

# Montane and Subalpine Vegetation of the Sierra Nevada and Cascade Ranges

JO ANN FITES-KAUFMAN, PHIL RUNDEL,  
NATHAN STEPHENSON, AND DAVE A. WEIXELMAN

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### Introduction

Montane and subalpine coniferous forests and other vegetation of the Sierra Nevada comprise one of the largest and most economically important sets of ecosystems in California. This region includes most of the area of both the eastern and western slopes of the Sierra from 600 to 1,500 m at its lower margin to 3,000 to 3,500 m at its upper limit. There has been a large and visible increase in research on Sierran vegetation since the original publication of *Terrestrial Vegetation of California* in 1977.

Over 90% of the entire Sierra Nevada was classified as vegetated, according to a GAP analysis by Davis and Stoms (1996). Areas classified as nonvegetated included lakes, rock outcrops, urban areas, and alpine areas with little or no vascular plant cover. In the southern Sierra Nevada, less than half the ground surface within the montane and subalpine zones is dominated by forest vegetation (Richards 1959). The remaining area includes lakes, wetlands, rock outcrops, talus slopes, meadows, and montane chaparral. Vegetation cover drops with increasing elevation, from 70%–100% in montane forests to <25% in subalpine forests (Vankat 1970). Across the full region of the Sierra Nevada, Cascade Range, and Modoc Plateau included in this chapter, lower montane mixed conifer and eastside pine encompass over half of the landscape (Table 17.1). Upper montane and subalpine vegetation comprise one-third of the area.

General patterns of vegetation vary with elevation, latitude, and location relative to the crest of the Sierra Nevada.

TABLE 17.1

Distribution of Forest Types in the Sierra Nevada, Cascade Range, Modoc Plateau, and Warner Mountains of California

Major Upland Forest Type	Area (ha)	Percentage of Area
Westside mixed conifer	1,674,395	33
Red fir	693,903	14
Jeffrey pine	159,687	3
Subalpine woodland	951,751	19
Eastside pine	1,304,731	25
Eastside mixed conifer and/or white fir	334,632	7

NOTE: Adapted from Table 21.3 in Franklin and Fites-Kaufman (1996).

Along the lower slopes to the west of the crest, forests dominate the landscape. The lower montane zone is composed of ponderosa pine–mixed-conifer (*Pinus ponderosa*) forest at lowest elevations and white fir–mixed conifer (*Abies concolor*) forest at somewhat higher elevations, including isolated groves with giant sequoia (*Sequoiadendron giganteum*). In the northern Sierra Nevada, Douglas-fir (*Pseudotsuga menziesii*) is prevalent, broadly overlapping with both ponderosa pine and white fir. Black oak is important throughout the lower elevations of the lower montane forests. Canyon live oak (*Quercus chrysolepis*) occurs in extensive patches in large, steep canyons. Tanoak (*Lithocarpus densiflorus*) is prevalent in areas of high precipitation in the northern Sierra Nevada. To the east of the crest and in the Kern River basin, Jeffrey pine (*Pinus jeffreyi*) replaces or mixes with ponderosa pine, sugar pine (*P. lambertiana*) is rare or absent and incense cedar (*Calocedrus decurrens*) is less common. Chaparral is common in the interface with the foothill woodlands at the lowest elevations but decreases in importance at higher elevations. Patches of nonforested vegetation are typically restricted to rock outcrops or sites that have had high severity fire or land use. Meadows or herbaceous-dominated sites occur but are limited in distribution on the west slopes but may be prevalent on the eastern slopes.

Above the lower montane zone, and forming a transition to the higher subalpine zone, is the upper montane zone comprised of a mosaic of conifer forest, meadows, and montane chaparral. On the western slopes and portions of the eastern slopes, red fir (*Abies magnifica*), Jeffrey pine (*Pinus jeffreyi*), and lodgepole pine (*Pinus contorta* subsp. *murrayana*) are the dominant forest species. White fir often broadly overlaps with these species. On the eastern slopes, red fir is less consistently present and often replaced by white fir.

The subalpine zone has a lower proportion of forested vegetation than the lower or upper montane zones. Nonforested vegetation dominates the landscape. Subalpine forests include several geographically restricted associations dominated by mountain hemlock (*Tsuga mertensiana*), western white pine

(*Pinus monticola*), whitebark pine (*P. albicaulus*), foxtail pine (*P. balfouriana*), and limber pine (*P. flexilis*). East of the crest, dominant vegetation also changes with elevation, but species composition differs from slopes west of the crest. Red fir is more restricted or absent in portions of the range east of the crest.

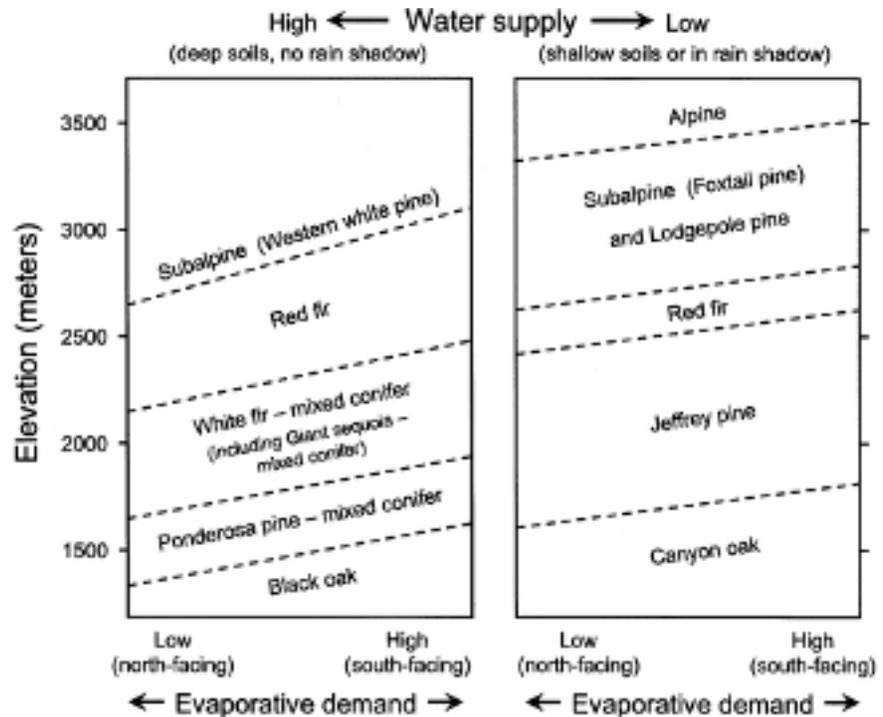
### Environmental Controls of Vegetation Distribution

Climate is the master controller of the distribution of vegetation types in the Sierra Nevada. In past studies, climatic controls of Sierran vegetation distribution have been summarized implicitly in diagrams in which the ordinate represents elevation; the abscissa, a moisture gradient (Rundel, Parsons, and Gordon 1977; Vankat 1982). In these diagrams, elevation serves as a surrogate for several climatic factors that change in concert with elevation (Fig. 17.1). The moisture gradient, in turn, represents local topographic or edaphic modifications on site water balance, such as those controlled by slope aspect, slope steepness, proximity to water, soil porosity, and depth to bedrock.

Some key features of the elevational climatic gradient for the forested zone of the Sierra Nevada can be summarized as follows. Though these data come from the southern Sierra Nevada, patterns are qualitatively similar throughout the range. Mean annual temperature declines relatively steeply with elevation, from ~12°C at 1,400 m elevation (near lower treeline, upper chaparral, and woodland limits) to ~1°C at 3,400 m (near upper treeline; Stephenson 1988). In contrast, mean annual precipitation changes relatively little with elevation in the forested zone, from ~1,050 mm at 1,400 m elevation, peaking at ~1,400 mm at about 2,000 m elevation, then declining slightly with increasing elevation beyond 2,000 m. However, the fraction of annual precipitation that falls as snow increases greatly with elevation, from only 20% to 25% near lower treeline (upper chaparral and woodland) to >95% at upper treeline (Stephenson 1988). Compared to lower elevations, the deeper snow pack and cooler temperature at higher elevations mean that snowmelt is completed later in the spring. Coupled with cooler temperatures and hence lower evaporative demand at higher elevations, this means that as elevation increases in the Sierra Nevada, the length and magnitude of the summer drought period experienced by plants decrease sharply (Stephenson 1998; Urban et al. 2000).

Unlike the elevational climatic gradient, previous characterizations of local moisture gradients have proven to be inadequate. Specifically, they failed to recognize the intrinsically different effects of evaporative demand and water supply on plant distributions (Stephenson 1998). For example, the “dryness” experienced by plants on south-facing slopes (high evaporative demand) is physiologically different from the “dryness” experienced by plants on shallow soils (low water supply), and these differences are reflected in the vegetation. The point is illustrated by a concrete example from the western slope of the southern Sierra Nevada. At roughly 1,800 m elevation, a north-facing slope with deep soils will likely be occupied by white fir–mixed

FIGURE 17.1 The approximate distribution of forest types in the southern Sierra Nevada relative to elevation, evaporative demand, and water supply. Only upland forest types (away from open water and meadow edges) are shown. Forest types intergrade extensively, so that boundaries between types are not sharply defined. In particular, intergradation between foxtail pines and lodgepole pines is so extensive that no boundary between the two types is shown, though foxtail pines dominate at the highest elevations; lodgepole pines, at lower elevations. Because deep soils able to retain abundant water disappear at high elevations, no upper treeline is indicated in the high water supply diagram. Modified from Stephenson (1988).



conifer forest. At the same elevation, a site that is “dry” due to a southern aspect is likely to support ponderosa pine–mixed conifer forest, whereas a site that is “dry” due to shallow soils is likely to support Jeffrey pine forest (see Fig. 17.1; see also Stephenson). The moisture gradient must therefore be decomposed into two separate gradients, reflecting evaporative demand and water supply.

In the Sierra Nevada, local topographic effects on evaporative demand (such as those determined by slope aspect) mostly influence the elevation at which different forest types are found (see Fig. 17.1). On average, a given forest type is found roughly 200 m higher on a steep south-facing slope than on a steep north-facing slope. Similar patterns have long been known from other mountain ranges, where vegetation types often occur at higher elevation on sunward slopes than on shaded slopes (see the citations in Stephenson 1998).

In contrast, local effects on water supply (such as those determined by soil depth or rain shadows) have little influence on the elevation of forest types. Instead, differences in water supply yield entirely different suites of forest types (Stephenson 1998). For example, on the western slope of the southern Sierra Nevada forests growing on deep soils tend to be dominated by firs. In contrast, forests experiencing reduced water supply, whether due to shallow soils or rain shadow effects, tend to be dominated by pines.

Factors affecting local site water balances operate across a broad range of spatial scales, contributing to complexity in the mosaic of vegetation types found in the Sierra Nevada (Urban et al. 2000). At scales of hundreds of kilometers for a given elevation, temperature decreases and precipitation increases from south to north in the range. Rain shadows

can affect vegetation patterns at scales of tens of kilometers, whereas soil depth can affect patterns at scales down to a few meters. Complexity is also added by the apparent competitive displacement of species from portions of otherwise broad habitat ranges. For example, on the moist western slopes of the Sierra, lodgepole pine tends to occupy extremes: either dry, rocky outcrops, or moist meadow edges. It is apparently displaced from deep, well-drained upland soils by red fir. At similar elevations in a rain shadow, red fir drops out and lodgepole pine occupies deep upland soils as well as meadow edges.

The north–south gradient in Sierran climate is partly a function of the location and annual migration of the jet stream (Minnich and Padgett 2003). The mean location of the jet stream lies in northern California and the Pacific Northwest, resulting in a pattern of increasing average annual precipitation from south to north in the Sierra Nevada. A north–south gradient of ambient temperature also occurs but is most prevalent during the winter. Elevations of the topographic crest increase from 2,000 m southeast of Mt. Shasta to 3,000 m at Lake Tahoe, and exceeding 4,000 m in Sequoia National Park. Broad patterns of vegetation are apparently related to these climatic gradients from north to south. Several dominant species in the relatively wetter north, for example, tanoak and Douglas-fir, are absent or sparse in the southern Sierra. The landscape distribution of other widely distributed species, such as ponderosa pine, varies from north to south along the western slopes of the Sierra. In the southern Sierra it dominates on all aspects, whereas in the northern Sierra it is often displaced by Douglas-fir on north- or east-facing aspects and lower slopes.

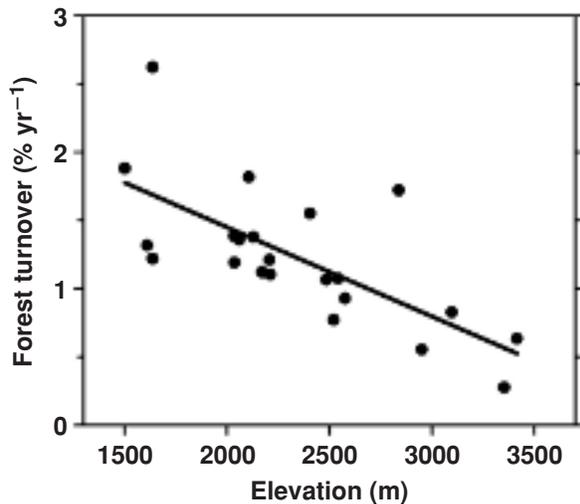


FIGURE 17.2 Forest turnover rate (the average of mortality and recruitment rates) declines with increasing elevation in the Sierra Nevada. Data are for all trees taller than breast height (1.4 m) in 22 long-term monitoring plots in Yosemite and Sequoia national parks. Redrawn from Stephenson and van Mantgem (2005).

Just as the elevational climatic gradient strongly controls the distribution of forest types, it also controls the pace of forest population dynamics. Tree mortality rates in undisturbed old-growth forests of the Sierra Nevada decline sharply with increasing elevation, as do tree recruitment rates. Thus, low-elevation forests (such as ponderosa pine–mixed-conifer forest) are the most dynamic, with turnover rates of trees taller than breast height (1.4 m) approaching 2% per year (Fig. 17.2). Forests near treeline (such as whitebark pine and foxtail pine forests) are the least dynamic, with tree turnover rates as low as 0.5% per year. Turnover rates of seedlings (<1.4 m tall) are higher, declining from about 10% per year at low elevations to 2.5% per year at high elevations (van Mantgem et al. 2006). The strong decline of forest turnover with increasing elevation may be related to parallel declines in forest productivity (Stephenson and van Mantgem 2005).

### Agents of Change

#### FIRE

Fire is one of the great shapers of the forested zone of the Sierra Nevada, perhaps surpassed in importance only by climate. Before the middle 1800s, fire-return intervals varied from a few years in low-elevation forests (black oak woodlands and ponderosa pine–mixed conifer forests) to 200 years or more in high subalpine forests (Fig. 17.3); Skinner and Chang 1996; Caprio and Lineback 2002; van Wagten-donk and Fites-Kaufman 2006). Fires were most widespread in drought years (Swetnam and Baisan 2003), typically with the greatest area burning from mid-summer through fall (Caprio and Swetnam 1995). Centennial-scale warm periods were associated with many small fires, whereas extended

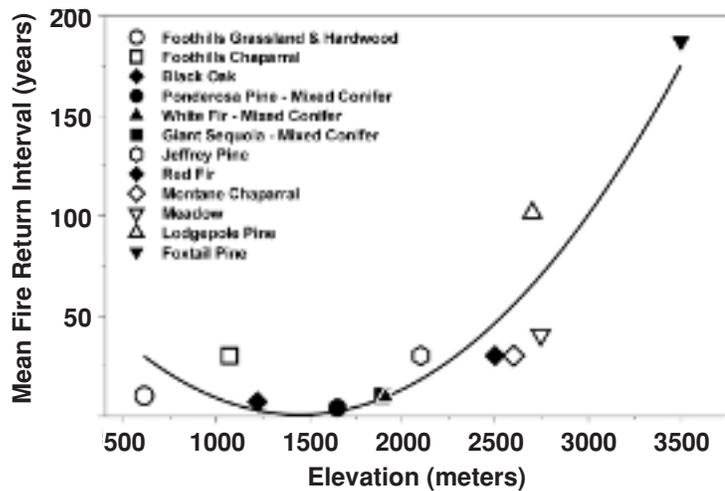
cool periods were associated with fewer and larger fires (Swetnam 1993). Although there is no doubt that many fires were ignited by Native Americans (Anderson and Moratto 1996), ignitions by Native Americans may not have been uniform across the landscape and lightning may have accounted for most ignitions in more remote areas (Vale 1998).

Historic patterns of fire and vegetation interactions varied throughout the Sierra Nevada (van Wagten-donk and Fites-Kaufman 2006). One of the fundamental outcomes of historic fire was heterogeneity in vegetation structure at within-stand to landscape scales. Forests often consisted of a heterogeneous mosaic of differing ages, vegetation structures, and species composition (Bonnicksen and Stone 1982; Fites-Kaufman 1997; Taylor 2004; North et al. 2004). Variation in fire patterns and effects at the scale of clumps of trees to small patches (majority less than 1 ha) created or modified forest gaps that were an integral part of the landscape (Bonnicksen and Stone; Stephenson et al. 1991). Trees within these patches are often multiaged (North et al. 2004), which may result from top-down effects of fire and El Niño events interacting with bottom-up site differences and species regeneration preferences (North et al. 2005a). Before the middle 1800s, forests experiencing frequent fires (such as ponderosa pine-, white fir-, and giant sequoia-mixed conifer forests) are thought to have been relatively open in structure across much of their distribution, particularly in the southern portions and eastern slopes of the Sierra Nevada (Kilgore 1973; Vankat and Major 1978; Parsons and DeBenedetti 1979; Stephenson 1996, 1999; Taylor 2004). In the relatively wetter northern Sierra Nevada, greater variation in forest density apparently occurred, corresponding in part with variation in fire (Fites-Kaufman 1997; Franklin and Fites-Kaufman 1996). In higher elevation forests with longer fire-return intervals (such as lodgepole pine or red fir forest), fires sometimes created forest gaps covering tens or even hundreds of hectares (N. Stephenson personal observation). However, large, uniform forest patches were by no means universal, and much of the forested landscape at high elevations retained a generally fine-scale patchiness similar to forests at lower elevations (Parker 1986).

Fire also played a role in the spatial pattern and landscape importance of nonconiferous forest vegetation components, especially shrubs, chaparral, and hardwoods (van Wagten-donk and Fites-Kaufman 2006). Patches of shrubs occurred more frequently at fine scales in many forest types, particularly where sprouting shrubs were present. Larger patches of shrubs (montane chaparral) occurred, especially at mid and higher elevations where white fir and red fir dominated nearby forests (Conard and Radosevich 1982; Leiburg 1902; Russell et al. 1998). Similarly, fire played a role in perpetuating black oak interspersed in mixed conifer forests or as large monotypic patches.

With the arrival of Euroamerican settlers and subsequent livestock grazing, fire suppression, and loss of Native American fire use, fire frequency plummeted. For example, for

FIGURE 17.3 Relationship between mean fire-return interval and elevation in the Sierra Nevada before the middle 1800s. Confidence in the fire-return intervals varies among vegetation types and is highest for the ponderosa pine-, white fir-, and giant sequoia-mixed conifer forests. Figure courtesy of Tony Caprio, modified from Caprio and Lineback (2002.)



much of the landscape in Sequoia and Kings Canyon National Parks the median date of last fire was 1875 (Caprio et al. 2002), followed by an unprecedented fire-free interval. Fire exclusion led to several notable changes in forests, particularly in the ponderosa pine-, white fir-, and giant sequoia-mixed conifer forests (Vankat and Major 1978; Parsons and DeBenedetti 1979; Stephenson 1996; Taylor 2004; van Wagtenonk and Fites-Kaufman 2006). For example, giant sequoia reproduction, which in the past depended on frequent fires to expose mineral soil and open gaps in the forest canopy, effectively ceased, and reproduction of other shade-intolerant species such as ponderosa pine was reduced.

