



## Review

## Presettlement and modern disturbance regimes in coast redwood forests: Implications for the conservation of old-growth stands

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## ABSTRACT

Coast redwood (*Sequoia sempervirens*), a western North American conifer of ancient lineage, has a paradoxical combination of late-successional characteristics and strong adaptations to disturbance. Despite its shade tolerance and heavy dominance of the canopy on many sites, redwood saplings are uncommon in upland old-growth stands. Information needed to ensure the conservation of old-growth redwood forests has been limited. In this review paper, we integrate evidence on redwood biology with data on the historic and modern disturbance regimes to help clarify the degree to which key attributes of redwood forests may have been dependent upon periodic disturbance. Available evidence suggests that episodes of fire, flooding, and slope failure prior to European settlement were frequent but predominantly of low to moderate severity and extent, resulting in broadly uneven-aged forests. The majority of fires prior to European settlement were apparently of human origin. Frequency and severity of the major disturbance agents have been radically changed in modern times. Fires have been largely excluded, and flooding has been altered in ways that have often been detrimental to old-growth redwoods on alluvial terraces. However, because of the apparent anthropogenic origin of most presettlement fires, the long-term evolutionary role of fire for coast redwood is ecologically ambiguous. With fire exclusion, redwood possibly could be displaced to some extent on upland sites by increasing abundance of fire-sensitive competitors. Alternatively, redwood may be able to maintain dominance by vegetative sprouting and new seedling establishment on root-wad mounds, fallen logs, and on soil exposed by slope failure. Future research priorities are suggested that will help resolve some of the current ambiguities.

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## 1. Introduction

Many conifer species in cool temperate forests occur in disturbance-prone environments and have biological traits suggesting adaptation to major natural disturbances. Examples of disturbance adaptations include a requirement of exposed mineral soil for good seedling establishment, high light requirements, rapid growth in open environments, early reproductive maturity, and thick bark on mature trees (Rowe and Scotter, 1973; Heinselman, 1973; Chandler et al., 1983). In conifer forests of the Pacific Northwest, the natural disturbance regime is spatially and temporally complex. In some climatic zones, frequent fires of low to moderate intensity historically led to a predominance of complex, multi-aged stands (Morrison and Swanson, 1990; Taylor and Skinner, 2003), while the fire regime in other locations was dominated by stand-replacement events (Stewart, 1986; Agee, 1993; Huff, 1995). Consequently, landscapes of old-growth conifers in some parts of the Pacific Northwest, as in parts of the northern Rocky Mountains and boreal forest, are a patchwork mosaic of largely single-generation stands, with the predominant age of canopy trees in each stand indicating the date of the last major fire (Heinselman, 1973; Hemstrom and Franklin, 1982; Barrett et al., 1991; Huff, 1995).

Maintaining natural vegetation complexes in parks and natural areas can be challenging in regions where extensive, stand-replacing events typify the natural disturbance regime. Impressive old-growth forests of particular species, which in some cases may have been a factor in the establishment of reserves, are often not self-sustaining and may succeed to other species in the absence of fire. At the same time, disturbances such as fire, wind, and ice storms also can have beneficial effects on the structure and function of old-growth stands, including nutrient cycling, modification of fuel loads, formation of cavity trees for wildlife, and promotion of complex canopy architecture (Chandler et al., 1983; Agee, 1993; Sillett and Van Pelt, 2007).

Although forests of coast redwood (*Sequoia sempervirens* D. Don (Endl.)) in northern California and southern Oregon are contiguous in many areas with fire-prone forests of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), the disturbance dynamics of redwood have been something of an enigma, and the role of disturbance in the ecology and perpetuation of old-growth stands has been debated for decades. Redwood has apparently been a dominant species in the California Coast Ranges for much of the Holocene (Sawyer et al., 2000a; Sawyer, 2006), which may argue for its adaptability to fluctuating climatic and fire regimes. But humans were present as ignition sources during most of this time (Moss and Erlandson, 1995), and fire histories of individual stands prior to the 17th century are not well known. Some ecologists have interpreted coast redwood as a species dependent upon fire, flooding, or landslides to create suitable mineral soil seedbeds and inhibit competition from more shade-tolerant species (Cooper, 1965; Stone and Vasey, 1968; Stone et al., 1969; Barbour et al., 1980). In a report to Redwood National Park, Stone et al. (1969) characterized redwood forest as a fire subclimax and predicted that without fire on upland sites, redwood gradually would be replaced by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), grand fir (*Abies grandis* Dougl. Ex D. Don) Lidl.) western redcedar

(*Thuja plicata* Donn) and tanoak (*Lithocarpus densiflorus* (Hook. & Arn.) Rehd.). Others have interpreted redwood as a late-successional species that is tolerant of fire but not dependent on it, and capable of self-perpetuation through gap dynamics and understory recruitment (Fisher, 1903; Roy, 1966; Veirs, 1982; Busing and Fujimori, 2002; Sawyer, 2007).

These widely varying interpretations can be attributed in part to two factors. First, redwood itself is a species with an unusual constellation of biological traits that defies easy classification into traditional categories of succession. On the one hand, redwood is a shade-tolerant species with great longevity, and old-growth stands are often highly uneven-aged (Fisher, 1903; Fritz, 1929; Veirs, 1982). On the other hand, redwood seedlings are generally uncommon in the understory of old-growth stands but can become established in large numbers on exposed mineral soil (Fritz, 1932, 1951; Person and Hallin, 1942; Roy, 1966). Like many fire-adapted species, mature redwoods have thick bark that allows mature trees to survive moderately intense fire, and redwood saplings can grow rapidly in open, disturbed habitats. In addition, redwood has some traits that enable it to rebound quickly even after severe fire. These traits—unusual among conifers—include vegetative sprouting (Fig. 1) from basal burls (lignotubers) and an ability to replace burned branches along the bole with new sprouts



Fig. 1. Large coast redwood tree with a fire-created basal hollow and two generations of vegetative basal sprouts. (Photo by John Stuart; reproduced with permission of the journal *Madroño*.)

from epicormic buds (Fritz, 1932; Roy, 1966). Redwood also has a remarkable mechanism for responding to flooding along alluvial terraces, where it can occur in nearly pure stands with impressively high biomass. Although redwoods may be killed by extended soil saturation following floods, well-drained alluvial deposits are often colonized by upward growth of roots from the existing root mass, and it sometimes establishes new layers of adventitious roots from the stem (Stone and Vasey, 1968; Zinke, 1977).

A second reason for the continued ambiguity on the role of disturbance is that redwood dynamics are difficult to study. The large size of old canopy trees makes it difficult to core trees with an increment borer, so good estimates of stand age structure and fire history usually must be obtained from cross-sections of stumps on cutover land. Most of the old-growth stands in private hands were already logged one or more decades ago; opportunities for new investigations of this type are limited and dwindling. Furthermore, accurate ring counts and crossdating in redwood are challenging because of the frequent occurrence of partial or missing rings (Fritz and Averill, 1924; Fritz, 1940; Waring and O'Hara, 2006) and relatively uniform (complacent) ring series (Brown and Swetnam, 1994).

The biological and cultural significance of coast redwood, a species of ancient lineage with fossil analogs that were once much more widely distributed in North America, western Europe, and Asia (Sawyer et al., 2000a), is sufficient to justify a renewed effort to study the ecology of this species. The redwood ecoregion has been identified by the World Wildlife Fund as being in the highest conservation priority class among ecoregions in the U.S. based on biological uniqueness, conservation status, and impending threats (Ricketts et al., 1999; Noss, 2000). Redwood National Park is one of 12 "natural" World Heritage Sites in the U.S. and is also an International Biosphere Reserve. It is important, therefore, to provide managers with the best available information on how the remaining old-growth redwood reserves should be managed to perpetuate the unique aspects of the redwood ecosystem. The first objective of this paper is to provide an analytical review and critical synthesis of scientific evidence on spatial and temporal variability in disturbance regimes in the redwood region prior to European settlement, and how these disturbances influenced the structure, composition, and dynamics of redwood forests. Second, we review how an alteration of disturbance regimes in modern times may affect the perpetuation of old-growth stands. Third, we highlight some of the major gaps in existing knowledge of redwood dynamics and suggest priorities and possible approaches for future research. Because of space limitations, we focus only on the types of natural disturbances common prior to European settlement and do not consider some of the more recent direct or indirect human impacts (e.g., climate change, invasive species, forest fragmentation, logging, grazing).

## 2. The redwood forest environment

Redwood is distributed in a narrow belt 900 km long along the Coast Range from central California to southern Oregon (Fig. 2). Width of the redwood zone is highly variable but is predominantly 12–32 km. The topography is characterized by hills and low mountains with rounded summits, steep slopes, and narrow canyons. Three subregions were recognized by Sawyer et al. (2000b). The northern and central subregions are underlain primarily by Franciscan sandstones, siltstones, conglomerate, and schists of Mesozoic age, while bedrock in the southern subregion is predominantly Cenozoic marine and non-marine sedimentary deposits. Redwood is found on a wide variety of soils ranging in texture from sandy loam to clay and from moderately acidic to alkaline.



Fig. 2. Natural range of coast redwood, showing the three main subregions recognized by Sawyer et al. (2000b). The southern boundary of the northern subregion is determined by the southern range limit of western hemlock. (Data and map from Save-the-Redwoods League.)

