South Coast Bioregion

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There is fire on the mountain and lightning in the air …

"Fire on the Mountain," MARSHALL TUCKER BAND, 1975

Description of Bioregion

Physical Geography

The South Coast bioregion includes the Southern California Coast and the Mountains and Valleys sections as defined by Miles and Goudey (1997). The region is bordered on the north by the Transverse Ranges, on the south by the U.S. border with Mexico, on the east by the Peninsular Ranges, and on the west by the Pacific Ocean (Map. 15.1). The Transverse and northern Peninsular ranges bound the Los Angeles Basin, an extensive floodplain comprising millions of years of alluvial outwash deposited by the Los Angeles, San Gabriel, and Santa Ana rivers. Minor mountain ranges occur within the basin, including the Palos Verde Peninsula on the west, Puente Hills on the east, and San Joaquin Hills on the south. The Orange and San Diego coastlines comprise a series of Pleistocene marine terraces and an uplifted peneplain now incised by east-west-running rivers including the Santa Margarita, San Luis Rey, and San Diego rivers. Other rivers traversing the San Diego coastal plain and emptying into San Diego Bay are the Sweetwater and Otay rivers (Schoenherr 1992).

The Transverse Ranges are one of the few east-west ranges in western North America and are composed of five mountain systems separated by broad alluvial valleys. These include, from west to east, the Santa Ynez, Santa Monica, Castaic or Liebre, San Gabriel, and San Bernardino mountains, with maximum elevations of 1,430, 949, 1,765, 3,074, and 3,508 m, respectively (Norris and Webb 1976). The Channel Islands are geologically part of this formation.

On the western end, the Transverse Ranges fork into a northern extension, the Santa Ynez Mountains and a southern extension, the Santa Monica Mountains (Map 15.1). Both extend nearly to the ocean leaving a very narrow coastal plain and both are relatively low-elevation mountains largely lacking significant coniferous forests. The Santa Ynez geology

is dominated by marine sediments predating the Tertiary and bears much resemblance to the Coast Ranges to the north (Norris and Webb 1976). The Santa Monica Mountains comprise a mixture of Miocene volcanic extrusions and more recent marine terrace deposits. The San Gabriel Mountains are a largely granite fault block, bounded on all sides by faults and with outlying extensions including the Verdugo Mountains to the west and Liebre or Castaic Mountains to the northwest. These mountains have experienced considerable uplift in recent geological time, contributing to the rather steep and highly dissected front that faces the Los Angeles Basin. The eastern-most San Bernardino Mountains are also a rapidly growing granitic fault block, but unlike the San Gabriel Mountains, they have conifer-dominated mid-elevation plateaus between 1,700 and 2,300 m, which includes Arrowhead and Big Bear lakes. Several features in this range represent the most southerly extension of Pleistocene glaciation in California (Sharp et al. 1959), indicative of lower summer temperatures in the region during the last glacial maximum (Owen et al. 2003).

The Peninsular Ranges are a north-south trending series of fault blocks, the bulk of which lie south of the U.S. border (Hinds 1952). In our region they include the San Jacinto Mountains in the north, with a maximum elevation of 3,300 m, and to the southeast the drier Santa Rosa mountains with several peaks over 1,800 m. To the west is another series of lower-elevation ranges separated by broad valleys and include the Santa Ana, Agua Tibia, and Laguna Mountains, mostly below 1,800 m. Unusual and potentially stressful substrates for vegetation include serpentine and breccias in the Santa Ana Mountains and gabbros in the Laguna Mountains and lower foothills to the west, including peaks such as Pinos, Guatay, Mother Grundy, Lawson, Lyons, Tecate, Otay, and Mt. Miguel, all below 1,500 m (Alexander 1993). These gabbro soils are, like serpentine, derived from mafic igneous rocks, and weather

MAP 15.1. The South Coast bioregion extends south from the east-west trending Transverse Ranges to Mexico and from the coast east to the north-south trending Peninsular Ranges.

into reddish iron- and magnesium-rich soils that have lower primary productivity but support a rich diversity of endemic plants (Schoenherr 1992).

This southwestern region includes the highest peaks outside of the Sierra Nevada; however, over 50% of the region is below 500 m (Davis et al. 1995). The extraordinary range of elevations represented in this region translates into a high diversity of vegetation types and fire regimes. The high ranges separated by broad valleys dissected by riparian corridors all play important roles in determining the extent of fire spread. The widespread distribution of substrates such as gabbro has possibly reduced fire frequency by limiting the rate of biomass productivity. The unusually rich diversity of mineral and gem deposits, many of which have been mined since the middle of the nineteenth century (Schoenherr 1992), have likely been responsible for early anthropogenic impacts on wildfire activity in remote mountainous regions (Leiberg 1900a).

Despite comprising only 8% of the land area of the state, this region contains 56% of the total human population (Davis et al. 1995). This pattern of development has placed immense pressure on natural resources and has created a fire management problem of extraordinary proportions.

Climatic Patterns

This is a region of mediterranean climate, consisting of cool, wet winters and hot, dry summers. Average rainfall varies spatially from 200 to 1,200 mm annually, two thirds of which falls November to April in storms of several days' duration, and dry spells of a month or more may occur during the wet season (Major 1977). The distribution of winter rainfall is strongly controlled by the orographic effect, and precipitation increases with elevation. Above 2,100 m a significant portion of winter precipitation comes as snow. Significant summer precipitation is rare near the coast but occasional Mexican monsoons from the Gulf of California affect the interior mountains (Douglas et al. 1993).

Mean winter temperatures near the coast are greater than 10°C and decrease toward the interior and with elevation. Coastal sites may occasionally experience subzero temperatures with lethal effects on some native species (Collett 1992). In the interior foothills and valleys, summer temperatures often exceed 40°C, but are more moderate at higher elevations and toward the coasts. Late spring and early summer marine air delays the onset of the fire season in the coastal mountains (Coffin 1959).

Lightning accompanies both winter and summer storms, and the proportion varies markedly between the coastal and the interior ranges (Fig. 15.1). In the interior ranges, lightning strikes peak in August, a pattern typical in other interior parts of California and the Southwest (van Wagtendonk and Cayan 2003); however, in the coastal ranges, lightning strikes peak later in the autumn (Fig. 15.1B). The coastal ranges also differ in that 35% of all strikes occur in winter and spring, whereas in the interior these two seasons represent less than 12% (Fig. 15.1A, B). Due to high fuel moisture, these winter and spring lightning strikes play essentially no role as ignition sources for wildfires (Conroy 1928), thus a substantially greater proportion of lightning strikes will be ineffective at igniting fires in these coastal ranges.

Regionally, lightning strike density is substantially greater in the interior mountain ranges, which receive several times more strikes than at comparable elevations in the coastal ranges (Fig. 15.2; Wilcoxin's signed rank test, $P <0.001$, n = 10). Broad comparisons of lightning strike density reveal roughly 25 to 40 lightning strikes per 100 km^2 per year for interior ranges, and this is 5 to 10 times higher than for coastal valleys (Fig. 15.2). Based on the density of fires ignited by lightning in these two regions (Keeley 1982) it appears that only 3% to 5% of all lightning strikes ignite a fire. In the interior ranges, lightning-ignited fires are predictable most years, whereas in the coastal ranges, they are sporadic. For example, in the Santa Monica Mountains, lightning-ignited fires occurred rarely in fire records between 1919 and 1980 (Radtke et al. 1982). Since 1981, there have been lightning-ignited fires on two dates, one in 1982 and one in 1998 (Santa Monica Mountains National Recreation Area fire records, supplied by Marti Witter, NPS, 2003). Thus, in the coastal ranges, lightning is a potential source of fire ignition but a relatively uncommon source. In the interior ranges, they are annual events, with the vast majority of lightning-ignited fires in forests and fewer than 20% in shrublands (Keeley 1982).

A factor of local importance in southern California is the Santa Ana wind. This foehn wind results from a high-pressure cell in the Great Basin, coupled with a low-pressure trough off the coast of southern California, which drives dry air toward the coast. These foehn winds may exceed 100 km hr^{-1} and bring high temperatures and low humidity. Santa Ana winds create the worst fire weather conditions in the country because several days or weeks of these winds occur every autumn, at the time natural fuels are at their driest (Schroeder et al. 1964). Under Santa Ana wind conditions, fire spread is rapid, sometimes covering 30,000 ha in a single day through fuels of any age class (Phillips 1971).