Forests became denser in many areas, with increased dominance of shade-tolerant species such as white fir and incense cedar (Parsons and DeBenedetti 1979; Bouldin 1999). More area came to be dominated by dense intermediate-age forest patches (Bonnicksen and Stone 1982; Stephenson 1987). Shrubs and herbaceous plants became less abundant than in the past (Kilgore and Biswell 1971; Harvey et al. 1980). Perhaps most importantly, dead material accumulated, causing an unprecedented buildup of surface fuels (Agee, Wakimoto, and Biswell 1978; van Wagtenonk 1985). Additionally, "ladder fuels" capable of conducting fire into the crowns of mature trees increased (Kilgore and Sando 1975; Parsons and DeBenedetti 1979). One of the most immediate consequences of these changes was an increase in severity of wildfires that was rarely encountered in pre-Euroamerican times (Kilgore and Sando 1975; Stephens 1995, 1998; van Wagtenonk and Fites-Kaufman 2006).

#### INSECTS AND PATHOGENS

Native bark beetles are the proximate cause of the majority of natural tree deaths in the Sierra Nevada (Ferrell 1996). Most often, beetles kill trees that were already stressed by drought, root disease, dwarf mistletoe infestation, or air pollution. A potential additional source of predisposing stress is increased forest density, brought about by fire exclusion

(Smith, Rizzo, and North 2005) and some logging practices (Sherman and Warren 1988; Ferrell; Barbour et al. 2002).

Among the native fungal root diseases, the most important are annosus root disease, armillaria root disease, and black-stain root disease (Ferrell 1996). Annosus root disease in particular is thought to be spreading more easily in overly dense forests resulting from fire exclusion (Slaughter and Rizzo 1999; Rizzo and Slaughter 2001). Additionally, cut stumps often prove to be the establishment points for the disease.

Of particular concern is white pine blister rust, an epidemic disease introduced from Asia. Blister rust attacks five-needled pines, and has now been found in all five-needled pine species in the Sierra Nevada. However, the first and most severely affected species in the Sierra Nevada is sugar pine, often the second or third most abundant tree species in mixed-conifer forests. Combined with other stresses, blister rust has been contributing to a long, steady decline in sugar pine populations, which is expected to continue into the future (van Mantgem et al. 2004).

#### WIND AND AVALANCHES

Compared to much of the rest of North America, wind is a less important force shaping forests of the Sierra Nevada. However, forest edges or substantially thinned forests (whether created by logging, fire, avalanche, or other cause) tend to be vulnerable to windthrow (Fosberg 1986). Wind can affect upper montane forests significantly, although it is not clear how much of the current patterns are confounded by thinning.

Avalanches are rare in lower elevation forests (such as the mixed-conifer forests; but see Fry 1933), instead tending to be most common in red fir, lodgepole pine, and subalpine forests (Kattelman 1996). Avalanches are most common on steep, north-facing slopes at these elevations, and often recur in given locations (avalanche paths). A moderate recurrence interval (every few decades) tends to result in dominance by aspen rather than by conifers; more frequent

recurrences can lead to avalanche paths that are chronically free of trees.

#### LOGGING

The number of large trees in the Sierra Nevada has declined significantly since the arrival of Euroamerican settlers (USDA Forest Service 2001). For example, in white fir-mixed conifer forests of the central and northern Sierra Nevada during the 57-year period from about 1935 to 1992, numbers of trees greater than 24 inches (61 cm) in diameter declined by 60% (Bouldin 1999). Trees >36 inches (91 cm) in diameter declined by >80%. Though all mixed-conifer species have been affected, declines have been most severe for large pines (ponderosa pine and sugar pine).

Bouldin (1999) attributed these declines mostly to logging, but also cited forest stress—caused by increased densities of small trees—as a contributing factor (see also Smith et al. 2005). Additionally, white pine blister rust, though most deadly to small trees, may have contributed to the decline in larger sugar pines.

Years of logging and losses of large trees have resulted in a significant rangewide decline in the area occupied by structurally complex old forest, particularly in the commercially valuable mixed conifer forests (Franklin and Fites-Kaufman 1996). The national parks of the Sierra Nevada and southern Cascades (Lassen, Yosemite, Sequoia, and Kings Canyon) contain some of the most extensive remaining tracts of old forest. According to General Land Office Survey Records from the late 1800s, much of the coniferous forests had large trees present across more than 50% to 70% of the landscape (USDA Forest Service 2001). Currently, estimates range from 5% to 15% for most forest types.

The exact progression of decline is poorly known both for changes in the early settlement period as well as more recent. The pattern varied by accessibility and factors influencing use, such as mining activity. For example, in the 1940s in the central and northern Sierra (Placer County through Plumas County) the proportion of remaining old growth in the pine belt was estimated to be 38% overall but ranged from 1% to 68% within individual sections (Weeks et al. 1942). Another variable in logging historically has been changing economic values of individual species. As late as the early 1960s, pines were logged preferentially over firs, which were considered to be of lower value (McKelvey and Johnston 1992; Beesley 1996).

#### AIR POLLUTION

Some of the worst air pollution in the United States is found periodically along the western flank of the Sierra Nevada, especially in the south (Peterson and Arbaugh 1992; Cahill et al. 1996; Bytnerowicz et al. 2003). Ozone is the most damaging air pollution constituent, particularly affecting ponderosa pine and Jeffrey pine. Ozone-sensitive individuals of these pines show extensive foliar injury at present ozone levels in the southern Sierra Nevada (Peterson and

Arbaugh; Duriscoe and Stolte 1992; Patterson 1993; Miller 1996; Bytnerowicz, Arbaugh, and Alonso 2003). Compared to ozone-resistant individuals, ozone-sensitive pines have lower photosynthetic rates, lose their needles earlier, and have diminished annual ring growth (Patterson and Rundel 1995; Miller). Smaller trees are the most severely affected. Pines in Sierra Nevada east of Fresno, particularly in Grant Grove and Giant Forest of Sequoia and Kings Canyon National Parks, show some of the most severe ozone damage in the Sierra Nevada (Peterson and Arbaugh; Duriscoe and Stolte 1992). Patterson and Rundel found that nearly 90% of Jeffrey pines in or near the Giant Forest sequoia grove showed visible signs of ozone injury; however, they ranked only 10% of the pines as showing severe injury.

Pines stressed by air pollution (compounded by crowding caused by fire suppression) are generally more susceptible to fatal insect attacks. In the face of chronic ozone pollution, they may continue to decline as they have in the Los Angeles basin to the south (Miller 1973, 1996; Ferrell 1996).

#### Lower Montane Vegetation

Lower montane vegetation is dominated by forests. These forests are often classified in varied ways but most broadly referred to as Sierra mixed-conifer forests. The dominant tree species—including ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and white fir (*Abies concolor*)—have broadly overlapping distributions that contribute to multiple, often imprecise systems of classifications. For example, in the central Sierra Nevada, Douglas-fir co-occurs with white fir in a broad zone. The distribution of ponderosa pine extends below Douglas-fir and up through much of the range of white fir. A high degree of local spatial diversity in occurrence of these dominant and other common trees—including sugar pine (*Pinus lambertiana*), incense cedar (*Calocedrus decurrens*), and black oak (*Quercus kelloggii*)—lead to highly varying mixtures of dominant species in any one site, particularly the size of most sample plots. In the *Manual of California Vegetation*, Sawyer and Keeler-Wolf (1995) described nine different tree series within the lower montane forest of the Sierra Nevada. Here we take a broader approach, recognizing the largely overlapping patterns of dominant tree distributions.

#### PONDEROSA PINE AND DOUGLAS-FIR-MIXED CONIFER

Ponderosa pine-mixed conifer forests dominate much of the lower montane zone (Fig. 17.4). In the northern Sierra, this belt may occur from 300 to 1,800 m (rarely higher, as around Lake Tahoe and northward), whereas to the south at Sequoia-Kings Canyon National Parks, it can range from 1,200 to 2,100 m. At middle and higher elevations, ponderosa pine forest co-occurs or is replaced by white fir forest, or in the northern Sierra by Douglas-fir on north- or east-facing slopes at lower elevations (Tables 17.2 and 17.3). Tanoak occurs in scattered locations from Eldorado County north



FIGURE 17.4 Stand of ponderosa pine, west slope of the central Sierra Nevada, approximately 1,000 m. Photograph courtesy of Jerry F. Franklin.

to the Yuba and Feather River basins, where it forms dense stands with variable amounts of ponderosa pine, Douglas-fir, or sugar pine where average annual precipitation is greater than 1,550 mm (Fites 1993).

At its lowest margin, ponderosa pine forest intermingles with chaparral. Stands of black oak or individuals of ponderosa pine and incense cedar may occur well down into chaparral and foothill woodlands on favorable sites, often deeper soils or drainages in the southern Sierra and north-facing aspects in the northern Sierra. Individual trees of ponderosa pine and incense cedar often occur along streams well below the normal lower forest limit. Throughout the Sierra Nevada large stands of canyon live oak (*Quercus chrysolepis*) dominate steep canyons. Ponderosa pine or Douglas-fir often occur interspersed with canyon live oak as individuals or small stands where soils are deeper. On shallower soils, in rain shadows (such as on the eastern flank of the Sierra Nevada), and at higher elevations, ponderosa pine is replaced by Jeffrey pine (*Pinus jeffreyi*). Within the elevation zone where ponderosa and Jeffrey pines overlap, hybrids occur (Haller 1962) but not consistently (pers. observation). Another high-elevation yellow pine, washoe pine (*Pinus washoensis*), is scattered in widely separate

stands along the eastern slope of the northern Sierra Nevada, Warner Mountains, and adjacent Great Basin ranges (Griffin and Critchfield 1972).

The characteristic structure and composition of ponderosa pine-mixed conifer forest are determined primarily by moisture and fire history. In the central Sierra (Fites-Kaufman 1997), topographic position and soil moisture influenced the importance of ponderosa pine and other co-occurring species. Fites-Kaufman found that ponderosa pine cover in remnant stands had strong positive correlations with potential annual solar radiation index (PASI) and negative association with lower one-third slope positions. Black oak was positively associated with upper slope positions. Douglas-fir was negatively associated with PASI. Fites-Kaufman also reported differences in fire-return interval averages and distributions related to topography and composition. North- and east-facing slopes and lower slopes had longer average fire return intervals, greater variation between intervals and a higher proportion of Douglas-fir. Ponderosa pine was often present in low amounts or absent. In the southern Sierra, ponderosa pine occurs more evenly across all aspects, perhaps reflecting either the absence of Douglas-fir or generally drier conditions (Stephenson 1998).

Shade tolerance, drought tolerance, and response to fire of dominant tree seedlings are important factors governing the composition and successional patterns in lower montane forests. Seedlings of ponderosa pine are intolerant of shade in comparison to Douglas-fir, white fir, incense cedar, and sugar pine (Fowells and Schubert 1951; McDonald 1976; Oliver and Dolph 1992; York, Battles, and Heald 2003), resulting in poor establishment of ponderosa pine in dense stands (Liliehalm et al. 1990; Fites 1993). Sugar pine, similarly to ponderosa pine, shows low growth rates in dense shade, but with moderate shade can have growth rates as high as the more shade-tolerant white fir and Douglas-fir (Oliver and Dolph 1992). Typically, ponderosa pine increases in relative density as total stand density decreases, whereas the reverse relationship is typical for white fir, incense cedar and sugar pine (Sellers 1970). Under appropriate conditions, ponderosa pine can grow to very large size in the Sierra, with trees reaching heights of 69 m and diameters up to 2.8 m (Van Pelt 2001). Ponderosa pine and incense cedar possess greater drought tolerance than white fir or Douglas-fir (Pharis 1966), allowing them to establish and dominate on xeric sites with open canopies.

Black oak, adapted to fire by sprouting from the root crown or epicormic buds, decreases in importance in dense forest stands. Although this oak is moderately shade tolerant in its early stages of growth, it requires full sun for good growth when mature (McDonald 1969). It seems to have been virtually eliminated by shading from dense stands of incense cedar in the Yosemite Valley (Gibbens and Heady 1964). Seedling abundance of black oak can be extremely high in relation to sapling and tree densities. Sellers (1970) counted 8,800 seedlings per hectare in a stand with only

47 saplings and tree oaks per hectare. Seedling density has been found to be related in some stands to the average diameter of surrounding black oaks, apparently due to their greater acorn production (Garrison et al. 2002). Seedling mortality is high, and growth during the first 25 years (ca. 10 cm dbh) is slow, followed by a period of increase in diameter. Growth slows as trees reach maturity at about 90 years, and few trees attain ages in excess of 350 years (McDonald 1969). Although mature black oak is intolerant of poor drainage or relatively mesic soils with poor aeration (McDonald), it is extremely drought resistant and may grow on sites too poor for ponderosa pine (Sellers 1970). It is often found in mixed stands with canyon live oak on poor soils and steep slopes in large canyons.

Fire tolerance of seedlings of tree species common in the ponderosa pine belt differ (van Wagtenonk 1983). Ponderosa pine and black oak are the most tolerant followed by sugar pine, Douglas-fir, incense cedar, and white fir (van Wagtenonk 1983; Kauffman and Martin 1987). This is due in part to the sprouting response of black oak, established at an early age, and bark thickness in the conifers (van Mantgem and Schwartz 2003).

Abundant evidence indicates that incense cedar and white fir have both increased their relative abundance and absolute densities in ponderosa pine forests since the turn of the twentieth century (Vankat 1970; Bouldin 1999). On mesic sites in the northern Sierra white fir, incense cedar, and Douglas-fir may not have changed as much as on more xeric sites (Fites-Kaufman 1997), although understory densities have increased dramatically (Bouldin 1999). Ponderosa pine and sugar pine regeneration has showed a decreasing trend (Ansley and Battles 1998; Gray et al. 2005). At low elevations in ponderosa pine-mixed conifer below the elevational limit of white fir and Douglas-fir, ponderosa pine has persisted as the dominant in the overstory and understory, particularly where a dense understory of *Chamaebatia foliolosa* occurs (Parsons and DeBenedetti 1979; Fites-Kaufman 1997).

Composition and structure in ponderosa pine forests vary, reflecting elevational and latitudinal gradients (Tables 17.2 through 17.5). At the lowest elevations, ponderosa pine and black oak dominate cover, with incense cedar present in varying amounts (Table 17.2). Tree cover ranges from 47% to 97% in ponderosa pine forests and from 60% to 100% in Douglas-fir forests (Table 17.4). In ponderosa-pine-dominated forests on xeric sites, *Chamaebatia foliolosa* often forms a dense, low growing shrub layer, averaging 30% to 78% cover. It is strongly rhizomatous, with deeply buried rhizomes, resprouting readily with fire and competing with conifer seedlings often to the detriment of species other than ponderosa pine. *Arctostaphylos* spp. are also common, with *A. viscida* most prevalent. The herbaceous layer is often sparse, particularly where forest density has increased. *Iris*, *Calochortus*, and *Polygala cornuta* are commonly present.

In contrast, forests on more mesic sites with Douglas-fir tend to have higher tree cover, averaging more than 80%, and a well-developed herbaceous layer (Table 17.4; Fites 1993).

Sugar pine, incense cedar, and white fir are common in both the overstory and the understory, as well as *Cornus nuttallii*. *Acer macrophyllum* occurs near drainages or on rockier soils with shallow subsurface water. *Taxus brevifolia* and *Torreya californica* occur occasionally, particularly in association with mesic drainages or moist soils. The shrub layer is variable in cover, ranging from trace amounts to >50%. Deciduous, shade-tolerant species are most common including *Philadelphus lewisii* at the lowest elevations, and *Corylus cornuta*, *Symphoricarpos mollis*, *Rosa* spp. at middle elevations. *Ceanothus integerrimus* is prevalent where recent disturbances have occurred. The herbaceous layer is not only well developed but often diverse, comprised of shade-tolerant species. The most common include *Adenocaulon bicolor*, *Trientalis latifolia*, *Osmorhiza chilensis*, *Disporum hookerii*, and *Galium triflorum*.

Basal areas range widely from 30 to 215 m<sup>2</sup> ha<sup>-1</sup> (Table 17.5). Similarly, tree densities also vary widely from 64 to 1,165 stems ha<sup>-1</sup>, in part due to different minimum diameters measured. Sellers (1970) reported that trees 60 to 90 cm dbh were 155 to 240 years old in Sequoia-Kings Canyon National Park, but Sudworth (1900) gave ages of 360 to 546 years for the same diameters.

Logging and fire suppression have both resulted in changes in the ponderosa pine and Douglas-fir forests (Vankat and Major 1978; Minich et al. 1995; Chang 1996; Franklin and Fites-Kaufman 1996; Bouldin 1999). Bouldin reported increases in overall tree density and the understory but decreases in density of trees >60 cm dbh. Pine species have been selectively targeted since early European settlement (Franklin and Fites-Kaufman) as well as large trees (McKelvey and Johnston 1992). Changes in density have been reversed where prescribed burning has occurred (e.g., Keifer and Stanzler 1995; Roy and Vankat 1999) but the area burned annually is minor compared to the historic role of fire (McKelvey et al. 1996). Density increases in the southern Sierra and San Bernadino mountains have been greatest on sites with higher precipitation (Minnich et al. 1995).

#### WHITE FIR-MIXED CONIFER

White fir-mixed conifer forest forms the dominant community on relatively deeper soils and higher elevation sites in the lower montane zone of the Sierra Nevada (Fig. 17.5). In the central and northern Sierra it is present on north or east aspects broadly overlapping with Douglas-fir at lower elevations. Depending on latitude, this community occurs from 1,250 to 2,200 m. Although white fir is the dominant species, up to six species of conifers may be present in individual stands—hence the common use of the name “mixed conifer.” This zone can be widely overlapping with the ponderosa pine and Douglas-fir forests discussed previously. In this section, the emphasis is on “mixed-conifer” forests dominated by white fir. Sugar pine and incense cedar are important associates, and giant sequoia may be dominant in terms of basal area in local groves (Rundel

TABLE 17.2  
Composition of Ponderosa Pine Communities in the Sierra Nevada

Cohort and Species	Composition				
	% of Stems/ha			% Cover	
	A	B	C	D	E
Overstory Trees (cm dbh)	>40	>40	>30	>2.5	>2.5
<i>Abies concolor</i>		21	17	5	29
<i>Pinus ponderosa</i>	71	39	48	38	27
<i>Pinus lambertiana</i>		14	4	8	13
<i>Quercus kelloggii</i>	28	23		6	4
<i>Calocedrus decurrens</i>			30	25	20
<i>Pseudotsuga menziesii</i>				11	16
Understory Trees			10–30 cm	<2.5 cm	<2.5 cm
<i>Abies concolor</i>			51	1	5
<i>Pinus lambertiana</i>			14	1	2
<i>Pseudotsuga menziesii</i>				2	1
<i>Calocedrus decurrens</i>			37	10	2
<i>Pinus ponderosa</i>			12	1	1
Understory Shrubs					
<i>Arctostaphylos</i> spp.			5	10	
<i>Ceanothus integerrimus</i>			<1	1	5
<i>Chamaebatia foliolosa</i>			29	51	
<i>Rhamnus crocea</i>			<1	1	
<i>Toxicodendron diversilobum</i>			<1	2	
<i>Rosa</i> spp.			1	1	2
<i>Symphoricarpos mollis</i>					2
Understory Herbs/grasses					
<i>Galium bolanderi</i>				1	1
<i>Iris</i> spp.				2	1
<i>Polygala cornuta</i>				1	1

NOTE: Data are from varied sources including northern, central, and southern Sierra Nevada. Columns a and b are from the General Land Office Survey data from the late 1800s on the western slopes of the Stanislaus, Sierra, and Sequoia National Forests and adjacent lands (n = 40 and 30; Hyde 2002). Column c is from the southern Sierra Nevada, summarized in Minnich et al. (1995) based on Vankat (1970; n = 12). Columns d and e are from data collected in the northern Sierra Nevada during the 1980s (Fites 1993). Column d represents the Chamaebatia type (n = 14); and column e, the Iris-Polygala type (n = 25).