The redwood region has a Mediterranean climate, with mild, rainy winters and generally cool, dry summers. Mean daily minimum temperatures in January range from 0.4–7 °C and mean daily maximums in July range from 14–30 °C. Temperatures seldom drop below –9 °C or rise above 38 °C. Mean annual precipitation is moderate to high, generally more than 100 cm, but as low as 72 cm in some parts of the southern subregion and more than 200 cm in the northernmost part of the range (Sawyer et al., 2000b). Even in the northern subregion, only 5% of the annual precipitation falls between early June and late September (Veirs, 1982). The dry summers, however, are moderated by cool temperatures, stratus clouds, and fog. The geographical distribution of redwood, a distinctly mesophytic species, generally follows the inland extent of these coastal influences. At the northern end of the range, redwoods blanket entire hillslopes, whereas in the south, redwoods are commonly restricted to small pockets sheltered in narrow valleys, often surrounded by shrublands and grasslands.

The highly fractured sandstones of the Coast Range, combined with active tectonic motion and high rainfall, result in some of the highest erosion rates in the continental United States even under natural conditions, and the rates are further accelerated following timber harvest, grazing, and development. Erosion and deposition processes help create some of the distinctive landforms upon which the redwoods grow, such as the alluvial flats. North coast alluvial flats are flat, broad surfaces that build up vertically, primarily through sediment deposition during infrequent floods. The spatial distribution of alluvial flats and terraces is related to bedrock geology. For example, terraces along the South Fork Eel River are common in the Wildcat and Yager Formations, but are absent in the Central Belt Franciscan mélange, where earthflows impinge on the river channel (Bickner, 1984). Redwood-bearing terraces on the Smith River are located west of the Coast Range thrust fault, which separates the ultramafic rocks to the east from the Franciscan complex to the west.

On alluvial flats, coast redwood often makes up more than 90% of the stand basal area (Sawyer et al., 2000b; Busing and Fujimori,

2002). On upland slopes, redwood is usually mixed with other evergreen conifer and broadleaved species such as Douglas-fir, grand fir, western hemlock, Sitka spruce (*Picea sitchensis* (Bong.) Carr.), tanoak, madrone (*Arbutus menziesii* Pursh), and California bay (*Umbellularia californica* (Hook. & Arn.) Nutt.). In the northern subregion in the vicinity of Redwood National Park, slope forests studied by Veirs (1982) had a mean of 70 canopy trees per hectare (range of 58–97 for trees >60 cm dbh), of which 41–95% were redwood. Total stand basal areas averaged 162 m<sup>2</sup>/ha (range 107–255), with redwood making up 43–97% of the total. Coast redwood stands contain some of the highest concentrations of biomass in the world, with some alluvial stands having more than 3000 metric tons per hectare (Westman and Whittaker, 1975; Busing and Fujimori, 2005).

Coast redwoods are also considered to be the tallest living trees on Earth, attaining maximum heights of 115 m (Sawyer et al., 2000c). Because of its great height and longevity, coast redwood reliably assumes a position in the upper canopies of most redwood forests. When present, the broadleaved evergreen trees, notably *Lithocarpus*, historically formed a shorter secondary canopy or understory.

### 3. Disturbance regimes prior to European settlement

#### 3.1. Historical fire regimes and lightning fire incidence

Historical fire regimes in redwood forests have been reconstructed primarily by dating fire scars on cross-sections from stumps or fallen trees (e.g., Brown and Swetnam, 1994), and in a few cases by determining establishment dates of even-aged cohorts of trees that apparently germinated or sprouted after fires (Veirs, 1982; Stuart, 1987). These methods provide conservative estimates of fire frequency because light surface fires may not always leave detectable scars or result in the establishment of a new cohort of trees. Many fire scars detectable near ground level may not be visible on stump surfaces (Norman, 2007), which in coast redwood are often more than a meter above ground. In cases where reliable calendar years could not be assigned to each scar because of problems such as sapwood decay in older

stumps, investigators have sometimes computed the average interval between consecutive scars on individual stumps as a minimum estimate of fire frequency (e.g., Jacobs et al., 1985; Finney and Martin, 1989). Fire-history studies in redwoods are subject to additional problems because the uniform ring patterns and frequent ring anomalies in redwood make crossdating difficult (and hence the assignment of reliable calendar dates to fire years). To date, only the fire scar records of Brown and Swetnam (1994), Brown and Baxter (2003), and Norman (2007) have been analyzed with the aid of crossdating techniques, and in the latter two studies, ring uniformity and anomalies made it difficult to assign some dates with a high degree of certainty.

Several methodological approaches were used in the 12 fire-history studies summarized in Table 1. While there is variability among the fire intervals reported, a general pattern is evident in the three redwood subregions of mean fire-return intervals between 6 and 25 years for most study sites (Table 1, Fig. 3).

Evidence on fire regimes in the more extensive redwood forests of the northern subregion, however, has been more limited and subject to differing interpretations (e.g., Fisher, 1903; Fritz, 1932; Stone et al., 1969; Veirs, 1982; Brown and Swetnam, 1994). Estimated fire intervals have ranged from less than a decade to several centuries, depending on site location and whether interpretations were based primarily on fire scars (Brown and Swetnam, 1994) or age cohorts of trees (Veirs, 1982). The available studies on stump cross-sections do agree, however, on the presence of numerous fire scars, even at stump height on mesic sites (e.g., Figs. 1–11 in Veirs, 1982). At a coastal site south of the Klamath River and near a Yurok Indian village (Plot 1 in Veirs, 1982), seven stumps each had 3–7 fire scars during the period 1700–1850, with a mean interval between consecutive scars of 21 years. Longer intervals of 100–400 years between consecutive scars are common on mesic, coastal sites in the Veirs stumptop data, especially in the 11th to 17th centuries, but even in those centuries, nominal scar dates (not crossdated) among trees within a 1 ha plot are well distributed among 20-year intervals. More recent studies from partially crossdated disks in the northern subregion on sites 3–11 km from the ocean suggest mean fire intervals of 6–26 years during the 16th to 19th centuries (Brown

**Table 1**  
Mean presettlement fire-return intervals for redwood forests reported by subregions.

Location	Scars	Point methods		Area methods		Data type	Fire interval (years)	Study/composite area (ha)	Source
		Cross dating <sup>a</sup>	Ring indicators	Basal sprouts	Age class				
Northern subregion									
Del Norte and no. Humboldt Cos.	X				X	I, C	20–500	1, 9	Veirs (1982)
Del Norte Redwoods SP	X	X				C	11–26	1, 8	Norman (2007)
E. of Prairie Creek Redwoods SP	X	X	X			C	8	45	Brown and Swetnam (1994)
Humboldt Redwoods SP	X			X		C	11–44	7	Stuart (1987)
Southern Humboldt Co.	X					I	25	12	Fritz (1932)
Central subregion									
Jackson State Demons. Forest	X	X				C	6–22	4–20	Brown and Baxter (2003)
Salt Point SP	X					I, P	9–12	~200	Finney and Martin (1989)
Annadel SP	X					P	6–23	14 trees	Finney and Martin (1992)
Southern subregion									
W. Marin Co.	X	X		X		C	8–13 <sup>b</sup>	10 trees	Brown et al. (1999)
Near Muir Woods	X					I, P	22–27	75	Jacobs et al. (1985)
San Mateo Co.	X					I, P	9–16	1–3	Stephens and Fry (2005)
Big Basin Redwoods SP	X					C	~50	Variable	Greenlee (1983)

Data types are P, point (individual stumps); C, composite over a plot or study area based on exact or estimated calendar dates; I, interval (mean number of years between scars on individual stumps; approximate or exact calendar dates not known).

<sup>a</sup> Crossdating techniques utilized in the indicated studies, but precise calendar dates not always possible in every case.

<sup>b</sup> Mostly from the post-European settlement period.

