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Chapter 1

Geology, climate and vegetation of the Sierra Nevada and the mixed-conifer zone: An introduction to the ecosystem

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Abstract

The Sierra Nevada bioregion occupies over 6 million hectares, ranging in elevation from nearly sea level to the highest peaks in the contiguous United States. Vegetation patterns and landscape mosaics are the combined result of geography, climate patterns, and human-derived and natural disturbances. The western slope rises gently with deeply incised river drainages. Annual temperatures and precipitation patterns are Mediterranean in nature, with wet winters and dry summers. The eastern escarpment drops steeply into the Great Basin and Mojave Desert and is largely within the rain shadow. Urban centers and extensive agricultural activities border much of the western slope, while the eastern side is sparsely populated. The transport, distribution and effects of air pollution are the consequence of geography, vegetation and patterns of urban and agricultural development. An understanding of air pollution in the Sierra Nevada bioregion begins with an understanding of the physical environment. This chapter details the key elements of the Sierran environment that influence the air pollution.

The Sierra Nevada as it exists today is the consequence of geologic and climatological forces, natural and anthropogenic disturbances, historic and modern management practices, and the complex interactions between them. This chapter describes the key physical and biological characteristics that influence the characteristics of Sierran landscapes and ultimately the effects, distribution and concentrations of ozone (O_3) in the mixed-coniferous forests of the Sierra Nevada bioregion.

1. Overview of the bioregion

The Sierra Nevada has been the topic of extensive ecological evaluation in recent years. In 1996 the *Status Report of the Sierra Nevada, a Final Report to Congress of the Sierra Nevada Ecosystem* was published (SNEP Science Team, 1996). Subsequently, an environmental impact statement resulting in new management directions was assembled by teams from the eleven National Forests that occupy the Sierras and USDA Forest Service researchers from the Pacific Southwest Research Station (US Forest Service, 2000). Both documents highlight the need to approach studies of biological and physical processes in an integrated manner; thus, in order to understand air pollution (O_3 in particular) in the region, one needs to have some understanding of the physiography, climate, and organisms. For this reason, the term "bioregion" has been adopted as a reminder of the complexity that exists.

The Sierra Nevada bioregion encompasses about 8.5 million hectares along the eastern border of California and into the western edge of Nevada (Fig. 1). The north-south axis of the bioregion is approximately 600 km long and the east–west axis is a little over 100 km wide. To the west of the Sierra Nevada is the agriculturally important Central Valley, roughly 800 km long and 100 km wide. The Central Valley is surrounded by four major mountain chains, the Sierras to the east, the Cascade Mountains to the north, the Transverse Ranges to the south, and the Coast Ranges to the west. The Coast Ranges have a profound influence on weather patterns across the Valley and thus ambient conditions in the bioregion. Most of California's 2200 km of coastline is skirted by mountains. Marine air masses strongly influence the environment along the coast, but the presence of mountainous barriers creates large differences in environmental conditions, in particular hot summers on the interior side compared to the coastal side. Where gaps occur in the Coastal Ranges, marine influences penetrate further inland. One of the largest gaps in the Coastal Ranges occurs at San Francisco, where marine air masses transport urban pollutants into the Central Valley and Sierra Nevada forest ecosystems. To the east of the Sierra Nevada range is the sparsely populated, arid Great Basin in the north and Mojave Desert in the south.

The western edge of the Sierra Nevada begins at less than 300 m in the valley grasslands and foothill woodlands. The western slopes rise gradually above the valley floor, dissected with deep westward facing river systems. The eastern edge of the uplift is a fault escarpment dropping steeply into the Great Basin and Mojave Desert. The northern part of the range forms rolling highlands with peaks generally less than 2700 m. Summits increase in elevation southward with elevations culminating at Mount Whitney (4418 m), the highest peak in the contiguous United States.

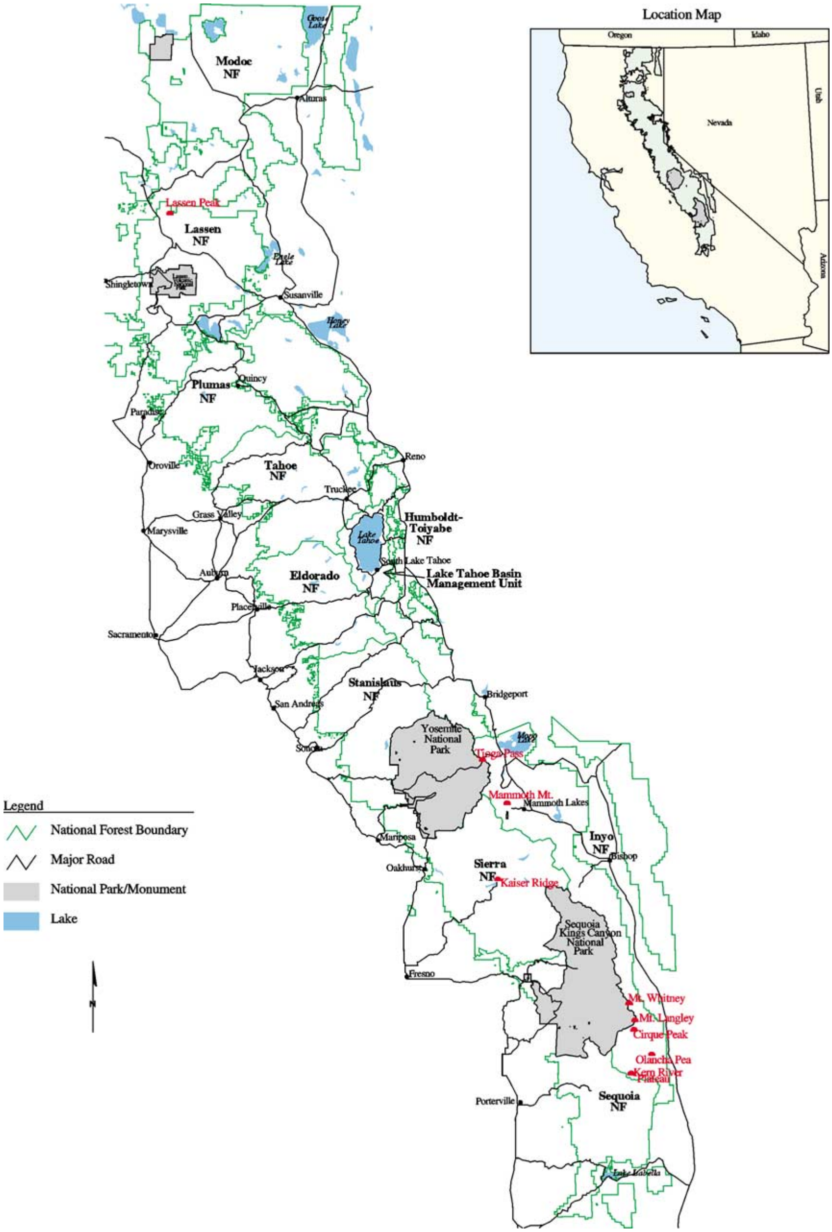

Figure 1. Map of the Sierra Nevada bioregion.

Table 1. Twelve major vegetation types comprise 68% of the Sierra Nevada landscape (data from the US Forest Service, 2000)

Plant community	Percentage of total area in the Sierra Nevada range
Sierran mixed-conifer forest	10
Blue oak woodland	10
West-side ponderosa pine forest	8
Lower montane mixed-conifer-oak forest	7
Red fir forest	6
Foothill pine-oak woodland	5
Jeffrey pine-fir forest	5
Lodgepole pine forest	4
Jeffrey pine forest	4
East-side pine forest	3
Red fir, western white pine and lodgepole–Western white pine forest	3
Non-native annual grasslands	3

Management of the region is complicated by ownership patterns. Of the 8.5 million hectares, 36% is privately held, and 41% is managed by the Forest Service and the Bureau of Land Management. Several state, local and federal agencies manage smaller portions, and three national parks (Yosemite, Sequoia–Kings Canyon and Lassen Volcanic National Parks) are interspersed within the 11 National Forests (Fig. 1).

