing detail.

It was nearly 55 million years ago that the earth began a prolonged cooling trend. Increasingly severe northern winters slowly diminished the range of ancient redwoods. Like the coast redwood today, their roots may not have tolerated the ground freezing. And with the building of western continental mountains, inland droughts became more frequent far from coastal storms. And thus, 20 million years ago, the redwoods retreated south and west, establishing their claim to the moist, temperate regions of California.

Then within the last two million years, the trend in global cooling climaxed four times in the Ice Ages. Massive ice fields, two miles thick, buried the continent as far south as the Ohio and Missouri Rivers. But in California, the low, coastal mountains were largely glacier-free. And here, extending 500 miles from Monterey County to the southwestern tip of Oregon, coast redwoods found safe refuge.

Mark Twain once quipped, "The coldest winter I ever spent was a summer in San Francisco!" Indeed, many visitors would agree. But it is the summer fogs of the Pacific Coast that breathe life into the redwood forest.

One tree requires prodigious amounts of moisture. As much as 500 gallons per day are required to replace the amount released by the leaves as water vapor. When the vapor condenses with coastal fog, light rains bathe the forest to help maintain a cool and damp microclimate during the dry summer months. Redwoods flourish only where summer fogs pervade, below 3000 feet and less than 40 miles from the sea.

The trees are renowned for their great height. Three hundred feet is common among stands of old-growth redwood. The task of supplying water to their uppermost branches is formidable and spike-tops result from times of moisture stress. Most astonishing is the comparatively small size of their winged seed: 60 seeds to a cone, 123,000 to a pound. A redwood may produce five million seeds per year, but less than one in a million may survive to become the tallest of all living things at more than 367 feet high. Such colossal height suggests profound longevity; and countless human milestones have lapsed in just one redwood's 2200 year lifespan.

When we consider the great age of the redwood forest, human activity among the trees has been a very recent event. For example, it is only within the last 150 years that redwoods have fallen on the cutting edge of the lumber industry. But the human chapter in redwood chronology begins with California's first inhabitants.

At least 15 Native American tribes came to occupy parts of their range, yet the most intimate associations evolved among northwestern cultures as late as 900 A.D.. To people of the northern forest, redwoods embodied the eternal spirit found in all things which live as equals.

"What remains of our ancient, ancient history, is recorded here among the ancient creatures, who have seen civilizations come and go. It's like our people. We have seen many flags fly over this land. And the creatures around us, they commit no wrong against us. They are in state of grace. So in the name of progress, we've seen much death and destruction, and how insensitive man is to the natural world. So it behooves us, then, all of us, to make corrections within the educational system where little children will be taught the truth about resources. So that when it comes their turn to accept the responsibilities of managing or helping manage a natural area, they will know how" (Coyote, West Coast Representative, Council of Elders).

Rituals, such as the Jumping Dance of the Yuroks, celebrated the renewal of life and the sanctity of the natural world.

Their settlements clustered along rivers or on the coast near streams, lagoons and bays. Houses were gabled and semi-terranean, built of redwood planks split by elk horn wedges and stone mauls. Footpaths connected neighboring villages, but for riverine fishermen like the Hupa and Yurok, canoes were indispensable. Shallow, 18-foot dugouts were hewn from redwood logs using fire and mussel-shell adzes. Although living redwoods were sometimes felled by burning, most tribal needs were met by the abundant supply of fallen wood.

If the Native American experience could be weighed in terms of impact upon the redwood forest, it would be measured by fire. Open meadows, or prairies, may have been maintained by periodic burning to enhance the availability of game and valued species of plants that thrive in fire-disturbed areas.

The charred trunks of many old redwoods can attest to the natural part that fire plays in a mature forest ecosystem. Periodic, low-intensity fires benefit the forest by recycling nutrients to the soil and burning ground vegetation that competes with redwood seedlings for water, nutrients and sunlight.