The overwhelming importance of Santa Ana winds is illustrated by the relationship between burning patterns and climate. Throughout the western U.S., there is a strong relationship between antecedent drought and fire activity (Westerling et al. 2002). However, in southern California during the twentieth century, there is a surprisingly weak relationship between antecedent drought and subsequent fire activity (Keeley 2004a). The important role of Santa Ana winds is also shown by the relationship between the Palmer Drought Severity Index and large fires. Those large fires occurring during the autumn months and most likely driven by Santa Ana winds occur regardless of whether or not there is a drought. The primary impact of antecedent drought appears to be one of extending the fire season, since large fires before and after the autumn Santa Ana season occur consistently during drought years.
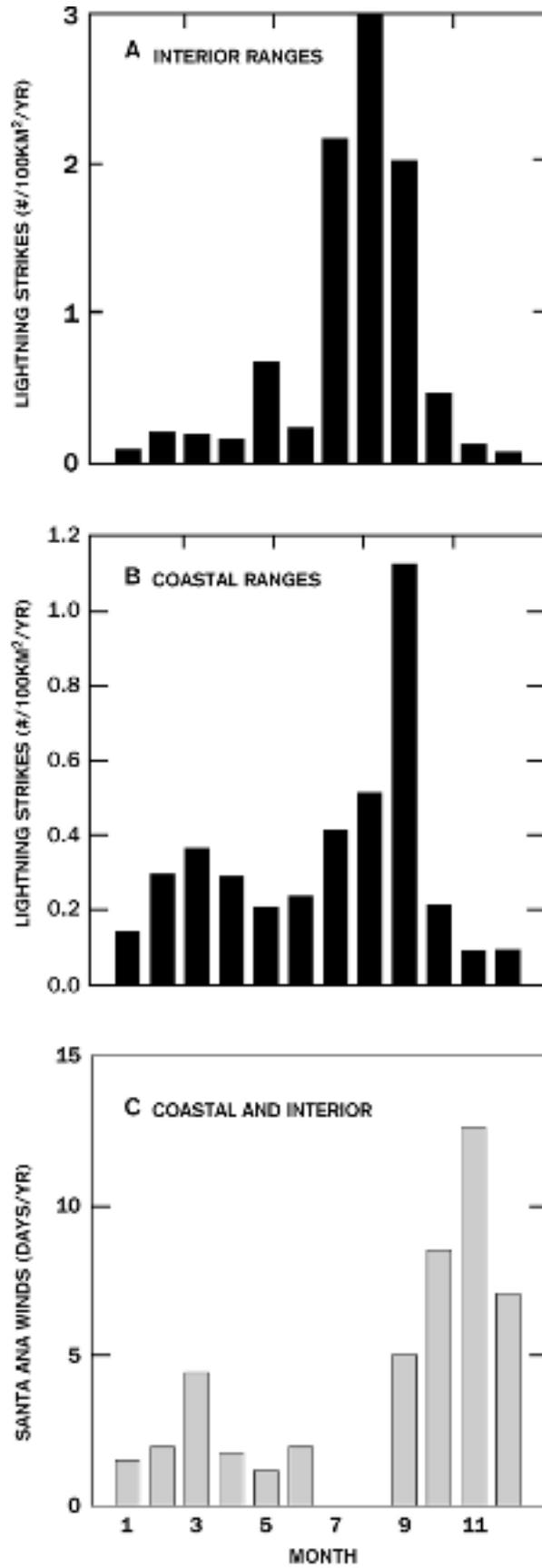
FIGURE 15.1. Monthly distribution of lightning strike density in the interior (A) and coastal (B) zones of southern California as defined by Miles and Goudey 1997 (data from van Wagtendonk and Cayan 2003) and Santa Ana wind days (C) for Los Angeles County (data from Weide 1968), based on (1) 3-mb decrease in mean sea level pressure from Santa Monica to Palmdale, (2) ≥10°C decrease in temperature from Santa Monica to Palmdale, (3) northerly wind speeds of 16 km per hour in the San Fernando Valley and 50 km per hour in the Riverside-San Bernardino area, and (4) relative humidity ≤30%.
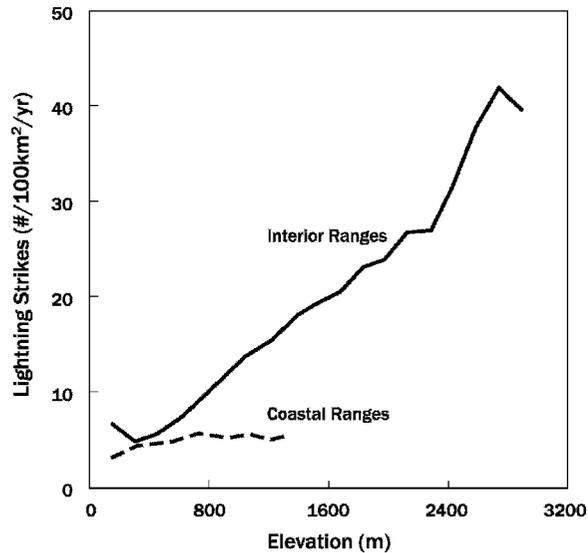
FIGURE 15.2. Elevational distribution of lightning-strike density for the interior and coastal ranges of the South Coast bioregion. Due to limited area in the highest elevations these were combined into the last elevational category plotted. (Data from van Wagtendonk and Cayan 2007.)

Although the weather conditions that produce lightning do not overlap with conditions that generate foehn winds, the seasons do overlap and Santa Ana winds may occur within days or weeks of a lightning-ignited fire (Fig. 15.1C). Although the vast majority of contemporary burning in the region is due to human-ignited fires during Santa Ana wind conditions, it is hypothesized that under natural conditions, occasionally lightning-ignited fires persisted into the autumn foehn wind season and these Santa Ana wind-driven fires accounted for the majority of area burned (Keeley and Fotheringham 2001a).

One of the difficulties in sorting out the role of climate in driving fire regimes is that human ignitions play a major role in this region and complicate the interpretation. For example, in focusing on just the decadal average Palmer Drought Severity Index for Riverside County, it is apparent that it matches closely the area burned during the twentieth century (Fig. 15.3). However, human population growth parallels these changes in area burned, and increased ignitions are likely a major contributor to the late-twentieth-century increase in burning in that county.

Ecological Zones

The South Coast bioregion is a complex mosaic of grassland, shrubland, forest, and woodland (Fig. 15.4) that forms a relatively fine-grained landscape relative to most wildfires, which usually burn large enough areas to encompass a diversity of vegetation types and associations. Thus, fire regimes vary on a rather course scale, and within a vegetation type there is limited association of fire regimes with specific plant associations. In this respect, there are two broad ecological zones: the coastal valleys and foothill zone and the montane
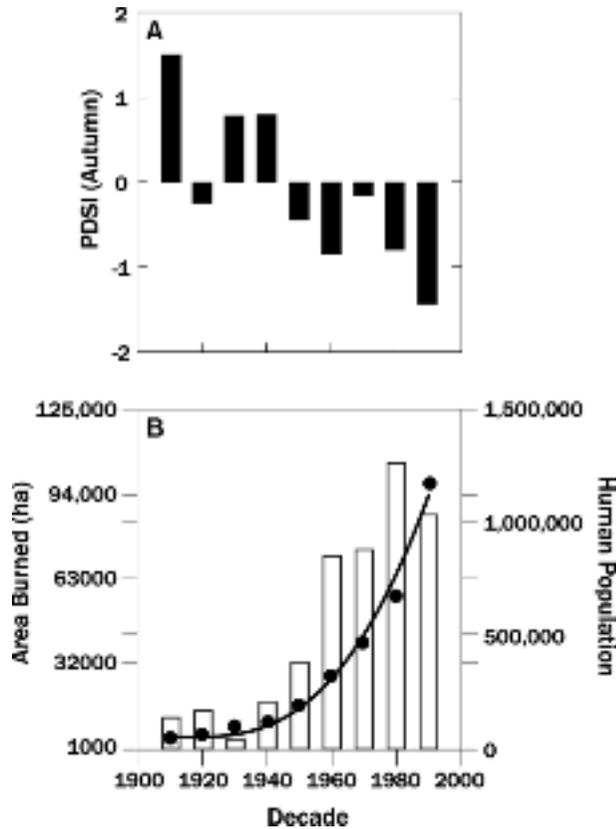

FIGURE 15.3. Decadal variation in Palmer Drought Severity Index (A), area burned (open bars), and human population (closed circles) for Riverside County (B). (Data from Keeley et al. 1999.)

zone. Within each of these zones, fire response is best examined at the scale of broadly defined vegetation types.