Because of the latitudinal distance and large elevation relief that contribute to striking climatic gradients, the ecosystems occupying the Sierra Nevada vary from desert shrublands to seasonal wetlands and from alpine meadows and stony fell fields to a rich diversity in forest types. More than 3500 native plant species occupy the Sierras, comprising about 50% of the natural diversity in California on only 21% of Californian land base (Shevock, 1996). Plants cover about 90% of the land base; the remaining areas are occupied by rock, water, or human settlement. At least 88 different plant communities, as defined by the *Manual of California Vegetation* (Sawyer and Keeler-Wolf, 1995), have been identified, 25% of which occupy 2400 hectares or less. Of the more common plant communities, particularly the forest types, large differences in the composition of understory species exists. This variability is dependent upon elevation and latitude.

By far, the most dominant vegetation types are yellow pine forest types—Sierran mixed-conifer, west side ponderosa pine, Jeffrey pine, and east side pine types (Table 1). However, unlike Pacific Northwest forests or the hardwood forests of the Appalachian ranges, Sierran forests are naturally patchy consisting of mixed-age mosaics of dense stands, open stands, and patches of shrubby vegetation types (Franklin and Fites-Kaufmann, 1996).

Humans have inhabited the bioregion for at least 10,000 years. Estimates of pre-European settlement populations vary greatly. Roughly 100,000 Native Americans occupied the Sierra Nevada bioregion in the century prior to European discovery, with the majority living on the western slope (Anderson and Moratto, 1996). Thirteen tribes had established permanent and seasonal settlements throughout the range. These peoples had established trade routes among tribes and were engaged in a number of ecological practices, such as irrigation and burning to maintain desirable plant species (Anderson and Moratto, 1996).

European settlement in California began with the Spanish missionaries in the late 1700s, but for the most part these activities were focused in the coastal plains and Coastal Ranges far west of the Sierra Nevada. Large influxes of Europeans began with the Gold Rush of 1849. Between 1847 and 1860 an estimated 150,000 to 175,000 people moved into the region (Duane, 1996). This resulted in large changes to the landscape not only caused by mining, hydrologic projects, and timber extraction but also by expansion of agriculture, particularly sheep and cattle grazing, all these land uses to support the mining camps and auxiliary enterprises. The decline in mining towards the end of the century was followed by the development of agriculture in the Central Valley, including annual crop production, horticultural fruit operations, and grazing. Population grew slowly to about 250,000–275,000 residents in 1960. In the 1950s and 1960s population growth in California's coastal communities increased the demand for timber, water, and recreational activities. Large water diversion and reservoir systems were installed, and timber harvest surged in the 1960s through the 1970s. By 1990 the population had grown 2.5 times to 650,000 people, mostly located in the central portion of the western slopes near Sacramento. Beginning in 1990, urban expansion of several cities and towns on the eastern edge of the Central Valley increased dramatically, and new foothill and forest communities were built or expanded to accommodate commuters, retirees, and recreationalists. Population forecasts indicate that between 1.8 and 2.0 million people may reside in the Sierra Nevada bioregion by 2040 (Duane, 1999).

In the sections that follow, geology, climate, current and prehistoric vegetation patterns are discussed in greater detail. Understanding the geographic features that make-up the bioregion and the climate that shapes air mass and vegetation patterns are critical to understanding the fate and transport of air pollutants. The presence of vegetation both influences the transport of atmospheric pollutants and can be profoundly affected by pollutants. However, these influences have taken place in a background of natural processes such as fire, drought, and mass wasting, and the biologic factors of disease and insects, and natural mortality. In order to successfully integrate all of the factors that impinge on the distribution of O_3 and the effects on ecosystems, each of these factors should be examined independently.

Table 2. Names and scale for geologic time periods

EON	ERA	EPOCH	Beginning (Millions of years)
Phanerozoic	Cenozoic	Holocene	11000 yr
		Pleistocene	1.8
		Pliocene	5
		Miocene	23
		Oligocene	38
		Eocene	54
		Paleocene	65
	Mesozoic	Cretaceous	146
		Jurassic	208
		Triassic	245
	Paleozoic	Permian	286
		Carboniferous	360
		Devonian	410
		Silurian	440
		Ordovician	505
		Cambrian	544

2. Geology and physiography

The Sierra Nevada is largely composed of Mesozoic granitic rocks of the Sierra Nevada batholith (Table 2). The batholith forms an extensive block that has been uplifted on the east along the Sierra Nevada fault system and tilted westward (Bateman and Wahrhaftig, 1966). It is overlapped in the Central Valley by the emplacement of sedimentary rocks and on the Modoc Plateau to the north by volcanic sheets. The geology and physiography changes from the northern to the southern end of the bioregion. In the north, the batholith is flanked on the west by a metamorphic belt, a terrain of strongly deformed and metamorphosed sedimentary and volcanic rocks of Paleozoic and Mesozoic age. In the south, only scattered remnants of metamorphic rock occur within the batholith mostly in the western foothills and the crest of the range south of Yosemite National Park (Fig. 1). Elevations at the crest generally increase southward from 2000 m southeast of Mt. Shasta to 3000 m at Lake Tahoe, and exceeding 4000 m from Tioga Pass in Yosemite to Mt. Langley and Mineral King in Sequoia National Park (Fig. 1). Summit elevations then decrease to 2500 m in the Tehachapi ranges at the southern end of the range. The topography in the northern province reflects the tilted block structure with a gentle western slope and a precipitous, dissected eastern escarpment. To the south, the western slope becomes increasingly steep and dissected. The trunk streams in the southern province have increased local relief in part due to the steepness of the terrain and the increased size and lower descent of Pleistocene glaciers.

Adding to the complexity of the southern terrain, several fault systems subdivide the southern part of the block. For example, the north to south Kern River fault extends from the basin and range province, dividing the Great Western Divide-Greenhorn Mountains from the Great Eastern Divide at Mt. Whitney.

3. Climate

Climate patterns in the Sierra Nevada are the outcome of elevation, latitude, the annual migration of the jet stream and the Pacific anticyclone. In addition, climate has profound effects on both the long-range transport of O_3 and the potential effects of O_3 on ecosystems. Although much of the pollutant loads are generated from distant urban locations, prevailing winds produced by surface heating (anabatic flows) coupled with terrain, control the infiltration patterns of O_3 into the mountains. Tropospheric synthesis of O_3 from urban-generated precursors is largely controlled by sunlight, humidity, and temperature (Seinfeld and Pandis, 1998). The Mediterranean climate that prevails along the west coast sets up an annual pattern of wet winters and dry summers, creating a corresponding "O_3 season" during summer and a "clean" season during winter.

The climate in the bioregion is an outcome of seasonal changes in global circulation. During winter, large latitudinal temperature gradients support a strong circumpolar vortex with the mean position of jet stream southward into northern California. Surface low pressure in the Gulf of Alaska produces a strong onshore flow of moist air into northern California and the Pacific Northwest. During summer, reduced latitudinal temperature gradients weaken the circumpolar vortex, and the mean position of the jet stream shifts northward into British Columbia. A Hadley subtropical anticyclone that covers most of the northeast Pacific Ocean replaces surface low pressure in the Gulf of Alaska.

3.1. Prevailing winds during the summer air pollution season

During summer, prevailing ground level winds are northwesterly as a consequence of the geostropic balance between the subtropical anticyclone over the east Pacific Ocean and thermal low pressure over the desert (Fujioka et al., 1999). The northwesterly direction of the prevailing winds drives air masses onshore to the coastal ranges. At the gap in the coastal ranges at San Francisco Bay, the onshore winds diverge into two air streams, one flowing northward into the Sacramento Valley and the other southeastward into the San Joaquin Valley (Fig. 2). Although the California coast is dominated by a cool, moist coastal marine layer—a steady-state feature that forms from the cooling and moistening of the tropospheric boundary layer overlying the cold California ocean current—the marine layer usually dissipates in the Central Valley from diabatic heating and mixing with warm air aloft (Glendening et al., 1986).