1971). On the eastern slopes of the Sierra, these forests occur on more mesic sites (such as along creeks or north-facing aspects), often replacing Douglas-fir in the north. Composition is shown in Table 17.6 for stands from a variety of areas throughout the Sierra including south, central,

and northern west-slope sites and the Lake Tahoe basin east of the crest. On drier sites at higher elevations, white fir may share dominance with incense cedar or Jeffrey pine. Near the upper margin of the white fir forest, white fir mixes with red fir in transition to red fir communities.

TABLE 17.3  
Composition of Mixed Douglas-fir Forests in the Sierra Nevada

Cohort and Species	Composition								
	% of Stems/ha						% Cover		
	A	B	C	D	E	F	G	H	I
Overstory Trees	>30.5 cm	>30 cm	>24 cm	>40 cm	>30 cm	>30 cm	>2.5 cm	>2.5 cm	>2.5 cm
<i>Abies concolor</i>	46	3	39	44	26	43	42	18	28
<i>Pseudotsuga menziesii</i>	16	16	34	34	7	14	30	50	32
<i>Calocedrus decurrens</i>	14	24	14	14	12	15	16	12	14
<i>Pinus lambertiana</i>	12	5	8	<1	13	6	13	11	17
<i>Pinus ponderosa</i>	4	46	5	<1	22	15		6	18
<i>Pinus jeffreyi</i>	4								
<i>Abies magnifica</i>	4								
<i>Cornus nuttallii</i>							19	14	
<i>Lithocarpus densiflorus</i>								25	14
<i>Quercus kelloggii</i>		6		<1				9	4
Understory Trees			9.5–23 cm	9.5–39 cm	10–30 cm	10–30 cm	<2.5 cm	<2.5 cm	<2.5 cm
<i>Abies concolor</i>				65	32	38	6	1	3
<i>Pseudotsuga menziesii</i>				25	6	12	1	2	2
<i>Calocedrus decurrens</i>				9	13	18	5	2	2
<i>Pinus lambertiana</i>					8	4	1		1
<i>Pinus ponderosa</i>					12	13			
<i>Cornus nuttallii</i>							12	7	
<i>Lithocarpus densiflorus</i>								17	15
<i>Quercus kelloggii</i>								1	2
<i>Acer macrophyllum</i>								1	
Understory Shrubs									
<i>Corylus cornuta</i>								7	
<i>Symphoricarpos mollis</i>								2	
<i>Rosa</i> spp.								2	2

NOTE: Data are from varied sources from the Eldorado north through the Lassen counties. (a) and (b) are from data collected in 1899 by Sudworth (Stephens 2000) with (a) representing a "large" stand (n = 4); and (b) an "average" stand (n = 5). (c) and (d) are from the Plumas National Forest, with (a) circa 1957 and (d) 1996 (Ansley and Battles 1998). (e) and (f) are from the central Sierra Nevada with (e) circa 1935 and (f) 1992 (Bouldin 1999). (g), (h), and (i) are from the Eldorado north through Lassen counties from data collected in the 1980s (Fites 1993). These represent different communities with g mountain dogwood type (n = 22). (h) tanoak-"moist" type (n = 118) and (i) tanoak-"dry" type (n = 22).

The structure of individual stands within white fir-mixed conifer forests is highly variable. This situation is due to the complex dynamics of stand mosaics and variable environmental conditions (North et al. 2002). Vegetation is often comprised of varying size patches of forests of varying

density interspersed with openings dominated by shrubs or herbs. Although previously, patches of forests with similar size trees were thought to be even-aged, detailed spatial patterns of trees in the Teakettle Experimental Forest in the Sierra Nevada suggest that groups of trees are often multiaged

TABLE 17.4  
Mean Canopy Cover (%) by Layer by Plant Community in the Northern and Central Sierra Nevada

Plant Community	Tree	Shrub	Herb	Graminoid	Total
White fir plant associations	92 (51–99)	14 (0–95)	5 (1–88)	2 (0–15)	95 (54–100)
Ponderosa pine associations	87 (47–97)	8 (0–70)	5 (1–18)	3 (0–15)	91 (50–99)
Ponderosa pine/bearclover	78 (50–95)	58 (50–95)	6 (1–45)	3 (1–5)	94 (75–99)
Ponderosa pine-canyon live oak	83 (65–97)	12 (1–44)	14 (1–55)	6 (1–12)	90 (65–99)
Douglas-fir associations	91(70–100)	13 (0–82)	22 (1–88)	4 (0–48)	96 (75–100)
Douglas-fir-tanoak-dogwood	96 (93–99)	6 (0–19)	23 (4–61)	1 (0–6)	98 (94–100)
Douglas-fir-tanoak	88 (60–98)	10 (0–41)	6 (1–18)	2 (0–18)	92 (75–99)
Douglas-fir-canyon live oak	76 (65–85)	2 (1–3)	6 (3–10)	3 (1–5)	87 (70–98)

NOTE: From Fites (1993). Ranges (low–high) of cover are shown in parentheses.

because recruitment patterns differ among species in response to climate and fire (North et al. 2005a).

On typical sites, white fir commonly comprises >70% of the stems or basal area (Rundel 1971; Fites 1993; Minnich et al. 1994; Barbour et al. 2002; Table 17.6). Mature trees of this species are commonly 50 to 66 m in height with diameters up to 2.2 m, and reach ages of 300 to 400 years (Van Pelt 2001). On productive sites, however, many large-diameter (>76 cm dbh) white fir can be >130 years old, having been recruited following fire cessation in the mid 1800s (North et al. 2005). Sugar pine is a typically an important associate in white fir forests. With the exception of giant sequoia, sugar pine is the largest member of the community, reaching heights up to 82 m and diameters of 3.5 m (Van Pelt). On shallower soils or drier sites, Jeffrey pine may co-dominate the tree layers (Barbour et al. 2002; Oakley 2003; Taylor 2004).

In white fir dominated forests, basal areas range from 49 m<sup>2</sup> ha<sup>-1</sup> on relatively xeric sites in the Lake Tahoe basin to 163 m<sup>2</sup> ha<sup>-1</sup> in Sequoia-Kings Canyon National Park (Table 17.7). Tree densities range from 539 to 722 stems ha<sup>-1</sup>. In mixed white fir and Jeffrey pine stands, basal areas are typically less than 100 m<sup>2</sup> ha<sup>-1</sup>. Densities are more variable than white fir dominated stands, ranging from 278 to 1,196 stems ha<sup>-1</sup>. Tree cover varies from 30% (North et al. 2002, 2004) to 95% (Table 17.4). Shrub cover varies from absent to 95% cover. Herbaceous and grass cover is also widely variable but is typically less important than shrub cover, averaging 1% to 5% (Fites 1993; North et al. 2005b).

In contrast to the lower elevation ponderosa pine- and Douglas-fir-mixed-conifer forests, white fir-mixed conifer forests tend to be comprised of a mosaic of trees and shrubs in varying densities. Four patterns of overstory-understory structure are most prevalent: (1) dense forest, with absent or poorly developed understory; (2) open to moderately dense forest with a sparse to well developed understory; (3) openings dominated by shrubs or herbs and grasses; (4) open forests with sparse understory on rocky sites (North et al.

2002). These patterns may be due to microsite variation in soil depth or rock component, snow accumulation, fungal pathogen occurrence, or site history and are then reinforced over time by variable regeneration responses of the understory. A mosaic of dense forest, open forest, and nonforested openings are particularly evident in granitic-derived soils such as in the Teakettle Experimental Forest. Although fire suppression has resulted in increased stem densities, the openings have persisted (North et al. 2004). This has been attributed to more favorable conditions for seedling establishment and survival under partial shade, where soil moisture is maintained in contrast to harsh conditions in openings with high soil temperatures and reduced soil moisture (Gray et al. 2005).

Understory trees and shrubs form an important element in white fir-mixed conifer forests. Dense thickets of white fir and incense cedar saplings have developed in many sites (Vankat and Major 1978; Bouldin 1999; Barbour et al. 2002), apparently due to a decreased fire frequency but also possibly as a result of climatic change (Millar and Woolfenden 1999). The most prevalent shrubs are *Ceanothus cordulatus*, *Quercus vaccinifolia* (in the northern Sierra), *Prunus emarginata*, *Symphoricarpos mollis*, and *Ribes* spp. (Fites 1993; Potter 1994; North et al. 2002; North et al. 2005b). *C. cordulatus* occurs in openings, particularly in response to fire or other disturbances or on harsh dry sites and is usually enriched with available forms of nitrogen (Oakley et al. 2003).

On glacial moraines with rocky soils, particularly derived from granitic substrates, *Q. vaccinifolia* (to the north) can form extensive stands with high cover. *Chrysolepis sempervirens* is often a co-associate of *Q. vaccinifolia* but is more shade tolerant and persists in the understory of moderately dense white fir forests, particularly in the southern or eastern Sierra.

On sites with subsurface water, *Rubus parvifolia* is common (less so on eastern slopes in the northern Sierra) and

TABLE 17.5  
Structure of Mixed Ponderosa Pine and Mixed Douglas Fir Forests in the Sierra Nevada

Important Species (In Order of BA Importance)	Min Diameter (cm)	Density (Trees ha <sup>-1</sup> )	Basal Area (m <sup>2</sup> ha <sup>-1</sup> )		Location	Date of Data	Source
			Mean	(min-max)			
Mixed Douglas-fir							
PP, DF, IC, SP, WF, BO	>30.5	229 (150-300)	130 (94-186)		Placer, Eldorado, Stanislaus National Forests	1899	Stephens 2000 (Sudworth)
WF, DF, SP, IC, JP, PP, RF	>30.5	235 (160-300)	215 (188-232)		Placer, Eldorado, Stanislaus National Forests	1899	Stephens 2000 (Sudworth)
	>30	57	70			1935	Bouldin 1999
	>30	64	30			1992	Bouldin 1999
DE, WE, SP, IC, PP, BO, MD	>9.4 (>24)	721 (219)	75 (67) <sup>a</sup>		Plumas National Forest	1996	Ansley and Battles 1998
DE, WE, SP, IC, PP, BO, MD	>24	157	58		Plumas National Forest	1957	Ansley and Battles 1998
DE, WE, IC, SP, MD	>2.5		80 (34-150)		Mesic sites on Lassen, Plumas, Tahoe, Eldorado National Forests	1980's	Fites 1993
DE, PP, IC, WF, SP, CL	>2.5		68 (23-104)		Xeric sites on forests listed previously	1980's	Fites 1993
Mixed Ponderosa Pine							
PP, IC, WF, BO, SP	>2.5	1977	133		Sequoia-Kings Canyon National Park	1969	Roy and Vankat 1999
IC, PP, WF, BO	>2.5	1165	107		Sequoia-Kings Canyon National Park	1996	Roy and Vankat 1999
PP, IC, WF, SP, BO	>2.5		61 (17-128)		Lassen, Plumas, Tahoe, Eldorado National Forests	1980's	Fites 1993

NOTE: Species abbreviations are as follows: BO, black oak; CL, canyon live oak; DF, Douglas fir; IC, incense cedar; JP, Jeffrey pine; MD, mountain dogwood; PP, ponderosa pine; RF, red fir; SP, sugar pine; WF, white fir.

<sup>a</sup>Standard deviation.



FIGURE 17.5 Old-growth mixed-conifer forest, Placer County Big Trees, Tahoe National Forest, approximately 1,500 m elevation. Dominant tree species (in declining importance) are *Pinus ponderosa*, *P. lambertiana*, *Pseudotsuga menziesii*, *Abies concolor*, and *Calocedrus decurrens*. Photo courtesy of M. G. Barbour.

*Acer glabrum* is found. *Salix scouleriana* also occurs on sites with a past history of large fires.

Herbaceous cover is mostly sparse in white fir forests (seldom >5%), except in occasional moist swales or drainage bottoms, where it may approach 100%. It may be completely absent over large areas with thick litter accumulation. Common species in denser, shady forests include *Hieracium albiflorum*, *Kelloggia galioides*, *Viola lobata*, *Festuca rubra*, and *Carex rossii*; and *Smilacina racemosa*, *Pedicularis semibarbata*, and *Phacelia hydrophyloides* occur in denser, shady forests. In more open forests, the herb layer is often diverse and can be rich (Mellmann-Brown and Barbour 1995; North et al. 2005b), including *Anaphalis margaritacea*, *Brodiaea elegans*, *Calyptridium umbellatum*, *Collinsia parviflora*, *Eriogonum nudum*, *Eriogonum wrightii*, *Eriogonum umbellatum*, *Erysimum capitatum*, *Lupinus* spp., and *Achnatherum* spp.

In many sites in white fir forests where a heavy carpet of litter coats the soil surface, herbaceous vegetation is restricted to scattered individuals of *Pyrola picta* and *Chimaphila menziesii*. The diversity of these and other mycorrhizal epiparasites (including *Allotropa virgata*, *Pyrola asarifolia*, *P. minor*,

*P. secunda*, *Hemitomes congestum*, *Pityopus californicus*, *Sarcodes sanguinea*, *Corallorhiza striata*, *C. maculata*, and *Cephalanthera austiniae*) is remarkable in the Sierra Nevada. The heavy snow cover and moderate winter temperature extremes may provide conditions allowing critical fungal activity in the root zone throughout the year.

Changes in white fir-mixed conifer forests have occurred since European settlement as in the ponderosa pine and Douglas-fir forests. Both increases in density, particularly of smaller trees (Bouldin 1999; Barbour et al. 2002; Taylor 2004; North et al. 2004) and decreases in large trees have occurred. The spatial pattern of the increase in density has not always been uniform, with at least some of the in-growth associated with aggregates of existing trees (North et al.), although overall there appears to have been an increase in uniform spatial structure compared to a more heterogeneous structure at the time of European settlement (Taylor). These shifts in composition have been attributed to fire suppression (Taylor) but may also be confounded with shifts in climate favorable for white fir (Millar and Woolfenden 1999). In xeric sites, with a higher proportion of Jeffrey pine, as in some areas such as the Lake Tahoe basin, preferential logging of pine over fir for mining contributed to the shift in composition (Lindstrom 2000). A contrasting trend was observed by Roy and Vankat (1999) over a 27-year period since 1969 in Sequoia-Kings Canyon National Parks. Total stand density actually declined, including stems of white fir, which was attributed to prescribed burning (and in unburned stands, self-thinning) during this period. The effect of prescribed burning on reduction in stem density, particularly in smaller diameter white fir, has been documented by monitoring in the parks (Keifer and Stanzler 1995).

Other less readily quantified changes in white fir-mixed conifer forests are on the distribution, size, and dynamics of large montane chaparral patches. Early explorers such as Leiburg (1902) documented the presence of large patches of chaparral amongst the white fir-mixed conifer and high-elevation red fir forests in the Sierra Nevada. Although the presence of some of these shrub patches have been attributed to shallow soils (Potter 1998), others are a result of fire (Russell et al. 1998; Nagel and Taylor 2005). Nagel and Taylor found lower historic fire frequencies in chaparral than in nearby forests in the Lake Tahoe basin and suggested that fire suppression has caused a reduction in chaparral area of 62%. It is unknown what role early settler fires played in creation or maintenance of large chaparral patches in the white-fir mixed conifer forests compared to historic fires from lightning or Native Americans. The shade-tolerant nature of white fir allows it to regenerate below chaparral (Conard and Radosevich 1982), with little effect on height growth (Oliver and Uzoh 2002). As a result, recruitment of white fir in chaparral can be nearly continuous over time (Conard and Radosevitch; Nagel and Taylor). Most of the shrubs sprout following fire, resulting in mortality of white fir regeneration and perpetuation of shrubs with fire. Nagel and Taylor found that it took nearly 30 years on average for

TABLE 17.6  
Composition of White Fir and Mixed White Fir-Jeffrey Pine Forests

Cohort and Species	Relative Composition (% of Stems/ha)							
	A	B	C	D	E	F	G	H
Overstory trees	*	*	>30 cm	>40 cm	>2.5 cm	*	*	*
<i>Abies concolor</i>	53	40	88	68	66	91	30	17
<i>Pinus lambertiana</i>	3	2	1		19		54	20
<i>Calocedrus decurrens</i>	2	1	<1	1	28		9	46
<i>Pinus jeffreyi</i> <sup>†</sup>	42	56		9	8			14
<i>Abies magnifica</i>			<1	19				
<i>Quercus kelloggii</i>							7	1
<i>Pinus</i> (mixed)						9		
Understory trees			10–30 cm	2.5–40 cm	<2.5 cm			
<i>Abies concolor</i>			84	73	5			
<i>Pinus lambertiana</i>			12		<1			
<i>Calocedrus decurrens</i>			<1	2	4			
<i>Pinus jeffreyi</i>				2				
<i>Abies magnifica</i>				17				

NOTE: Data are from varied sources including northern, central, and southern Sierra Nevada. Columns a and b are from General Land Office Survey data from the Lake Tahoe basin in the late 1800s (n = 313 trees). Column c is from data collected in 1969 in Sequoia-Kings Canyon National Park adapted from Vankat and Major (1978; Minnich et al. 1995; n = 16). Column d is from the Lake Tahoe Basin, collected in 2000 (Barbour et al. 2002; n = 140). Column e is from Eldorado north through Lassen National Forest collected in the 1980s (Fites 1993; n = 17). Columns f, g, and h are from General Land Office Survey data collected in the late 1800s from the Stanislaus, Sierra, and Sequoia National Forests and adjacent lands (Hyde 2002; n = 29, 19, and 11, respectively).

\*From General Land Office Survey Data, minimum diameter likely >20 cm dbh.

<sup>†</sup>Includes some ponderosa pine.

white fir to grow to a height of 30 cm, significantly smaller than the typical height of chaparral stands of that age.

#### GIANT SEQUOIA

The giant sequoia (*Sequoiadendron giganteum*) groves of the central and southern Sierra Nevada present a special case of mixed-conifer forests. These groves are typically dominated by white fir, or at higher elevations by red fir, with sugar pine as an important component (Rundel 1971). Giant sequoias are commonly third in abundance in these groves, although their basal area often exceeds that of other species (Fig. 17.6, Table 17.8). Drier or lower elevation areas of giant sequoia groves often include ponderosa pine, Jeffrey pine, incense cedar, and black oak as associated species. Douglas fir is present in some of the northern groves, and the North Calaveras Grove is notable for an extensive understory of *Taxus brevifolia*.

The natural occurrence of giant sequoia is restricted to some 67 to 75 groves (depending on how they are defined) on the west slope of the Sierra Nevada (Rundel 1972b;

Willard 2000). From Placer County to the Kings River, there are eight disjunct groves, separated by as much as 90 km. South of the Kings River there is a much more continuous belt of groves, never separated by more than about 7 km, extending through Tulare County. The size of individual groves varies greatly from the tiny Placer County Grove with just six trees to the large Redwood Mountain and Giant Forest Groves that are approximately 1,000 ha in area and contain more than 20,000 giant sequoias each. The northern disjunct groves largely occur at elevations of 1,400 to 2,000 m, with south-facing slopes favored. The major group of groves south of the Kings River generally occurs at higher elevations up to 2,450 m, with individual trees reaching 2,700 m, and favor north-facing slopes. Overall, giant sequoia groves occupy about 14,600 ha, with roughly 90% of this area in public ownership (Stephenson 1996).

Giant sequoias have attained a special fame because of their huge size and longevity. They are the largest trees in existence, with bole volumes of nearly 1,500 m<sup>3</sup> and heights measured up to 307 feet (Van Pelt 2001). Precise tree dates as old as 3,266 years have been measured in giant sequoia



FIGURE 17.6 *Sequoiadendron giganteum*, with an enormous fire scar, in Calaveras Big Trees State Park, South Grove, approximately 1,500 m elevation. The tree is approximately 5 m in diameter, breast height. Photo courtesy of M. G. Barbour.

stumps, giving this species an age exceeded only by *Pinus longaeva* and *Fitzroya cupressoides*. Contrary to widespread public impressions, many of the largest giant sequoias owe their size less to their age and more to their rapid rate of growth. Revised estimates of the age of the General Sherman Tree, for example, are now about 1,650 years, rather than early estimates of more than 3,500 years (Stephenson and Demetry 1995; Stephenson 2000). Fire scar records from giant sequoias have allowed the establishment of a 2,000-year record of regional fire history for the Sierra Nevada, and shown the importance of climate in maintaining nonequilibrium conditions (Swetnam 1993).