Unlike most trees, redwoods contain very little pitch that might fuel prolonged burns. Their bark is also one-foot thick at the base and a poor conductor of heat, thus insulating their life-supporting tissues from fire.

All the tissues responsible for transporting water and nutrients from the soil to the leaves in exchange for photosynthetic sugars lie just beneath the bark. As redwoods grow from seedling to giant, the innermost tissues die and become heartwood. Fires do sometimes penetrate the bark and burn the heartwood from within. Yet the burning of these cavernous scars, known as "goose pens" to early settlers, seldom kills mature redwoods. The vast reservoir of water stored within their tissues can resist most heartwood burns.

Centuries later, scars from major fires may no longer be seen. Redwoods not only conceal the damage with an accelerated growth of tissue, but they can buttress gradual leans of 40 feet or more to restore their balance in unstable soils.

Even when fires succeed in destroying a redwood trunk, root collar burls at the base of the stump survive. New growth sprouts from dormant buds within the collar to form concentric stands of trees which, in turn, mature and die to propagate further circles of redwood. In this way, a parent tree may never truly die because its roots and genetic code live on.

It was this flirtation with immortality that impressed English botanist A.B. Lambert when he first described the coast redwood in 1828. Their rounded cones and branchlets of needles forming flat sprays were very similar to the bald cypress and suggested the genus Taxodium. But unlike the deciduous cypress, coast redwoods were evergreen, retaining their branchlets for three or four years. And the redwood's ability to regenerate from the root collar was extremely rare among conifers. Lambert chose to name the species sempervirens, or "ever-living."

Another botanist, Stephen Endlicher, challenged Lambert's designation of Taxodium. He noted that redwoods produce a second type of needle unlike bald cypress, with smaller needles bristling about the stem on leading shoots and juvenile growth. In 1847, he proposed a new genus, Sequoia, most likely in honor of the great American Indian scholar who invented the Cherokee alphabet.

Sequoia sempervirens had first been described by the Spanish in 1769, when Portola's expedition explored Monterey Bay "over plains and low hills, well forested with very high trees of a red color, not known to us... they are named redwood from their color."

The dark, rich hues of the heartwood, bark and swollen knobs of burl are due to the presence of tannic acids, or tannin. Not only is tannin a potent fire-retardant used in fire extinguishers, but the astringent nature of the acid makes the wood unpalatable to nearly all fungi and insects, especially termites. Fallen logs decay very slowly, a quality not unnoticed by early loggers.

Although the Spanish colonization of California was largely built of adobe, the subsequent flood of emigrants during the Gold Rush of 1849 increased the demand for lumber. Within six years, California swelled from 15,000 to more than 223,000 people. Many came by sail, choking San Francisco's harbor with ships abandoned by their crews for the Motherlode. While few found fortune in the gold fields, many struck it rich supplying the miners with lumber. By 1850, the rush for redwood was on.

Pioneer steam, wind and water-powered mills were built near Albion and Mendocino, or wherever coastal headlands would permit the loading of schooners. Humboldt Bay championed the boom in spite of hazardous sandbars. Within three years, Eureka boasted six sawmills and 3000 people. No less than 143 ships and 20 million board feet of lumber left Humboldt Bay for San Francisco in 1853.

Although many of the mills soon failed due to over-production and an unstable market, survivors, like William Carson, made Eureka the jewel of the redwood empire. When his mansion was completed in 1886, citizens hailed Eureka for having "no cyclones, few tramps, little poverty, and never lost a dollar by dishonest officials."

The wealth of the lumber barons was enriched by the tremendous productivity of the redwood forest. While reports of one and a half million board feet per acre may have been exaggerated, they are not suprising. When we consider the biomass, or living weight, of the trunks alone, old-growth redwoods contain as much as 1540 tons per acre, or more than eight times the amount produced by a mature tropical rain forest!