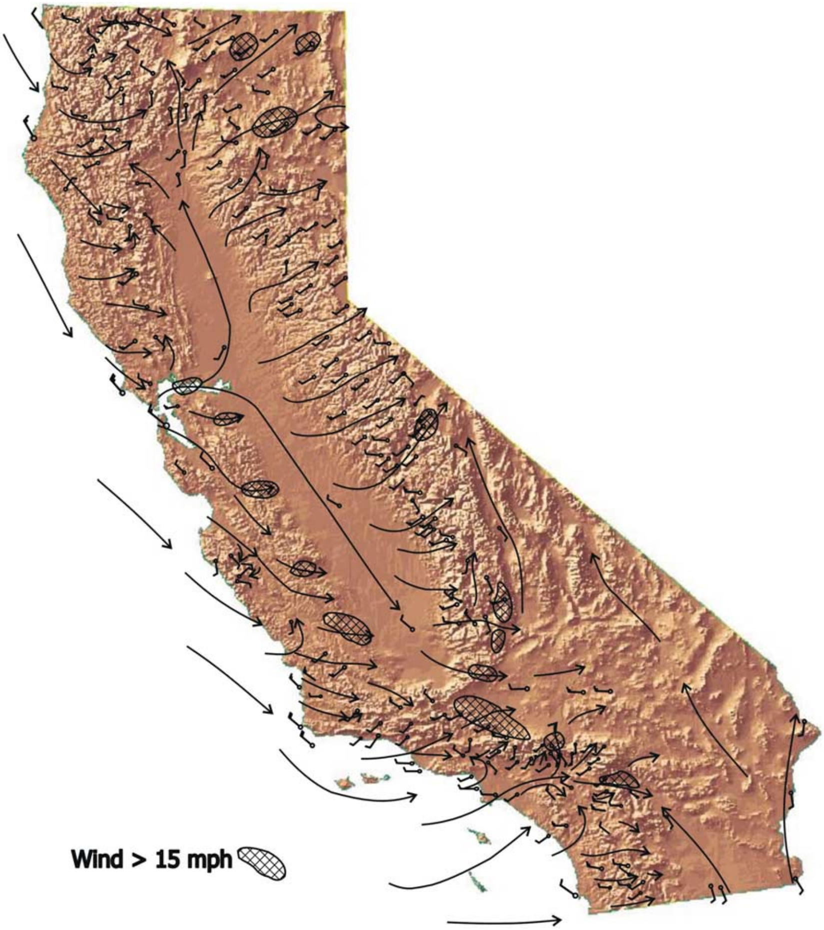

Figure 2. Prevailing wind patterns for July.

Warm boundary layer air masses overlying the Central Valley in summer are stratified by weak thermal inversions at 1000–1300 m. Daylight land heating generates local anabatic winds (cf. Edinger et al., 1972; Hayes et al., 1984) from the southwest and west on the western slope (Fig. 2; Ryan, 1982), which transport polluted air masses to the crest of the Sierras. Local winds predominate because upper air wind speeds are $< 10\ \mathrm{m\,s^{-1}}$ below 700 mb (3000 m). Marine air funnels through low gaps in the Sierra Nevada into the Mojave Desert, including Walker, Tehachapi and Mammoth Passes, as well as through Trinity Gorge into the Modoc Plateau. Afternoon surface winds on mountain slopes are typically westerly or southwesterly at right angles to local contours, and wind speeds range from 3–5 $\mathrm{m\,s^{-1}}$ on most slopes and as high as 5–10 $\mathrm{m\,s^{-1}}$ on exposed slopes and passes (Schroeder et al., 1967; Ryan, 1982; Zack and Minnich, 1991). The regions that experience the highest winds tend to have high winds almost daily because surface onshore pressure gradients are a constant feature. During winter, the combination of strong horizontal mixing aloft in the presence of the jet stream, weak insolation, and strong thermal inversions overlying the Central Valley reduces transport of pollution into the Sierra Nevada.

In summer, the stable stratification of boundary layer combined with upslope flows results in uniform relative humidity gradients. Although the afternoon relative humidity in the Central Valley is normally less than 30%, adiabatic cooling (cooling due to volumetric expansion) combined with limited mixing upslope result in increases of relative humidity as high as 40–50% at 2000 m in the bioregion.

3.2. Temperature

A stronger north to south gradient in ambient temperature exists in winter than in summer. In winter, the more southerly position of the jet stream is coupled with latitudinal temperature gradients and lapse rates (the rate of temperature decrease with increasing elevation), reflecting the equivalent barotropic structure of the atmosphere. Mean January temperatures in the southern Sierra Nevada average 6 °C in the lower foothills on the western slopes, and then decrease to 0 °C at 2000 m as compared to 1500 m in the northern Sierras. Temperatures decrease to -6 °C at 3000 m along the crest of Sierras. Persistent ground inversions in low-lying basins result in temperatures of -2 to -6 °C in the high east side plateaus from Modoc to Lake Tahoe and Mammoth Lakes, then increase to 4 °C in the lower Owens Valley and northern Mojave Desert.

Because the jet stream and associated latitudinal temperature gradients are far north of California during summer, the profile of decreasing temperature with elevation is virtually the same from the northern to southern Sierra Nevada. Mean July temperatures in the Central Valley range from 26–28 °C. On the west slope of the Sierras temperatures decrease to 24 °C at 1000 m, 20 °C at 2000 m and 14 °C at 3000 m. Values then increase to 20 °C on the high leeward plateaus and basins from Modoc to Mammoth and to 24–28 °C in the Mojave Desert.

3.3. Precipitation

Most precipitation in the Sierra Nevada falls during winter. Summer is a season of protracted drought except for occasional afternoon thundershowers (Fig. 3). Winter precipitation results from extratropical cyclones and associated waves

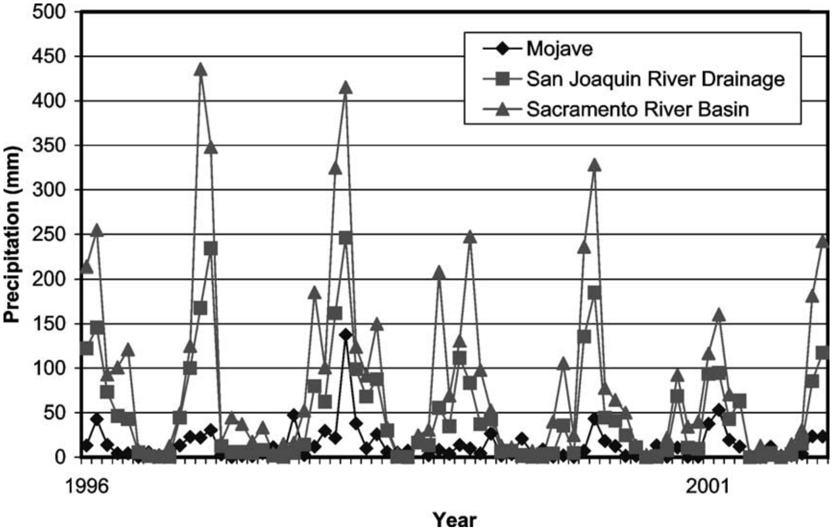

Figure 3. Annual precipitation patterns for the eastern Sierra Nevada (Mojave—diamonds), southern Sierra Nevada province, western slopes (San Joaquin River basin—squares), and northern province western Sierra Nevada slopes (Sacramento drainage—triangles). (Source: Western Regional Climate Center, Desert Research Institute, Las Vegas, Nevada.)

of the jet stream moving into California from the North Pacific Ocean between November and April. Before the passage of cold fronts, the presence of a deepening trade wind "marine layer" results in long periods of steady rain in stable air. Post-frontal precipitation consists of convective showers concentrated over high terrain. Because most precipitation falls during the prefrontal zone, strong gradients in mean annual precipitation in the Sierras result primarily from mechanical lift over mountain barriers rather than from thermal convection. The dominance of southwesterly winds in prefrontal zones (Minnich, 1984) generates intense physiographic lift on the south- to southwest-facing escarpments that lie at right angles to storm winds. The average annual precipitation also gradually decreases southward because the mean position of the jet stream lies in northern California and the Pacific Northwest (Fig. 4). In the northern Sierras orographic lift along the uniformly gentle western slope produces an average annual precipitation of 60 cm along the lower foothills to 150–200 cm at the crest of the range north of Lake Tahoe. To the east, rain shadows are associated with average annual precipitation of 20–60 cm in the Modoc Plateau, and 60–80 cm in the Lake Tahoe Basin. The topographic complexity of the southern Sierras results in large variability in average annual precipitation along the west slope. Steep southwestern exposures have average annual precipitation of 100–150 cm at Yosemite, the upper San Joaquin drainage, Kaiser Ridge, Se-