The most important single habitat feature characterizing giant sequoia groves is the presence of soil moisture availability through the dry summer months (Rundel 1972a; Anderson et al. 1995). This moisture is necessary but not sufficient for the presence of giant sequoia. Climatic changes during the Pleistocene and early Holocene has cleared impacted giant sequoia distribution (Rundel 1972a). Even with available summer moisture, the upper height limit of giant sequoia appears to be controlled by water stress (Rundel 1973).

Fire prevention in giant sequoia grove areas over much of the late nineteenth and most of the twentieth centuries led to a sharp reduction in giant sequoia reproduction as shade-tolerant white fir thickets became established in grove understories (Aune 1994). Difficulties and imprecision in determining pre-Euro-American grove structure has helped fuel a debate between “structural restorationists,” who believe that forest structure should be restored mechanically before fire is reintroduced (Piirto and Rogers 2002), and “process restorationists,” who believe that simple reintroduction of fire is appropriate (Stephenson 1994). It appears that restoration of fire without a preceding mechanical restoration may restore the pre-Euro-American structure of sequoia groves, at least within the bounds of our imprecise knowledge of past grove structure (Stephenson 1999).

### Upper Montane Vegetation

Upper montane vegetation types grow at elevations above white fir and mixed-conifer series of the Sierra Nevada. The elevation of this transition from lower montane forests occurs at about 1,800 m in the central and northern Sierra Nevada and at about 2,200 to 2,500 m in the southern Sierra. Its lower elevation appears to correspond best with mean freezing elevation during winter storms (Barbour et al. 1991). The percentage of total precipitation that falls as snow in this zone is 70% to 90%, which is dramatically more than an average of 33% in the lower montane. Consequently, the upper montane experiences deeper and longer lasting snowpacks than any other place in California: 2.5 to 4.0 m deep and duration nearly 200 days (Barbour and Minnich 2000; Fig. 17.7a).

In addition to coniferous forests, montane meadows, aspen, montane chaparral, and nonforested rock outcrops are prevalent in this zone, as described in subsequent sections. Three major community types of distinctive conifer composition form the upper montane forests. These are red fir forests, lodgepole pine forests, and Jeffrey pine forests. These communities receive most of their annual precipitation in the form of snow. Summers are generally dry, although infrequent but locally intense summer convective storms may occur in August and September. Fires are clearly an aspect of the natural environment of these upper montane forests, but are often less frequent than found in lower montane forests and with more variable intensities and severities (van Wagtenonk and Fites-Kaufman in press).

### RED FIR

Red fir forests, with an overwhelming stand dominance of red fir (*Abies magnifica*), lie in a belt immediately above montane white fir and mixed-conifer associations. This belt generally occurs in an area roughly 300 to 500 m in elevational width, extending from about 1,800–2,400 m in the northern Sierra Nevada to about 2,100–2,750 m in the southern Sierra. Although largely a Californian

TABLE 17.7  
Composition of Mixed White Fir-Jeffrey Pine Forests in the Sierra Nevada

Cohort and Species	Relative Composition (% of Stems/ha)				
	A	B	C	D	E
Overstory (dbh)	>30 cm	>40 cm	>40 cm	>30 cm	>20 cm
<i>Abies concolor</i>		40	81	23	21
<i>Pinus lambertiana</i>		9			
<i>Calocedrus decurrens</i>	14	7		6	3
<i>Pinus jeffreyi</i>	86	28	10	62	76
<i>Abies magnifica</i>		6	8		
Understory	10–30 cm			10–29 cm	10–29 cm
<i>Abies concolor</i>	33	64		33	29
<i>Pinus lambertiana</i>		2			
<i>Calocedrus decurrens</i>	33	9	1	13	12
<i>Pinus jeffreyi</i>	33	9		52	56
<i>Abies magnifica</i>		8			

NOTE: Data is from Varied Sources and Locations in the Sierra Nevada. Column a is from Sequoia-Kings Canyon National Park collected in 1969, reported in Minnich et al. (1994), adapted from Vankat and Major (1978; n = 7). Column b is from the Lake Tahoe Basin collected in 2000 (Barbour et al. 2002; n = 70). Column c is from the Lassen National Park collected in the 1990s Taylor (2000) (n = 33). Columns d and e are from the central Sierra Nevada; column d, from 1935; and e, from 1992 data (Bouldin 1999).

species, red fir extends north through the Cascade Range into southern Oregon. The southern limit of red fir is Sunday Peak in northern Kern County. Populations of red fir in the Klamath range of northern California and in the southern Sierra Nevada are *A. magnifica* subsp. *shastensis*, a distinct form from the subsp. *magnifica* of the central and northern Sierra Nevada. Mean annual precipitation in red fir forests is generally in the range of 1,000 to 1,300 mm, with the great majority of this falling as winter snow. Snow packs of 2.4 to 4 m or more depth are not unusual during the winter months (Rundel, Parsons, and Gordon 1977).

The dense canopy cover in red fir forests reduces light penetration and wind and, as a consequence, slows the drying of surface and ground fuels and reduces the frequency of lightning ignitions. Fires in these forests often are ignited by lightning strikes in late summer, and then smolder slowly for several months until early winter snows put them out (Kilgore and Briggs 1972). High intensity fires associated with wind and/or drought also can occur (van Wagtenonk and Fites-Kaufman 1996). Stephens (2001) found a fire-return interval of about 25 years for red fir forests near Mammoth in the eastern slope of the Sierra Nevada. Adjacent stands of Jeffrey pine had fires at a return interval of only 9 years.

Red fir is a large and long-lived conifer, with heights of 62 m and diameters reaching 3 m (Van Pelt 2001). Stands of red fir forest are often virtual monocultures of this species (Fig.

17.7b). At its lower margin, red fir often mixes with white fir and sugar pine, and less commonly with giant sequoia. Despite their significant overlap in range, there is no known hybridization between red and white fir. At higher elevations red fir can be found with lodgepole pine, Jeffrey pine, and mountain hemlock (Potter 1998). Western white pine is a common associate in the northern and central Sierra Nevada, but less so in the southern Sierra.

The structure of red fir forests is commonly formed of relatively even-aged stand mosaics from a hectare to several hectares or more in size. Broad surveys of stand densities and basal areas of red fir forest have been carried out in many parts of the Sierra Nevada, with early data sets summarized in Rundel et al. (1977; data from Schumacher 1928 and Dunning and Reineke 1933). Oosting and Billings (1943) reported a mean basal area of 102 m<sup>2</sup> ha<sup>-1</sup> for mature stands of red fir forest in the northern Sierra Nevada, whereas Vankat (1970) found a similar mean of 92 m<sup>2</sup> ha<sup>-1</sup> in Sequoia National Park.

Red fir begins to set seed at an age of 40+ years, and good seed crops are produced at 2- to 6-year intervals. Seed is disseminated by wind but generally no more than a distance of approximately 1 to 1.5 tree heights from the parent tree. Initial seedling growth is best in shade with soil litter no more than 8 mm in depth (Gordon 1970), but as seedlings grow to be saplings growth is best in full sunlight. Seedling growth beneath mature forest canopies is very

TABLE 17.8  
Structure of Giant Sequoia, White Fir, and Mixed White Fir-Jeffrey Pine Forests in the Sierra Nevada

<i>Important Species (In Order of BA Importance)</i>	<i>Min. Diam. (cm)</i>	<i>Density (Trees/ha)</i>	<i>Basal Area (m<sup>2</sup> ha<sup>-1</sup>)</i>	<i>Location</i>	<i>Date of Data</i>	<i>Source</i>
<b>Giant Sequoia</b>						
GS, WF, SP, RF	>2.5	1009	955	Sequoia-Kings Canyon National Park	1969	Roy and Vankat 1999
GS, WF, SP, RF	>2.5	618	367	Sequoia-Kings Canyon National Park	1996	Roy and Vankat 1999
<b>Mixed White Fir</b>						
WF, SP, IC	>2.5	757	163	Sequoia-Kings Canyon National Park	1969	Roy and Vankat 1999
WF, SP, IC	>2.5	722	141	Sequoia-Kings Canyon National Park	1996	Roy and Vankat 1999
WF, JP, RF, IC, SP	>1	539	49	Lake Tahoe basin	2000	Barbour et al. 2002
WF, IC, JP, SP, PP			86	Eldorado, Tahoe, Plumas, Lassen National Forests	1980's	Fites 1993
<b>Mixed White Fir-Jeffrey Pine</b>						
JP, IC, WF, LP	>2.5	533	91	Sequoia-Kings Canyon National Park	1969	Roy and Vankat 1999
JP, IC, WF, LP	>2.5	844	105	Sequoia-Kings Canyon National Park	1996	Roy and Vankat 1999
JP, WF, SP, IC, RF	>1	278	45	Lake Tahoe basin	2000	Barbour et al. 2002
WF, JP, RF, WP, PP, SP	>4	1196	80	Lassen National Park	1998	Taylor 2000

NOTE: GS = giant sequoia, WF = white fir, SP = sugar pine, RF = red fir, IC = incense cedar.



FIGURE 17.7 (a) *Abies magnifica* forests occupy a climatic zone that experiences a deeper and longer lasting snowpack than anywhere else in California. (b) An old-growth red fir forest, with a single-canopy layer and modest regeneration, 2,200 m elevation, Tahoe National Forest. Overstory trees average 0.8 m dbh and an age of about 250–350 years. Photograph (a) courtesy of M. G. Barbour, (b) courtesy of J. Franklin.

slow. Shade-tolerant seedlings may grow only 3 cm a year for 60 to 80 years or more under these conditions (Gordon 1973). In years of heavy seed crops, favorable microsites such as forest openings and gaps are filled with large numbers of seedlings, which slowly thin to saplings and finally mature to become a new group of mature canopy trees. Large gaps for colonization may be produced by wind damage, fire, logging, or outbreaks of insects and fungal pathogens. It is these processes that produce the observed mosaics of relatively even-aged stands.

The dense shade and thick litter accumulation beneath mature red fir canopies restricts the growth of most understory plant species. The most common understory shrubs present in the central and northern Sierra Nevada are *Ribes roezleii* and *Symphoricarpos vaccinioides* (Oosting and Billings 1943). Herbaceous cover seldom exceeds 5%, with the most common species being *Hieracium albiflorum*, *Poa bolanderi*, *Pedicularis semibarbata*, and *Aster breweri*. Epiparasitic herbs such as *Sarcodes sanguinea*, *Pterospora andromeda*, *Coralorhiza maculata*, and the related *Pyrola picta*, *Orthila secunda*, and *Chimaphila umbellata* are common. Openings with gravelly granitic soils often have greater herb cover, with

*Arabis platysperma*, *Viola purpurea*, *Eriogonum nudum*, *Gayophytum nuttallii*, *Monardella odoratissima*, *Calyptidium umbellatum*, *Elymus elymoides*, and *Wyethia mollis* as typical species (Rundel et al. 1977; Potter 1998).

Broader open areas with rocky soils or where fires have opened gaps support montane chaparral species such as *Ceanothus cordulatus*, *C. velutinus*, *Arctostaphylos patula*, *Chrysolepis sempervirens*, and *Ribes roezlii*, with *Prunus emarginata* and *Salix scouleriana* on wetter sites and *Quercus vac-cinifolia* on rocky outcrops (Potter 1998).

Small lightning-caused fires within red fir stands may kill local groups of trees and open up a gap with appropriate soil conditions for colonization by lodgepole pine seedlings. Such local populations of lodgepole pine are relatively transitory, however, as fir seedlings regenerate well beneath such open canopies. In a time frame of 1 or 2 centuries, red firs overtop and shade out the lodgepole pines.

#### JEFFREY PINE

Jeffrey pine (*Pinus jeffreyi*) replaces the lower yellow pine forests of ponderosa pine on drier sites in the upper montane



FIGURE 17.8 Open lodgepole pine stand near the edge of a wet meadow, upper montane zone. Photography courtesy of J. Franklin.

zone of the Sierra Nevada. Its belt of primary occurrence lies at 1,520 to 1,830 m in the northern areas of the range, and at 1,600 to 2,600 m in the southern Sierra Nevada. On the western slopes of the range, Jeffrey pine most commonly occurs in mixed stands with white fir and incense cedar at lower elevations (and Sierra juniper in the north), and with red fir and lodgepole pine at higher elevations (Potter 1998). These stands are generally open, with canopy cover in the range of 40% to 65%, or less on rocky sites. Stand basal area for all tree species in Jeffrey pine stands in Sequoia National Park have been reported over a range of 31 to 62 m<sup>2</sup> ha<sup>-1</sup> (Vankat 1970). The largest trees reach heights up to 61 m, with diameters up to 2.5 m (Van Pelt 2001).

The relatively long needles of Jeffrey pine and relatively open structure of these stands make for dry surface and ground fuels that burn readily. Thus, fires in Jeffrey pine stands burn more frequently than those in adjacent red fir forests (Stephens 2001).

Relatively pure stands of Jeffrey pine occur on the east slope of the Sierra Nevada south of the Tahoe Basin (Fig. 17.8), mixing only at higher elevations with lodgepole pine and red fir. This dominance in areas that might otherwise seem appropriate for ponderosa pine may relate to colder temperatures. Jeffrey pine commonly shares dominance with white fir and Sierra juniper in the Tahoe and Toiyabe National Forests (Vasek 1976). On the eastern slopes of the central and southern Sierra Nevada, Jeffrey pines typically form relatively pure stands at 2,590 to 2,740 m elevation in a belt between red fir forests above and pinyon-juniper woodlands below. Typical understory shrubs beneath the open canopy Jeffrey pine stands on this east slope include *Arctostaphylos patula*, *A. nevadensis*, *Ceanothus prostrata*, *C. cordulatus*, *Artemisia tridentata* and *Purshia tridentata* (Vasek; Stephens 2001).

Washoe pine (*Pinus washoensis*), a high elevation cousin of ponderosa pine, is locally important in the northern Sierra Nevada and southern Cascade Range (Haller 1961; Smith 1994). Although seldom a stand dominant, it is the



FIGURE 17.9 Stands with *Pinus jeffreyi* can occur on the west slope of the Sierra Nevada in the upper montane zone, but pure stands can also be found at 2,000 m on the eastside, as shown here. Mono County. Photograph courtesy of M. G. Barbour.

most important species above 2,400 m in the Bald Mountain Range and at about 2,290 m on dry slopes in the Warner Mountains (Haller in Rundel et al. 1977). It reaches co-dominant status with Jeffrey pine on Mt. Rose at elevations of 1,950 to 2,560 m. Red and white fir are less abundant in these stands.

The open understory of Jeffrey pine forests represents a mosaic of microsites with varying litter accumulation, shading, and moisture availability. Grasses are common on drier sites, including *Elymus elymoides*, *Deschampsia elongata*, and *Achnatherum occidentale*, whereas *Wyethia mollis* and *Monardella odoratissima* are also frequently present.

#### LOGEPOLE PINE

Open stands of lodgepole pine forests make up a widespread upper montane forest/woodland over much of the Sierra Nevada, tolerating both shallow rocky soils and semisaturated meadow edges, in an elevational belt within and above the red fir zone (Fig. 17.9) (Potter 1998). These forests, strongly dominated by *Pinus contorta* subsp. *murrayana*, generally occur at elevations of about 1,830 to 2,400 m in the northern Sierra Nevada, and rise to 2,440 to 3,350 m in the south. Stands of lodgepole pine may reach much lower; however, with cold air drainage down glacial canyons. The lodgepole zone is characterized by a short growing season of as little as 2 to 3 months, and the great majority of the 800 to 1,500 mm of annual precipitation falls as winter snow. The generally low stature and open stand structure of lodgepole pine forests is a function of these severe climate conditions and the thin, nutrient-poor soils that characterize this zone. Commonly there are few understory shrubs and little soil litter accumulation in these stands.

Unlike the Rocky Mountain subspecies of lodgepole pine (*P. contorta* subsp. *latifolia*), which has a life history often tied closely to stand-replacing crown fires and often occurs in large even-aged cohorts, Sierran lodgepole pine does not

require fire for seedling establishment and typically occur in multiaged stands (Parker 1986). Large stand-replacing crown fires are rare in Sierran lodgepole pine stands (van Wagtendonk and Fites-Kaufman 1996).

Over much of its range in the Sierra Nevada, lodgepole pine attains heights of no more than 15 to 20 m, although individual trees may reach heights of 30 m and diameters of 60 to 130 cm under better conditions with good soil resources (Rundel et al. 1977). Stands of lodgepole pine forest sampled in Sequoia National Park at elevations of 2,600 to 3,100 m had a mean density of 3,390 trees ha<sup>-1</sup>, including saplings, and a basal area of 58 m<sup>2</sup> ha<sup>-1</sup> (Vankat 1970).

More than any other Sierra conifer, lodgepole pine is relatively tolerant of poor soil aeration, and thus grows well around the margins of wet meadows and other moist areas (Rundel and Yoder 1998). Many upper montane and subalpine meadows in the Sierra Nevada exhibit invasion of young lodgepole pines moving inward from their drier margins. It is not clear how much this process has been influenced by changes in fire frequency or grazing over the last 150 years. Comparative photographic studies have shown changes in lodgepole pine stand densities in Yosemite (Vale 1987) and Sequoia National Parks (Vankat 1970). Attempts at restoration of plant communities in disturbed areas of lodgepole pine forest have shown low to poor success (Moritsch and Muir 1993).

Lodgepole pine is the overwhelming dominant within its forest community, mixing occasionally with red fir, and with scattered Jeffrey pine and western white pine, and mountain hemlock at higher elevations (Potter 1998). It may occasionally form a treeline krummholz, growing with whitebark, limber, or foxtail pine. Scattered shrubs such as *Arctostaphylos nevadensis*, *Ribes montigenum*, and *Quercus vaccinifolia* are present within stands of lodgepole pine forest, but understory vegetation is generally sparse. Lake edges and wet meadows in the lodgepole zone support fringes of low ericaceous shrubs, most notably *Cassiope mertensiana*, *Vaccinium caespitosum*, *Phyllodoce breweri*, and *Kalmia polifolia*. Fast-moving streams are generally characterized by relatively dense populations of willows (*Salix* spp.).

### Subalpine Vegetation

The subalpine landscape is comprised of a mosaic of subalpine forests/woodlands, meadows, rock outcrops, and scrub vegetation types. Although forests often comprise less than half or a third of the landscape, they have been the most studied vegetation types within the subalpine zone and are therefore emphasized in this section. Subalpine forests are open stands of conifers occurring on generally sandy soils or rocky slopes at elevations above the upper montane forest stands of red fir and lodgepole pine. Stand densities are low and trees rarely exceed 25 m in height (Fig. 17.10). Many, but not all, species form shrubby krummholz forms of growth near their upper elevational limits.

The elevational distribution of subalpine forest communities varies with latitude. In the Lake Tahoe basin, such

stands begin around 2,450 m and extend up to treeline at 2,750 to 3,100 m (Graf 1999), whereas in the southern Sierra Nevada the range is more typically 2,900 to 3,660 m (Rundel et al. 1977). Both upper and lower limits of subalpine species distributions are driven by a variety of factors, including soil resources, water availability, and climatic limiting factors.

Subalpine forests are characterized by a relatively short growing season with cool temperatures. Frequently the season of vegetative growth lasts no longer than 6 to 9 weeks, and frosts can occur at any time of the year. Annual levels of precipitation are 750 to 1,250 mm. With the exception of occasional summer thunderstorms, almost all of this precipitation falls as winter snow. Wet years with abundant snowfall can limit growth as these may produce late-lying snowfields that reduce the length of the growing season (Armstrong et al. 1988). Winds are often severe, particularly around exposed ridges. Such wind conditions may produce snow-free winter areas that lower soil temperatures and increase plant water stress.