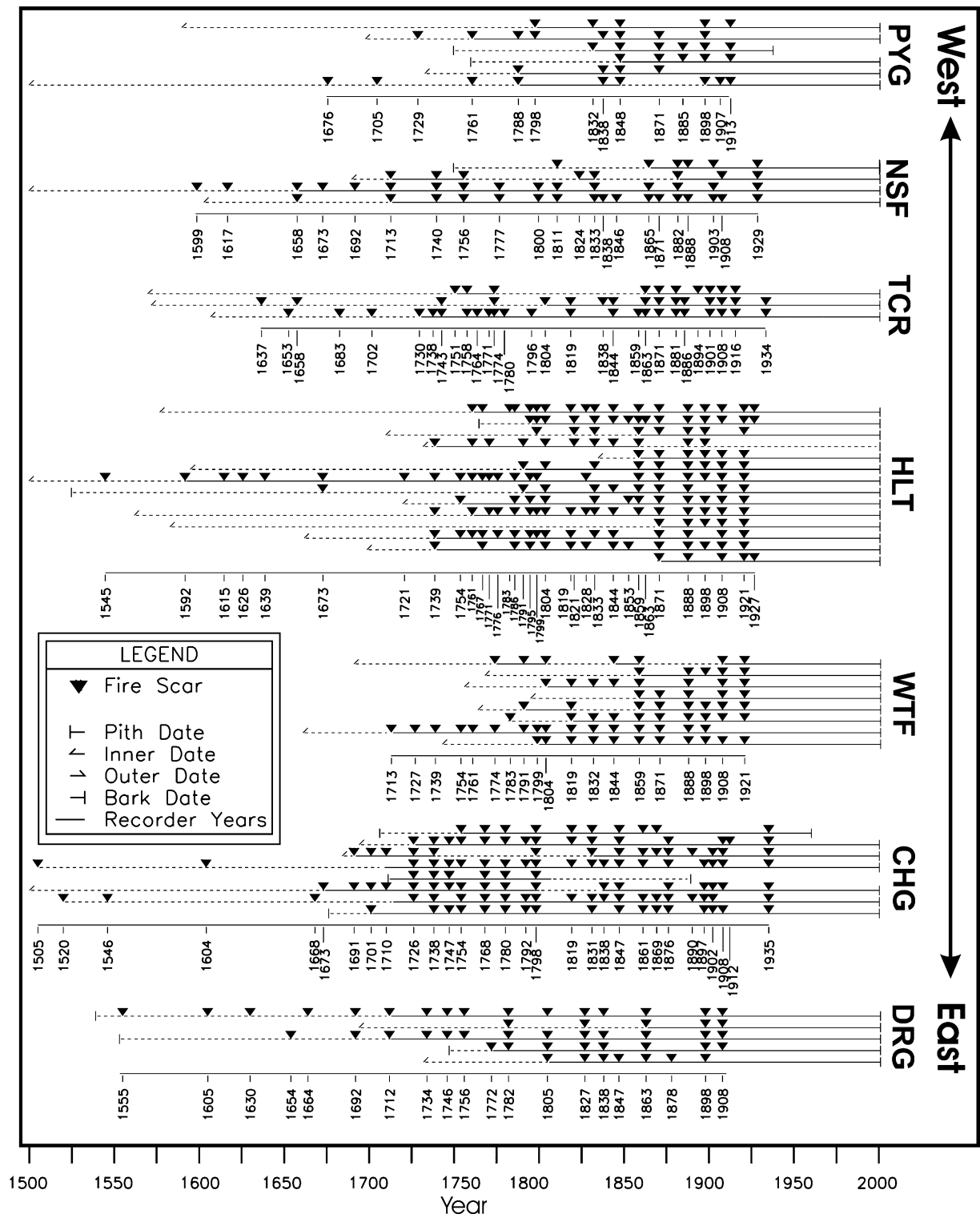


Fig. 3. A fire chronology for 7 old-growth redwood stands at the Jackson State Forest in the central subregion. Each line shows fire scar dates on an individual tree. The “West-East” gradient shown on the right side of the figure refers to a ~25 km ocean-inland gradient across which study sites were distributed. (From Brown and Baxter, 2003; reproduced with permission of the Northwest Scientific Association.)

and Swetnam, 1994; Norman, 2007). The data of Norman (2007), collected from disks cut near ground level, indicate mean fire intervals of 11–26 years across a range of sites in the watershed of Mill Creek, a tributary of the Smith River (Fig. 2).

Three predominant climatic gradients in the redwood region potentially influenced spatial variations in fire frequency: a west-east gradient of increasing summer temperature and decreasing

humidity, a north-south gradient of decreasing winter precipitation and increasing summer temperature, and a fog-mediated gradient where cool, moist conditions prevail on foggy days and warm, dry conditions prevail on fog-free days (Jacobs et al., 1985; Stuart and Stephens, 2006). However, natural gradients in fire frequency may have been overridden in some places by historical fire-use patterns of Native Americans, causing fire frequencies to

be much higher than expected in coastal regions and in upland areas surrounding streamside village sites or in areas of resource procurement (Brown and Swetnam, 1994; Norman, 2007).

Lightning is less common along the central and north coast of California than further inland, and few lightning strikes result in fires because of the dome of cool, moist air and summer fog near the coast. In a study of approximately 1,000,000 lightning strikes in California between 1985 and 2000, van Wagtendonk and Cayan (2008) reported mean densities of 3.0 lightning strikes/100 km<sup>2</sup>/year in the North Coast and Central Coast bioregions. These were only 15–23% as frequent as in the Sierra Nevada and Klamath Mountain bioregions of the state's interior (Minnich, 2006). The mean annual number of lightning fires in areas with significant redwood forests was low, ranging from 0.07 to 0.4/100 km<sup>2</sup>/year, with mean fire sizes ranging from 0.01 to 2.85 ha. Corresponding mean rotation periods for lightning fires ranged from ca. 2700 to 171,000 years in different ranger districts (Keeley, 1981). Lightning fires were most frequent and had the highest mean sizes in the northern redwood subregion.

Between 1950 and 2003, there were only three lightning-ignited fires larger than 120 ha in redwood forests (Oneal et al., 2006). The 1985 Gorda Rat and 1999 Kirk fires in the central subregion burned 2179 and 2177 ha, respectively, of redwood stands in Monterey County, and the 2003 Canoe Fire in Humboldt County burned 4468 ha of mostly old-growth redwood forest (Fire Resource and Assessment Program, 2007; Scanlon, 2007). Most fires spread as low-intensity surface fires, but dried redwood foliage ranks high in flammability characteristics compared to 12 other western conifers (Fonda et al., 1998), and even fires with low flame heights can climb up redwood bark and reach the crowns, leading to “torching” in some trees (Scanlon, 2007).

Although lightning strikes in redwood forests are normally associated with humid weather conditions that are not conducive to the spread of large fires, a small fire smoldering for weeks or months could erupt after a shift toward drier, windy conditions on a later date, as happened in the central and southern subregions after dry lightning strikes in June 2008. For fires of all causes, Gripp (1976) found that 89% of fires larger than 120 ha in the northern subregion between 1955 and 1974 were associated with three synoptic weather patterns: Pacific High (Postfrontal) type, Great Basin High type, and the Subtropical High Aloft pattern. Dry east winds (föhn winds) are produced by the Pacific High and Great Basin High types, while abnormally high temperatures and low humidity characterize the Subtropical High Aloft pattern.

The majority of fires prior to 1850 were probably ignited by Native Americans, assuming that the lightning regime over the past several hundred years is similar to that of recent times. Native Americans regularly used fire to clear vegetation near their villages and along travel routes, to culture plants for food and basketry materials, to improve game populations, and for other domestic and cultural reasons (Lewis, 1993; Keter, 1995; Anderson, 2006). Annual or nearly annual burning occurred closest to villages and in areas used for agriculture and the culture of acorns in tanoak and oak groves, with increasingly longer fire intervals further away in moist conifer forests (Vale, 2002; Anderson, 2006; Stuart and Stephens, 2006).

### 3.2. Historical windstorm frequency and severity

Severe wind events result from the passage of mid-latitude cyclones that form annually over the North Pacific between October and March. According to NOAA climatological data for Eureka, California, peak wind gusts over 100 km/h have occurred during each month from November to April over the course of an 83-year period. Northern California tends to be south of most of the storm centers and there is latitudinal reduction in peak wind

speeds from north to south through the redwood range. This latitudinal disturbance gradient was evident in the exceptionally severe 1962 Columbus Day storm (Lynott and Cramer, 1966).

In a study on the effects of three severe windstorms on partially logged old-growth stands, Boe (1966) found that trees on the leeward sides of harvest units and the leeward side of a low ridge were most susceptible to failure. Uprooted redwoods were four times as common as snapped trees in his study. Forty-one percent of snapped redwoods had evidence of internal decay, compared to only 10% of uprooted trees. As internal decay in redwoods is often associated with past fires (Fritz, 1932), fire regimes may alter the proportion of snapped versus uprooted trees in a stand. Severe winter storms contribute to the complexity of redwood canopies by snapping tops and branches. This episodic disturbance leads to reiterative growth of new leaders and provides a distinctive habitat for flora and fauna of the redwood forest (Sawyer et al., 2000c; Sillett and Van Pelt, 2000).

Compared to other temperate forests in North America, catastrophic windthrow has been uncommon in closed-canopy, old-growth redwood forests during the 20th century, which is somewhat surprising given the great height and relatively shallow root systems of redwood trees. Few redwoods were killed in the closed forests of Jedediah Smith State Park during the severe Columbus Day storm of 1962, and the majority of the fallen trees were either Douglas-fir or redwood that toppled because Douglas-fir fell into them (Sturgeon, 1964). Within the boundaries of parks and reserves, no windstorms during the 20th century appear to have caused massive windthrow leading to the establishment of young, even-aged cohorts over several hectares or tens of hectares (collective observations of present authorship team). Old-growth redwoods likewise appeared to have had a low incidence of severe windthrow in the late 19th century. Fisher (1903, p. 16) noted that “when a strong wind follows a long rainy season, redwoods exposed on high ridges may sometimes be blown down, but no considerable tracts of forest are ever overthrown.”

### 3.3. Historical flood frequency and severity

Floods in north-coastal California are caused by regional storms during winter months generated as the North Pacific High and jet streams shift southward. The heaviest rainfall events on the West Coast occur when the mid-latitude jet stream dips down into the subtropics and entrains warm, moisture-rich air. Highest precipitation occurs when a large, slow-moving storm with subtropical moisture runs into a mountain range perpendicularly.

Inter-annual variations in climate are linked to the El Niño/South Oscillation phenomenon. Annual flood peaks in coastal rivers at the northern portion of the redwood range are significantly smaller during El Niño conditions; south of 35°N latitude, floods are significantly larger during an El Niño phase (Andrews et al., 2004). Major regional storms before settlement were at least as intense as those in recent decades (Harden, 1995).