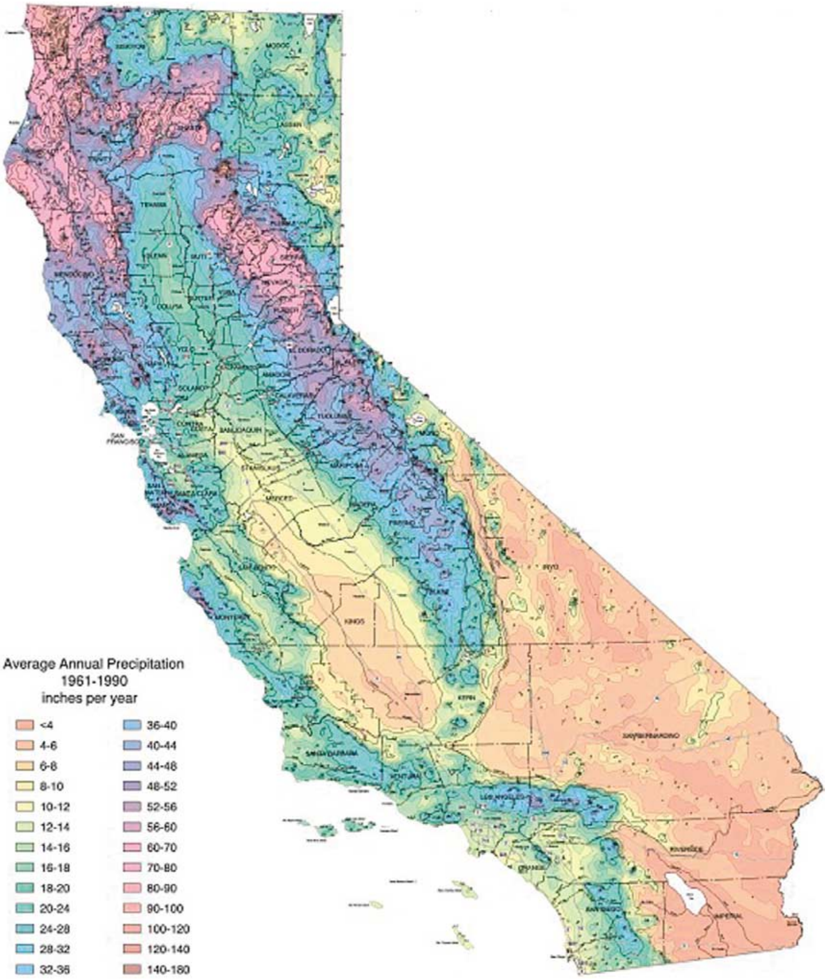

Figure 4. Annual precipitation for the state of California. (Source: Western Regional Climate Center, Desert Research Institute, Las Vegas, Nevada) (1 inch = 2.54 cm).

quoia National Park to the Great Western Divide, and the Greenhorn Range. Leeward slopes on the coastal front receive 50–100 cm, including the upper Tuolumne River, Mono Creek Basin, the upper Kings River, and the Kern River plateau northward to Mt. Whitney. The average annual precipitation seldom exceeds 50 cm in the southern Sierras and Tehachapi ranges due to low altitude and rain shadows extending northeastward from the western Transverse of southern California and South Coast Ranges.

3.4. Snowfall

The ratio of liquid equivalent snowfall to the average annual precipitation (S/AAP) shows a linear relationship between snowfall and altitude (Minnich, 1986; Barbour et al., 1991). The lower limit of reliable snowfall at 1000–1200 m approximates the moist adiabatic lapse rate from mean sea surface temperatures to the storm freezing line. In the southern Sierras S/AAP ratios increase to 25% at 1750 m, 75% at 2750 m and 100% at 3000 m (Minnich, 1986). Average snow lines are about 200–400 m lower in the northern Sierras (Barbour et al., 1991). The total liquid equivalent snowfall increases rapidly with increasing AAP northward in the Sierras. With an AAP of 150 cm near Yosemite, the water equivalent snowfall reaches 50 cm at 1900 m and 75 cm at 2200 m. At Mt. Lassen (AAP, 200 cm), 50 cm water equivalent amounts are reached by 1400 m and 100 cm by 2000 m. Interannual snow levels in California tend to increase with increasing total annual precipitation largely due to enhanced advection of moist subtropical air masses during El Niño events (Minnich, 1986). Hence, extraordinary snow accumulations during very wet years are frequently limited to the highest elevations (> 2800 m), with middle elevations producing storm runoff.

3.5. The North American monsoon

During the summer months of July to September the annual migration of the jet stream northward reduces delivery of moist air, and consequently most of the range experiences an annual drought. However, the North American monsoon, a deep layer of moist, unstable tropical air, periodically causes afternoon thunderstorms, especially in the eastern Sierras. The monsoon arrives from the tropical Pacific and Gulf of California around an anticyclone in the mid-troposphere centered over the southwestern US desert. South to southeasterly winds aloft transport tropical moisture into southeastern California and the eastern Sierras. Total summer precipitation (July–September) average 5–10 cm at most.

Lightning from afternoon thunderstorms are a frequent ignition source for wildfires. The distribution of lightning strikes recorded by electromagnetic direction finders reflects the spatial pattern of afternoon summer thunderstorms. Lightning detection rates range from 2.0 $\mathrm{km}^{-2}\,\mathrm{yr}^{-1}$ along the crest of the Sierras to $< 0.5\ \mathrm{km}^{-2}\,\mathrm{yr}^{-1}$ in the Sierra foothills (Minnich et al., 1993; GEOMET, 1994).

4. Vegetation

The Sierran mixed-conifer forest is one of several ecosystems that form broad belts from the Cascade Range to the Tehachapi Mountains. With increasing elevation along the western slope, chaparral and foothill woodlands are replaced by mixed-conifer and subalpine forests that extend to the tree line about 3000 m in the north to 3500 m in the south. Descending the leeward (east side) escarpments are narrow belts of subalpine and mixed-conifer forest that are replaced by pinyon–juniper woodlands and desert scrub communities at lower elevations. (More detailed descriptions of these ecosystems can be found in Barbour and Minnich, 2000.)

4.1. Foothill woodland

Foothill woodland, which grows along the lower western foothills to as high as 1000 m in the north and 1700 m in the south, consists of open cover of gray pine (*Pinus sabiniana*) in association with open parks of the deciduous valley oak (*Quercus lobata*), and blue oak (*Q. douglasii*), and the evergreen interior live oak (*Q. wislizenii*), scattered understory cover of California buckeye (*Aesculus californica*), toyon (*Heteromeles arbutifolia*), California coffeeberry (*Rhamnus californica*), western redbud (*Cercus occidentalis*), and exotic annual grassland (Griffin and Critchfield, 1976). The tree layer is typically 15–30 m tall, while shrubs are $<$ 6 m.

4.2. Chaparral

Chaparral, which consists of evergreen sclerophyllous shrubs in carpet-like stands 2–6 m tall, is most abundant on steep eroding slopes between 500 and 2000 m. The dominant species is frequently chamise (*Adenostoma fasciculatum*). Other common shrubs are in the genera California lilac (*Ceanothus*), manzanita (*Arctostaphylos*), scrub oak (*Quercus*), mountain mahagony (*Cercocarpus*), California coffeeberry (*Rhamnus*), and toyon (*Heteromeles*). North of the Tuolumne River, stands are found mostly on southern exposures of the major gorges or on hogback ridges near Placerville and San Andreas. As terrain complexity and the steepness of the western escarpment increases southward, chaparral expands into a narrow zonal belt from the Tuolumne River to the Kern River, and locally eastward onto the southern exposures of the Merced, San Joaquin, Kings, and Kaweah watersheds, as well as the western and eastern flanks of the Greenhorn Mountains. Scattered patches occur in the Tehachapi Ranges.