Most of the subalpine areas of the Sierra Nevada were subjected to repeated glaciation during the Pleistocene, and thus have thin and poorly developed soils with little organic matter. The small amounts of litter accumulation and open stand structure of subalpine forests means that fire is rare. Because of the solid granite parent material, areas with deeper soil accumulation can become waterlogged for much of the year. For these reasons, the length of the growing season is a function of early season limitation due to low temperatures and snowfields, and late season limitations due to drought. Studies of the dynamics of alterations of treeline elevation over the past several millennia using tree ring chronologies have reinforced the significance of complex interactions of both temperature and water availability in determining such changes (Lloyd and Graumlich 1997; Bunn et al. 2005). Responses of high-elevation forests to future global warming may depend strongly on water supply.

Treeline growth of multistemmed trees and shrubby krummholz growth of conifers varies with latitude in the Sierra Nevada. Treeline in the northern Sierra Nevada is dominated by whitebark pine (*Pinus albicaulis*), which frequently occurs with a krummholz form of growth near its upper limit (Fig. 17.11). Several other species may also form krummholz growth forms, including Sierra juniper, mountain hemlock, lodgepole pine, and rarely Jeffrey pine. Further south in the central Sierra Nevada, limber pine (*Pinus flexilis*) is the dominant treeline species, particularly on the east slope of the range, often occurring with lodgepole pine. Finally, treeline in the southern Sierra Nevada is characterized by open stands of foxtail pine (*Pinus balfouriana*), a species that does not typically develop krummholz growth forms. Despite similarities in adaptations to their high elevation environment, these three subalpine pines come from very different lineages and are not closely related.

The genetic structure of many subalpine pines, most notably *P. albicaulis*, *P. flexilis*, and *P. balfouriana*, is strongly



FIGURE 17.10 (a) Mixed subalpine woodland dominated by white-bark pine, with a prominent understory of pinemat manzanita. Slide Mountain, 2,700 m, east of Lake Tahoe. (b) Subalpine stands are typically fragmented by intervening meadows and barrens, as here in Yosemite National Park above Tuolumne Meadows. Photograph (a) courtesy of M. G. Barbour, (b) from J. Fites-Kaufman.

influenced by the seed-caching behavior of Clark's nutcracker (*Nucifraga columbiana*). These birds actively gather huge quantities of pine seeds and disperse them, often into caches where multiple seeds may germinate (Tombach and Kramer 1980; Tombach 1982, 1986).

Tree-ring analyses of upper treeline species in the Sierra Nevada have been compared to instrumental records to understand growth responses to temperature and moisture availability. Extrapolating these data back before instrumental records has given a long-term record or estimated temperature conditions. Rates of annual tree growth in fox-tail pine, lodgepole pine, and western white pine are influenced by positive nonlinear interactions between summer temperature and winter precipitation (Graumlich 1993). Although maximum growth rates occur under conditions of high winter precipitation and warm summers for all three species, substantial species-to-species variation occurs in the response to these two variables (Graumlich 1994).

Lloyd and Graumlich (1997) reconstructed a 3,500-year history of fluctuations in treeline elevation and tree abundance in the southern Sierra Nevada using tree-ring records. Treeline elevation was higher than at present throughout most of this period. Declines in the abundance of live trees and treeline elevation occurred twice during the last 1,000 years. An elevational decline from 950 to 550 years BP coin-

cided with a period of warm temperatures (relative to present) in which at least two severe, multidecadal droughts occurred. A second decline from 450 to 50 years BP was apparently triggered by an increase in the rate of adult mortality in treeline forests. This latter decline occurred during a period of low temperatures lasting for up to 400 years and was apparently caused by a sustained failure of regeneration in combination with an increased rate of adult mortality.

Pollen and microfossil records from Sierran lakes have provided additional useful data in interpreting late Holocene changes in subalpine species occurrences. The upper altitudinal limits of many subalpine conifers began to decline about 2,500 years BP, coincident with the beginning of Neoglacial cooling (Anderson 1990).

Tree-ring studies of recent growth trends of whitebark pine and lodgepole pine in a subalpine forest of the southern Sierra Nevada have shown a dominant trend of increasing basal area increment over time in all age classes of both species (Peterson et al. 1990). This increased growth rate in subalpine trees is widespread and relates to the complex interactions of many factors including ambient CO<sub>2</sub> levels and their effect on water use efficiency (Graumlich 1991; Bunn et al. 2005). Climatic variables account for a relatively small portion of the variance in short-term tree growth, and there is no clear relationship with long-term growth.



FIGURE 17.11 Krummholz of *Pinus albicaulis*, above Sonora Pass, 3,200 m elevation. The “trees” are crowded together into a continuous hedge about 60–70 cm tall (note blue back-pack for scale). Photograph courtesy of M. G. Barbour.

#### MOUNTAIN HEMLOCK

Mountain hemlock (*Tsuga mertensiana*) has a broad range extending from the coastal ranges of Alaska south through British Columbia, and the Pacific Northwest into the Sierra Nevada. In the northern Sierra Nevada it may be found in upper montane forests of red fir and lodgepole pine (Potter 1998), but it is more characteristic at higher elevations near treeline where it is often the most common tree species but often mixed with Sierra juniper and whitebark pine. Mountain hemlock thrives in moist but well-drained mountain soils, often showing a preference for north-facing slopes. This is in contrast to stands in the Cascade Range where greater summer precipitation and cooler temperatures provide broader topographic conditions for growth (Parker 1994, 1995). In the central Sierra of Yosemite National Park it often grows up to 30 m in height in extensive groves with a virtually closed canopy. Seedlings are relatively shade tolerant compared to other subalpine conifers and do well under this type of canopy. At higher elevations, however, mountain hemlock is more scattered and often assumes a lower, shrubby growth form.

South of Yosemite, mountain hemlock becomes increasingly restricted to small stands growing on favorable microsites in cold moist valleys and sheltered ravines where snow banks remain late into the summer. Unlike pure stands of the central and northern Sierra Nevada, these scattered trees in the southern portions of the range are commonly found mixed with lodgepole pine, foxtail pine, western white pine, and red fir. The southernmost occurrence of mountain hemlock is below Silliman Lake in northern Tulare County where there is a small grove of about 60 trees with heights up to 24 m, diameters to nearly 90 cm, and healthy reproduction (Parsons 1972).

#### SIERRA JUNIPER

Sierra juniper (*Juniperus occidentalis* subsp. *australis*) is one of the most striking trees of the Sierra Nevada with its short

but massive trunk appearing to grow out of seemingly solid granite substrate. This Sierran subspecies of western juniper is differentiated from the subspecies *occidentalis*, which grows in the Cascade Range with ponderosa pine and Great Basin sagebrush. Sierra juniper occurs on shallow soils from 2,100 to more than 3,000 m elevation, often growing with Jeffrey pine, red fir, whitebark pine, mountain hemlock, and/or lodgepole pine. More than any other subalpine tree, Sierra juniper shows a remarkable ability to colonize and grow successfully out of small fractures in granite domes that would not support other species.

At the lower margins of lodgepole pine forest in the Tahoe Basin, there are mixed stands of Sierra juniper with red fir and Jeffrey pine, but these associated tree species are replaced by western white pine and mountain hemlock with increasing elevation. The largest Sierra juniper is reported to occur farther south in the Stanislaus National Forest, where there is a tree 26 m in height and 4 m in diameter (Lanner 1999). Sierra juniper may occur mixed in lodgepole pine stands up to treeline, where it increasingly takes on a krummholz form of growth. Some of these junipers are reported to reach ages of over 1,000 years (Graf 1999).

#### WESTERN WHITE PINE

Western white pine (*Pinus monticola*) is locally abundant in subalpine habitats along the west slope of the Sierra Nevada, where it may occur in small pure stands but more commonly is found mixed with lodgepole pine, Jeffrey pine, mountain hemlock, and red fir (Potter 1998). Although Sierran trees of this species may reach 40 m in height and 2.5 m in diameter, these sizes are smaller than those reached by the same species in the northern Rocky Mountains and Pacific Northwest (Van Pelt 2001). Western white pine generally maintains a tree form of growth up nearly to treeline, where it is commonly replaced by whitebark pine or foxtail pine on rocky ridges. Seedlings are reported to be relatively few compared to other subalpine conifers (Parker 1988).

A detailed analysis of tree distributions in a subalpine watershed dominated by western white pine has been made for Emerald Lake in Sequoia National Park. This watershed extends from 2,804 m at Emerald Lake up to 3,415 m at Alta Peak. A complete census of 1,206 trees in the watershed showed western white pine as the strong dominant with 71% of the individual trees and 83% of the basal area (Table 17.9). Lodgepole pine, largely restricted to mesic benches, was second in abundance with 17% of the trees, but formed only 3.5% of the basal area. Foxtail pine comprised 9.5% of the trees and 13.7% of the basal area, with these largely occurring on high north-facing ridges in the watershed. Small numbers of Jeffrey pine and red fir were largely restricted to the lowest elevations in the watershed in mesic bench habitats (Table 17.9).

#### WHITEBARK PINE

The most widespread treeline conifer in the Sierra Nevada is whitebark pine (*Pinus albicaulis*), which occurs abundantly

TABLE 17.9  
Total Census Data for Conifers in the Emerald Lake Watershed (2804–3415 m) of Sequoia National Park

Species	Relative Density (%)			Relative Basal Area		
	Mesic Bench	SW-facing Ridge	N-facing Ridge	Wet Meadow	Steep Talus Slope	
<i>Pinus monticola</i>	71.2	48.7	27.7	9.0	8.4	6.2
<i>Pinus contorta</i> subsp. <i>murrayana</i>	16.7	68.3	17.8	1.5	11.4	1.0
<i>Pinus balfouriana</i>	9.5	—	16.8	77.0	4.4	1.8
<i>Pinus jeffreyi</i>	0.9	100.0	—	—	—	—
<i>Abies magnifica</i>	1.7	65.0	35.0	—	—	—
Total	100					

Species	Relative Basal Area (%)			Habitat		
	Mesic Bench	SW-facing Ridge	N-facing Ridge	Wet Meadow	Steep Talus Slope	
<i>Pinus monticola</i>	82.4	57.8	30.3	8.1	3.8	0.1
<i>Pinus contorta</i> subsp. <i>murrayana</i>	3.5	81.7	10.7	1.2	6.3	0.1
<i>Pinus balfouriana</i>	13.7	—	9.0	90.4	0.5	0.1
<i>Pinus jeffreyi</i>	0.2	100.0	—	—	—	—
<i>Abies magnifica</i>	0.2	92.1	7.9	—	—	—
Total	100					

NOTE: Relative density and relative basal area data are based on a population of 1206 trees of all size classes in the basin. The habitat data show the relative proportion (%) of density and basal area of each species within five watershed habitats (Rundel et al. unpublished data).

from the Lake Tahoe area south to Mount Whitney, as well as in the higher Cascade Range, Warner Mountains, and Klamath range of northern California. It frequently occurs in the central Sierra with lodgepole pine, mountain hemlock, and Sierra juniper, whereas in the southern Sierra of southern Fresno and northern Tulare Counties it slightly overlaps in range with foxtail pine. Growth form of whitebark pine is variable, depending on the severity of growing conditions. On more favorable sites it can form small trees 10 to 15 m in height, but often exhibiting gnarled and twisted branches in response to winds. A second canopy layer of prostrate *Arctostaphylos nevadensis* is common (see Fig. 17.10a). In more exposed locations, whitebark pine readily takes on a multistemmed krummholz form of growth, and finally at treeline a low mat of growth <1 m in height (see Fig. 17.11). Growth is very slow in these, as in other treeline species, but longevity is great. Arno (1967) reported a tree 43 cm in diameter to be 800 years in age. Studies in Yosemite National Park have reported good seedling establishment in stands from 2,950 to 3,250 m elevation (Parker 1988).

A watershed study of subalpine dominated by whitebark pine (*Pinus albicaulis*) was carried out for Eastern Brook Lakes, a watershed of 250 ha extending from 3,170 to 3,780 m elevation on the eastern slope of the Sierra Nevada (Peterson et al. 1989). Only lodgepole pine and whitebark pine were present, with multistemmed trees and shrubby growth forms. The density of pine stems in the watershed, including multiple stems on single individuals if they reach 1.4 m in height, was 3,290 stems ha<sup>-1</sup>, with whitebark pine comprising >90% of these stems. Krummholz individuals of both pine species formed 39% of the total number of stems. The basal area of pines varied from 1.6 to 21.0 m<sup>2</sup> ha<sup>-1</sup> in subunits of the watershed, with lodgepole pine accounting for more than half of this basal area. The mean leaf area index of canopies of lodgepole pine was calculated to be 4.1 m<sup>2</sup> m<sup>-2</sup>, compared to 4.6 m<sup>2</sup> m<sup>-2</sup> for whitebark pine.

The protein-rich and fat-laden pine nuts of whitebark pine form a staple food supply of Clark's nutcrackers (Tomback 1982, 1986). These birds collect massive numbers of these seeds and cache them in the soil. Studies in

the Sierra Nevada have reported that single adults Clark's nutcrackers can cache as many as 89,000 pine nuts in a season, far in excess of their short-term nutritional needs. These caches are the primary means of reproduction for whitebark pines, and thus have strong genetic consequences. Genetic variation is highly structured in within the natural groupings of krummholz thickets and upright tree clumps. Genetic studies have shown that multiple individuals are present within krummholz thickets, and genetic relationships often resemble half- to full-sibling family structure (Rogers et al. 1999). At lower elevations, most (72%) of the tree clumps contained more than one genotype; the remaining clumps appeared to be multi-stemmed trees.

#### LIMBER PINE

Limber pine (*Pinus flexilis*) is widespread in scattered stands over an area of the east slope of the Sierra Nevada from Mono Pass south to the Inyo National Forest east of Sequoia National Park. In this belt it appears to fill the niche occupied by whitebark pine to the north. Although also present in the higher Transverse and Peninsular Ranges of Southern California, limber pine is more typical of the White Mountains in California and eastward across the Basin and Range Province to the Rocky Mountains. Within its Sierra range, limber pine occupies steep, eroded, and/or nutrient-poor sites at or near treeline. It may occasionally be found on more mesic sites but under such conditions has been considered to be a pioneer species. Like whitebark pine, treeline individuals of limber pine frequently form low cushions of krummholz growth.

Studies of limber pine across sites in the Sierra Nevada and southern California concluded that its distribution and abundance are limited by competition from other species. It is most dominant and persists longest on steep, dry slopes at higher elevations. Trees reaching 2,000 years of age have been reported, but such great ages may be atypical.

Although similar in general appearance, limber pine is not closely related to whitebark pine. However, limber pine in its development as a subalpine species has convergently evolved large pine nuts that rely on Clark's nutcrackers rather than on wind for seed dispersal (Tombach and Kramer 1980; Carsey and Tombach 1994).

#### FOXTAIL PINE

The dominant subalpine and treeline pine of the southern Sierra Nevada is foxtail pine (*Pinus balfouriana*). The disjunct distribution of this species—the southern Sierra Nevada and the Klamath Mountains of northern California—is unusual, but in some respects mirrors the disjunction of *Abies magnifica* var. *shastensis* between the southern Sierra Nevada and the Cascade and Klamath Ranges. These two subspecies of foxtail pine are well differentiated, with the southern Sierra Nevada taxon (subsp. *austrina*) morphologically distinct in many characteristics of the foliage, bark, cones, and seeds from populations from the subspecies *balfouriana*

restricted to the Klamath Mountains (Mastrogriuseppe and Mastrogriuseppe 1980).

Despite this morphological differentiation and nonexistent gene flow between the subspecies, there are much higher levels of differentiation among populations within the Klamath Mountains subspecies than between the two subspecies (Oline et al. 2000). This high genetic differentiation is attributed to genetic divergence among small isolated populations in the northern subspecies. In many respects the subsp. *austrina* shows closer links to its cousin, Great Basin bristlecone pine (*Pinus longaeva*) in the White Mountains. Foxtail pine is closely related to both Great Basin and Rocky Mountain bristlecone pine, with the three species forming a close evolutionary lineage.

In the Sierra Nevada, foxtail pine is restricted to the higher elevations of 2,600 to 3,660 m south of the Middle Fork of the Kings River. At its lower elevational limits it may occur in open stands with lodgepole pine, Jeffrey pine, western white pine, red fir. At higher elevations, however, it forms relatively pure but low density stands. Vankat (1970) sampled foxtail pine stands at 3,170 to 3,290 m elevation in Sequoia National park and reported a mean canopy cover of 26%, with a basal area of 31 m<sup>2</sup> ha<sup>-1</sup> and a density of 418 tree ha<sup>-1</sup>. Not surprisingly, the mean basal area of adult foxtail pine and density of seedlings declined with increasing elevation from forest to treeline stands (Lloyd 1997). These declines were also associated with lower nutrient inputs from aboveground litter and lower litter C:N ratio. However, neither nitrogen concentration of seedling needles or nitrogen relative accumulation rate differed significantly across elevations. Models of site moisture availability and irradiance coupled with field measurements of stand characteristics and tree ring records suggest that there are strong correlations of microsite conditions with age-class structure and ring-width patterns (Bunn et al. 2005).

Foxtail pine is shade intolerant at all stages of growth and prefers shallow, well-drained soils on exposed sites. Like other subalpine pines, it has deep, spreading root systems that tap snowmelt in fractures of the rocky granite soil. Unlike whitebark and limber pine, which typically form krummholz at treeline, foxtail pine retains an upright form of growth throughout its elevational range. Despite its high elevation of occurrence, foxtail pines can reach large sizes. A tree at 3,250 elevation on Alta Peak was reported to be 24 m in height and 2 m in diameter. Mastrogriuseppe and Mastrogriuseppe (1972) suggested that foxtail pine may well reach ages of 2,500 to 3,000 years.

### Nonconiferous Vegetation

#### DECIDUOUS FOREST

A number of broad-leaved tree species are also found in the Sierra Nevada. Those associated or intermixed with

coniferous forests, such as black oak, big-leaf maple, and mountain dogwood have already been discussed in previous sections. Here the primary focus is on the more widespread species that occur widely, in particular aspen (*Populus tremuloides*). But first, a brief synopsis of other common deciduous species and their distribution is included. The majority of the deciduous forest types and species discussed are associated with riparian or wetland sites. Due to space limitation, there is not a comprehensive treatment of riparian vegetation but rather a broad overview of some of the dominant trees.

Most of the deciduous trees in the Sierra and northeastern California are associated with riparian areas or subsurface water but may also occur on particularly rocky soils. Buckeye (*Aesculus californica*) occurs in small patches in the lowest margins of yellow pine forests on the western slopes of the Sierra. White alder (*Alnus rhombifolia*) is common along perennial streams and seeps in the montane forests on the western slopes of the Sierra, generally between 750 and 2,400 m. It often occurs intermixed with conifers but also by itself in small patches where the root zone is perpetually saturated. *Cornus sessilis*, a low growing tree or tall shrub <5 m tall (Hickman 1993) may be found associated with white alder or at higher elevations and on the eastern slopes in association with the prevalent shrub *Alnus tenuifolia*. On steep eastern slopes, *Betula occidentalis* occurs between 1,500 and 2,750 m in the southern Sierra, but is lacking in the central and northern Sierra. It grows in groves of multistemmed trees 6 to 9 m tall along streams draining into the Owens Valley. The taller *Populus balsamifera* subspecies *trichocarpa* occurs in riparian areas with low stream gradients and high channel sinuosity (Merrill, Benning, and Fites 2006), more commonly on the eastern slopes. *Salix* species are also common in riparian areas on both slopes of the Sierra, with most growing as shrubs. The ecological relationships of the numerous *Salix* species and their individual patterns have been little studied.