In the coastal and foothill zone, the distribution pattern of grasslands, sage scrub, chaparral, and woodlands is driven largely by a combination of soil moisture and disturbance. At the arid end of the gradient, herbaceous and semi-woody subshrub associations predominate, with woodlands and chaparral at the moister end of the gradient. However, there is an important interaction between soil moisture and disturbance, such that under xeric conditions, far less disturbance is required to displace the dominant woody association with herbaceous vegetation (Keeley 2002a).

Southern California grasslands include small, highly fragmented patches of native grassland and more widespread, anthropogenically created non–native-dominated annual grasslands. The native grasslands are dominated by perennial bunchgrasses, purple needlegrass *(Nassella pulchra)*, pine bluegrass *(Poa secunda)*, and Junegrass *(Koeleria macrantha)*, and are distributed on fine-grained soils in localized patches within a mosaic of shrublands and woodlands (Huenneke 1989, Keeley 1993). Native grasslands also include a rich diversity of annual forbs but very few native annual grasses. Significant native grasslands still persist in valleys and shallow slopes on clay soils, which, due to the water-holding capacity of these fine-grained soils, are stressful substrates for competing shrubs.

FIGURE 15.4. Landscape mosaic of southern oak woodland, grassland, sage scrub, arid chaparral on south-facing exposures (slopes on right side of photo), and mesic chaparral on north-facing slopes. (Photo by J. Keeley, location near Black Mountain north of Ramona, San Diego County.)

Most of the grasslands in the region lack any native grasses and are dominated by non-native annual grasses and forbs. They bear little resemblance, in both ecology and distribution, to native grasslands. Most annual grasslands were derived from fire-induced type conversion of shrublands and subsequent invasion by non-native grasses and forbs. They exhibit no strong relationship with soil type or precipitation regime and are the result of anthropogenic disturbance (Cooper 1922, Wells 1962, Keeley 1990b, 1993, 2002a). Although these generalizations are broadly applicable across the region, on a more limited scale there are some annual grasslands that do appear to be derived from native grassland as a result of intensive livestock grazing (Oberbauer 1978) or soil tillage (Kellogg and Kellogg 1990, Stromberg and Griffin 1996).

Semi-deciduous sage scrub dominates lower elevations along the coast and in interior valleys, and in these two subregions, sage scrub forms very different species assemblages (Davis et al. 1994). Thus, it is not surprising that there are significant differences in fire response between coastal and interior sage scrub associations. This appears to be driven partly by floristic differences (Kirkpatrick and Hutchinson 1977) and partly by the impact of the more arid conditions in interior valleys. As treated here, the interior sage scrub is equivalent to the Riversidian Division and the coastal sage scrub is included within the Venturan and Diegan divisions (Axelrod 1978).

At lower elevations, the taller stature evergreen chaparral replaces sage scrub on north-facing exposures or on deeper soils (Fig. 15.5), and with increasing elevation completely displaces it throughout much of the foothills and lower montane. Chaparral comprises a rich array of different floristic associations (Sawyer and Keeler-Wolf 1995), some of which, such as chamise and black sage *(Salvia melliflora)*, have such broad distributions that they include more than a single fire regime. Although fire response between dominants of different associations varies, different associations are often subject to similar fire regimes because of the fine-grain distribution of associations due to small-scale topographic variation. For example, monotypic stands of the facultative seeder chamise *(Adenostoma fasciculatum)* on south-facing slopes are often juxtaposed with diverse north-facing slopes of obligate resprouters such as scrub oak *(Quercus berberidifolia)*, California coffeeberry *(Rhamnus californica),* and chaparral cherry *(Prunus ilicifolia)*, sometimes separated by ridge tops dominated by the obligate seeder hoaryleaf ceanothus *(Ceanothus crassifolius).* Most fires burn broad portions of the landscape; thus these three associations typically burn in the same high-intensity fire. Although fire severity may vary in these different associations, the impact of fires on community resilience may be as much a function of pre- and post-fire climate as it is floristic differences.

Within chaparral-dominated landscapes, there are isolated patches of serotinous cypress species, Tecate cypress *(Cupressus forbesii)* or Cuyamaca cypress *(Cupressus arizonica)* (Hickman 1993). They typically occur above 1,200 m in widely disjunct populations, perhaps as relicts of a once-wider distribution. They range from 330 to 1,700 m, primarily on north-facing slopes, and all populations appear to date back to the last fire (Armstrong 1966, Zedler 1977). These small-stature cypress form even-aged monotypic stands from less than 1 ha to more than 100 ha in size, typically embedded within a sea of chaparral, and usually on fine clay soils derived from gabbro or other ultramafic substrates (McMillan 1956, Zedler 1995a).

Several pines are closely associated with chaparral shrublands. In the eastern Transverse and northern Peninsular ranges are pockets of knobcone pine *(Pinus attenuata)* (Minnich 1980a, Pequegnat 1951, Vogl 1973), a species more common further north in the coastal ranges. Coulter pine *(Pinus coulteri)* is widely distributed above 1,200 m throughout

FIGURE 15.5. Mosaic of sage scrub surrounding patch of larger-stature chaparral in the Santa Ana Mountains, Orange County, at approximately 700 m. (Photo by J. Keeley.)
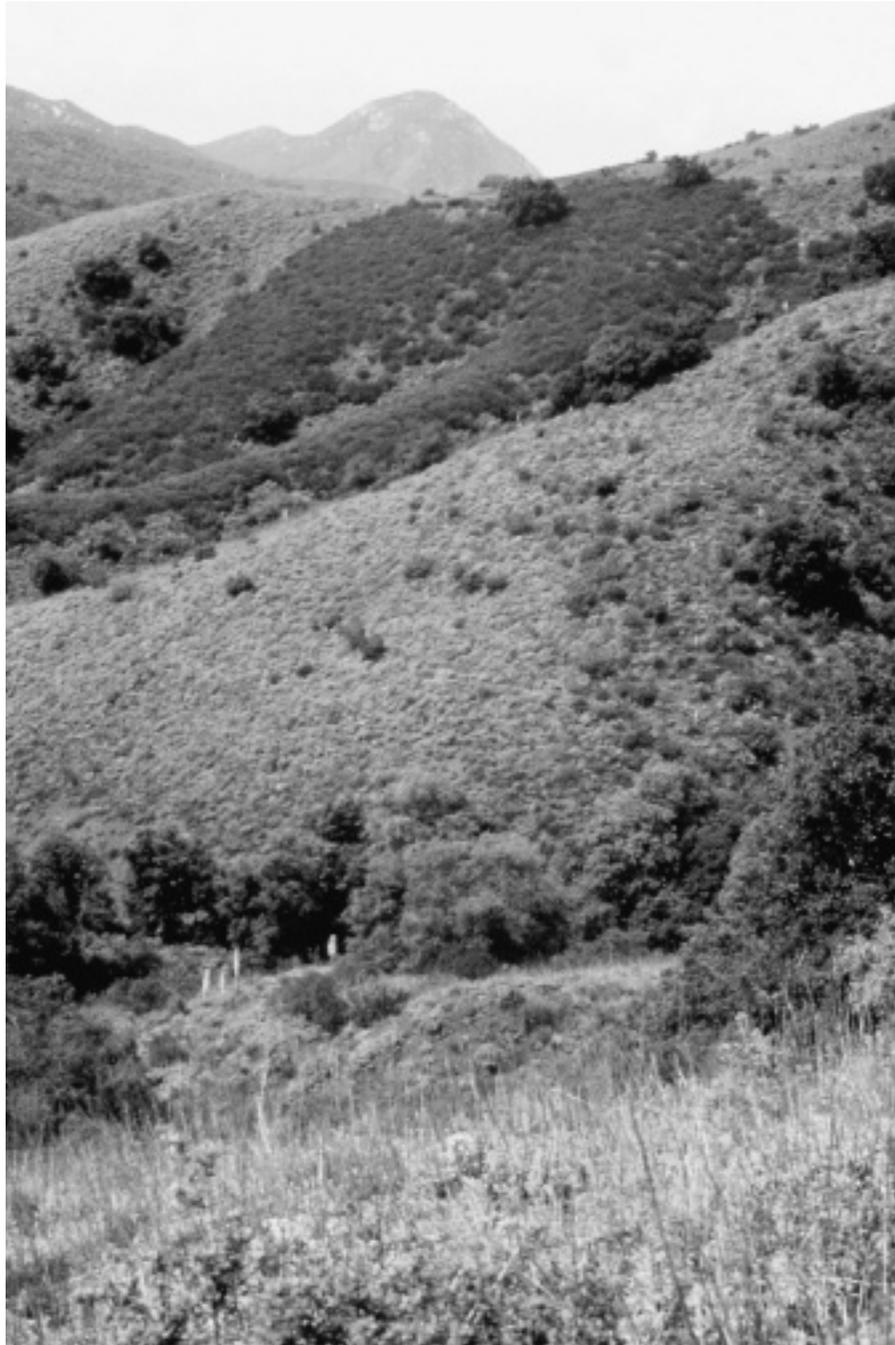
the Transverse and Peninsular ranges, occurring in both chaparral and mixed conifer forests (Griffin and Critchfield 1972). A closely related species is Torrey pine *(Pinus torreyana)*, a rare endemic restricted to a few coastal populations in San Diego County, with one disjunct population on Santa Rosa Island.