4.3. Mixed-conifer forest

Forming an extensive belt from 1000 to 2200 m in the north and 1500 to 2600 m in the south, mixed-conifer forest is a multi-layered community in which the cover contributed by each layer and the species composition is variable, especially along climatic gradients from the moist western slope to the drier eastern escarpment and southward through the range (Griffin and Critchfield, 1976; Barbour and Minnich, 2000). The tree component consists of overstory conifers 30–60 m tall and a middle layer 5–20 m tall of deciduous and evergreen hardwoods. The dominant species on the west slope south to the Greenhorn Mountains are ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*), and sugar pine (*Pinus lambertiana*). Although stands are mixed throughout the range, *P. ponderosa* tends to be dominant in basins and southern exposures, *A. concolor* on northern exposures, *C. decurrens* in canyons, and *P. lambertiana* on steep north-facing slopes. Discrete groves of giant sequoia (*Sequoiadendron giganteum*) occur in shallow basins from Kings Canyon southward to near Johnsondale in the northern Greenhorn Range. A few groves occur as far north as Calavaras State Park. Douglas-fir (*Pseudotsuga menziesii*) is an important associated species north of Yosemite. Important hardwood species include California black oak (*Quercus kelloggii*), canyon live oak (*Quercus chrysolepis*) and California laurel (*Umbellularia californica*) on steep slopes and canyons, as well as mountain dogwood (*Cornus nuttallii*) and big-leaf maple (*Acer macrophyllum*) near streams. California nutmeg (*Torreya californica*) and Pacific yew (*Taxus brevifolia*) are important midstory associates north of Mineral King and Yosemite. West slope forests north of Lake Tahoe have midstory of Pacific madrone (*Arbutus menziesii*) and tanbark oak (*Lithocarpus densifloris*).

In the semiarid Tehachapi ranges, eastern escarpment of the Sierra Nevada, Modoc Plateau, leeward ranges and basins of the Kern Plateau, and the Mono Creek basin, mixed- conifer forest consists primarily of Jeffrey pine (*Pinus jeffreyi*) and *Abies concolor*, with scattered colonies of *P. lambertiana* and *Calocedrus decurrens*. Sierra western juniper (*Juniperus occidentalis* ssp. *australis*) is an important associate along the eastern escarpment from Olancha Peak to Susanville. Mid-story hardwoods on leeward sites of the west slope and the Tehachapis consist mostly of *Q. kelloggii* and *Q. chrysolepis*. On the eastern escarpment, *Q. chrysolepis* occurs as far north as Mt. Whitney; *Q. kelloggii* occurs only near Mt. Whitney.

The Sierran mixed conifer forest has open cover of low shrubs with dense patches on steep slopes and in forest openings. The shrub layer is typically open with cover inversely related to the cover to tree overstory. Important species are in the genera mountain misery (*Chamaebatia*), *Ceanothus*, *Arctostaphylos*, chinquapin (*Chrysolepis*), *Rhamnus*, various stone fruit shrubs (e.g. *Prunus*), and oak (*Quercus*). Dominant shrubs in dry forests include the green leaf manzanita (*Arctostaphylos patula*), and mountain whitethorn (*Ceanothus cordulatis*), as well as species common to the Great Basin including mountain mahogany (*Cercocarpus ledifolius*), Great basin sagebrush

(*Artemisia tridentata*), and rabbitbrush (*Chrysothamnus nauseosus*). Herbaceous cover is insignificant except near streams and meadows due to summer drought.

4.4. Subalpine forest

Subalpine forest consists of moderate sized conifers (20–40 m tall) dominated mostly by lodgepole pine (*Pinus contorta*) and red fir (*Abies magnifica*). *P. contorta* is dominant on shallow soils of glaciated slopes, while *A. magnifica* is dominant on gentle slopes with deep soils below areas of glaciation. *P. contorta* also grows at wet sites along the edges of meadows and lakes subject to cold-air drainage, sometimes downslope within the mixed-conifer forest belt. Subalpine forests lack mid-story hardwood species of mixed-conifer forest except for quaking aspen (*Populus tremuloides*) stands that grow mostly in talus slopes and riparian sites. Shrub cover is open and consists of *Arctostaphylos patula*, *Ceanothus cordulatis*, bush chinquapin (*Chrysolepis sempervirens*), and gooseberry (*Ribes* spp.) Forests frequently exhibit a homogeneous aspect, as well as local patchiness resulting from stand-replacement fires. Western white pine (*Pinus monticola*) is a common associate throughout the Sierras. Other associated species include limber pine (*Pinus flexilis*) in the southern Sierras, whitebark pine (*P. albicaulis*) in the northern Sierras, foxtail pine (*P. balfouriana*) from Mineral King to Kersarge Pass, and mountain hemlock (*Tsuga mertensiana*) north of Yosemite.

4.5. Pinyon–juniper woodland

Pinyon–juniper woodland grows on the eastern escarpment of the Sierras and the Tehachapi ranges. Stands consist of short-statured conifer forests (10–20 m tall) dominated by singleleaf pinyon pine (*Pinus monophylla*) south of Reno and western juniper (*Juniperus occidentalis* ssp. *occidentalis*) on the Modoc Plateau. Utah juniper (*Juniperus osteosperma*) is a widespread associated species from Mono Lake to Mt. Lassen. California juniper (*Juniperus californica*) is an important associate in the southern Sierra and the Tehachapi Mountains. Stands grow with open subcanopy of *Cercocarpus ledifolius* above 2000 m but more extensively with Great Basin sage scrub dominated by *Artemisia tridentata, Chrysothamnus nauseosus*, and antelope bush (*Purshia glandulosa*). Gaps in woodland canopy are found in areas of recent stand-replacement fires (e.g., Wangler and Minnich, 1996).

5. Holocene climate and vegetation change

Boundaries that define ecosystems or vegetation types are generally constructs for human convenience. The true boundaries of a particular vegetation type are both gradual and subject to modification dependent upon short- and long-term climate and disturbance events (Thompson, 1988, 1990). Attempts to define the cause and effect of ecosystem changes as determined by vegetation characteristics are confounded by natural variability and processes. To separate "natural changes" from those caused by human activities (human influences on landscape processes), research efforts have focused on reconstructing Sierran landscapes prior to European invasions and the last glaciation.

Modern Holocene climates began roughly 11,000 years ago with global warming that lead to the thinning and retreat of the Canadian (Laurentide) and Eurasian ice sheets (Table 2). It is assumed that the extant vegetation patterns began to form with the establishment of the modern climate regime. Reconstruction of Holocene vegetation patterns relative to climatic conditions is often compared to existing conditions in an effort to separate anthropomorphic effects from natural ecological processes.

The modern global climate became established at the beginning of the Holocene, after which Sierran ecosystems soon developed their modern aspect and distribution. An emerging body of proxy evidence, including pollen, macrofossils from woodrat middens, lake stands, tree rings, stable isotope data, astronomical cycles, and global climate models, reveal important climatic fluctuations during the Holocene. However, broadscale post-glacial vegetation changes appear to be small, in part because the natural selection processes that result in changes in recruitment of species new to the landscape or distribution patterns require several generations to reach mature phases (Davis and Botkin, 1985; Sauer, 1988; Thompson, 1988, 1990). Although many species were apparently adjusted to their modern ranges by 6000 B.P., others were still undergoing range adjustments in the late Holocene (Nowak et al., 1994) and are continuing to shift today.

The most well-known evidence for cooler wetter climates in California during the late Pleistocene (the epoch preceding the Holocene) is found in evidence of extensive ice sheets along the crest of the Sierras, pluvial lakes in the Great Basin, and pinyon-juniper woodlands, rather than the desert shrublands that cover modern deserts (Bartlein et al., 1998; Van Devender, 1990; Spaulding, 1990). Glacier equilibrium line altitudes were about 1000 m below the firn lines of modern cirque glaciers in the Sierra Nevada (Broecker and Denton, 1990; Burbank, 1991; Dawson, 1992).

By the early Holocene (8000 B.P.), the Laurentide ice sheet had collapsed (Dawson, 1992), and the climate appears to have been warmer and drier than at present. Direct thermal evidence for warmer temperature comes from bristlecone pines (*Pinus longaeva*) that were analyzed for stable hydrogen isotopic composition (Feng and Epstein, 1994). Temperatures reached maximum values at 6800 B.P. and have been cooling ever since.