Distribution and floristic composition of riparian deciduous forests and other nonforested communities have been related to geomorphic valley types (Harris 1988), channel morphology, and soil conditions (Herzog 2000; Merrill, Benning, and Fites 2006), proximity to watercourse and time since fire (Russell and McBride 2001), solar radiation, canopy cover, and litter depth (Russell et al. 2003). Stream diversions or reductions in stream flow and flood events can alter physiology, morphology (Smith et al. 1991), and establishment and survival (Rood et al. 2003) of riparian hardwood species. Smith et al. (1991) observed decreased stomatal conductance and reduced leaf size and area in *Populus*, *Salix*, and *Betula* in the eastern Sierra in response to reduced streamflow from diversions, particularly under the more stressful conditions of hot, dry weather. Increased streamflows on the Truckee River for an endangered fish (*Chasmistes cujus*) resulted in extensive seedling recruitment of *Populus fremontii* (Rood et al.). Historically, mining affected riparian areas, particularly in the central and northern



FIGURE 17.12 Mature *Populus tremuloides* stand, 2,500 m elevation, central Sierra Nevada, with James Barry standing in it. The aspen stand is on a slope, and just below it is a wet meadow where aspens are few. Photo courtesy of M. G. Barbour.

Sierra, where it still continues, but the influence on composition and structure of riparian deciduous forests has been little studied (Kattleman and Embery 1996).

Of all of the deciduous species (aside from black oak), aspen is the most widely distributed in the Sierra and northeastern California and is the most widely distributed native North American tree species (Little 1971). It occurs in a diversity of habitats. Aspen occurs where there is adequate moisture in the soil profile but will not grow in soils saturated at the surface for long periods. In the Sierra, aspen generally occurs in pure groves fringing wet or moist meadows, and on slopes watered by springs or seeps or subsurface water (Fig. 17.12; Potter 1998).

Aspen is shade intolerant and requires high light conditions to regenerate. Aspen sprouts vigorously from roots following fire and fire is often attributed to playing a critical role in the perpetuation of aspen, particularly where competition from conifers may occur. Fire not only enhances reproduction but also reduces competition and reduction in light from conifers. Aspen regenerates mostly through vegetative reproduction; adventitious shoots or suckers arise on a long and extensive lateral root system. After disturbances, numerous root suckers of aspen sprout from an extensive root system. This results in a dense stand of trunks, all of which belong to the same clone. In some cases, aspen has been negatively affected by browsing of livestock and deer. When young suckers are browsed extensively over a period of years, their vigor is reduced and aspen regeneration suffers. Management agencies are beginning to address potential effects to aspen including the lack of fire, growth of conifers into aspen stands, and over-browsing of young aspen (Shepperd et al. 2006).

Depending on the elevation, water table, and geographic region, a great variety of shrub and herbaceous species are found in the understory within the aspen type in California (Potter 1998; Manning and Padgett 1995; Sawyer and Keeler-Wolf 1995; Weixelman, Zazmudio, and Zamudio 1999). Weixelman, Zazmudio, and Zamudio reported that the types of plants in the understory of aspen stands were related to soil moisture. Stands with predominately graminoid understories had a shallower depth to soil saturation than sites with predominately shrub or herbaceous understories. In aspen stands associated with meadows, a dense, often tall graminoid and herbaceous layers are characteristic. Common understory shrubs include *Rosa woodsii*, *Salix* spp., and *Ribes* spp. Common understory herbs and grasses include *Elymus glaucus*, *Elymus elymoides*, *Poa wheeleri*, *Lupinus* spp., *Ligusticum grayii*, *Senecio triangularis*, and *Osmorhiza* spp.

Aspen stands not associated with meadows are found on sloping sites where subsurface water is adequate for aspen but too deep for meadow species. This includes talus at the base of slopes. These aspen stands are most vulnerable to conifer encroachment with absence of fire. Here the understory flora is more similar to drier upland communities. *Symphoricarpos* spp. are the most prevalent shrubs, with *S. mollis* common on west slopes and upper montane forests and *S. vaccinioides* in more xeric eastslope forests. Common herbaceous and graminoid species include *Monardella odoratissima*, *Thalictrum* spp., *Hackelia* spp., *Angelica breweriana*, *Wyethia mollis*, *Collinsia* spp., and *Poa bolanderii*.

The biology, distribution, and dynamics of aspen in the Sierra Nevada have been monographed by Barry (1971). He concluded that aspen groves were generally climax, only successional to red fir, and then requiring approximately 200 years for a complete transition to red fir forest.

## MEADOWS

Meadows are found scattered through virtually every forest type of the montane and subalpine zones of the Sierra Nevada, Cascades, and Modoc Plateau in California. They are most prevalent in upper montane and subalpine zones in the Sierra Nevada and Cascades, and in montane portions of the Modoc Plateau. Although their total area is a small percentage of the mountainous terrain, meadows are among the most species-rich vegetation types and are heavily used for both recreation and livestock grazing. Development of meadows or adjacent areas for residences or commercial structures has long occurred (Kattlemann and Embury 1996), and it continues with increased population growth (Duane 1996; Manley et al. 2000).

The single most important factor in explaining the distribution of meadows is the existence of a shallow water table that provides for high soil moisture content the year around (Wood 1975). The importance of overall water table levels and seasonal patterns of water table in plant community composition and dynamics has been noted by many studies of Sierra

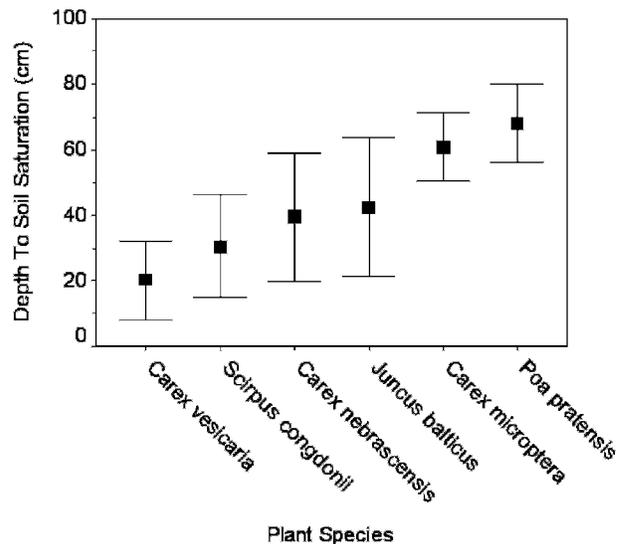


FIGURE 17.13 Average depth to soil saturation ( $\pm$  S.E.) for selected plant species in meadows in the Sierra Nevada. Modified from Weixelman et al. (1999).

meadows (e.g., Bennet 1965; Benedict 1983; Ratliff 1985; Halpern 1986; Allen-Diaz 1991; Weixelman, Zamudio, and Zamudio 1999; Fig. 17.13).

The origin of Sierra meadows has often been attributed to the filling in of glacial lakes and valleys. Although this explanation is valid for some higher elevation meadows, it oversimplifies the variety in meadows types and modes of formation (Rundel, Parsons, and Gordon 1977). Meadows form where there is an accumulation of fine-textured soil in combination with a shallow water table (Ratliff 1985). Meadows typically form in basins, along permanent or intermittent streams, or below springs or seeps. Benedict and Major (1982) further separated out two types of subalpine meadows in the southern Sierra based on physiographic factors. The most typical, found throughout the Sierra, is one with vegetated margins (Fig. 17.14); and the second, with arid, sandy margins.

Other factors that affect meadow size, composition, and structure include climate change, fire, and herbivores. Climate influences meadows directly through modification of water tables and indirectly through enhancement or detriment of periodic tree invasion (Bartolome et al. 1990; Norman and Taylor 2005). The role of fire in meadows of the Sierra Nevada and northeastern California has been little studied but seems to vary by elevation and fire patterns in adjacent forested or nonforested communities. In dry meadows in northeastern California in the Lassen National Forest, Norman and Taylor found that fire occurred frequently (return interval of 11–14 years) in adjacent forests prior to European settlement. Just south, in the eastern portion of Plumas county Blank et al. (1995) found abundant evidence of fire over the last several thousand years using charcoal depositions. It is less clear what the role of fire was in wetter meadows, particularly at higher elevations, but it is



FIGURE 17.14 Wet meadow, about 1,800 m elevation in the central Sierra Nevada, with aspen at the upland edge. Note the heterogeneity of meadow communities (different shades of gray) within the wetland. Photograph courtesy of J. Fites-Kaufman.

surmised to have been infrequent (DeBenedetti and Parsons 1979; Dull 1999; Berlow et al. 2002).

Grazing, which reduces fuel, may confound interpretations of the role of fire potentially causing an underestimation of the role of fire, potentially causing it to be underestimated (Norman and Taylor 2005). Fire in subalpine meadows can influence composition and may be related to drought (DeBenedetti and Parsons 1979; Dull 1999). Interesting effects are establishment or increases in bryophytes. Native Americans often preferentially burned meadows and other riparian areas (Kimmerer and Lake 2001) including many areas in the Sierra and northeastern California (Lindstrom 2000; Anderson 2006). Stevenson (2004) assessed the impact of grazing on Sierran meadows and concluded that grazing and position along a moisture gradient explained 23% of species presence, and that grazing impact was greatest on megaforbs (almost half of ungrazed meadow indicator species were megaforbs).

Although the most commonly studied herbivory effects are from domestic livestock, other herbivores may influence meadows. Berlow et al. (2002) found that gopher mounds influenced the establishment of *Artemisia rothrockii*.

Overall, meadows are characterized by dense cover of graminoid and herbaceous species. Shrubs may or may not be present. Sierran meadows can be classified into four broad

types based on vegetation composition and water table depth: (1) open wet meadow, (2) open dry meadow, (3) shrub meadow, and (4) woodland meadow (see Table 17.10). These broad meadow types may be further classified based on vegetation, elevation, water table, landform, hydrology, and soil characteristics (Bennet 1965; Benedict and Major 1982; Ratliffe 1985; Allen-Diaz 1991; Sawyer and Keeler-Wolf 1995; Weixelman, Zamudio, and Zamudio 1999; Stevenson 2004). Meadow types tend to intergrade across the landscape. For example, an open wet meadow type may grade into a shrub meadow type within a short distance. This is due to the fact that hydrologic conditions, which control the growth of meadow vegetation, can change over short distances. A meadow site also can change vegetation composition over time. An open wet meadow type that experiences a flood that results in the establishment of willows may change to a shrub meadow type. Allen-Diaz (1991) documented the importance of fluctuations in water table on meadow composition. One of the most prevalent meadow types in the Sierra, characterized by presence of *Deschampsia caespitosa* and *Carex* spp. was associated with higher fluctuations in water tables than in any other types in the Sagehen basin in the northern Sierra.

The open wet meadow type is composed predominately of perennial sedge, rushes, and grasses. Dominant species generally spread by rhizomes and often form dense sod over large areas. Soils in this type are saturated in the rooting zone for a majority of the growing season. Soils are generally dark loams due to large amounts of organic material (Weixelman, Zamudio, and Zamudio 1999). The open wet meadow type occurs throughout virtually every forest type of the Sierra and Pacific Northwest floristic provinces and as inclusions in the northern and coastal prairie and sagebrush steppe (Barbour and Major 1977). In the Sierra Nevada and Cascade ranges, open wet meadows usually occur above 1,200 m elevation (3,940 ft) in the north and above 1,800 m elevation (5,900 ft) in the south. *Carex nebrascensis* is a common dominant in open wet meadows across the Sierra Nevada and Southern Cascades (Allen-Diaz 1991).

Subtypes of the open wet meadow type exist, depending on dominant species, presence of an organic layer, elevation, and disturbance. The subtype dominated by *Sphagnum* spp. and sedges is characterized by an acidic peat layer that is subject to oxidation if the meadow vegetation is disturbed. At higher elevations, above 2,340 m, *Carex scopulorum*, *Carex subnigricans*, or *Carex angustata* often dominate open wet meadows (Allen-Diaz 1991; Weixelman, Zamudio, and Zamudio 1999). Many plant communities indicative of disturbance exist within the open wet meadow type. For example, a plant community that increases with disturbance is the *Juncus balticus* community. Overgrazed wet meadows have more herbs and fewer grasses and grasslike species than less intensively grazed or ungrazed (by livestock) meadows, and taller species are replaced by lower growing species (Ratliffe 1985). Willows may become established on sites

TABLE 17.10  
Dominant Plant Species by Major Meadow Type for the Eastern Sierra Nevada

Meadow Type	Dominant Vegetation	Average Cover (%)	Constancy (%)
Open wet meadow	<i>Carex nebrascensis</i>	18	62
	<i>Carex utriculata</i>	15	40
	<i>Carex vesicaria</i>	11	20
	<i>Juncus balticus</i>	3	40
	<i>Deschampsia cespitosa</i>	8	60
	<i>Poa pratensis</i>	4	51
	<i>Achillea millefolium</i>	4	33
	<i>Muhlenbergia filiformis</i>	2	20
	<i>Stellaria longipes var longipes</i>	2	41
Open dry meadow	<i>Carex douglasii</i>	23	75
	<i>Poa secunda</i> subsp. <i>juncifolia</i>	12	75
	<i>Muhlenbergia richardsonis</i>	12	62
	<i>Juncus balticus</i>	5	62
	<i>Leymus triticoides</i>	5	18
	<i>Poa pratensis</i>	5	18
	<i>Poa bulbosa</i>	4	12
	<i>Achnatherum</i> spp.	2	18
	<i>Lupinus</i> spp.	2	25
	<i>Polygonum douglassii</i>	2	50
	<i>Gayophytum diffusum</i>	2	37
	Shrub meadow	<i>Salix lemmonii</i>	35
<i>Salix eastwoodiae</i>		31	8
<i>Poa pratensis</i>		25	78
<i>Carex nebrascensis</i>		21	67
<i>Salix geyeriana</i>		18	67
<i>Ribes inerme</i>		8	32
<i>Juncus balticus</i>		6	64
<i>Achillea millefolium</i>		3	75
Woodland meadow	<i>Populus tremuloides</i>	35	66
	<i>Elymus glaucus</i>	21	40
	<i>Pinus contorta</i> subsp. <i>murrayana</i>	15	45
	<i>Poa pratensis</i>	11	73
	<i>Juncus balticus</i>	7	33
	<i>Achillea millefolium</i>	4	93
	<i>Osmorhiza chilensis</i>	4	62
	<i>Salix scouleriana</i>	1	37

NOTE: Average cover (%) and constancy (%) is given for each species (from Weixelman et al. 1999).

that are flooded with some regularity, and when this occurs, this type can be converted to the shrub meadow type. Trees may also encroach in this type due to lack of fire (Sharsmith 1959) or lowered soil moisture (Wood 1975).

Wet meadows are remarkably variable, in effect a mosaic of half a dozen habitats and associations. Cluster and indicator species analyses of data from the Golden Trout Wilderness in the southern Sierra Nevada suggest that deep channels, emergent habitats, and mudflats are rich in obligate wetland species, and they have a low similarity of species composition with other meadow habitats and communities (Table 17.11; Murrell-Stevenson 2004). A large portion of total meadow biodiversity is found on overhanging banks of meandering stream channels, and also in the understory of willows. Indicators of banks include *Marchantia polymorpha*, *Muhlenbergia filiformis*, *Salix geyeriana*, *Stellaria longipes* var. *longipes*, and *Trifolium monanthum* var. *monanthum*. Willow understory plants include *Dugaldia hoopesii*, *Fragaria virginiana*, *Geum macrophyllum*, *Pedicularis groenlandica*, *Ribes divaricatum*, *Sphenosciadium capitellatum*, and *Thalictrum fendleri*.

The open dry meadow type is found at all elevations and is characterized by meadow species adapted to drier conditions. Soils are not saturated within the rooting zone for any part of the growing season, and saturation is often much deeper than the rooting zone (Allen-Diaz 1991; Weixelman, Zamudio, and Zamudio 1999). Graminoid species that characterize this type at higher elevations include sedges such as *Carex exserta* and grasses such as *Trisetum spicatum* and *Poa stebbinsii*. At lower elevations the sedge *Carex douglasii*, and grasses such as *Poa secunda* spp. *juncifolia*, *Poa pratensis*, *Danthonia* spp., and *Achnatherum* spp. tend to dominate. A subtype of the open dry meadow type is the short-hair sedge type found at higher elevations in the Sierra Nevada. This community is characterized by a tough *Carex exserta* sod that will withstand considerable disturbance. Klikoff (1965) measured the net photosynthesis of three meadow species and found their responses to moisture stress paralleled their natural distributions. As leaf water potential declined from about  $-0.2$  to  $-1.5$  MPa, the net photosynthesis of *Carex exserta* from dry meadows did not significantly decline, but the rates of *Potentilla breweri* and *Calamagrostis breweri* from wet meadows fell sharply to 10% of the initial rates. Short-hair sedge and its associates, *Antennaria* spp., *Lupinus breweri*, *Achnatherum occidentale*, and *Trisetum spicatum*, do well on dry, gravelly soils.

The shrub meadow type is a transitional type that is characterized by open meadow interspersed with clumps of shrubs, usually willow, with 10% to 40% cover across the meadow. Common willow species include *Salix geyeriana* and *S. lemmonii*. This type occurs on landforms where there is periodic flooding during the growing season. The occurrence of floods allows the establishment of willow species from seed and provides the needed moisture for the seed to germinate. Survival of willows has also been

related to water table depth and soil moisture (Conroy and Svejcar 1991).

The woodland meadow type, also found scattered above 1,800 m, is typified by scattered sedges, grasses, and herbs interspersed with lodgepole pine and/or aspen. Depending on the elevation, water table, and geographic region, a great variety of herbaceous species are found within this type. Common grasses include *Agropyron* spp., *Poa wheeleri*, *Elymus glaucus*, and *Bromus carinatus*. In some cases these meadows represent remnants of the wet meadow type that has dried out and been invaded by forests. In other cases, these are sites that normally would support tree cover but have a water table close enough to the surface to support a dense cover of herbaceous species. The causes and dynamics of lodgepole pine establishment and survival in Sierra meadows have had some study but the patterns seem to vary and no one dynamic model exists. Wood (1975) and Helms (1987) found that most lodgepole pine seedlings become established in meadows in years of low snowpack. Others suggest that the nature of the soil may influence whether lodgepole pine is able to invade a meadow (Ratliff 1985; Howell 1931). Helms (1987) suggested that drier meadows were more conducive to encroachment of lodgepole pine, regardless of precipitation. Norman and Taylor (2005) could find no relationship between climate and lodgepole pine invasion in drier eastside meadows in northeastern California. Fluctuations in water table may result in cyclical establishment, survival, and then mortality of lodgepole pine, depending upon the water levels (Bartolome et al. 1990). There may also be feedbacks with fire, tree invasion, and water tables. The role of fire in reduction of invading trees was discussed previously. However, feedbacks with tree invasion, water tables, and fire have not been studied. A prescribed burn that resulted in a patch of high severity in a lodgepole pine stand in the Lake Tahoe basin in the 1990s resulted in the transformation of the site to a meadow. State park ecologists surmised that transpiration of the lodgepole pine had lowered the water table, effectively preventing hydric conditions associated with meadows (Fites-Kaufman, pers. obsv.).

Productivity of meadows varies with moisture status and elevation. Herbage produced on Sierra Nevada meadows in California ranges from less than  $336 \text{ kg ha}^{-1}$  on drier meadows to over  $4,484 \text{ kg ha}^{-1}$  on moist to wet sites (Ratliff 1985). In Sequoia-Kings Canyon National Park subalpine meadows dominated by *Carex exserta* had 24% of the total annual productivity of montane meadows dominated by *Deschampsia* and *Carex* (Stohlgren et al. 1989). Removal of herbage by clipping resulted in some increases in above-ground productivity of 30% to 35% in the first 4 years but also showed declines of 15% to 20% with increased removal. It is unclear whether the increased above-ground productivity was accompanied by decreased below-ground productivity, although monitoring has shown lower levels of root depth and density with intense compared to moderate or no grazing (Weixelman and Zamudio 2001).