Bigcone Douglas-fir *(Pseudotsuga macrocarpa)* occurs in low- to high-density populations between 400 and 1,800 m, although small populations at lower and higher elevations do occur (Gause 1966). Approximately two thirds of this forest type (19,000 ha) are distributed in the San Gabriel Mountains

(Stephenson and Calcarone 1999). They are most abundant on north-facing slopes, particularly on interior sites (Bolton 1966, Minnich 1978). This tree was heavily exploited for timber during the early settlement period because it was the lowest elevation conifer in the region (Minnich 1988). This, plus increased fire frequency accompanying settlement in the Los Angeles Basin, are considered factors accounting for the upward movement of its elevational boundary (Gause 1966). Today, it is commonly restricted to rather steep ravines in association with canyon live oak *(Quercus chrysolepis)* amidst a sea of chaparral and oak woodland (McDonald and Litterell 1976).

Riparian woodlands and shrublands today occupy a relatively small percentage of the region, as it is estimated that 90% of them have been lost (Faber et al. 1989). Historically, the greatest extent of riparian habitat was the Los Angeles coastal plain, much of which was a vast seasonal wetland (Gumprecht 1999). Riparian woodlands have the potential for affecting landscape patterns of fire spread. The dominant woody taxa willow *(Salix)*, alder *(Alnus)*, cottonwood *(Populus)*, elderberry *(Sambucus)*, maple *(Acer)*, mule fat *(Baccharis)*, ash *(Fraxinus)*, arrow weed *(Pluchea)*, poison oak *(Toxicodendron)*, and sycamore *(Platanus)* are almost all important components of riparian communities throughout the Northern Hemisphere. Nearly all are winter deciduous (Rundel 1998), and in foothill and coastal environments this contrasts with a landscape otherwise dominated by either summer deciduous or evergreen life forms.

Woodlands dominate undisturbed valleys and north-facing slopes, most commonly including the evergreen coast live oak *(Quercus agrifolia)*, sometimes in association with the much rarer evergreen Engelmann oak *(Quercus engelmannii)*. Typically these woodlands are relatively open and in many instances are best considered oak savannas. Today, the understory consists mostly of non-native grasses and forbs, and these are the primary fuels that carry fire. Prior to human entry into California, the oak understory is thought to have comprised coastal sage scrub subshrubs (Wells 1962), and examples of this association are still readily observed today along Highway 101, north of Gaviota Pass in Santa Barbara County. This plant community has long been in direct competition with human development; thus extensive portions of woodlands have been lost. Interior live oak *(Quercus wislizenii)* is another evergreen oak that often forms closed-canopy forests on mesic sites, often mixing with broadleaf chaparral shrubs. Valley oak woodlands occur in several valleys of the northwestern Transverse Ranges. These represent a southern extension of such woodlands and are covered in more detail in the Central Coastal section by Borchert and Davis, Chapter 14.

One largely endemic association is the California black walnut *(Juglans californica)*-dominated woodland, widely distributed in the foothills of the Los Angeles Basin (Quinn 1990). This winter-deciduous tree often forms associations with arborescent forms of evergreen chaparral shrubs such as Christmas berry *(Heteromeles arbutifolia),* chaparral cherry *(Prunus ilicifolia)*, and holly-leaf redberry *(Rhamnus ilicifolia)* (Keeley 1990a).

In the lower montane zone, winter-deciduous California black oak *(Quercus kelloggii)* woodlands often dominate between the lower-elevation evergreen sclerophyllous chaparral and the higher-elevation evergreen conifers. This winter-deciduous woodland is more widespread in the other interior ranges of the region.

Montane forest types considered here all exhibit substantial ecological overlap with Sierra Nevada forests. They include yellow pine, mixed conifer, and lodgepole pine forests. Two yellow pines, ponderosa *(Pinus ponderosa)* and Jeffrey *(Pinus jeffreyi),* segregate out according to specific climatic parameters, with the latter being predominant on drier and/or colder sites (Thorne 1977, Stephenson 1990). At their lower margins they are associated with Coulter pine *(Pinus coulteri)* and at higher elevations with white fir *(Abies concolor)*. On more mesic slopes, white fir and incense-cedar *(Calocedrus decurrens)* dominate with a smaller percentage of sugar pine and Jeffrey pine. Lodgepole pine *(Pinus contorta* var. *murrayana)* forests have limited distribution in the highest elevations of the eastern Transverse and northern interior Peninsular ranges. Unlike the lodgepole populations of the northern Rocky Mountains, these southern California pines are not fire-dependent serotinous species, and in this respect are most similar to the Sierra Nevada lodgepole pine forests.

Overview of Historic Fire Occurrence

Prehistoric Period

Chaparral genera, including manzanita *(Arctostaphylos)*, California-lilac *(Ceanothus)*, mountain-mahogany *(Cercocarpus)*, flannelbush *(Fremontodendron)*, Christmas berry *(Heteromeles arbutifolia)*, cherry *(Prunus)*, oak *(Quercus)*, coffeeberry or redberry *(Rhamnus),* and sumac or sugarbush *(Rhus)*, were present in the south coast region since at least mid to late Miocene—5 to 15 million years ago (Axelrod 1939). Even then, fire was part of this environment, as middle Miocene deposits in the Santa Moncia Mountains contain charcoal and partially burned chaparral fragments (Weide 1968). Chaparral shrub species as well as big-cone Douglas-fir forests were present in southern California since at least middle Pliocene (Axelrod 1950b) and were present much further east into what is today desert habitat (Axelrod 1950c). Throughout the Pliocene and Pleistocene epochs, the region was dominated by closed-cone cypress and pines and included Monterey cypress *(Cupressus macrocarpus)*, Bishop pine *(Pinus muricata)*, and Monterey pine *(Pinus radiata)*, species that today are displaced 560 km northward (Axelrod 1938, Axelrod and Govean 1996, Ledig 1999, 2000). The closed-cone character indicates fire has been a predictable feature of this landscape for at least a couple million years, and this is supported by fossil charcoal records (Johnson 1977). The fact that these species typically burn in stand-replacing crown fires, and are moderately long-lived obligate seeders sensitive to short fire-return intervals (Keeley and Zedler 1998), and growth rates were lower than those today due to 40% less CO_2 during much of the Pleistocene (Ward et al. 2005), suggests the hypothesis that fires were infrequent, on the order of once or twice a century.