Anderson (1990) found that Sierra Nevada forests from Mammoth Lakes to Tioga Pass had been established by 10,000 B.P., but that early forests were more open and contained abundant shrubs, such as *Chrysolepis sempervirens*, compared to current forests. Open forests may reflect both drier conditions and limited soil development after deglaciation. *Pinus contorta* experienced successive disappearance from lower elevation sites (Anderson, 1996). The evidence from pollen studies documents the development of a lower montane forest and giant sequoia community that existed around a small meadow between 12,500–8,800 B.P. (Koehler and Anderson, 1994). Scuderi (1987a) found that the Sierra Nevada tree line at Cirque Peak was 70 m higher than at present, with the maximum elevations occurring between 6500 and 3500 B.P. Similarly, the tree line was 125 m higher in the White Mountains (LaMarche, 1973).

Submerged pine stumps dated 6300 to 4800 B.P. reveal that Lake Tahoe was below sill heights for centuries (Lindstrom, 1990). Nearby Walker Lake, which drains the eastern Sierra Nevada south of Lake Tahoe, was shallow and desiccated from 5300–4800 (Benson et al., 1991). Clark and Gillespie (1997) provide evidence that Holocene glaciers in the Sierra Nevada may have been entirely absent during much of the Holocene.

Pollen profiles along the crest of the Sierra Nevada record an increase in subalpine conifers, especially *Pseudotsuga menziesii* and *Abies magnifica*, by 6000 B.P.—apparently reflecting increasing effective precipitation (Anderson, 1990). A period of cooler moister climate occurred about 5000 to 3000 B.P., sometimes referred to as the Neoglacial. Evidence includes enlargement of alpine glaciers and small interior lakes and subtle shifts in vegetation. Pollen and macrofossil data suggest that *Pinus contorta* experienced a return to lower elevation sites by 1700 B.P. Early Holocene tree lines in the southern Sierra Nevada persisted until 3500 B.P. Scuderi (1987a) argued that tree lines fell by about 70 m in elevation in the years 3400 and 2400 B.P. in response to cooler, wetter conditions (c.f. Lloyd and Graumlich, 1997). Similar trends in the White Mountains, about 20 km to the east, have been documented (LaMarche, 1973). Climatic deterioration may have led to the establishment of modern mountain glaciers. A lake core from below Conness glacier indicates the formation and growth of the glacier at 3400 B.P. (Konrad and Clark, 1998). High water levels were recorded at Walker Lake (Benson et al., 1991) and Mono Lake (Stine, 1990).

The Neoglacial was followed by an extended period of reduced precipitation from 2000 to 600 B.P. that culminated in profound drought at 1000 B.P. Evidence for regional drought is found in low water levels at Walker Lake (Benson et al., 1991) and Mono Lake (Stine, 1990). Relict tree stumps rooted in current lakes, marshes, and streams in the Sierra Nevada were attributed to severe drought that occurred from 1000–700 B.P. (Stine, 1994). Scuderi (1987b) established that tree-ring widths in *Pinus balforiana* were inversely related to glacial expansions and found a period of pronounced warmth from 1200–1000 B.P. A summer temperature reconstruction from tree-ring data from subalpine conifers in the southern Sierras by Graumlich (1993) showed a period with temperatures exceeding late 20th century values from 900 to 675 B.P. At Cirque Peak in the southern Sierras, Scuderi (1987a) found a lowering of tree lines at 1400 and 900 B.P.

During the Little Ice Age (700–200 B.P.) a small glacial advance left fresh moraines below hundreds of modern and extinct cirque glaciers (Burke and Birkeland, 1983; Clark and Gillespie, 1997). Scuderi (1990) found a sharp decline in indexed ring width beginning in 1600 B.P. Graumlich (1993) also identified a period of cold temperatures from 1450 to 1850 B.P. Lloyd and Graumlich (1997) describe a decline in tree line and tree line forest abundance from 450 to 50 B.P. The Little Ice Age is associated with high stands in the Mojave Desert (summarized in Enzel et al., 1992) and at Mono Lake (Stine, 1990).

5.1. Holocene climatic change or singular events?

One important question is whether vegetation and fire regimes in the Holocene fluctuated in response to long-term climatic change or within a background of a stable climate punctuated by singular events. The Medieval Drought and Little Ice Age—the two periods for which we have the best evidence—have been interpreted from both standpoints. Stine (1994) proposed that climate change associated with the Medieval Drought involves reorientation of the mid-latitude storm tracks, but this is not supported by time-averaged GCM maps (Bartlein et al., 1998). Alternatively, Enzel et al. (1992) thought that snow accumulation in the Sierras, high precipitation and stream flow in southern California, and high lake stands could be explained from singular flood producing events in a single season.

The evidence supports the singularity hypothesis. Precipitation variability during the Holocene has lasting impact on the terrestrial landscape only where water is stored with a long residence time, i.e., in the form of lakes (high stands) and ice (moraines). The effects of precipitation variability on soil water and vegetation are fleeting. Indeed, the paleobotanical record from the Holocene suggests that ecosystems exhibit small, but constant rates of change under a strong influence of inertia. A few great floods will accumulate in snowpacks, glacial advances, and Holocene lakes, but they are ambiguously expressed in changes of tree line and vegetation records gleaned from pollen cores.

6. Fire in Sierran mixed conifer forest

One of the most important ecological processes in the Sierran mixed-conifer forests is recurrent fire, which shapes species composition and forest structure. But the details of past ecologically driven recurrence rates and fire intensities are controversial. Forest fire suppression has altered natural fire patterns, forest structure and species composition. Suppression has reduced the number of fires, resulting in increasingly dense forest stands and accumulations of ground and standing fuels. At the same time, disturbance from logging has further increased the number and density of small trees, shrubs and understory species, contributing to the flammability of forests. Compounding these effects, O_3 and other air pollutant have contributed to increased susceptibility to drought and changes in litter and ladder fuels. Identifying the many contributing factors to the structural changes in mixed-coniferous forests and developing approaches to restoring forests to an equilibrium status first requires an understanding of how fires function in the ecosystem.

The Mediterranean climate of winter storms and dry summers results in unfavorable temperature and moisture conditions for decomposition (Hart et al., 1992), leading to fuel build-up and fire hazard (Rundel et al., 1988; Barbour and Minnich, 2000). The fire season in the Sierras begins in early summer, within 2 months after the last winter storms. By this time, most species have completed growth flushes, and the fuel moisture of live plants as well as litter and dead fuels has reached flammable thresholds. In mixed-conifer forest, the growth flush occurs after snow melt, usually from May to July (Royce and Barbour, 2001a, 2001b). The onset of drought begins soon after because moisture is rapidly depleted in porous soils, especially in glaciated terrain. Summer thundershowers have limited effect on soil moisture. Lysimeter data for the Sierra San Pedro Mártir in Baja California and the San Jacinto Mountains show that summer rain is countered by high summer transpiration rates, with limited wetting of the root zone (Franco-Vizcaíno et al., 2002).

Although Sierra Nevada mixed-conifer forests experienced gradual fluctuations in distribution and species composition as the result of climatic variability and disturbance, lengthening fire intervals due to suppression very likely have placed forests beyond the range of "normal" landscape-scale structures in association with extended subcanopy successions and broad-scale coarsening of patch mosaics. Before fire control was instituted ca. 1900, surface fires mediated surface fuel accumulation and selectively eliminated subcanopy sapling and pole size conifers, leaving open stands of mature trees. Stand densities (stem dbh $>$ 10 cm) in California ranged from 100–200 ha^{-1} dominated by ponderosa pine, Jeffrey pine, and white fir (McKelvey and Johnston, 1992; Minnich et al., 1995). Under suppression management, the near absence of fires Jeffrey led to stand-densification, with an age-specific trend toward dominance by juvenile, pole-size classes of *Abies concolor* and *Calocedrus decurrens* (Kilgore, 1973; Vankat, 1977; Vankat and Major, 1978; Weatherspoon et al., 1992; SNEP Science Team, 1996). Regional stem density increases of 100–200 stems ha^{-1} (dbh $>$ 10 cm) over the past 60 years were reported in the San Bernardino Mountains of southern California (Minnich et al., 1995). The density of ponderosa pine stands regenerating from nineteenth century logging often exceed 500 stems ha^{-1} (Albright, 1998). In the Sierra Nevada, tree densities (stems $>$ 10 cm dbh) have climbed to 500 ha^{-1} on west slope ponderosa pine forest (Ansley and Battles, 1998; Roy and Vankat, 1999).