The long-term (10,000 years) flood history of coastal California has been inferred through analysis of tree rings, pollen and plant fossils, radio-isotopes, and floodplain stratigraphy (Malamud-Roam et al., 2006). Early Holocene climate was marked by rising temperatures and reduced moisture, culminating in a severe dry interval about 5000–7000 years ago. This was followed by a cooler, moister period, with wet winters along the coast. During the last 2000 years there has been a general drying trend throughout California, and the period of A.D. 950–1150 was very dry. In contrast, the Little Ice Age (A.D. 1450–1800) was unusually cool and wet. Floodplain sediments in the Sacramento River basin provide evidence that very large floods occurred as many as 10 times during the last 600 years (Malamud-Roam et al., 2006), and such floods would likely have occurred along coastal rivers as well.

A range in flood frequency and patterns of flood deposits over thousands of years can be discerned through studies of floodplain stratigraphy. For example, in the Tall Trees Grove in Redwood National Park, about 1.2 m of silt and sand were deposited by a minimum of seven floods over 810 years and about 3.2 m of sediment was deposited by 12 floods during the last 3520 years (Fig. 4). In Rockefeller Grove in lower Bull Creek, 15 flood deposits totaling almost 9 m deep were deposited over a 1000-year period, averaging 59 cm of deposition every 67 years (Zinke, 1981). A single flood event can deposit more than 1.5 m of sediment (Zinke et al., 1996). Along Pfeiffer-Redwood Creek, at the southern end of the redwood's range, measurements covering a 600-year period point to a minimum recurrence interval of flooding of once every 140 years (Evarts and Popper, 2001).

Flood deposits can often have a positive effect on both health of mature redwoods and establishment of new regeneration. Typically, overbank deposits are dominated by silt-sized sediment, with small amounts of fine sand and clay. The topmost layers tend to be finer than those lower in the soil column, and usually there is a larger proportion of sand in deposits near the stream and less sand inside the alluvial flat. The probability of overbank flooding decreases as the floodplain level rises following floods, so the probability of fresh mineral deposits being available for redwood seed germination decreases with time unless the channel bed fills in at the same rate. Alternatively, massive floods occasionally can act as stand-replacement events. In Cuneo Creek, a tributary of Bull Creek, Stone and Vasey (1968) found that up to 26 m of sand and gravel were deposited about 9500 years ago, which may have destroyed much of the existing stand at the time (Zinke, 1977). To date, there have not been studies relating depositional characteristics with specific watershed attributes.

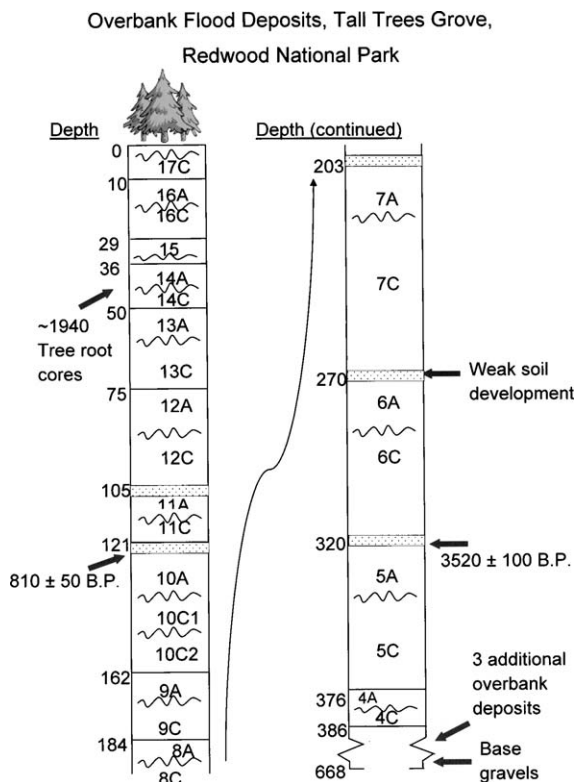


Fig. 4. Stratigraphy of an alluvial flat in Redwood National and State Parks showing thick overbank deposits in the older (lower elevation) section of the sediment column, and thinner, younger deposits near the surface of the flat. Seventeen flood events are represented in this soil column. Depths are shown in cm. (D.K. Hagans, unpublished data, Redwood National and State Parks.)

Along the channel margins of north-coastal rivers, alders (*Alnus rhombifolia*, *A. rubra* Bong.) commonly colonize fresh flood deposits during mudflows. If the channel bed is not further mobilized by floods, the alder stands develop and begin to trap fine sediment and organic debris. Further growth of riparian trees can stabilize stream banks and protect them from erosion (Lisle, 1989), thus helping to preserve the alluvial flats.

#### 3.4. Historical incidence of landslides

Mass movement processes, both slow-moving and rapid, are common in the Coast Ranges, but redwood stands are exposed to different types of landslides in the various terrains. About 30% of the Redwood Creek landscape in the northern subregion shows evidence of earthflows or other mass movement features (Harden et al., 1995), which occur primarily in highly sheared Franciscan mélange, a unit within the Franciscan complex. Because they typically move 0.3–15.3 m/year, and their gooey silt- and clay-rich soils dry out severely in the summer, they are commonly unforested. In contrast, forested earthflows have slower movement rates, which allow redwood trees to grow on their surfaces, as are common on schist hillslopes in Redwood National Park.

On harder sandstones and siltstones, rapid mass movements, such as debris slides, mudflows and debris flows, are well documented. The northern and central Coast Ranges have many colluvial-filled bedrock hollows, which periodically evacuate during large storms through debris avalanches. After evacuation, they slowly refill through soil creep and can remain stable for more than 7000 years. Colluvial hollows cover an estimated 20% of greywacke and shale slopes (Marron, 1982), which reflects the importance of debris avalanching in the erosional development of these slopes. Because redwood stands in the southern part of the redwood range tend to be clustered in narrow stream channels, they are especially vulnerable to debris avalanches and flows. Steep, inner gorge hillslopes adjacent to larger streams are also especially susceptible to debris slides and avalanches (Marron, 1982). Limited pollen dating suggests high landslide activity between 11,000 and 14,500 years B.P., and increased landslide activity is associated with wetter climatic periods (Muhs et al., 1987). Debris slide frequency in coastal California increases during periods of high-intensity storms, such as occurred in the late 1930s (Reid, 1998a).

California is riddled with faults, and the Coast Ranges have frequent earthquakes. In January, a 1700 magnitude 9+ earthquake occurred in the western U.S. from Washington to northern California along the Cascadia subduction zone (Atwater et al., 2005). Increased overbank deposition at that time has been documented in the Navarro River basin (Constantine et al., 2005). Although earthquake-induced landslides are well documented in southern and central California (Muhs et al., 1987), the spatial and temporal distributions of such landslides in the northern Coast Ranges are presently unknown.

## 4. Structure and dynamics of old-growth stands

### 4.1. Age and size distributions

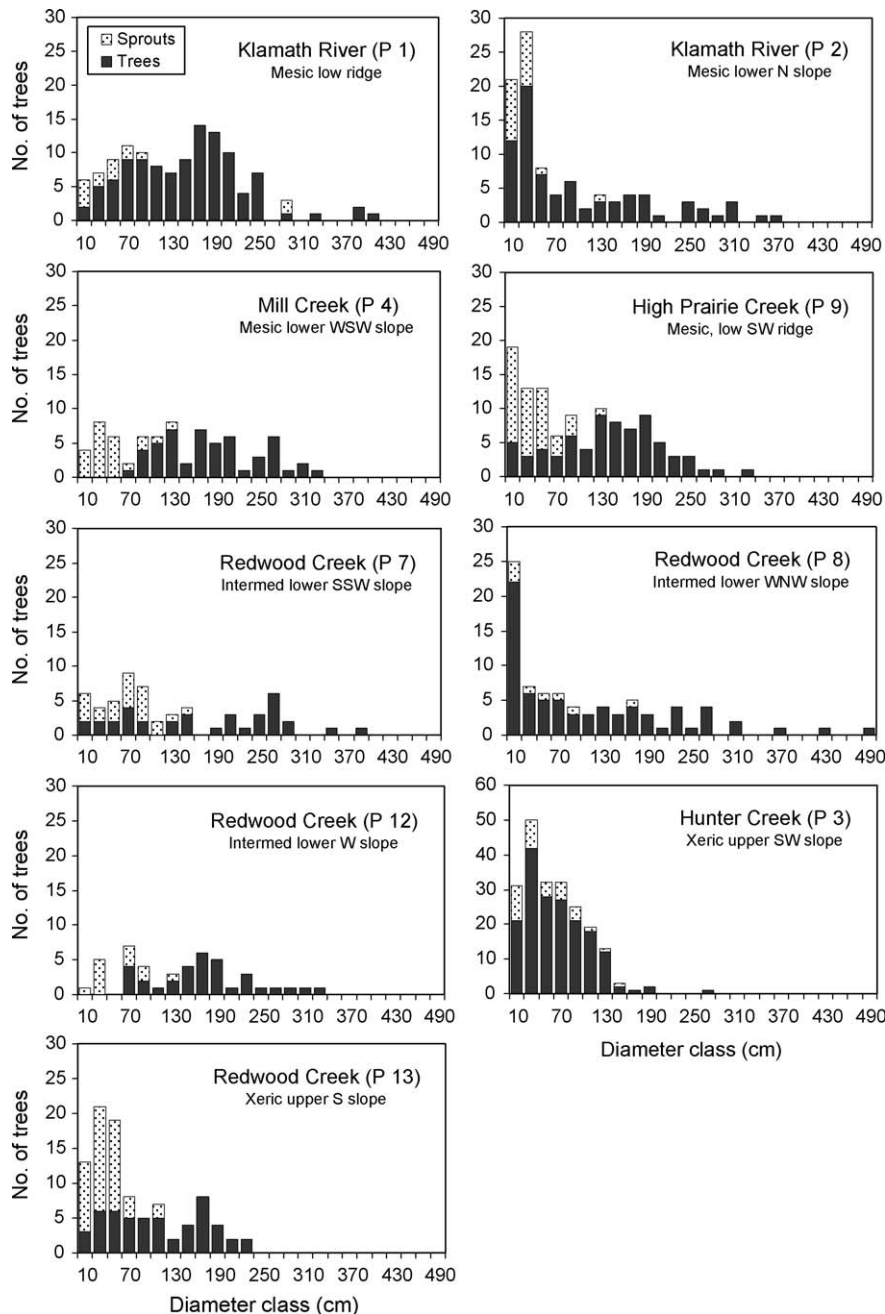
The general import of the evidence reviewed above on presettlement disturbance frequency is that intervals between major stand-replacing events appear to have been long in coast redwood forests except possibly for landslides in some locations where unstable soils are situated on steep slopes bordering rivers and streams. Given the prevailing regime of mostly low- to moderate-severity disturbance and the shade tolerance of redwood, one would expect old-growth redwood forests to be predominantly uneven-aged, a property noted but not documented as early as Fisher (1903).