Harvesting such wealth was difficult for early loggers. Armed with little more than an axe atop springboards to clear the root collar burls, two men might spend a week felling one redwood giant. Their inverted undercut reduced breakage by allowing the tree to slide off the stump when toppled. Then before the tree was sawed into logs, the bark was stripped and burned to facilitate hauling and avoid clogging the mill's machinery. Often, logs cut from the largest redwoods had to be split with dynamite before they could be "dogged" together in trains.

Teams of oxen dragged the trains over an elaborate network of trestles and cross-timbered skidroads. At nearly $5000 per mile, skidroad construction was the most costly aspect of early logging until the coming of the railroads in 1875. Steam locomotives not only opened up more remote sections of forest to logging, they inspired the creation of the first steam-powered winch, seven years later. Known to loggers as bull donkeys, they soon replaced the oxen teams just as rails replaced the skidroads.

The revolution in logging afforded by machines increased production dramatically. By the time caterpillars became commonplace in the 1930's, more than one third of the redwood forest had been logged. Six hundred million board feet were cut each year. The postwar housing boom saw 398 mills work the redwood coast by 1948, and for 24 years, production topped one billion board feet! Few privately owned stands of old-growth timber survived. By 1989, more than 1,900,000 acres of virgin redwood, 95% of the original forest, had been cut down.

Ninety-five percent! It is both remarkable and sobering to tally the cost of America's growth this last century. And had it not been for the crusades of early conservationists, many more redwoods would have fallen.

As early as 1852, the California state legislature wrestled with attempts to place redwood forest lands into public ownership. But public support was neither widespread nor persistent enough to enact legislation until Andrew P. Hill rose to champion the cause in 1899.

"Andrew Hill, who was a very famous painter and photographer from San Jose, California, was commissioned to take pictures in the redwoods; and this particular park was where he wanted to take the pictures. The people who Hill gathered around him, who happened to be very noted people (David Starr Jordan of Stanford University was president of Stanford, Benjamin I. Wheeler of Berkeley and Father Kenna of Santa Clara, and the noted journalist by the name of Josephine McCracken), formed a group to look into how the redwoods that we know today could be preserved" (Tony Look, Co-Founder of the Sempervirens Fund).

In 1900, McCracken described the peril menacing Big Basin: "Greed, rapacity and vandalism will hack and cut and mutilate the grandest and most magnificent forest that can be found on the face of the globe."

In May of that year, Hill led a party of eight conservationists to explore Big Basin's redwoods. So profound was their experience that they rallied together near Sempervirens Falls to form the Sempervirens Club, dedicated to the preservation of Big Basin as a public park.

"They passed the hat for a contribution from each of the people who went. They had the grand total of $36 to start this movement which, today, has been so successful with many millions of dollars contributed and bought. It then went to the state legislature again and this time, Father Kenna, of the University of Santa Clara, was the prime mover of the legislators in Sacramento. And between Mr. Hill and himself, they were able to persuade the legislature to appropriate $250,000 to buy 3600 acres of redwoods in the Basin itself" (Tony Look).

As Reverend Kenna addressed the legislature, "Senators... these redwoods are predominantly Californian, unique in their species and situation, and as a forty-niner, I beg you to stay the hand that would harm those that still remain, to recall the glories of those vast virgin forests now no more." On March 16th, Governor Gage signed the bill appropriating funds for the purchase of Big Basin as California's first redwood park. Unfortunately, Big Basin's charter did not extend protection to north coast redwoods.

It is in the northwest regions of California that the largest sequoias grow in pure stands atop alluvial flats. Redwoods thrive along river banks in areas prone to flooding. When excessive amounts of silt smother the roots of other conifers, redwoods keep pace with the rise in soil by producing new roots from their root collar burls. As many as seven successive root systems have been counted on fallen trees. Although redwoods lack taproots, they remain extremely wind firm by interlocking their six-foot deep roots with those of neighboring trees.

Efforts to preserve the northern redwoods coincided with the construction of the state highway from Eureka to San Francisco in 1917. When the road passed through the remote Dyerville-Bull Creek Flat area of Humboldt County, it opened up the most spectacular pure stands of old-growth redwood to logging. Since virtually all lands adjacent to the highway were owned by timbermen, three prominent conservationists were compelled to take action.