Post-suppression increases in fuel loadings and increasing vertical fuel continuity with the addition of pole-size stems have resulted in a shift from surface fires to stand-replacement burns, with the size of stand-replacement burns in the order of thousands of hectares. Forests frequently have been replaced by montane shrublands, *Quercus chrysolepsis* and *Q. kelloggii* which may persist for decades (cf. Kauffman and Martin, 1990).

In the reconstruction of pre-suppression fire regimes, forest ecologists universally agree that the open forest structure is an outcome of recurrent surface fires, but there is disagreement on the fire intervals, intensities, severity, and size as well as its effect on regional and microscale stand structure. There are two end member models, whose findings depend primarily on the methods employed.

One end-member is a model of short-fire intervals with low intensity proposed in fire scar dendrochronology studies. Pre-suppression intervals estimated from this method in Californian mixed-conifer forest are generally less than 20 years (McBride and Laven, 1976; Kilgore and Taylor, 1979; Finney and Martin, 1989; Swetnam, 1993). Estimates for white fir forest are from 9 to 42 years in the Oregon Cascades (McNeil and Zobel, 1980; Agee, 1993). Because fire intervals were assumed to be short, it was deduced that pre-suppression fire intensities were low, consuming mostly litter, shrubs, seedlings, immature trees, and senescent groups, leaving vigorous stand structures (Kilgore and Taylor, 1979; Kilgore, 1981; Parsons and Swetnam, 1989; Swetnam, 1991, 1993). The extrapolation of site-based fire scar records to a spatial fire pattern is not explicit and requires assumptions concerning whether synchronous fire scar years between sampling sites represent single or multiple burns. The size of burns cannot be deduced except with high resolution sampling. A detailed analysis by Kilgore and Taylor (1979) correlates fire scar records with stand age data in the central Sierra Nevada. They found that fires recurring at 15 to 18 years were small and patchy ($<$ 800 ha), but cleared out most immature trees, with limited survival of young subcanopy trees joining the canopy layer.

The other end-member model is based on landscape scale, spatially-explicit reconstruction of fire history of mixed-conifer forest from time-series aerial photographs of the Sierra San Pedro Mártir of Baja California where fire suppression is not practiced (Minnich et al., 2000). Forests there consist of open, mixed-aged stands of mature trees (65–145 trees ha^{-1}) and few poles (15 ha^{-1}), with increasing pole size stem densities with time-since-fire. In the landscape model, Minnich et al. (2000) found that the open forest structure is a outcome of moderate to large intense surface fires with fire intervals of about 2–3 events per century. Fires were frequently greater than 1000 ha and occasionally as large as 8000 ha. Most burn area is accomplished by the largest 10 percent of events. Subcanopy flame lines produced fatal foliar scorch 10–20 m above the ground, killing pole-size trees and a few overstory trees. Stand-replacement burns (gaps mostly < 10 ha) were limited to exposed steep slopes and ridges—often stands with subcanopy of montane chaparral and *Quercus chrysolepsis*. Long fire intervals were attributed to the gradual build up of subcontinuous shrub cover, conifer recruitment, and litter accumulation, with the time-dependence between fuel accumulation and burning leading to non-random patch dynamics. Over time, most burned stands were older than 40 to 50 years, but there were rare cases of fire sequences within less than 20 years. The trend of longer fire return intervals in Sierra San Pedro Mártir is not exclusively the result of climatic gradients; mean annual precipitation in Sierra San Pedro Mártir (70 cm) is well within the range of many forests of southern California and portions of the Sierras. A greater percentage of total rainfall is used by Sierra San Pedro Mártir forests compared to Sierran forests, where increased precipitation can result in increased runoff and percolation with increased latitude (Franco-Vizcaíno et al., 2002). Seasonal plant-soil water availability are more related to the timing of precipitation events rather than the total annual accumulation; in both Sierra San Pedro Mártir and the Sierras the rainy season occurs between November and April. Because of the granitic parent material typical of both northern and southern forests, porous soils are generated. A forest population model was proposed in which the forest canopy layer is the result of vigorous selective elimination of subcanopy trees by intense understory fires. Most subcanopy trees, largely first generation trees after fire, perish in landscape-scale fires, leaving only a few to join the canopy layer. The rate of entry into the overstory class is balanced by low mortality rates in the overstory class.

Site-based field and modeling studies have assumed that fire scar dendrochronology estimates reflect regional fire-return intervals and landscape-scale dynamics. However, fire interval estimates must include the “long-tailed” fire size distributions, i.e., most events are small, and relatively few large events account for most burned area (Minnich and Chou, 1997; Malamud et al., 1998). The high frequency of small events due to lightning strikes and spot burns suggests that any randomly selected fire scar dendrochronology sampling site has a high probability of recording small local burns. Hence, the assumption that all fire scar year dates represent large burns may lead to underestimation of fire-return intervals. Moreover, small fires cumulatively remove little standing biomass because they have insufficient energy release to maintain flame lines (fires are small because they are low in intensity). Conversely, although the elimination of small fires in time-series landscape fire histories in Sierra San Pedro Mártir leads to overestimation of return intervals, fire size frequency distributions predict that the cumulative area of small fires over long time scales is small.

To develop plausible models of presuppression fire regimes in the Sierra Nevada—which is essential to understanding air pollution effects on mixed-conifer forest ecosystems—it is important to elucidate the role of small, low intensity fires in landscape-level dynamics. This will require high resolution fire scar dendrochronology sampling studies that can characterize and distinguish mass burns and microfires. Such studies have shown promise in the ponderosa pine forest of the Colorado Front Range. Veblen et al. (2000) found that while open lower elevation ponderosa pine forest were characterized by frequent surface fires, high elevation forests of *Pinus ponderosa* mixed with *Pseudotsuga menziesii* had longer fire intervals and included extensive stand-replacement fires.

7. Forest dynamics and climatic change

In the Sierra Nevada, Swetnam (1993) found large variability in fire scarring over the past 2000 years in long-lived giant sequoia forests. A pattern of infrequent, large fires during a cool period from 1500 to 1000 B.P. was followed by frequent small fires during a warm period from 1000–700 B.P. Fires have been infrequent and larger since 700 B.P. During periods of high fire frequency, the fuels were maintained at low levels, resulting in a patchy pattern of small fires. During low fire frequencies, more fuels accumulated and resulting fires were more widespread, producing coarse spatial patch structure.

However, the dynamics of mixed-conifer forest are also dependent on cumulative fuel build-up at scales of decades rather than short-term effects of growth, litterfall, and fuel moisture by climatic variability. Landscape models have, typically, not accommodated the effects of regional patch mosaics. A time lag exists between fuel accumulation, and fires that tend to be self-limiting and time-dependent (Minnich and Chou, 1997). Fire occurrence is therefore constrained in space and time by the rate of fuel accumulation and previous fire history. Because old-growth stands are preferentially burned regardless of short-term climate variability, the linkage between climate and fire occurrence in long-lived mixed-conifer forest is at the scale of centuries. Hence, the effect of precipitation variability is modulated by patch structure in which changes in regional fire hazard result in only small portions of stand achieving flammability thresholds. Correlations between climate variability and fire occurrence should be scaled as a running mean averaged for the mean fire interval. This scaling will reveal periods of greater or lesser burning in response to long-term fluctuations in precipitation.

8. Other natural disturbances

The Sierra Nevada experiences other forms of disturbance: floods, avalanches, and ongoing tectonic processes continually alter the landscape. The annual spring run-off of snow melt swells streams and periodically results in catastrophic floods downstream. Avalanches are generally restricted to the higher elevations above the mixed-conifer zone, but occasional avalanches at lower elevations create debris zones that provide sources for insect outbreaks (Kattelmann, 1996). The southern province is still uplifting in relation to plate motions of the San Andreas fault. Volcanic eruptions have occurred as recently as the 1800s in the central part of the range. In the past decade several areas in the central region near Mammoth Lakes have experienced total tree kill due to high soil CO_2 levels related to volcanic activity. Most of these events have been small and local relative to the entire area occupied by the Sierras, but at the decade or century scale, few areas of the Sierras have escaped the influence of natural disturbances.