Systematic data on age and size distributions are limited to two studies by Fritz (1929) and Veirs (1982) based on field counts of rings on stumps in cutover old-growth stands. Fritz (1929) reported ring counts from >630 stumps on a 12 ha plot near the Eel River in the central subregion. Veirs (1982) examined stumps on nine 1-ha plots distributed on a variety of near-coastal, intermediate, and xeric slope forests in the vicinity of Redwood National Park in the northern subregion. The investigators in both cases reported highly uneven-aged stands, with the range of ages exceeding 1000 years. In the study of Veirs (1982), the mean age of trees more than 200 year old (i.e., those in the canopy layer) was 549 years, and 7% of the canopy trees were >1000 years old. Corresponding mean and maximum redwood diameters were 158 and 488 cm, respectively. Busing and Fujimori (2002) came to similar conclusions about redwood longevity (6–12% of trees

>10 cm dbh surviving to age 1000 years) based on observed mortality rates on a large permanent plot on an alluvial site.

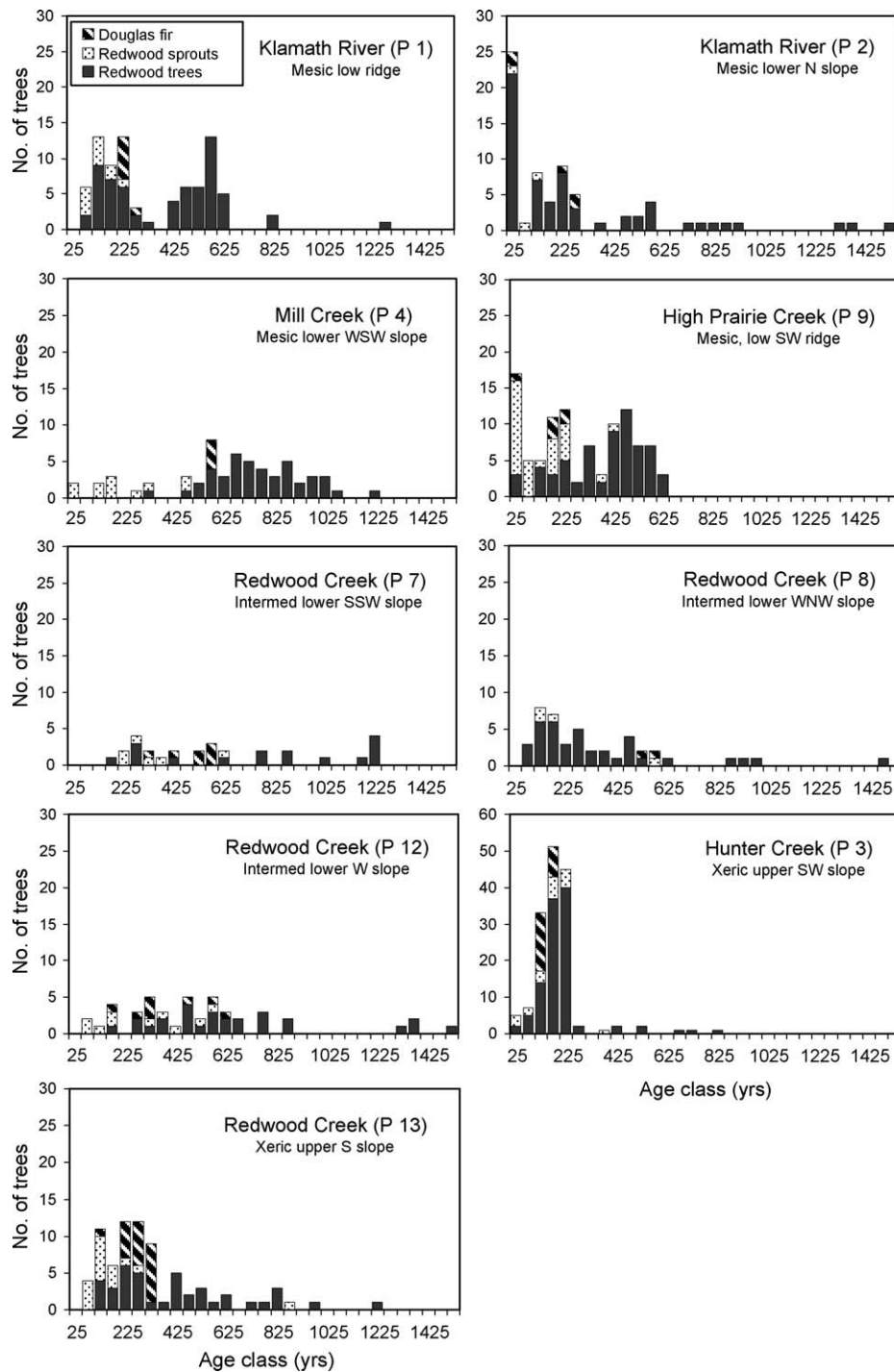
As in most tree species, redwood diameter–age relationships reveal considerable scatter; trees 200 cm dbh can vary in age from 400 to 1200 years (Veirs, 1982). At the same time, however, there is a clear and significant relationship between diameter and age in uneven-aged stands (mean  $r^2$  among stands = 0.67; Veirs, 1982). The shapes of size distributions resemble the corresponding age distributions except that peak age classes are represented by broader size class peaks (Figs. 5 and 6), a consequence of the wide range of sizes for trees of a given age class.

In spite of the broad range of ages on most plots, only 2 or 3 of the 9 plots in the Veirs (1982) study had size or age distributions approximating a negative exponential or rotated sigmoid curve, which are often found in uneven-aged, old-growth forests where



**Fig. 5.** Size distributions (midpoints of 20 cm diameter classes) of redwood trees and redwood sprouts on nine 1-ha plots in old-growth stands in the vicinity of Redwood National Park, northern subregion. P1–P13 correspond to plot numbers in Veirs (1982). Note different scale for Plot 3. (Plotted from the original field data of Veirs, 1982.)





**Fig. 6.** Age distributions (midpoints of 50-year classes) of redwood and Douglas-fir for the nine 1-ha stands shown in Fig. 5. On each stump, rings were counted on the clearest radius with the widest rings to reduce problems caused by partial rings. About 30% of the stumps could not be aged because of internal decay or damage from logging, but this percentage was similar among small, medium, and large trees. (Plotted from the original field data of Veirs, 1982.)

most disturbances are small treefall gaps (e.g., Rebertus and Veblen, 1993; Goodburn and Lorimer, 1999; Busing and Fujimori, 2002; Antos and Parish, 2002). The remainder of the Veirs plots had highly irregular, unimodal, or bimodal distributions with varying degrees of skewness (Fig. 6). The mesic, near-coastal sites had the greatest departure from the negative exponential form, with 3 of the 4 plots having strongly unimodal or bimodal age distributions. Population dynamics of species with great longevity and limited recruitment have not been extensively studied, and so demographic trends in the absence of major disturbance are not well

known. However, a stable population would likely require at least a shallowly descending age distribution to compensate for mortality, as appears to be the case in a number of the Veirs plots (Fig. 6). Busing and Fujimori (2002) documented that mean annual rates of redwood ingrowth and mortality were equal (each 0.29%) over a period of three decades in an old-growth stand with a descending monotonic size distribution.

Irregular age distributions on upland sites could have various causes, including natural disturbance, climatic shifts, and limited sample sizes. Direct evidence of moderate disturbance, however,

was present on all of the study areas of Veirs (1982) and was probably a significant factor in shaping the irregular age distributions. He found that most plots contained one to several age cohorts of Douglas-fir (Fig. 6), a species normally dependent on fire-created openings for successful canopy recruitment. Direct evidence of fire, such as fire scars or burned-out snags and hollow shells, was also present on all plots. Periodic landslides may have occurred on some sites, especially the steep, unstable slopes above Redwood Creek (Stone et al., 1969). But if landslides affected the study sites, they were not severe, stand-replacement events on the plots themselves (note the broad range of ages in Fig. 6 on Plots 7, 8, 12, 13, all on slopes above Redwood Creek).