Approximately 90% of the past 1.6 million years were cooler conditions, and contemporary plant associations in the region developed only during the last 8,000 years, which comprises the Holocene Epoch. Prior to the Holocene, we know certain dominants currently in southern California were displaced hundreds of kilometers southward and toward lower elevations. For example, the Vizcaino Desert region of

central Baja California at 27°N latitude had chamise chaparral only 10,200 years B.P. (Rhode 2002). At comparable elevations (780 m), the present southern boundary of chamise chaparral is more than 500 km north of this Pleistocene population. Further north in Baja California at 30°, Wells (2000) reported a diverse chaparral assembly at 550 to 600 m elevation between 10,000 and 17,000 years B.P., which is more than 400 m lower than that at present. In southern California, late Pleistocene floras were distributed 800 to 900 m lower (Axelrod 1950a, Anderson et al. 2002), likely due to the higher precipitation during glacial episodes (Robert 2004).

There is a relatively scant fossil record for coastal sage scrub species; for this reason, Axelrod (1978) proposed that this is a largely Holocene plant community in southern California. However, arid environments, such as those where sage scrub predominates, seldom preserve much of a fossil record. Illustrative of this is the fact that the nearly ubiquitous chaparral shrub chamise is absent from the fossil record, save some relatively recent packrat midden sites.

The present distribution of vegetation types is a product of Holocene drying and coincides with the first entry of humans into the region. The concomitant emergence of contemporary climate, vegetation distribution, and humans presents a challenge to accurately discerning natural and anthropogenic fire regimes. However, although humans were present more than 10,000 years B.P., a widespread presence significant enough to have an impact on the local ecology is undoubtedly much younger, perhaps only the last few thousand years or less (Jones 1992). Throughout the first half of the Holocene, lightning was likely the dominant or only ignition source in most parts of the region. It has been hypothesized that the coastal region burned when the occasional August or September lightning-ignited fire persisted until picked up and carried by the autumn foehn winds (Keeley and Fotheringham 2003). At the other extreme would have been montane coniferous forests subjected to frequent lightning ignitions, which would have burned on much shorter intervals, controlled largely by the rate of fuel accumulation (Minnich 1988).

By the middle Holocene, a great diversity of Indian groups had settled in the region, and fire was one management practice they all held in common. Numerous uses for burning have been reported, but the one that likely had the greatest impact was burning shrublands for type conversion to herb-dominated associations (Timbrook et al. 1984, Keeley 2002a). The clearest statement of this management practice is a 1792 report by Spanish explorer Jose Longinos Martinez who wrote, "in all of New California from Fronteras northward the gentiles have the custom of burning the brush" (Simpson 1938). It has been said that Native American presence was widespread and touched every part of this region (Anderson et al. 1998). This view would be supported by the fact that the archeological record in San Diego County alone has over 11,000 Indian sites documented, and they are distributed within all 32 USGS 7.5-min quadrangles (Christenson 1990). Two thirds of the settlements were in the coastal valleys and foothills in what currently is chaparral or sage scrub vegetation.

The sudden emergence of charcoal deposits and replacement of woody elements by herbaceous taxa around 5,000 yr B.P. in coastal southern California (Davis 1992) is perhaps a reflection of Native American burning for type conversion. Burning is also a likely contributing factor to the demise of closed-coned cypress along the San Diego coast 1,800 yr B.P. (Anderson and Byrd 1998), because it is not tied to climatic patterns that might account for the extirpation of this species in the area. Cessation of Indian burning following settlement is thought to have been a major contributor to an apparent nineteenth century lowering of the elevational distribution of oak woodlands (Byrne et at. 1991).

Historic Period

Much of our historical information is from written records that often contain misinformation and exhibit various biases. Early reports on fire cause are suspect when it comes to evaluating lightning ignitions. For example, Sargent (1884) reported for 1881 that 340,000 acres burned in California forests, but none were attributed to lightning, whereas hunters, campers, and Indians were thought to be the primary sources of ignition. This report is highly suspect because today we know lightning accounts for a significant portion of all wildfires in the state. Undoubtedly, this source of ignition was not suspected because weather conditions during lightning storms are not conducive to rapid fire spread, and when distant lightning-ignited fires did become noticeable it was often days or weeks later when weather conditions had changed.

The first Spanish settlement in California was the Mission San Diego de Alcala, founded in 1769. In addition to initiating a relentless wave of settlers over the subsequent centuries, these first Europeans most dramatically changed the landscape with the introduction of a wide selection of grasses and forbs (Mack 1989). These non-natives spread rapidly, perhaps facilitated by the highly disturbed landscape resulting from a long history of frequent Indian burning (Keeley 2001, 2004c) and further promoted by the Mexican vaqueros habit of expanding grazing lands by burning off the brush (Kinney 1887).

American occupation and subsequent statehood brought increased competition for grazing land (Kinney 1900, Plummer 1911). In rural San Diego County, a typical late nineteenth-century land-use pattern involved homesteads of 65 ha centered in small grassy potreros or dry meadows that were generally too small to provide a sound economic basis for subsistence (Lee and Bonnicksen 1978). Chaparral dominated the slopes surrounding these potreros (e.g., Fig. 15.4), and stockmen routinely burned the shrublands to supplement meadow grazing with additional forage and to allow easier movement from one canyon to another.

In remote areas, sheep herders routinely used fire to enhance mountain-grazing lands, and miners used fire to open the brush and facilitate exploration. Post-settlement increases in sedimentation have been interpreted to be at

least partially the result of this increased fire frequency (Cole and Wahl 2000). Surveys done in the three southern California forest reserves in the late nineteenth century provide some of the best quantitative data on pre–fire-suppression burning patterns. For the chaparral zone, which comprised 50% (San Bernardino) to 90% (San Gabriel) of the new reserve landscapes, USGS biologist J. B. Leiberg presented estimates of burning in annual reports filed in the late 1890s. Based on the area of chaparral in each reserve, and his estimate of how much chaparral had burned in the previous four to nine years, I calculate that he observed rates of burning, expressed as percentage of chaparral landscape burned per decade, of 2.8%, 3.3%, and 5.4% for the San Jacinto (Leiberg 1899a, 1900c), San Bernardino (Leiberg 1899b, 1900b), and San Gabriel (Leiberg 1899c, 1900a) Reserves, respectively. Even this limited extent of burning cannot be entirely ascribed to natural sources. For example, Leiberg (1899c) stated, "It is also noteworthy that the worst-burnt areas in the three reserves examined are to be found in the San Gabriel Reserve in the region of the most extensive mining operations." Although Leiberg's estimates likely did not capture all of the burning on these landscapes, they do indicate that natural fire rotation intervals in the lower-elevation chaparral zone were on the scale of once or twice a century or less, and certainly not on the scale of every few decades as was apparently the case in higher-elevation conifer forests.

These historical records suggest a pre-suppression model of burning in chaparral landscapes of many modest-sized summer lightning-ignited fires that burned a relatively small portion of the landscape, punctuated one to two times a century by massive autumn Santa Ana wind–driven fires (Keeley and Fotheringham 2001a). This model is supported by the historical record of infrequent large Santa Ana fires over the past 500 years (Mensing et al. 1999). It is also supported by life history characteristics of many dominant woody species that are resilient to long fire-free intervals and sensitive to short intervals on the scale of once a decade (Keeley 1986, Zedler 1995a).

Although remote regions were experiencing limited burning, rapidly developing rural areas reported some rather massive wildfires. In 1878, one of the largest fires in Los Angeles County history burned 24,000 ha, and in 1899, well over a quarter million hectares burned in a single fire centered in Orange County (Barrett 1935, Lee and Bonnicksen 1978). In San Diego County, it was reported in 1885 that "At least one third of the land covered with brush, grass and oak timber in the southern part of this county has been burnt off by settlers within the past eighteen months, doing a great deal of damage, not only as regards pasturage, timber, and bees, but also decreasing the reservoirs of water, which the absence of brush will effect...," and in 1889, a huge 37,000-ha fire burned coastal shrublands in the county (Barrett 1935).

It has been proposed that a view of the natural southern California fire regime can be gained by examination of burning patterns south of the U.S. border, where it is presumed humans have had less impact on the natural fire regime. These studies are discussed in the sidebar on fire regimes in southern California and northern Baja California (sidebar 15.1).