"And they are credited with being the founders of the Save-the-Redwoods League. They were Madison Grant, Henry Fairfield Osborn and John C. Merriam. John C. Merriam was a paleontologist at the University of California, and he interested his good friend, Stephen Mather, who was the first director of national parks, to join the group along with Franklin K. Lane, who was the Secretary of the Interior at the time. For a short time, Mr. Lane served as the President of Save-the-Redwoods League during its founding. And then, John C. Merriam followed. And the Save-the-Redwoods League, from a $100 contribution, began to start buying up groves in 1919 and 1920 which would eventually be protected for their great antiquity and their beauty. Save-the-Redwoods League grew from a handful of people to an organization which, today, has 50,000 people throughout the United States that contribute to help save these parks. The League determined that it was necessary to actually buy it with donated funds, buy these groves with donated funds, and then combine that, hopefully, with some state monies eventually to create a whole system of groves that could be protected. There was no unified California state park system. So the Save-the-Redwoods League, in 1926 and 27, began a campaign to urge that a bond issue be voted by the voters of California to establish a California State Park System. And that state park system came into being in 1928 with the establishment of the first parks; and the redwood parks became the core of that California state park system" (John Dewitt, Executive Director of the Save-the-Redwoods League).

"Well, I think that the California state park system, of course, was ahead of most everyone in thinking in terms of the future, and in setting aside areas in California that were unique to California in its culture and in its natural history. So that I think California was recognized for the kind of far-sighted thinking that was involved. Now, they're beginning to recognize how important tourism is toward their economic welfare; so that there was always that conflict between the economics and the intrinsic values of the redwoods. People that are coming out of our big metropolitan centers really have little or no understanding of what it's like to be in the out-of-doors and what their responsibility is" (William Penn Mott, Jr., former Director of the National Park Service).

"It's very important that when people visit parks that they realize that they are actually the caretakers. They are the ones who are determining whether that park and whether those redwood trees will be as nice tomorrow as when they found them today" (John Mott, California State Park Ranger).

"I took a bunch of kids from inner Oakland on a hike once through a state park. These were kids who were on their last chance. They were in a continuation school and it was their last shot at education before they were kicked out of the system, totally. And it really wasn't anything I did. It was the park itself. The weather was perfect. The day was perfect. And all of a sudden, these kids saw a snake that happens to be on the endangered species list. And one little boy looked up at me and said, 'You know, this place ain't been trashed yet!' And he figured it out. There was something special about having places that haven't been trashed yet and keeping them that way" (Mimi Guiney, California State Park Ranger).

"The future of redwood forests has a lot to do with the future of the human race. And that the future of this redwood tree is your future and my future as well. What this means is, as we come to this consciousness of the significance of the 'sempervirens sequoia,' we're coming to realize that, literally, the very future of this lovely little planet we call Earth is intertwined with the reality of the future of these redwood forests" (Verl Clausen, Executive Director of the Sempervirens Fund).

Although nature has been responsible for placing the coast redwood on the edge of a continent and, geologically, on the edge of survival, the forces that have brought economic prosperity to the redwood coast have also brought the old-growth forest to the edge of extinction. The value of preserving the last remaining stands of old-growth is not merely a question of economics. It is a choice between a rich or an impoverished existence for man. Perhaps the IUCN, the International Union for the Conservation of Nature, explains it best when they state, "We have not inherited the Earth from our parents, we have borrowed it from our children."

Jim Snyder
28th May 1989

"We, of Sempervirens Fund, simply invite you to join with us in the continuation of caring about our relationship to the coastal redwoods, and realizing that that relationship is one that touches our own lives as well. So that, standing together, we can be assured of renewing, each generation, the reality that they, and we, will, in the full sense of the phrase, be 'sempervirens,' always-living" (Verl Clausen).