Although there is little evidence of catastrophic natural disturbance in upland redwood stands in the past century, in a few places there are sizable stands of “older mature” but not ancient forest on rather mesic, maritime sites that were not logged (e.g., the extensive mature redwood-Douglas-fir forests at West Ridge in Prairie Creek Redwoods State Park and similar stands in the central Headwaters Forest Preserve; C.G. Lorimer and S.P. Norman, personal observations; see also Plot 3 in Fig. 6 in this paper). The paucity of large trees suggest that these sites may have experienced episodes of severe fire or winds, or some other abrupt change in the disturbance regime, a century or so prior to European settlement.

#### 4.2. Understory dynamics and canopy recruitment

In some parts of its range, coast redwood trees produce copious amounts of seed in nearly every year. Germination rates are low, in part because of a prevalence of empty seeds and fungal attack (Olson et al., 1990), but many seedlings in spring and early summer may be found in forest litter, on mineral soil, and on logs. However, most are killed before autumn by desiccation or damping-off fungi (Davidson, 1971). Virtually all redwood seedlings germinating on forest floor litter fail (Davidson, 1971).

Because of the affinity of coast redwood for mineral soil seedbeds, the frequent surface fires evident in the tree-ring record may have had some benefit to redwood seedling establishment, but direct contemporary evidence of enhanced redwood seedling establishment after fire is lacking. In fact, 5 years after the lightning-caused Canoe Fire, which burned >4000 ha in mostly old-growth forest, Douglas-fir regeneration was abundant but few redwood seedlings were present (S.P. Norman, personal observations). Based on evidence from forest age structure, fires sometimes aided the establishment of competing shade-tolerant conifers such as western hemlock and grand fir (Veirs, 1982). At the same time, however, recurrent fires also generally prevented these fire-sensitive species from living long enough to comprise a significant proportion of the canopy on upland sites (Veirs, 1982).

On alluvial sites, periodic floods provide excellent mineral soil seedbeds for redwood seedling establishment, although mortality in subsequent years can be high (Becking, 1996). Flooding also reduces populations of competing species such as tanoak (Stone and Vasey, 1968). For these reasons, alluvial flats generally have many more redwood seedlings and saplings than upland slope sites. For example, on an alluvial site at Bull Creek in the central subregion, Busing and Fujimori (2002) reported redwood seedling and sapling densities of 537/ha (>0.1 m tall and <10 cm dbh), which was higher than all other species combined.

In the absence of fire in upland old-growth forests, successful establishment of new redwood seedlings may be dependent upon small soil disturbances, such as root-wad mounds and gravity-induced soil movement on slopes, as well as fallen logs, to provide suitable seedbeds. Canopy gaps of various ages have been reported to occupy 13–27% of the land area in various old-growth stands, with uprooting more common than bole snap (Hunter and Parker,

1993; Busing and Fujimori, 2002). Hunter and Parker (1993) found that 43% of the total gap area was caused by slope failures, especially on steep, concave slopes. These slope failures were small or localized, averaging 751 m<sup>2</sup> in area (range 79–3437 m<sup>2</sup>).

Naturally fallen logs, which cover up to 10–20% of the forest floor on upland sites, may offer another important substrate for conifer seedling establishment (Bingham, 1984; Bingham and Sawyer, 1988; Porter, 2002). In the Pacific Northwest, logs serve as water reservoirs in forests that experience a summer dry period (Harmon and Cromack, 1987; Gray and Spies, 1995) and offer more stable moisture regimes for drought-sensitive seedlings (Marra and Edmonds, 1994). At two old-growth slope sites in the northern subregion, redwood seedlings, saplings, and taller understory trees (heights of 5 cm to 15 m+) on logs had mean densities ranging from 6–44/ha, accounting for 35–74% of the total number of redwood recruits in these size classes (Bingham, 1984; Porter, 2002). Redwood understory trees established on woody debris are often large and vigorous (>6 m tall). However, the frequency with which saplings on logs establish root systems in mineral soil and successfully reach the canopy is not presently known.

Redwood seedlings and saplings grow slowly in the shaded understory, but once established, they have a remarkable capacity to persist. These young trees are often damaged by falling debris, tipped over or suppressed to the point of leader dieback, only to sprout new upright leaders from dormant buds in their burl or lower stem. Even 2-year-old seedlings will sprout after injury (Finney, 1993). Although redwood sprouting is generally reduced in older stems (Boe, 1965; Powers and Wiant, 1970), an unusual trait is that trees of virtually any size and age can sprout. Sprouting from burl or other dormant buds in redwood stems is important in maintaining or improving competitive status of redwood on sites where high fire frequency or intensity would otherwise eliminate non-sprouting, slow growing trees and other woody plants (Rydellius and Libby, 1993).

Repeated burning and sprouting can result in groups of sprouts around the remains of one or more predecessor stems, a sprout clone of the original seed origin individual (Roy, 1966). Although many sprouts do not attain canopy status while the parent stem is still alive, some sprouts apparently can reach the canopy if the parent stem snaps off. On three upland sites, Stuart (1987) traced the origin of large basal sprouts on living redwood trees to historically documented fires. The frequency of basal sprouting following bole breakage on standing, single-stemmed trees or partial uprooting of trees during normal gap dynamics has not been investigated. But this potentially could be a significant factor in maintaining redwood dominance in old-growth stands, given the observed high frequency of stump sprouting after logging of old-growth stands. Neal (1967) reported a sprouting frequency of 93% for stumps smaller than 90 cm in diameter and 44% for stumps of the largest size class (>295 cm diameter).

Age distributions of upland old-growth stands in the northern subregion indicate that redwood usually does not have more than about 15 trees per hectare in each of the several youngest 50-year age classes (Fig. 6). But dense populations of redwood saplings may not be necessary to ensure replacement of existing canopy trees. If the stands with descending age distributions in the Veirs (1982) data set represent reasonably stable populations, they would require only 10–20 trees per hectare to cross the minimum size or age threshold for canopy status (60 cm or 200 years) in each century to maintain the existing level of redwood dominance. Bingham (1984) and Porter (2002) found that total redwood recruits in the sapling and understory tree classes (0.5–15 m+ tall) in that region averaged 13–44/ha, including those on fallen logs. Because of uncertainties about the long-term success of seedlings on fallen logs, it is unclear if this level of recruitment is adequate to sustain current levels of redwood canopy dominance.

#### 4.3. Stand development after major disturbances

Some redwood stands in presettlement times were probably occasionally affected by severe events that killed most of the existing trees over at least limited areas, although field evidence is scanty. Most of our knowledge of stand development after stand-replacement events comes from observations following logging. These observations suggest that vegetation development after severe events is often strongly shaped by vegetative sprouting of redwood and associated hardwoods.

Pre-disturbance tree densities may be low in old redwood stands (e.g., 60 trees/ha), and so the spatial arrangement of sprout regeneration may be highly aggregated. Redwood sprouts grow very rapidly in full sunlight and typically outgrow other species (Waring and O'Hara, 2008). Seedling-origin redwoods are capable of rapid growth, but an initial delay in establishment and slow early growth makes them less competitive. Tanoak sprouts and Douglas-fir seedlings have rapid initial growth rates similar to those of redwood sprouts (Wensel and Krumland, 1986). During the stand initiation phase, Douglas-fir seedlings can be overtopped by tanoak sprouts, but the sustained height growth of Douglas-fir will often cause it to emerge through a tanoak overstory and eventually overtop the tanoak (Hunter and Barbour, 2001; Sawyer, 2007). By age 10–20 years, tanoak sprouts also begin to fall behind redwood sprouts and will usually then lapse into the understory (Fig. 7). Broadleaves such as Pacific madrone, red alder, and bigleaf maple (*Acer macrophyllum* Pursh) have slower growth rates than redwood sprouts and like tanoak, are generally relegated to subordinate positions, where they may die back and resprout in response to competition or disturbance such as fire (Waring and O'Hara, 2008).

The occurrence of one or more fires soon after canopy removal can alter competitive relationships by killing seedlings of Douglas-fir and most other conifers. Vigorous sprouts from the burned redwood seedlings or saplings, however, begin growth earlier and grow much faster than the new cohorts of Douglas-fir and other conifer seedlings. Thus, fires during the regeneration phase of a stand can shift the competitive advantage among species from newly established seedlings to sprouting redwoods with established root systems (Rydelius and Libby, 1993).

Less severe disturbances with residual canopy cover result in fewer sprout clumps and reduced sprout growth in redwood and other species. At light intensities lower than approximately 30%, height growth is marginal, and the long-term survival of redwood sprouts is questionable despite their relatively high tolerance to shade (O'Hara et al., 2007).

Rapid growth of redwood and Douglas-fir during the first 150 years of stand development results in a steep decline in stand density from self-thinning of both sprouts and seedling-origin

trees. Reineke (1933) described maximum stand densities of 7400 trees/ha at a mean stand diameter of 12.5 cm dbh, 2500 trees/ha at 25 cm dbh, or 870 trees/ha at 50 cm dbh. In an unmanaged even-aged stand in Mendocino County, redwood density declined from 642 to 268 trees/ha from age 65 to 137 years, while quadratic mean diameter increased from 50 to 97 cm (Allen et al., 1996). Despite the fast growth and rapid self-thinning of even-aged redwoods, this older second-growth stand still had more than three times the density of typical old-growth stands.