There are strong environmental links between tree disease organisms, wood chewing insects, and drought. The activities of insects and microbial disease organisms have significant effects on the structure of mixed-coniferous forests and ecological processes. Although the roles of insects and microbes—such as pollination, nutrient cycling, food sources, and vectors of disease—are critical to the function of forest ecosystems, episodic outbreaks have resulted in the loss of large patches of trees and shifts in species composition when host-specific epidemics occur. Both the abiotic environment and the biological activity of these organisms are inextricably linked in ways that are becoming more distinguishable. Compounding these effects are the effects of air pollution on individual trees and ecological function (SNEP Science Team, 1996).

8.1. Drought

The shrublands, grasslands, and forest ecosystems are well adapted to the annual cycle of wet winters and dry summers. However, nearly every decade has been punctuated by one or more dryer than normal years (Graumlich, 1993), with the most recent episode occurring between 1987 and 1992. The stress incurred by the dry conditions may kill trees directly, but more often leaves them vulnerable to insect and pathogen attack. The recurrence of periodic droughts through time has been recorded in pollen records, tree rings, and fire scars (e.g., Anderson, 1990; Stine, 1994). However, little instrumental data exists before 1900.

Most soil water available for growth in mixed-conifer forests is in the form of snow. Early snowfall insulates soils from freezing, which allows for some percolation of melt water, extends the growing season, and allows trees to prepare for the winter season by storing metabolites for spring regrowth. Many conifers remain photosynthetically active during the winter (Havranek and Tranquillini, 1995). As the snow melts in the spring, soil water is restored by percolation of melt water. By early to mid-summer most soil water is depleted, but pines and other tree and shrub species may exploit water reserves trapped in fractured bedrock (Hubbert et al., 2001). In "normal" years the depletion of soil water coincides with completion of the annual growth flush. Where snowfall is low for several consecutive years, the recharge of the soil water is low and the growth potential is slowed. When several dry winters occur sequentially, mortality increases, particularly in highly competitive, overly dense stands, or stands with pre-existing damage or stresses. After the 1987–1992 drought, the Forest Service estimated tree loss at more that 2 billion board feet, especially on the east side of the range where mortality reached 80% of the standing volume in some areas (USDA Forest Service, 1994). Forest management activities such as logging can alter soil hydrologic properties at a small scale, and fire exclusion contributes to increased mortality by incidentally encouraging stands of less drought resistant firs and denser stands of pines (Aber et al., 2000). However, the episodic loss of trees and stands due to drought is a normal part of the ecological cycle.

9. Biological disturbances

Insects and pathogens are generally considered part of the natural cycle in Sierran ecosystems. In the mixed-conifer forests, bark beetles, mistletoes, root diseases, and white pine blister rust are the key insects and pathogen pests that attack conifers. Of these, only white pine blister rust (*Cronartium ribicola*) is an introduced species. It primarily attacks *Pinus lambertiana* in mid-elevations but has been recently observed in *P. monticola* and *P. albicaulis* in the subalpine forest (Ferrell, 1996). Annosus root disease, black-stain root disease, and armillaria root disease are somewhat host specific; and although they do not generally kill trees directly, they do predispose trees to subsequent attack by bark beetles. Mistletoes also tend to weaken trees, which results in beetle infestations. The most serious pests in mixed-conifer forests are the bark beetles. Western pine beetle, pine engraver, and mountain pine beetles are the most prevalent; but fir engraver, Douglas-fir beetle and Jeffrey pine beetles contribute to mortality in *Abies concolor, Pseudotsuga menziesii,* and *Pinus jeffreyi,* respectively (Ferrell, 1996). All of the pests usually function as members of biotic complexes (USDA Forest Service, 1994). In many cases, infection by a pathogen weakens trees, making them susceptible to secondary attack by beetles. An increasing body of literature indicates that beetles specifically seek out trees weakened by biotic or abiotic stresses.

9.1. Insects

The most damaging insect family in Sierran conifers is the bark beetle. Several species that are either host-specific or generalists are common. The Jeffrey pine beetle (*Dendroctonus jeffreyi*) breeds almost exclusively in *Pinus jeffreyi*; the Douglas-fir beetle (*Dendroctonus pseudotsugae*) is exclusive to *Pseudotsuga menziesii*; and the western pine beetle (*Dendroctonus brevicomis*) attacks *P. ponderosa*. Fir engravers (*Scolytus ventralis*) attack most fir species, including *Abies concolor*, *A. magnifica*, and granf fir (*Abies grandis*). The mountain pine beetle (*Dendroctonus ponderosae*) breeds in most of the mixed-conifer pine species. Bark beetles are always present in the forest and are an important component in the normal ecological processes. Typically they breed and subsequently kill trees that are decadent, diseased, weakened by lightning and fire damage, or experiencing reduced growth because of site condition. Beetles often infest downed trees after wind throw, avalanches or floods and the debris piles from these events have been identified as local sources for several large-scale outbreaks. Beetles, particularly the larvae, are important food sources for several bird species and a number of predatory insects (Ferrell, 1986).

All major bark beetle species operate in the same manner. Adults emerge from larval galleries in the spring or summer and search for susceptible hosts. The attack begins by boring through the bark into the cambial layer of a tree. Many attacks are unsuccessful. In healthy pines and firs, the tree responds by exuding pitch, which either pushes the adult out, (referred to as “pitching-out”) or blocks its progress. Even when the adult successfully reaches the cambium and begins excavating egg chambers and laying eggs, trees can respond by filling the chambers with pitch, effectively entombing the eggs. When an attack is successful, the female excavates a tunnel and lays her eggs. The larvae hatch in one to several weeks and begin excavating galleries that are generally perpendicular to egg chambers. The specific pattern laid down by the female and the subsequent direction of the larvae excavations are often characteristic to the species. Damage to the tree occurs by two primary mechanisms. The first mechanism is simply girdling the tree or a major branch, as the larvae eat their way through the wood. The alternative source of mortality is secondary fungal infection. As the female excavates the egg gallery, fungal spores can be left behind serendipitously; or in the case of the western pine beetle, the females have a special pouch-like structure attached to head that contains spores of blue-stain fungus. As the female chews through the wood, spores are dislodged and germinate.

Minor attacks may not kill trees. But at least two species, western pine beetle and the fir engraver, are known to release pheromones upon successful attack that attracts other beetles to the same trees (DeMars and Roettgering, 1982; Ferrell, 1986). Thus, a single tree may be host to a large infestation, leaving other trees in the stand unaffected.

All major bark beetles have caused serious outbreaks resulting in severe tree mortality. The fir engraver, for example, was responsible for the loss of 1.2 million trees in the Sierras between 1977 and 1978 (Ferrell, 1986). In 1923 a major storm event in the Inyo National Forest caused a large blowdown that was the incubator for serious outbreak of Jeffrey pine beetle. In the next 3 years, more that 13 million board feet of Jeffrey pines on 32,000 acres were lost. Western pine beetle can kill millions of trees in a year during serious outbreaks.

Episodic insect kills are considered natural events, but the current high levels of infestation and mortality are a concern for forest managers in planning for long-term sustainability. Since many insects and pathogens can only inflict serious injury on trees already experiencing environmental stress, serious outbreaks are increasingly being interpreted as symptoms of existing stress, rather than the cause of poor forest health (Wickman, 1992). Drought, fire, logging, urbanization (and the fragmentation, human contact, and opportunity for spread of infectious agents associated with urbanization), and air pollution are key abiotic factors that interact with biological pests. Fire weakens trees making them susceptible to insect and pathogen infestation; once outbreak occurs, dead and dying trees provide fuel for fires. After large catastrophic fires, natural and plantation reestablishment of forests can create overly dense stands where competitive stress among individuals weakens trees. This condition is exacerbated by fire exclusion. Overly dense stands appear to be one of the primary starting places for outbreaks of disease and insect pests. Past logging practices in conjunction with fire exclusion have also resulted in densification of the native forests.

10. Summary

Sierra Nevada landscapes are constantly changing. Episodic events such as fires, floods, and pathogen outbreaks exist in a background of global shifts in climate and tectonic activity. Human activity, either directly or indirectly, has the potential for altering the direction of natural processes. Of all of the many ecologically modifying activities, air pollution may be the most insidious. Although rarely catastrophic in nature, increasing evidence suggests that air pollution may exacerbate drought conditions, modify nutrient cycling processes, and contribute to shifts in species composition. A better understanding of transport, concentrations, and distributions of anthropogenic air pollutants is essential to evaluating their effects, and ultimately, protecting critical resources.

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