Current Period

The nineteenth-century pattern of large fires has continued through the twentieth century, and Moritz (1997) demonstrated that the probabilities for large fires in the central coastal region have not changed due to fire suppression. Recent decades have experienced an increasing frequency of smaller fires (Moritz 1997, Keeley et al. 1999). Throughout the century, there has been a growth in fire frequency that parallels human population growth (Keeley and Fotheringham 2003). Much of the population growth has been in coastal valleys and foothills, where natural fire frequencies were lowest. In the latter half of the twentieth century, fire rotation intervals shortened and average fire size decreased in all southern California counties (Conard and Weise 1998, Keeley et al. 1999, Weise et al. 2002). Human impacts on montane environments have been slower to develop, although air pollution has caused substantial changes in forest structure (McBride and Laven 1999).

Major Ecological Zones

Burning patterns in the lower-elevation coastal valley and foothill zone show that, despite vigorous fire-suppression efforts throughout the twentieth century, over half of the landscape has burned within the past several decades (Fig. 15.6A, B, C). This in fact is an underestimate of the extent of twentieth century burning because these data are for just national forest lands (Stephenson and Calcarone 1999), and much of the foothill landscape outside the forests have experienced higher rates of burning (Keeley 1982).

Widespread burning should not be interpreted to suggest that fire-suppression activities have had no impact. Considering the fact that humans account for more than 95% of all fires (Keeley 1982), it seems reasonable that the primary impact of suppression has been to maintain these landscapes closer to their natural fire regime than if fires were not suppressed (Keeley et al. 1999). Within this zone it appears that roughly 10% to 25% of the landscape has never had a recorded fire (Table 15.1). Based on estimates of burning made by Leiberg, and discussed in the historical section, it would appear that this proportion of unburned landscape is not likely to be far outside the natural range of variability for the region.

Burning patterns for the montane zone (Fig. 15.6D, E, F) suggest that vigorous fire-suppression efforts throughout the twentieth century have had a substantial impact in excluding fires from this landscape (Stephenson and Calcarone 1999). Roughly 50% to 75% of these forests have never had a recorded fire (Table 15.1), which is likely outside the natural range of variability for these conifer forests. Effective fire exclusion in this zone contrasts markedly with the foothill zone where suppression has not been effective at excluding fire (Fig. 15.6A, B, C).
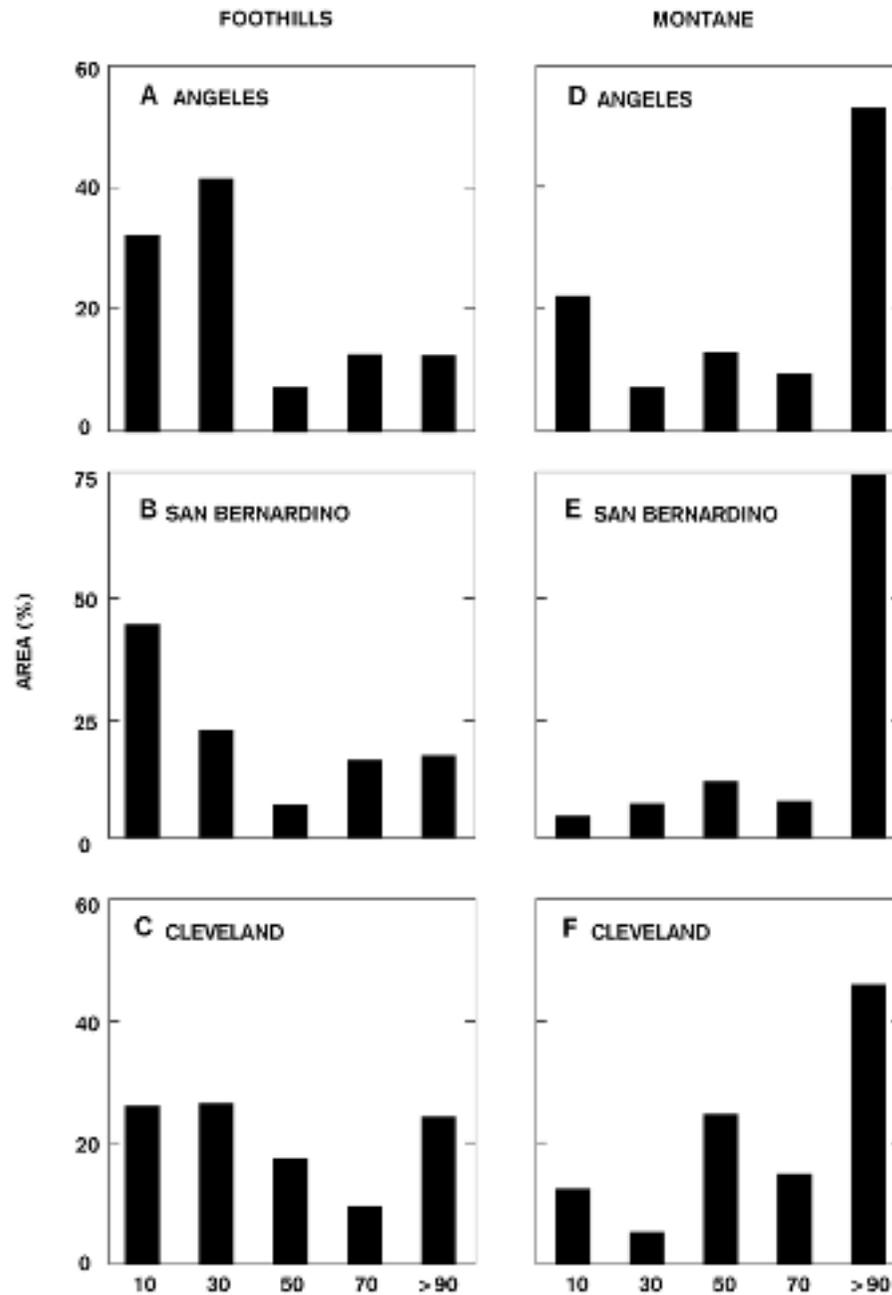
FOOTHILLS   MONTANE

FIGURE 15.6. Time since last fire for foothill (A, B, C) and montane (D, E, F) environments in the Angeles, San Bernardino, and Cleveland USFS national forests. The Angeles includes most of the San Gabriel Mountains and surrounding foothills, the San Bernardino includes the San Bernardino and San Jacinto mountains and the Cleveland includes largely the Santa Ana and Laguna mountains. (Data from Stephenson and Calcarone 1999.)

Grasslands

A substantial proportion of native bunchgrass rootstocks survive grassland fires and resprout as moisture becomes available in autumn (Table 15.2). These grasses flower and disperse seeds in the first post-fire spring, and seedling recruitment is commonly very abundant in the second and the next few post-fire years (Keeley 1990b), although recruitment may only be successful in years of high precipitation (Hamilton et al. 1999). These patterns are the same for a rich diversity of native herbaceous perennial forbs as well, including species of *Calochortus*, *Dichelostemma*, *Sanicula*, and *Lomatium* among others. Although annual species (both native and non-

native) lack much long-term seed storage, annual recruitment and seed production ensure a ready seed bank at the time of fire, and low-intensity fires generated by herbaceous fuels enhance seed survival.

Grasslands are resilient to a wide range of fire frequencies. Although annual fires are not part of the natural fire regime, they present little threat to either herbaceous perennial or annual species. This is because both life history types are adapted to persisting through the dry season with dormant rhizomes, bulbs, or seeds. Surviving fire apparently presents no greater challenge than the long summer drought. In the absence of fire for extended periods of time, natural grassland patches persist because of the greater competitive ability of

Dodge (1975) postulated that burning patterns were likely to be different between chaparral and coniferous forests on the two sides of the U.S. border because, unlike the United States, south of the border fire suppression was not practiced outside of towns and there was a common practice of setting fire to the brush as soon as sufficient dead material had accumulated to carry a fire. He found that the most significant difference between the vegetation of these two regions was the near total absence of grass and other herbaceous plants by the end of summer due to intense grazing by cows and horses. With the lack of fire suppression, frequent burning of the shrublands, and over-grazing in Baja California, he suggested land use patterns were at the same stage as was the case north of the border in the late nineteenth century.