## 5. Disturbance regimes in modern times

### 5.1. Current fire regimes

Fire has become substantially less common in most redwood forests in recent decades compared to the period prior to about 1930 (Brown and Baxter, 2003). In contrast to most of western North America, this reduction is thought to reflect reduced human ignitions (Stuart and Stephens, 2006), rather than changes in climate or fire suppression (e.g., Agee, 1993; Westerling et al., 2006).

Oneal et al. (2006) analyzed large fires that burned in the redwood region since 1950 and demonstrated that fire rotations were longer in the northern part of the range (1083 years) than in the central (717 years) or the southern regions (551 years). Fire rotation periods averaged 3309 years on flat terrain and 423 years on steep terrain, but they found no difference between south and north aspects. Fire rotations decreased from the lowest elevation class (1841 years) to the highest class (53 years). There was no consistent trend in fire rotations in zones starting near the coast and moving up to 50 km inland, apparently because of variability induced by the presence of low elevation forests on flat terrain extending along inland streams and rivers. Areas with a high ratio of annual potential evapotranspiration to annual precipitation had shorter fire rotations (117 years) than the wettest sites (1183 years).

Recent fire management has been generally successful at suppressing wildfires in the coast redwood forest, in part because burning conditions are not as severe as in the drier forests to the east. For example, since 1960, only four large fires occurred in redwood forests of the northern subregion, ranging from 1300–4500 ha in size.

In contrast to some other regions of the western U.S., little evidence is currently available on the effects of fire exclusion in redwood forests on litter and duff loading or on potential fire behavior. However, in a study of litter accretion and decomposition for coastal and inland old-growth redwood forests in Humboldt County, Pillers and Stuart (1993) found that litter would reach its equilibrium loading in 12–25 years. This equilibrium loading time is similar to fire-return intervals prior to fire exclusion, suggesting

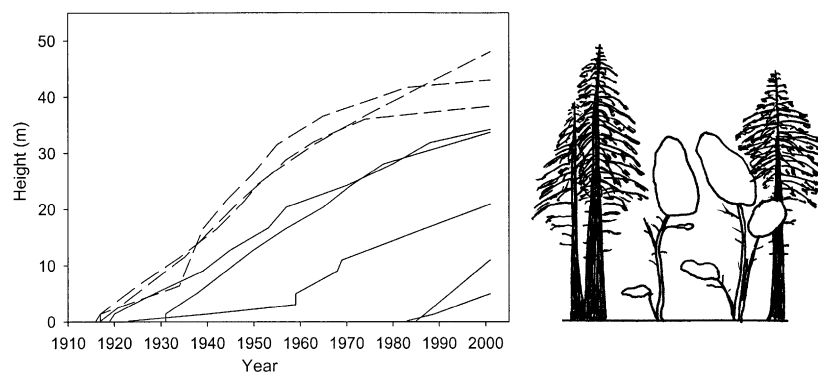


Fig. 7. Stand development and a schematic diagram of representative second-growth redwood (dashed lines) and tanoak trees (solid lines) growing adjacent to each other. Mendocino County, central subregion. (Adapted from Waring and O'Hara, 2008.)

that fire exclusion on that site may not have resulted in greater litter loads. They also found that moist coastal forests reached equilibrium sooner than drier interior forests and that there was a straight-line relationship of litter decomposition to summer average relative humidity ( $r^2 = 0.99$ ).

Larger dead and live fuel loads, on the other hand, have likely increased during the fire exclusion era, although the potential effects on fire behavior are uncertain. Fire behavior reports from the California Department of Forestry and Fire Protection during the 2003 Canoe Fire indicated relatively short flame lengths in litter but apparently long residence times at the bases of large trees (Scanlon, 2007). Almost all of the mortality of old-growth redwood trees was associated with surface fires enlarging basal hollows, which led to reduced structural support and stem breakage. Douglas-fir trees of all sizes were killed due to long fire residence times in bark and litter mounds at their bases (Y. Valachovic, Univ. of California, Cooperative Extension, personal communication, 2007).

Effects of fire exclusion on vegetation dynamics have not been formally studied in the redwood region, despite early predictions about successional replacement of redwood by other shade-tolerant species (e.g., Stone et al., 1969). Many stands contain numerous and sizable redwood understory trees (Fig. 5) which, barring the introduction of devastating pests or pathogens, will help perpetuate redwood dominance for centuries to come. Most of the competing species are shorter in stature and have shorter life spans than redwood. Western hemlock, for example, has a maximum life span of 300–500 years; tanoak probably did not often exceed 250 years of age (Veirs, 1982; Burns and Honkala, 1990) and is currently threatened by an exotic pathogen (Maloney et al., 2005). The southern and central subregions are outside the current range limits of western hemlock. It is also possible that the sprouting ability of redwood seedlings and saplings, even in the absence of fire, may result in low mortality rates that could compensate for low redwood seedling recruitment.

Despite these considerations, the dynamics of competition and canopy recruitment of these species are poorly known and should be investigated further. Many redwood subcanopy trees could be legacies from earlier fire or climatic regimes. Subcanopy redwoods 30 cm dbh, for example, have mean ages of 80–140 years on various slope sites in the northern subregion (Veirs, 1982), with estimated establishment dates in the mid-19th to early 20th centuries. No studies are available on historic changes in understory trees of redwood or competing species in the absence of fire. Even with shorter life expectancies and more frequent turnover, competitor species could still substantially increase their abundance in the forest canopy. In parts of the northern subregion where redwood is heavily dominant in the overstory and western hemlock is abundant in the understory, hemlocks in some cases already have successfully captured canopy space vacated by mortality of large redwoods (Fig. 8). The future trajectory for these young hemlock canopy trees is unclear and will depend on inherent age-mortality relationships.

## 5.2. Effects of altered flooding and erosion patterns

Timber harvest and road construction can alter downstream redwood forest dynamics through increased erosion, sedimentation, and altered flood regimes. However, the effects of timber harvest and road construction on increasing flood peaks is controversial, and several studies in the Pacific Northwest show contradictory results. Land-use activities increase the magnitude of small flood peaks through the effects of clearcuts on evapotranspiration and interception, and the integration of road drainage with natural drainage networks (Jones and Grant, 1996; Ziemer, 1998; Reid and Lewis, 2005). Nevertheless, the sample size of large floods (>10-year return period) is too small to detect the



**Fig. 8.** Effects of fire exclusion on the future composition of redwood stands are not well known. In this stand with a dense understory of western hemlock, deaths of several large redwoods in recent decades (note redwood snag in middle ground left of center) have allowed a number of hemlocks (center and right) to attain canopy status. (Jedediah Smith Redwoods State Park, northern subregion. Photo by Craig Lorimer.)

effects of timber harvest on large floods by statistical methods, and increases in peak flow in clearcut basins were not detected for flows with a 2-year return interval or greater (Thomas and Megahan, 1998; Ziemer et al., 1996).

Even without an increase in flood magnitude, however, the frequency of flooding on alluvial flats may change, depending on the nature of channel adjustments. For example, where channel aggradation reduces the flood capacity of river channels, flood frequency increases. Channel aggradation at Freshwater Creek in Humboldt County has reduced the capacity to convey the bankfull discharge by about 34%, and flood frequencies have generally doubled (Reid, 1998b). Lisle (1981) documented channel-bed aggradation of 1–4 m in nine north-coastal rivers during the 1964 flood, which persisted five to 15 years before declining to stable bed levels.

In contrast to the mixed evidence of land-use changes on flood frequency and magnitude, it is well established that land-use changes have increased erosion rates and sediment yields. Landslide frequency has increased in harvested and roaded areas (Harden et al., 1995; Montgomery et al., 2000). About 80% of the debris slide mass in Redwood Creek from 1954–1981 was associated with roads or timber harvest units (Pitlick, 1995). Debris slides increased tenfold in the past 50–150 years in Lone Tree Creek, Marin County, which corresponds to the introduction of grazing and grassland conversion in the area (Lehre, 1982). In addition to increased landslide frequency, debris flows tend to travel farther down channels in logged areas because the absence of riparian trees and down wood increases the momentum of the debris flow (Lancaster et al., 2003). Overbank deposition on a redwood-forested floodplain

in the Navarro River basin increased greatly after logging events in 1850 and 1931 (Constantine et al., 2005).

Accelerated bank erosion and deposition in channels and on floodplains are common responses to increased sediment production in redwood-dominated watersheds. For example, the channel of Redwood Creek in Redwood National Park locally filled more than 4.5 m since 1936 (Nolan and Marron, 1995), and the volume of sediment stored on the valley floor increased by almost 1.5 times over 1947 levels (Madej, 1995). In this watershed, elevated streambeds persisted for decades (Madej and Ozaki, 1996). Accelerated erosion rates and channel filling may cause flood deposits to contain coarser gravel instead of silt, affecting soil moisture retention of floodplain soils and burying streamside trees with gravel (Fig. 9A). A storm in 1955 initiated many landslides on recently logged slopes in upper Bull Creek in the South Fork Eel River watershed. The resulting sediment pulse decreased channel

capacity by aggrading the river channel up to 5 m and large log jams formed. The transport of logs and sediment induced bank erosion downstream, and more than 400 old-growth trees in Rockefeller Grove were toppled (Lowdermilk, 1962). Channel widths in Bull Creek that were about 20 m before the 1955 storm were estimated to be about 100 m after the storm (Smith and Sutherland, 2006). Combined aggradation from floods in 1955 and 1964 deposited at least 7 m of fill at the nearby Cuneo Creek Bridge (Short, 1993; Smith, 2004).