TABLE 17.11  
Indicator Species for Habitats in Subalpine Meadows of the Golden Trout Wilderness

<i>Indicator Species by Habitat</i>	<i>Importance Value</i>	<i>P Value</i>	<i>Cluster Level</i>
Gravel Bars			
<i>Agrostis scabra</i>	15.4	0.01	1
<i>Calamagrostis stricta</i> subsp. <i>inexpansa</i>	16	0.011	1
<i>Eleocharis acicularis</i> var. <i>acicularis</i>	14.5	0.017	1
<i>Epilobium hornemannii</i>	12.5	0.037	1
<i>Gayophytum humile</i>	15.4	0.008	1
<i>Salix lemmonii</i>	11	0.027	1
<i>Taraxacum officinale</i>	15.2	0.011	1
Mudflats			
<i>Limosella aquatica</i>	16.5	0.011	1
Gravel Bars and Mudflats			
<i>Gnaphalium palustre</i>		0.001	1
Gravel Bars	27.6		
Mudflats	21.3	0.018	3
<i>Veronica serpyllifolia</i> subsp. <i>humifusa</i>		0.001	1
Gravel Bars	25.3		
Mudflats	5.2	0.06	3
<i>Ranunculus cymbalaria</i> var. <i>saximontanus</i>		0.001	1
Gravel Bars	25.3		
Mudflats	19.9	0.022	3
Saturated			
<i>Eleocharis pauciflora</i>	11.4	0.044	1
Deep Standing Water			
<i>Lemna trisulca</i>	12.6	0.085	3
<i>Perideridia lemmonii</i>	9.5	0.055	2
<i>Veronica americana</i>	46.5	0.001	3
Overhanging Banks			
<i>Stellaria longipes</i> var. <i>longipes</i>	16.8	0.011	2
<i>Trifolium monanthum</i> var. <i>monanthum</i>	29.3	0.004	3
<i>Salix geyeriana</i>	16.4	0.026	2
<i>Muhlenbergia filiformis</i>	16	0.049	2
<i>Marchantia polymorpha</i>	10.5	0.058	1
Willow Understory			
<i>Pedicularis groenlandica</i>	10.8	0.05	2
<i>Ribes divaricatum</i>	10.7	0.055	2
<i>Dugaldia hoopesii</i>	15.4	0.018	2
<i>Fragaria virginiana</i>	21.6	0.007	2
<i>Geum macrophyllum</i>	42	0.001	2
<i>Sphenosciadium capitellatum</i>	18.4	0.021	2
<i>Thalictrum fendleri</i>	42.2	0.001	2

(continued)

TABLE 17.11 (continued)

Indicator Species by Habitat	Importance Value	P Value	Cluster Level
Dry			
<i>Agrostis idahoensis</i>	11.5	0.038	1
<i>Carex stramineiformis</i>	14.5	0.015	1
<i>Poa pratensis</i>	13.2	0.027	1
<i>Antennaria rosea</i>	10.9	0.051	1
<i>Carex subnigricans</i>	13.2	0.03	1
<i>Elymus trachycaulus</i> subsp. <i>trachycaulus</i>	12.6	0.019	1
<i>Koeleria macrantha</i>	11.7	0.043	1
<i>Pyrocoma apargioides</i>	13.6	0.012	1
Moist			
<i>Dodecatheon alpinum</i>	12.4	0.039	1
<i>Deschampsia cespitosa</i>	11.5	0.026	1
<i>Gentianopsis holopetala</i>	13	0.03	1
<i>Ranunculus alismifolius</i>	13.5	0.031	1
<i>Pedicularis attollens</i>	15.4	0.016	1
Dry/Moist			
<i>Carex capitata</i>	10.9	0.041	2
<i>Juncus orthophyllus</i>	15.7	0.033	2
Rocky Gravelly Banktops			
<i>Poa secunda</i> subsp. <i>juncifolia</i>	18.2	0.032	3
<i>Elymus glaucus</i> subsp. <i>glaucus</i>	21	0.001	3
<i>Juncus balticus</i>	20.2	0.02	3
<i>Penstemon heterodoxus</i>	24.4	0.015	3
<i>Senecio integerrimus</i> var. <i>exaltatus</i>	15.1	0.034	3
<i>Artemisia rothrockii</i>	38.1	0.002	3
<i>Castilleja praeterita</i>	32.6	0.006	3
<i>Lupinus lepidus</i> var. <i>ramosus</i>	30.9	0.002	3
<i>Muhlenbergia richardsonis</i>	46.9	0.001	3
<i>Elymus glaucus</i> subsp. <i>glaucus</i>	21	0.001	3

NOTE: The table presents indicator species for habitats along meandering stream channels and in nonchannelized portions of meadows. For each species, importance value, significance value (as an indicator), and clustering level (1–3) are presented. From Murrell-Stevenson (2004).

#### OUTCROPS AND MONTANE CHAPARRAL

Although open rock outcrops constitute a significant area within the coniferous zone of the Sierra Nevada, the colonization and development of vegetation on outcrops have been rarely discussed in the literature. The general pattern of succession on granite outcrops in the montane zone of the southern Sierra Nevada has been described in some detail by Rundel (1975), and his observations may have general applicability to other parts of the range. Successional development is primarily related to physiographical weath-

ering, leading to the formation of fracture lines suitable for colonization of woody plants. Biological modification of the outcrop by primary colonization of cryptogams and herbaceous plants is relatively unimportant in succession.

Two species of crustose lichens, *Rhizocarpon bolanderi* and *Lecanora gibbosa*, are the earliest colonizers on granite outcrops in the southern Sierra Nevada, although a variety of other species of lichens may also be present. Bryophytes are also early colonizers, particularly *Grimmia* species, which form mats along the margins of small drainage channels on

the outcrop surfaces. Small discontinuous mats of *Polytrichum juniperinum* and *Ceratodon purpureus* are common along seepage zones and in areas of shallow soil accumulation. Despite this widespread primary colonization by lichens and bryophytes, only rarely do these species play a significant role in the establishment of woody perennials on the outcrops.

Significant colonization of perennial species first occurs on outcrops when physiographical succession proceeds from a bare granite surface to the formation of fracture lines with prominent crevices. These crevices, 2 to 5 cm wide at the surface, collect windblown sand and organic matter, thereby providing a substrate for vascular plant colonization. *Epilobium canum* subsp. *latifolium* is the most widespread colonizer, but *Lomatium torreyi* may be more abundant locally. In moist, shaded crevices, *Pellaea breweri*, *P. bridgesii*, *P. mucronata* var. *californica*, *Onychium densum*, *Cheilanthes gracillima*, and other ferns dominate.

Primary colonization of woody plants in crevices is the most important stage in succession leading to the development of broad soil mats. In moist years, seeds of a variety of shrubs and trees are able to germinate and become established in pockets of granitic sand and organic matter within crevices. The most important montane colonizers are ponderosa pine, Jeffrey pine, incense cedar, *Arctostaphylos patula*, and *A. viscida*. Less commonly, black oak, canyon live oak, white fir, and *Ceanothus cordulatus* are present. In the subalpine zone, Sierra juniper, *Arctostaphylos nevadensis*, lodgepole pine, foxtail pine, whitebark pine, and *Quercus vaccinifolia* colonize outcrops in a similar manner. There is no evidence that the establishment of these species requires any previous biological succession on outcrops. Recent research on root growth of conifers and water use has demonstrated that rock fractures in granitic bedrock are important sources of water for young and mature pines (Hubbert et al. 2001).

This shrub-dominated vegetation is generally called montane chaparral (Fig. 17.15). On south-facing slopes with skeletal, coarse-textured soils, montane chaparral can maintain itself, but on less stressful locations, it can be overtopped by conifers, at which time the shade-intolerant shrubs die, leaving only long-lived "skeletons" on the forest floor to indicate that the forest is relatively recent. By experimentally manipulating montane chaparral, Conard and Radosevich (1982) were able to show the competitive effects of the shrubs (as a consequence of both shading and extraction of soil moisture) on young trees.

Alternatively, soil mats may evolve from weathered, broken outcrop surfaces. Shallow sands with little or no organic matter here support modest diversity of herbaceous perennials, including *Calyptridium umbellatum*, *Eriogonum nudum*, *E. wrightii* var. *subsaposum*, *Lomatium torreyi*, *Streptanthus tortuosus*, and mats of *Polytrichum juniperinum* and *Ceratodon purpureus*. With only 2 to 5 cm of granitic soil, dense carpets of herbaceous annuals may cover outcrop surfaces, particularly *Linanthus montanus*, *Phacelia oregones*, and *Eriogonum*



FIGURE 17.15 Montane chaparral, northern Sierra Nevada, approximately 1,700 m elevation. Dominants include *Arctostaphylos patula* and *Quercus vaccinifolia*. Photo courtesy of M. G. Barbour.

*spergulinum*. As outcrop soils reach 5 to 15 cm in depth with moderate amounts of organic matter, these species are replaced or overshadowed by a community of herbs characteristic of open areas within yellow pine forest communities. Woody trees and shrubs are able to colonize soils of this depth without reliance on crevice microhabitats.

In the northern Sierra Nevada, nongranitic outcrops are also present but have been little studied. Rock types include both volcanic and sedimentary or metasedimentary. Most of these outcrops are at the lower elevations along the western slopes of the Sierra Nevada, but a few occur in the upper montane and subalpine zones. The vegetation varies with elevation and location relative to the crest. Vegetation may be similar to adjacent areas but sparse and limited to fractures or small pockets of soil.

### The Cascade Range

Low-elevation ponderosa pine and Douglas-fir forest, white fir-mixed conifer forests, and upper montane red fir forest typical of the Sierra Nevada continue northward into the Cascade Range. The southern Cascades in California include Lassen Peak and Mt. Shasta. Unlike the Sierra Nevada, the crest of the mountains is less well defined, and therefore elevational and east-west gradients in vegetation can vary from that of the Sierra. North of Mt. Shasta, the Klamath Mountains form a barrier to precipitation resulting in vegetation on the western Cascade slopes more similar to east slopes of the Cascades near Lassen Peak (Skinner and Taylor 2006). Similar to the Sierra, vegetation changes in response to elevation and aspect (Taylor 2000; Beaty and Taylor 2001) but may also vary more noticeably with changes in soil substrate (Parker 1991).

Substrate may be more important in the Cascades because of the relatively young soils of volcanic origin and the strong contrasts in available nutrients and water depletion patterns in Andisols. In general, mixed ponderosa pine, Douglas-fir, and white fir forests occur on western slopes at elevations below 1,700 m. Canyon live oak occurs on

rockier soils in large canyons. On eastern slopes and more xeric sites, more open pine forests dominated by varied mixtures of ponderosa pine and Jeffrey pine occur (Smith 1994; Bekker and Taylor 2001). At higher elevations above 1,700 m, forests dominated by white fir are found on more mesic sites, but more typically mixed forests of Jeffrey pine and white fir occur up to 1,900 m on west slopes and 2,100 m on eastside slopes (Parker 1991). Above this zone, large areas of mixed white fir and red fir forests occur, followed at the highest elevations by mountain hemlock. Lodgepole pine occurs throughout the drier eastern portions of the Cascades in wet areas or lowlands with cold air drainages or on recently geologically disturbed areas. Parker surmised that lower elevation forests in Lassen National Park are more similar to those in the Sierra, whereas higher elevation subalpine forests are more similar to those of the central Cascades or Klamath mountains. Overall, little attention has been focused on variation in understory shrubs and herbs between the northern Sierra and southern Cascades.

On west slopes near Lassen Peak, low-elevation montane forests are similar to those described for the Sierra, with mixed stands of ponderosa pine, black oak, white fir, sugar pine, Douglas-fir, and incense cedar (Beaty and Taylor 2001). Beaty and Taylor identified five communities with ponderosa-pine-dominated forests occurring on south and west aspects, mixed Douglas-fir and white fir forests on north and east aspects, and mixed forests with all species but dominated by white fir, sugar pine, and incense cedar on west aspects between 1,370 and 1,770 m elevation. White-fir-dominated forests and mixed white fir-red fir forests occurred at higher elevations and on north- and northeast-facing slopes.

Understory in the lower montane forests of the southern Cascades is mostly similar to that of the northern Sierra, but some distinct plant associations have been identified (Fites 1993). Fites described mesic white fir- and Douglas-fir-dominated forests near Burney with *Acer circinatum* and *Paxistima myrsinites*, species more common in Pacific Northwest forests than the Sierra Nevada. As in the Sierra, *Arctostaphylos viscida*, *A. patula*, *Rosa* spp., and *Symphoricarpos mollis* occur. *Ceanothus velutinus* replaces *Ceanothus integerrimus* in importance, except for the western-most slopes. *Chrysolepis sempervirens* is more common than in the Sierra Nevada. On mesic sites, *Cornus nuttallii* and *Corylus cornuta* occur, whereas *Acer macrophyllum* may be locally abundant near streams or where rocky soils with subsurface water occur.

Eastern slope montane forests are heavily dominated by ponderosa and Jeffrey pines. Understory shrubs on the east slope reflect a strong Great Basin affinity: *Purshia tridentata*, *Artemisia tridentata*, *Arctostaphylos patula*, *Cercocarpus ledifolius*, *C. betuloides*, and *Ceanothus velutinus* are all important (Smith 1994). These forests are similar to those that occur in the Modoc Plateau and are described in more detail below.

Red fir dominates most upper montane forests, intermixed broadly with white fir at the lower boundaries and with western white pine at mid and higher elevations. Parker

(1991) suggests that western white pine is more prevalent in red fir forests in Lassen National Park than in the Sierra, but Potter (1998) also described several red fir plant associations with western white pine as prominent in a classification of upper montane forests in the central and southern Sierra Nevada. Little information exists on understories of upper montane forests in the Cascades. Some prevalent shrubs that occur in the Sierra Nevada upper montane forests also occur in the Cascades, including *Arctostaphylos nevadensis*, *A. patula*, and *Ceanothus cordulatus*.

Subalpine forests in the southern Cascades differ from those of the Sierra Nevada, particularly the central and southern Sierra (Parker 1991). Lodgepole pine is less important, and mountain hemlock and whitebark pine are most characteristic (Parker; Taylor 1995). Foxtail pine and limber pine are noticeably absent, although they are also absent in subalpine forests of the central and northern Sierra such as around Lake Tahoe. Taylor documented upward shifts in mountain hemlock distribution on Lassen Peak between 1842 and 1910 in response to climatic warming that began at the end of the Little Ice Age (1850–1880).

#### Fire, Mudflows, Avalanches, and Successional Studies

Vegetation dynamics and succession in the southern Cascades are in response to mudflows, avalanches and fire. Mudflows and avalanches were studied earlier (Beardsley and Cannon 1930; Dickson and Crocker 1953; Bailey 1963; Heath 1967); and fire history and effects of fire suppression, more recently (reviewed by Skinner and Taylor 2006).

Major mudflows and avalanches have been a regular environmental feature on Lassen Peak and Mt. Shasta. The flows have killed large areas of coniferous forests, resulting in primary succession of conifers and shrub species on bare substrates. Sudden release of water on the south slope of Mt. Shasta during the summers of 1924 to 1926 spread detritus over several square kilometers to a depth of >5 m. These flows, studied by Beardsley and Cannon (1930) and Dickson and Crocker (1953), included not only large boulders but also considerable fine volcanic mud. The original mixed-conifer forest community in the area of the flow was dominated by incense cedar, white fir, ponderosa pine, and sugar pine, with a scattering of black oak. Conifer species showed early signs of injury in the mudflow area, and within a few months virtually all trees were dead in areas where mud reached over 1 m in depth. The direct effect of the mudflow on conifers was attributed to deprivation of oxygen from the roots. Willows in the area survived for several years, but eventually succumbed to desiccation of their substrate.

The recolonization of areas devastated by mudflows and avalanches on Lassen Peak was studied intensively by Bailey (1963) and later by Heath (1967), who described a successional series covering flows dated over the last 1,500 years. The early establishment of conifers is limited only by the availability of disseminules and the physical stresses of the

environment, and some establishment occurs the first year. In the early stages of recolonization high-elevation species such as lodgepole pine, western white pine, and mountain hemlock do well, but they are eventually replaced by white fir and Jeffrey pine, which gradually increase in dominance. A later study of colonization on a debris flow from 1915 showed similar but slower patterns at higher elevation sites (Kroh et al. 2000). This flow occurred in the upper montane red fir and lodgepole pine forests. Colonization was slow for the first 15 years and did not peak until 40 years after the debris flow. Tree growth of the early colonizers has been slow. Both the slower recolonization pattern and the slower growth rates may be a reflection of the harsher, high-elevation environment or varied substrate conditions such as those underlain by soil versus lahar deposits or large tephra deposits.

The effects of fire are less dramatic than the primary succession ensued by mudflows and avalanches but has been a consistent force shaping forests in the southern Cascades for many centuries (Skinner and Taylor 2006). Fire-return intervals are similar to those of the Sierra Nevada, but the pattern of variation varies with landscape location. On western slopes in lower montane forests, more mesic sites on northern or eastern aspects and lower slope positions have the highest historical fire frequencies (Beaty and Taylor 2001). However, this pattern changes on the eastern portion of Lassen National Park, on Prospect Peak, where longer intervals between fires were found on more xeric west and south-facing slopes (Taylor 2000). Apparently, the more xeric sites occurring in the rain shadow of Lassen Peak have less fuel production and continuity. Repeat photographs from sites originally shot in 1925 show increases in forest density, particularly of the understory and dominated by young white fir (Taylor). Size structure data in the Caribou and Thousand Lakes Wilderness areas also suggest increased understory densities, particularly of white fir (Bekker and Taylor 2001; Taylor and Solem 2001). Although less dramatic, Taylor also reports increased density of the understory of some red fir forests.

Some of the landscape patterns of fire in the southern Cascades are a result of variation in the substrate from more recent volcanic flows or more resistant volcanic material. Taylor (2000) attributed longer fire-return intervals in some of the Jeffrey pine sites on Prospect Peak, to adjacent bare areas resulting from lava and scoria deposits in the mid-seventeenth century that act as a barrier to fire spread.

### Modoc Plateau

Within the Modoc Plateau, extensive areas of relatively level upland east of the Cascade-Sierran ridge are broken by the block-faulted Adin Range. These areas are high enough to support coniferous forest vegetation. Because of the rain shadow effect of the Cascades, precipitation in the conifer zone averages only about 600 mm yr<sup>-1</sup>, most falling as winter snow.

The vegetation of the Modoc plateau and Adin Range has been described by Smith (1994) and Vasek (1978). Riegel et al. (2006) summarized vegetation and fire patterns across northeastern California. The vegetation is a mosaic of coniferous forest communities (39% of the area), open woodlands with heavy cover by shrubs (43%), and shrublands (17%). The woodlands are discussed in Chapter 23 (this work) and scrub in Chapter 22 (this work).

The most prevalent forests are those dominated by varying mixtures of ponderosa and Jeffrey pine (Smith 1994). The following description of vegetation is based largely on the detailed work of Smith. In closed forest stands, white fir and incense cedar are important, with black oak present in low numbers. Individual species of conifers sort out along environmental gradients in the Modoc Plateau in patterns similar to those described earlier for the Cascades and Sierra Nevada. Stands dominated by *Juniperus occidentalis* (mostly subsp. *australis*) are typically associated with dry, rocky substrates, although they may occur also on heavy soils on south-facing slopes.

On the other end of the gradient, white fir and incense cedar dominate relatively mesic sites such as on north aspects, higher elevations, or deeper, less rocky soils. Forests are typically open with tree canopy covers ranging from 10% to 50%. Under these open tree canopies an understory of several shrub species and numerous grasses and herbs are typically present, often similar to those found in the adjacent Great Basin steppe. *Purshia tridentata*, *Artemisia* spp., and *Haplopappus bloomeri* are common understory shrubs. *Cercocarpus ledifolius* is prevalent on sites with shallow or rockier soils. *Arctostaphylos patula*, *Ceanothus prostratus*, *Ame-lanchier pallida*, *Ceanothus velutinus*, *Ribes cereum*, and *Prunus* spp. may occur on sites with deeper soils or higher moisture levels. At least several species of grasses or herbs are typically present. The most common grasses include *Elymus elymoides*, *Achnatherum occidentale*, *Festuca idahoensis*, and *Poa* species. *Wyethia mollis* is a widespread herb that some believe expands and persists on sites with historic heavy grazing.