Minnich (1983) used Landsat remote imagery to compare patterns of burning in sage scrub and chaparral shrublands between 1972 and 1980 on both sides of the border. He concluded that during this nine-year period, fires were larger north of the border. However, fire size was not compared statistically, and critics have suggested there is no difference evident in these data (Strauss et al. 1989, Keeley and Fotheringham 2001a). The primary motivation for concluding fires were larger north of the border was based on the inclusion of two fires reported in written historical records north of the border (Minnich 1983). Because written records were not available south of the border, it has been argued that this is a biased comparison (Keeley and Fotheringham 2001a). To compensate for the lack of written records south of the border, Minnich (1989, 1995, 1998; Minnich and Dezzani 1991; Minnich and Chou 1997) estimated fire size for an 80-year period south of the border using historical aerial photographs, and concluded that during this period, large fires were absent from the northern Baja California landscape. The conclusion from these studies is that the smaller fires south of the border are reflective of the natural southern California fire regime and larger fires north of the border are a modern artifact of fire suppression and illustrate the need for doing landscape-scale prescription burning in southern California.

This conclusion has been criticized because historical records show that prior to fire suppression in southern California, large fires were always part of this landscape (Barrett 1935), and through the twentieth century there has been no increase in frequency of large fires (Keeley et al. 1999, Mensing et al. 1999, Weise et al. 2002). Additionally, it has been proposed that the present fire regime in Baja California is not likely representative of the natural regime, and that it is largely the result of contemporary land use practices (Keeley and Fotheringham 2001a, 2001b). These latter authors contended that the patterns observed north and south of the border should not be the basis for southern California fire management policy.

More recent studies have focused on north-south comparisons of mixed conifer forest structure in the San Bernardino and San Jacinto Mountains in southern California with the San Pedro Martir Mountains of Baja California (Savage 1997; Minnich et al. 2000, 2001; Stephens and Gill 2005). These studies have attributed differences in forest structure to differences in fire suppression policy. Although the general conclusions are consistent with accepted dogma, there are reasons to question whether the more open forests, with minimal in-growth of white fir, reported for Baja California are primarily a result of different fire management practices.

Climate could play a bigger role than fire management practices. For example, north of the border yellow pine forests on the more arid end of the precipitation gradient commonly exhibit characteristics of Baja forests—for example, lack of white fir in-growth (Laven 1978, Dolph et al. 1995). Because the San Pedro Martir Mountain Range is approximately 3° latitude further south, there is little justification for ruling

out climatic factors as explanations for differences in forest structure.   There are clear north-south gradients in distribution of both winter (Keeley and Fotheringham 2001a, 2001b) and summer storms (Douglas et al. 1983). Indeed, the precipitation reported for 2,000 m in the San Pedro Martir (Minnich 1987b, Minnich et al. 2000) is comparable to what would be received at 500 to 1,000 m lower elevation north of the U.S.-Mexican border (NOAA Climatogical Summary).

Climatic differences are also suggested by differences in fire seasons north and south of the border (Stephens et al. 2003), and by patterns of tree distribution (Minnich 1987b). For example, ponderosa pine and big-cone Douglas-fir reach their southernmost distribution more than 200 km north of the Baja mountain range San Pedro Martir, and this is very likely climatically controlled (Thorne 1977, Stephenson 1990). Even trees that co-occur in both regions exhibit different patterns of distribution. Minnich (1987b) lists several examples, but the point is well illustrated by incense cedar. This conifer is widespread in forests of southern California (Thorne 1977, Minnich et al. 1995), yet in the San Pedro Martir it is concentrated along stream courses.

Also limiting the usefulness of these regions for understanding fire management north of the border is the fact that Jeffrey pine and mixed conifer forests of Baja California have experienced twentieth century reductions in the mean fire return interval over what was observed in pre-settlement times (Stephens et a. 2003). Some of this may be the result of a fire suppression policy that has been in effect for several decades in the national parks of Baja California. However, fire exclusion is not solely dependent on fire suppression activities, but rather may result from consumption of herbaceous fuels by livestock grazing (Savage and Swetnam 1990)—and Baja California forests have had a long history of livestock grazing (Henderson 1964, Stephens et al. 2003).

Until we have a clearer understanding of the extent to which climate and grazing determine forest structure in the mountain ranges south of the border, it would be prudent to rely on more direct measures of fire suppression impacts on forests of southern California for directing fire management.

TABLE 15.1

Fire frequency in foothills (below 900 m) and montane (above 1500 m)
portions of the three southern California USFS national forests

	Percentage of Area Burned							
	Foothills				Montane			
	NUMBER OF RECORDED FIRES				NUMBER OF RECORDED FIRES			
	0	1	2	≥3	0	1	2	≥3
Angeles	11	34	33	22	52	31	14	3
San Bernardino	16	38	25	21	73	22	4	1
Cleveland	24	37	24	16	45	47	8	0

NOTE: From Stephenson and Calcarone 1999.

TABLE 15.2
Fire-response types for important species in grasslands in the South Coast bioregion

	Type of Fire Response			
Lifeform	Sprouting	Seeding	Individual	Species
Herbaceous perennial	Yes, as a normal phenological response, not fire stimulated	No, dormant seed bank; seeds are produced by first year resprouts and generate seedlings in subsequent post-fire years	Aboveground portions of plants usually dead at time of fire	Mariposa lilies *(Calochortus* spp.*)*, blue dicks *(Dichelostemma capitatum)*, Lomatium *(Lomatium* spp.*)*, needlegrass *(Nassella* spp.*)*, sanicle *(Sanicula* spp.*)*
Herbaceous perennial	None	Yes, largely from current year seed bank	Plants dead at time of fire	Oats *(Avena* spp.*)*, bromegrasses *(Bromus* spp.*)*

TABLE 15.3
Natural fire regime characteristics for grasslands
in the South Coast bioregion

Temporal
  Seasonality — Summer–fall
  Fire-return interval — Moderate–long

Spatial
  Size — Moderate–large
  Complexity — Low

Magnitude
  Intensity — Low
  Severity — Low
  Fire type — Crown

grasses over shrubs on fine-grained soils. These substrates retain moisture in the upper-soil profiles and reduce percolation to deeper soil layers, which is lethal for shrub taproots that depend on it for surviving summer drought. Annual grassland persistence in the absence of fire is more complicated and a function of plant community interactions as discussed below.

FIRE REGIME–PLANT COMMUNITY INTERACTIONS

Historically, fire-return intervals were likely heavily influenced by proximity to Native American settlements (Keeley 2002a), being frequent in those areas, but on remote sites, where lightning was the primary ignition source, more on the order of one to several times a century (Table 15.3). Today, grassland fires are almost entirely ignited by humans, and fire frequency is very high, particularly at the interface

of urban areas. Historically, it is to be expected that most fires burned in summer and fall, but wherever human ignitions have been or are a factor, the fire season is extended to include late spring and early winter, and year round during droughts.

Anthropogenic burning beginning with Native Americans and continued by Euro-American settlers has greatly expanded grassland distribution at the expense of sage scrub, chaparral, and woodland (Wells 1962; Keeley 1990b, 2002a; Hamilton 1997). Initially these "grasslands" were likely dominated by native forbs, as the state lacks aggressive colonizing native annual grasses. It is to be expected that where these type conversions occurred adjacent to native grasslands that bunchgrasses such as purple *(Nassella pulchra)* and nodding needlegrass *(Nassella cernua)* would have invaded, although the long and extreme summer drought in this region might have made persistence on well-drained course substrates precarious. One native bunchgrass, foothill needlegrass *(Nassella lepida)*, which is a common component of coastal sage scrub (Keeley and Keeley 1984), likely persisted in these disturbance-maintained grasslands. However, prior to European entry into California, these "grasslands" probably were dominated by annual forbs, many of which were important food resources for Native Americans (Timbrook et al. 1982, Keeley 2002a).

During the first half of the nineteenth century, California grasslands, both bunchgrass-dominated and annual forb-dominated grasslands, were rapidly and thoroughly invaded by non-native grasses and forbs brought by the European colonizers (Mack 1989). Overgrazing and drought during the mid- to late nineteenth century are commonly given as causal factors behind our present non-native–dominated grasslands. However, some species, such as wild oats *(Avena fatua)* and black mustard *(Brassica nigra)*, appear to have dominated rapidly in the absence of overgrazing (Heady 1977). The primary factors driving the rapid non-native invasion of grasslands over much of the landscape were: (1) Holocene climate warming, which favored annuals over perennials; (2) long co-evolution of European annuals with human disturbance, which selected for aggressive colonizing ability; and (3) the disequilibrium in native ecosystems created by high frequency of burning by Native Americans (Keeley 2002a), which favored rapid invasion.