As channels aggrade, the local water table can be raised (Fig. 9C). The surface water level in Redwood Creek is closely related to the water table measured in adjacent alluvial flats (McFadden, 1983). Consequently an increase in channel surface water level can inundate the root zone in the alluvial flats, to the detriment of redwoods growing there.

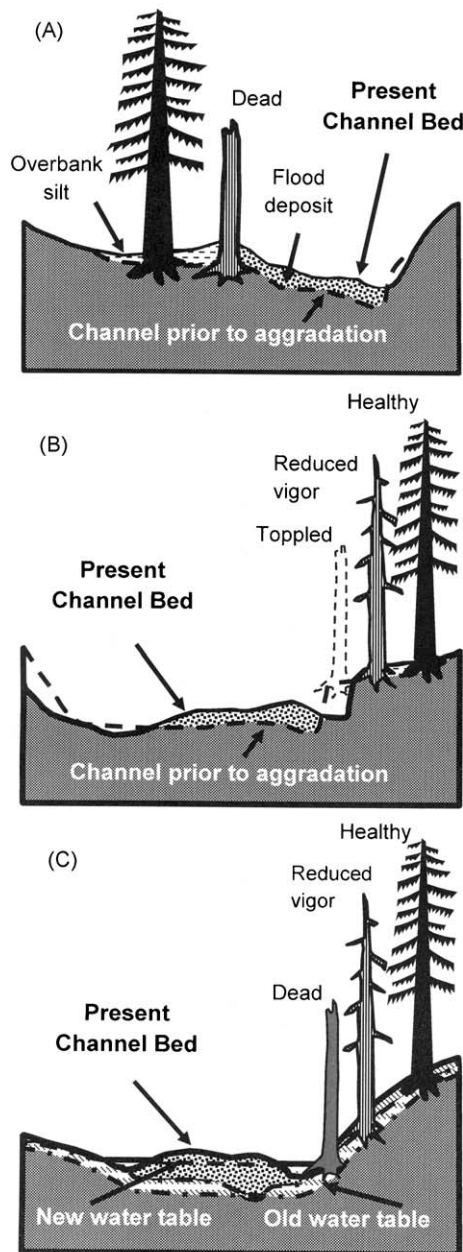
Diversion of water can also affect channel stability. A common response to dam construction is sediment starvation downstream, where river channels then cut downward into the bed, disconnecting the floodplain from the river (Williams and Wolman, 1984). A seasonal dam at Benbow Lake, California, has caused undercutting of the upstream alluvial flat by wave-generated erosion in the reservoir, toppling old redwood trees (Madej, 2001). In the Navarro River basin, even culvert construction and maintenance has changed floodplain dynamics by initiating channel incision (Florsheim and Mount, 2001). Excavation caused a decrease in base level, and knickpoints then migrated headward and incised channels in the floodplain where there had not been channels previously, thus affecting the water table of the floodplain and the redwoods growing there.

## 6. Conclusions

In the several centuries prior to 1850, old-growth forests of coast redwood appear to have been subjected primarily to frequent disturbances of low to moderate intensity, leading to highly uneven-aged stands. These disturbance regimes differ markedly from those of some coastal Douglas-fir forests to the north (e.g., Olympic Peninsula; Huff, 1995), but the highly irregular age structures are similar to those of long-lived, late-successional species found in other temperate regions of both the northern and southern hemispheres (Lusk and Ogden, 1992; Daniels et al., 1995; Pollmann, 2004; Parish and Antos, 2004). Stand-replacing events probably did occur, especially from landslides and destructive floods, but there is currently no large-scale evidence on their frequency, extent, or subsequent vegetation response. The few stand-level case studies on sites susceptible to landslides or repeated flooding (Redwood Creek, Bull Creek) suggest more than a thousand years between catastrophic events.

Fire, wind, and flood regimes of coast redwood forests have always been dynamic, but fundamental aspects of each have been altered during the last century at multiple scales. Fires have generally been excluded, wind dynamics have been altered through increased edge environment, and accelerated erosion has modified sedimentation and flooding regimes of some of the finest alluvial stands. A pressing question is to what extent these changes will have deleterious long-term consequences for a suite of desired forest attributes, including stand composition, structure, and diverse habitat elements for flora and fauna.

Fire exclusion has led to a marked reduction in burning across most of the species' range, but because historical fires were largely set by people, the relevance of this change for the forest is ecologically ambiguous. While frequent fire may have occurred for centuries in coast redwood, such fire may not have been the evolutionary force that it was in ponderosa pine forests (*Pinus ponderosa* Dougl. ex Laws.) that often shared similar frequencies (Agee, 1993). Because of redwood's ancient lineage (the oldest



**Fig. 9.** Impacts of channel aggradation on riparian redwood trees, resulting in gravel deposition (A), bank erosion (B), and water table changes (C). (Graphic provided by Redwood National Park.)

fossils from the genus *Sequoia* are from Jurassic deposits in southern Manchuria; Endo, 1951), the environments that forged many of its biological traits are now obscure. Some traits that appear to be fire adaptations may have evolved partly in response to other disturbances (e.g., vegetative sprouting in response to herbivory or wind damage).

Most redwood fire scar records on existing trees only extend back to the early 1600s, yet prior centuries likely experienced different climatic and cultural fire regimes. Although it is clear that upland redwood stands are not dependent upon severe fire for regeneration or continued dominance, the degree to which upland redwoods are dependent upon surface fires to provide mineral soil seedbeds, stimulate sprouting, and inhibit competition from other shade-tolerant species is still uncertain. Redwood may or may not be able to maintain dominance over the long run under the current disturbance regime of small treefall gaps from normal senescence and small-scale wind disturbance; the interpretive difficulty is that compelling demographic evidence is lacking for upland sites, and none of the published studies of fire history have revealed evidence of redwood stands that existed for one or more generations of trees (500+ years) without fire.

### 6.1. Recommendations for further research

In spite of the obstacles to studying redwood forest dynamics, key questions could feasibly be tackled using a multi-faceted research approach—stand history analysis, paleoecological methods, temporary field studies, permanent plot records, field experiments, and computer simulation—to provide multiple independent lines of evidence. Several research priorities, arranged by themes, are described below.

Some significant voids in our knowledge of the historic disturbance regime remain. In order to understand the full range of disturbance under which ancient redwood trees developed, knowledge of fire regimes prior to the 18th century is critical. In particular, the centuries prior to the Little Ice Age may provide a better analog for future redwood fire regimes than the period for which we have fire data. Such studies will be among the most difficult to conduct because cross-sections from large and old trees must be obtained near ground level, and crossdating will be challenging. It is possible, however, that crossdating might be facilitated by comparisons with ring chronologies of redwoods and other species growing on xeric and other stressful sites.

A more integrated understanding of historic redwood disturbance regimes could be achieved if methods are expanded to include evidence of other disturbance besides fire. Examination of ring chronologies for releases from suppression and cohort establishment, not otherwise linked with fire scars, could provide evidence on impacts and frequency of wind disturbance, normal treefall dynamics, floods, and landslides. New techniques, such as LIDAR, make it possible to identify past landslides and to identify areas with potential slope stability problems (Dubayah et al., 2005). With such techniques, the relative importance of climate, fire, seismic activity, land use, and geology in initiating mass movements can be discerned and subsequent forest recovery studied.

A second research priority is contemporary data on the response of redwood and associated species to fire. Most of our existing knowledge of species response to fire is derived from fire-history studies of tree-ring data, which are subject to dating errors and ambiguities concerning the origin (sprout vs. seedling) of post-fire cohorts. Surprisingly little direct evidence is available on redwood seedling establishment and sprouting after recent fires. Valuable data, especially using permanent plots, could be obtained both from paired burned and unburned plots on sites with recent wildfires, as well as from designed experiments incorporating

prescribed burns of different intensities and in different seasons on various sites.

A third priority is investigating the long-term effects of fire exclusion on future wildfire behavior and future stand trajectories. A resolution of successional trajectories in the absence of fire will require a systematic life-table approach. This would need to account for (1) establishment rates of redwood vs. competing species since the onset of fire exclusion, (2) their relative growth and survival rates in understory and gap environments, (3) survival and growth of sprouts following uprooting or snapping of the parent trees, (4) differences in the maximum tree heights and longevities of the species, and (5) the relative abilities of each species to re-establish and survive beneath the canopy of another species (cf. White et al., 1985a,b; Daniels et al., 1995; Lorimer et al., 2001; Taylor and Lorimer, 2003; Daniels, 2003 for analogous investigations in other forest types). Some evidence can be obtained with short-term temporary plot data, but long-term permanent plots (as in Busing and Fujimori, 2002) will be needed to make stronger inferences. Computer simulation could be a valuable means of examining the long-term implications of the basic demographic data (e.g., Cole and Lorimer, 2005; Choi et al., 2007).

Analogous research is needed on the effects of altered flooding regimes on alluvial redwood stands. Key research needs include the influence of watershed attributes and human impacts (dams, agriculture and logging, housing development, etc.) on flooding frequency, the spatial distribution of inundation and deposition, characteristics of flood deposits, and potential for stream channel recovery.

Finally, the effects of predicted climate change on future fire, wind, and flood regimes in coast redwood forests are important for formulating proactive management strategies for both old-growth and second-growth forests. An improved understanding of how past climatic variation influenced historic disturbance regimes, and the precise climatic mechanisms involved, can provide a basis for forecasting redwood forest composition and dynamics during periods of future climate change.

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