Current basal areas in older remnant forest stands range from 14 to 57 m<sup>2</sup> ha<sup>-1</sup>, mostly 23 to 34. Smith (1994) reported large pine trees ranging in age from 200 to 446 years. Laudenslayer et al. (1989) reviewed information on historic forests in northeastern California and compared their structure and composition with current patterns. Previously, forests were more open, larger trees were present throughout more of the landscape, shrubs were less prevalent, and perennial grasses were more dominant in the understory. Densities were highly variable. Currently, they range from 182 to 250 trees ha<sup>-1</sup>, whereas in the early 1900s they ranged from 35 to 190 trees ha<sup>-1</sup> (Laudenslayer et al. 1989).

### Warner Mountains

The Warner Mountains, running north-south along the Nevada border in northeastern California, reach a crest elevation of 2,130 to 2,440 m, with a maximum elevation of

3,013 m at Eagle Peak. A few early studies of vegetation (Haller 1961; Milligan 1969) have been supplemented by others since the first publication of this book (Vale 1977; Riegel, Thornburgh, and Sawyer 1990; Schierenbeck and Jensen 1994; Smith 1994). Floristically and climatically, the mountains are influenced by both California and the Great Basin (Pease 1965; Riegel, Thornburgh, and Sawyer; Schierenbeck and Jensen 1994). Vegetation patterns differ from other mountain ranges in California, and in particular the Sierra Nevada. Two typical Sierran conifers, red fir and sugar pine, are absent as well as mountain hemlock and Douglas-fir (Griffin and Critchfield 1972). *Pinus washoensis* (Washoe pine), a high-elevation form of ponderosa pine, is an important member of the upper montane communities, comprising up to 50% to 70% of the mature trees (Haller).

Little information exists on forest quantitative structure for the Warner Mountains, but floristic composition was sampled in detail by Riegel et al. (1990), Schierenbeck and Jensen (1994), and Smith (1994). On more productive sites in mature stands, basal areas varied from 34 to 43 m<sup>2</sup> ha<sup>-1</sup> (Smith 1994). Higher elevation Washoe pine dominated forests had lower basal areas averaging 21 m<sup>2</sup> ha<sup>-1</sup>.

Vegetation varies among the more gentle western slopes, with greater soil development and the steeper, rockier, and drier eastern slopes. At the lowest elevations, sagebrush- and juniper-dominated communities occur, similar to adjacent vegetation the Modoc Plateau (Vale 1977). Moving up in elevation, a mosaic of forests comprised of white fir alone or with yellow pines (ponderosa, Jeffrey, and Washoe pines), occur with open herb and scrub-dominated communities and meadows or aspen patches (Fig. 17.16). At the highest elevations, whitebark pine and lodgepole pine occur, sometimes mixed with white fir at the lower limits of their distribution.

On the less productive eastern slopes, a lower proportion of forest cover is present (Vale 1977; Schierenbeck and Jensen 1994). Riegel, Thornburgh, and Sawyer (1990) described four series including mountain mahogany, aspen, white fir, and whitebark pine. The white fir series included varied amounts of yellow pines. On the eastern slopes of the Warner Mountains, in the wilderness area, Schierenbeck and Jensen sampled vegetation and mapped their spatial extent. They estimated that white fir and mixed white fir and yellow pine forests comprised half of the area, northern juniper woodlands 13%, white bark pine 10%, mountain mahogany scrub 9%, montane meadows 7%, and big sagebrush scrub 7% of the area. Small amounts of montane black cottonwood, subalpine sage, and montane riparian scrub vegetation also occurred.

Vegetation structure and composition have been altered by a combination of fire suppression and historic grazing (Vale 1977). Although older white fir are present in the overstory and white fir has probably always been important in the forests of the Warner Mountains as with other similar areas to the south in Plumas County (Leiburg 1902), there has been an



FIGURE 17.16 White fir-pine forests and woodlands on volcanic substrates in the montane zones of the Warner Mountains. Fragmentation of the stands is caused by unstable slopes, wet meadows, and rock outcrops. Photograph courtesy of D. Weixelman.

apparent shift in the last century or more to less pine regeneration and greater white fir regeneration (Vale 1977; Schierenbeck and Jensen 1994). Vale also noted migration of conifers into sagebrush scrub and other shrub and herbaceous dominated communities. He attributed this at least in part of heavy grazing in the early part of the twentieth century.

### Productivity and Carbon and Nutrient Cycles

Relatively little research has been conducted on productivity and carbon and nutrient cycling in the Sierra Nevada, Cascades of California, and northeastern California. Nevertheless, the relatively small body of work in these areas suggests that there are some unique patterns in the Sierra Nevada because of interaction of the relatively productive forests coupled with a Mediterranean climate and low decomposition rates. This section contains a brief summary of existing information and sets the stage for implications for conservation, restoration, and future research.

The majority of research and data on productivity in the Sierra Nevada has focused on timber volume production, or tree bole production as summarized in Helms and Tappeiner (1996). The most productive ponderosa pine-mixed conifer sites can grow 17.5 m<sup>3</sup> yr<sup>-1</sup> (Oliver 1997). Red fir and mixed red fir-white fir can also be productive, growing up to 15 to 16.4 m<sup>3</sup> yr<sup>-1</sup>. The drier, eastside ponderosa pine forests are one-third as productive, with production of 5.6 m<sup>3</sup> yr<sup>-1</sup> (Oliver 1972). Westman (1987) characterized all forms of above ground biomass production in a white fir and red fir stand in Sequoia National Park and stated that these stands were near the high end of production levels in North America. Standing biomass was 43 kg m<sup>-2</sup> and 97 kg m<sup>-2</sup> in red fir and white fir stands, respectively. This was comparable to Douglas-fir forests in the Pacific Northwest but two to three times that in ponderosa pine forests in the southwest United States, three to six times deciduous forests in the eastern

United States, and seven times greater than balsam fir in New York. The white fir stand showed above ground production of 1,630 to 2,200 g m<sup>-2</sup> yr<sup>-1</sup>. Production in white fir was 1.3 to 2.7 times greater than that in red fir (810 to 1,030 g m<sup>-2</sup> yr<sup>-1</sup>). Westman (1987) attributes the greater production in a younger white fir stand to high stem densities (550 stems ha<sup>-1</sup> <26 cm dbh) and the high leaf production of these younger white firs. As discussed in the previous sections, increased stem densities of smaller trees have occurred throughout much of the Sierra Nevada in the last 100 years.

Litter accumulation rates have been documented for a few sites along the western slopes of the Sierra Nevada. Hart and Firestone (1991) measured 4,000 kg ha<sup>-1</sup> yr<sup>-1</sup> of litter fall in ponderosa-pine-dominated mixed conifer forests. Stohlgren (1988) included both litter and wood (<15.2 cm diameter) and measured production of 4,355 kg ha<sup>-1</sup> yr<sup>-1</sup> for a mixed white fir, sugar pine, and incense cedar stand and 6,364 kg ha<sup>-1</sup> yr<sup>-1</sup> for a giant sequoia stand.

These relatively high aboveground production rates and standing aboveground biomass levels are coupled with some of the lowest documented litter and small wood decomposition rates in temperate and boreal forests. Hart et al. (1992) reported decomposition constants of 0.08 and 0.18 yr<sup>-1</sup>. They suggested the low levels relative to other temperate forests was due to a temporal separation of warm temperatures and moist conditions that severely limited decomposition. Stohlgren (1988) estimated that 57 to 62 years would be required for 95% decay for all detritus (<15.2 cm diameter) and 27 to 30 years for the litter alone.

These rates are similar to what Wagener and Offord (1972) reported for piles of logging slash decomposition in northeastern California, measured over a 27-year period. They contrasted their findings with those from slash piles in the Pacific Northwest with 90% decay in 16 to 20 years and suggested the difference was due to the lack of "wet rots" in California. Harmon et al. (1987) found high rates of decomposition of down white fir logs and suggested other factors than fungi, as, for example, carpenter ants, may be important in decomposition in the Sierra Nevada.

More recent research has been conducted on nutrient fluxes and properties in the Sierra Nevada and northeastern California than on productivity and decomposition. Nitrogen is considered a primary limiting nutrient for plant growth in this portion of California. Frazer et al. (1990) summarized estimates of net N-mineralization and reported levels from 3.4 to 15.6 mg N m<sup>-2</sup> d<sup>-1</sup> in the forest floor or top 15 cm of soil. Powers (1990) compared a temperature and vegetation gradient and found lowest levels (2.4 kg ha<sup>-1</sup>) in soils under red fir forests and highest levels (23.4 kg ha<sup>-1</sup>) in soils under mixed conifer forests during the dry season (June–October). Both Powers (1990) and Hart and Firestone (1989) reported higher net N mineralization in younger than older forests, although Davidson et al. (1992) found two to three times greater gross mineralization in old growth forests. Davidson et al. (1992) suggest that microbial assimilation of NO<sub>3</sub><sup>-</sup> may be an important pathway in these forests.

The presence of nitrogen-fixing plants can result in greater net N mineralization and greater soil nitrogen and may play an important role in uptake and conservation of nitrogen released during fires. Erickson et al. (2005) found net N-mineralization rates 200% greater, and higher soil N concentrations under *Ceanothus cordulatus* patches than in adjacent forests in white fir-mixed conifer forests on the western slopes of the Sierra Nevada. Similarly, Johnson (1995) reported higher soil nitrogen levels below patches of *Ceanothus velutinus* on the eastern slopes of the Sierra Nevada. *Chamaebatia foliolosa*, widespread under open ponderosa pine stands, is an active nitrogen-fixer (Rundel et al. 1981).

## Conservation and Restoration

The most serious challenges facing conservation and restoration of Sierra Nevada vegetation are population growth, climate change, nonnative species invasions, and changes in fire–vegetation interactions. All factors affecting vegetation such as fire, air pollution, grazing, recreation, invasive species, logging, fuel treatments, mining, and water diversions are largely influenced in magnitude or extent by population growth in California. These varied factors and their influence on the Sierra Nevada were described extensively in the Sierra Nevada Ecosystem Project Final Report to Congress in 1996 (Wildland Resources Center 1996).

According to forecasts by Duane (1996), the human population of the Sierra Nevada bioregion is forecast to triple from 1990 to 2040. He further states that the population "more than doubled from 1970 to 1990, and its current population is approximately four times the peak population during the gold rush (1849–1852). This assessment of population increase does not include the impact of increased population in other parts of California that influence the Sierra Nevada through recreation or transported air pollution.

Along with current and future direct impacts of more people on Sierra Nevada vegetation, there are accumulations of changes in vegetation since European settlement that have greatly influenced the current state of vegetation. This includes increases in forest density and accumulated surface fuels (McKelvey et al. 1996; van Wagtendonk and Fites-Kaufman 2006). Although these changes may be due in part to climate change (Millar and Woolfenden 1999), there is no doubt that the absence of fire has played a key role in these changes. The Sierra Nevada has some of the most productive forests in North America, and these coincide with a long and consistent fire season (J. F. Franklin personal comm., personal observation). This leads to more rapid vegetation growth and fuel accumulation rates combined with high fire likelihood and subsequent potential for high severity fire than any other location in the western United States.

The high human population in the state contributes to higher levels of fire ignitions (Stephens 2005). Social concerns and lack of consensus about approaches and extent of

treatments to restore or deal with the historic and continued fuel accumulations compound the situation. These issues include concerns about air-quality degradation from smoke from prescribed burning, the expense of treatments, and disagreements about the relative merits and effectiveness of mechanical versus fire treatments. Despite the proven success of prescribed burning in restoration of vegetation in national parks of the Sierra Nevada, the treated area is limited compared to that which would be required to influence a large portion of the landscape. The same is true for all types of restoration and fuel treatments on national forest lands. As stated by some "it has taken 100 years to get here and it will take that long to get out of it" (J. van Wagendonk, personal communication).

Although much focus has been placed on characterization and understanding of historic patterns as a benchmark for restoration, changing climate along with changing social preferences may require another template for restoration. This can be more difficult than following a historic template, because the options are more open. It is clear that failing to address climate change along with potential increases in air pollution may result in even greater changes to Sierra Nevada vegetation as well as human populations. A 125% increase in the number of small wildfires that cannot be readily suppressed and turn into large wildfires has been forecasted (Fried et al. 2004). This forecast included a potential increase in the area burned by 41% and an increase in fire severity. The higher severity is in part a reflection of the current, overly dense forests in much of the Sierra Nevada, particularly the relatively mesic and productive montane forests. Climate is predicted to get warmer in the Sierra Nevada, resulting in longer fire seasons (Fried et al.).

Concurrent with increased fire is the threat of increased air pollution, based on the sheer increase in human population in California. Already, evidence of air pollution damage has been documented in the southern Sierra Nevada and mean levels of ozone along the western slopes of the central Sierra Nevada are among the highest in the country (Cahill et al. 1996; Carroll et al. 2003). Although the chronic effects of air pollution on Sierra Nevada forests have not reached the magnitude of those in southern California, the question remains when that might occur. Some of the most important effects of pollution are changes in the physiology and growth of trees that make them more susceptible to drought, particularly through decreased root growth. Although the Sierra Nevada has not experienced a recent drought of the magnitude of that which resulted in extensive and unprecedented mortality in southern California mountains, reconstructed climatic history of the Sierra Nevada from tree rings of the long-lived foxtail pine and western juniper indicate that severe droughts are not uncommon (Graumlich 1993). Forests that are denser are more susceptible to drought-related mortality, particularly from secondary effects of insect attack (Ferrell 1996).

A hard look at these future impacts of population increase, fire, forest and vegetation density, air pollution, and inevitable drought by all societal factions is desperately needed. Although we view the changes that have occurred in vegetation of the Sierra Nevada as great since European settlement to now—they may be minor compared to the future.

Invasive nonnative species present a potential serious threat to several plant communities in the Sierra Nevada. Such species have the potential to cause fundamental changes in natural community structure or ecosystem processes through crowding out of native species, altering natural fire cycles, changing hydrologic flow, impacting soil moisture availability, and/or altering soil nutrient levels (D'Antonio and Kark 2002; Brooks et al. 2004). Broad surveys carried out within Sierran national parks have shown that nonnative plant species richness is negatively correlated with elevation (Gerlach et al. 2003). Montane coniferous forests have about one-third as many nonnative species as the foothill oak savannas, and fewer than half of the species were shared between these communities (Keeley, Lubin, and Fotheringham 2003). Although there are relatively few nonnative species that pose present threats to native species and communities in the coniferous forests of the Sierra Nevada, there are a number of alien species present in small amounts that have the potential to have serious impacts on native ecosystems should they expand their range (Gerlach et al.).

As would be expected, nonnative species are most abundant in disturbed sites such as along roads and adjacent to developed areas. Within more natural montane and subalpine communities, nonnatives are generally most successful in invading wet meadow or riparian sites, although there are notable exceptions. *Bromus tectorum* (cheat grass), a widespread problem in rangelands across the Intermountain West, has until recently been only a minor invader of dry ponderosa pine forests in the Sierra Nevada. As has been found in similar forests in eastern Washington, *B. tectorum* seems to require persistent gaps and thus an environment with high frequency of canopy disturbance (Pierson and Mack 1990). There is recent evidence, however, that cheat grass is rapidly invading ponderosa pine forests in Kings Canyon National Park (Merriam et al. 2004).

The diversity and relative abundance of nonnative species in montane coniferous forests of the southern Sierra Nevada has been shown to be a function of fire severity and time since fire (Keeley, Lubin, and Fotheringham 2003). High-intensity fires create gaps that decrease tree canopy coverage and increase light levels and nutrients for an ephemeral successional flora. Few nonnative species in this habitat have persistent seed banks, so the time since fire is an important determinant of colonization success. Unburned coniferous forests are largely free of alien species, whereas some burned sites had a significant alien presence, which presents a challenge for fire restoration of these forests. The U.S. Forest Service has experimented with the deliberate

seeding of nonpersistent wheat to protected burned watersheds of ponderosa pine in the Sierra Nevada. This treatment, although slowing some potential erosion, reduces the diversity of native herb species and inhibits the establishment of pine seedlings (Keeley 2004).

Only a few nonnative species have been ecologically successful invaders at elevations >2,500 m, although there is concern that this situation could change in the future, particularly under conditions of disturbance and global change (D'Antonio and Kark 2002). Two nonnative species are widespread and ecologically successful above 2,500 m in the Sierra Nevada. The most widely established of these is *Poa pratensis* (Kentucky blue grass), which has invaded wet to moist meadows (Gerlach et al. 2003). This perennial grass is dispersed in the feces of cattle and horses, and then establishes persistent soil seed pools. It readily displaces native species once established. *Taraxacum officinale* (dandelion) is widespread along trails up to 3,000 m or more, but is not an aggressive invader of non-disturbed communities (Gerlach et al.).

### Areas for Future Research

The most important areas of future research are those centering on relationships between agents of change and vegetation. These include altered fire regimes, air pollution, nonnative invasive species, rapid climate change, and resource use or extraction. It is the interaction of these factors that is most critical for study.

Although there has been a considerable increase in the study of historic fire regimes and patterns in the Sierra Nevada in the past 20 years, there remains an emphasis on data at a site or point scale and not a landscape basis (van Wagtendonk and Fites-Kaufman 2006). The spatial complexity of fire behavior and severity and how they affect long-term patterns of fire-return intervals is unknown. There is a need to further understand the relationships between fire regime patterns and climate, which will improve the strength of predictions on future fire patterns (Moody, Fites-Kaufman, and Stephens 2006). Concurrent is a need to quantify rates of biomass and fuel accumulations and distributions in relation to climate, fire and land-use activities. Although there is a general basis for inferring that increased biomass and fuel accumulations lead to increased fire behavior and severity, very little research has been conducted on crown fire behavior and the relationship of fire behavior magnitude to high vegetation densities and varied configurations. There is little quantitative data on the relative effectiveness of varied mechanical or burn treatments in modifying fire behavior and effects. Further, there is little research on the effects of varied vegetation treatments on vegetation structure, composition, and function.

Although there has been some research over the years on overall vegetation patterns and underlying mechanisms, there are still some key areas that have had little or no focus. Have there been upward shifts in the lower boundaries of Sierran coniferous forests in the last century along the

eastern and western boundaries? Some changes are apparently due in part to one or several high severity fires in the past century, such as in Stanislaus County to the west of Yosemite National Park or along the eastern front north or Sierra Valley in the Diamond Mountains. However, it is unclear if some thresholds have been crossed that prevent successful tree regeneration and survival due to repeated high severity fire due to postfire vegetation shifts or creation of microclimates unsuitable for tree regeneration at these limits of tree distribution. What is the role of invasive plants in postfire or land-use activities, and how have they influenced subsequent fire and vegetation composition and structure? What are the landscape and long-term consequences of nonnative pathogens such as white pine blister rust or the potential invasion of sudden oak death?

Within forested stands, there has been little study of historic or current patterns of regeneration and recruitment of dominant tree species and how these have varied by forest type or ecosystem. For example, has regeneration been continuous or punctuated? What was the role of fire and climate in regeneration and recruitment patterns? What would the resulting stand structure look like with an active fire regime, such as frequent fire? Would the distributions of fire-induced mortality differ among forest types and with changing climate?

There has been little formal study of differences or gradients in vegetation composition, structure and dynamics from the south to the north in the Sierra. How do climate patterns vary and what role do they play in the vegetation composition, species turnover, and dynamics?

There is a need to better understand the impacts of an increasing human population on Sierran vegetation. Effects of air pollution have been studied and documented to some degree in the southern Sierras but chronic levels of high ozone are also documented in the central Sierra. What are the effects of lower but chronic levels of pollution in combination with vegetation that is dense from fire suppression?

Overall, nonforest vegetation has received far less research attention than forested vegetation of the Sierra Nevada. Relatively little research has been conducted on chaparral and shrublands and rock outcrops or herbaceous dominated sites have had little to no attention.

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