Annual grasslands thrive on frequent fires due to copious seed production and high seed survival under low-intensity fires. These non-native–dominated grasslands originated from disturbance and are not restricted by substrate, being found on soils that support most other vegetation types (Wells 1962). In the absence of fire or other disturbances, their persistence is a function of recolonization ability of woody associations (Wells 1962; DeSimone and Zedler 1999, 2001). Chaparral species colonize open grassland sites poorly, because species most tolerant of open xeric sites have weak dispersal and species with high dispersal establish poorly on open sites (Keeley 1998b). In the absence of disturbance, sage scrub species recolonize much more readily than chap-

arral (McBride 1974, Freudenberger et al. 1987, Callaway and Davis 1993).

Sage Scrub

In coastal communities the most common subshrubs are obligate resprouters after fire (Table 15.4), including California brittlebush *(Encelia californica)*, saw-toothed goldenbush *(Hazardia squarrosa)*, and coastal buckwheat *(Eriogonum cinereum)*; although in the long absence of fire these species are capable of continued basal sprouting and canopy regeneration (Malanson and Westman 1985). Many subshrubs are facultative seeders and regenerate after fire from resprouts and dormant seed banks, although on many sites resprouting is the dominant means for recapturing post-fire sites (Malanson and O'Leary 1982). The most common facultative seeders include bush monkeyflower *(Mimulus* spp*)*, California sagebrush *(Artemisia californica)*, purple sage *(Salvia leucophylla)*, and black sage *(Salvia mellifera)*. Seeds produced by the first-year resprouts are largely non-dormant and produce a massive flush of seedlings in the second post-fire year (Keeley and Keeley 1984, Keeley et al. 2006b). Several of these species are known to produce polymorphic seed banks with a portion of the seeds having deep dormancy broken by smoke or other combustion products (Keeley and Fotheringham 2000). Deerweed *(Lotus scoparius)* is the only obligate-seeding woody species typical of coastal sage scrub, and it exhibits massive seedling recruitment in the first post-fire year from dormant seed banks. In this, and all other legumes, chemical cues such as smoke play no role in stimulating germination; rather, heat shock triggers germination in the first post-fire year. As a consequence, germination may be triggered in the absence of fire on open substrates due to solar heating of the soil. For example, deerweed continues to recruit at low levels in subsequent years, particularly following high rainfall (Keeley et al. 2005b). This species is not long lived, perhaps a decade or two, and occasionally is subject to mass die off as was observed on many 5-year post-fire sites in spring following the extremely wet El Niño winter of 1997–1998 (J. Keeley personal observations).

Two larger-stature evergreen shrubs, laurel sumac *(Malosma laurina)* and lemonadeberry *(Rhus integrifolia)*, are widely dispersed throughout coastal sage scrub. They are both vigorous resprouters but have very different seedling recruitment dynamics. The former species often has substantial seedling recruitment following fire (Keeley et al. 2006b), whereas the latter species typically recruits under fire-free conditions (Lloret and Zedler 1991).

Much of the post-fire woody flora in southern California is rather promiscuously distributed in both chaparral and coastal sage scrub (Keeley et al. 2005b). Some species such as deerweed, golden yarrow *(Eriophyllum confertiflorum)*, California buckwheat *(Eriogonum fasciculatum)*, chaparral mallow *(Malacothamnus fasciculatus)*, laurel sumac, and black sage are equally common in both vegetation types. Coastal sage communities also have a very rich annual and herbaceous perennial flora, many of which are ephemeral post-fire

TABLE 15.4
Fire-response types for important species in sage scrub in the South Coast bioregion

Lifeform	Type of Fire Response			Species
	Sprouting	Seeding	Individual	
Shrub	Fire stimulated	Fire stimulated	Top-killed	Laurel sumac *(Malosma laurina)*
Shrub	Fire stimulated	None	Top-killed	Lemonadeberry *(Rhus integrifolia)*
Subshrub	Fire stimulated	Polymorphic seed bank, a portion is dormant and fire stimulated	Top-killed or killed	California sagebrush *(Artemisia californica),* coastal buckwheat, *(Eriogonum cinereum),* California buckwheat, *(Eriogonum fasciculatum),* bush monkeyflower *(Mimulus aurantiacus),* purple sage *(Salvia leucophylla),* black sage *(Salvia mellifera)*
Subshrub	Fire stimulated	No, dormant seed bank; seeds are produced by first year; resprouts generate seedlings in subsequent post-fire years	Top-killed	California brittlebush *(Encelia californica),* saw-toothed goldenbush *(Hazardia squarrosa)*
Suffrutescent	None	Fire stimulated	Killed or present only as dormant seeds	Deerweed *(Lotus scoparius)*

followers. The floristic overlap between chaparral and sage scrub in both the annual and the herbaceous floras is even more pronounced than with woody species; thus, they are discussed in the chaparral section. On the more mesic slopes, rhizomatous grasses, including giant wildrye *(Leymus condensatus)* and species of bent grass *(Agrostis* spp.*),* often dominate, particularly under high fire frequencies.

INTERIOR SAGE SCRUB

This more arid interior version of sage scrub lacks some of the most vigorous resprouting species, and the facultative seeders on these sites tend to behave more like obligate seeders, as fire-caused mortality often can be 100% on interior sites. Resprouting success appears to be more closely tied to plant age than to fire severity. In a study of several thousand burned shrubs it was found that for both California buckwheat and California sagebrush, mortality was not related to height of the burned skeleton, suggesting fire severity was not a factor determining resprouting (Keeley 1998a, Keeley in press). Rather, stem diameter (an indicator of plant age) was the primary determinant of resprouting success: as stems increased in diameter their probability of resprouting declined, a phenomenon shared by the northern California coastal scrub dominant coyote brush

(Hobbs and Mooney 1985). Less resprouting in older plants appears to derive from the loss of functional adventitious buds due to wood production, and may be the result of the evolution of secondary wood in taxa derived from herbaceous perennial ancestors (Keeley in press). Other interior shrubs regenerating heavily from seed are black sage, white sage *(Salvia apiana),* deerweed, and chaparral mallow, and all except brittlebush are shared with coastal sage scrub associations. Most of these species have light wind-dispersed seed, so if populations are extirpated from a site they readily disperse in from nearby source populations (Wells 1962; DeSimone and Zedler 1999, 2001).

Interior sage scrub communities have a similar ephemeral post-fire flora of annual and herbaceous perennial species that overlap greatly with coastal sage scrub and chaparral associations (Keeley et al. 2005a, b).

FIRE REGIME–PLANT COMMUNITY INTERACTIONS

Historically, fires burned primarily summer to winter but today the bulk of this landscape burns in the fall (Table 15.5). As with grasslands, human ignitions have increased both the frequency of fires (Wells et al. 2004) and length of the fire season, and during severe droughts, fires can burn year round. Size of fires is extremely variable and can be very large,

TABLE 15.5
Natural fire regime characteristics for sage scrub in the
South Coast bioregion

Temporal	
Seasonality	Late summer–fall
Fire-return interval	Moderate–long
Spatial	
Size	Moderate–large
Complexity	Low
Magnitude	
Intensity	Moderate
Severity	Low–high
Fire type	Passive-active crown

on the order of thousands of hectares, but modal fire size has decreased (Keeley et al. 1999), due to increased human ignitions coupled with increasingly effective fire suppression, as well as habitat fragmentation.

Natural lightning-ignited fires are rare in the low-elevation coastal sites; however, under autumn Santa Ana wind conditions fires would have readily burned in from adjoining chaparral and woodlands. Contemporary burning patterns in the western end of the Transverse Ranges result in much of this vegetation burning at roughly five-year intervals, and nearly all of this type burns before 20 years of age (McBride and Jacobs 1980, Keeley and Fotheringham 2003). It is unlikely that natural lightning-ignited fires ever burned at such a short fire-return interval. Although this vegetation is reasonably resilient to high fire frequencies, the current levels are near the lower threshold of tolerance, and many such sites are experiencing accelerated non-native invasion (Keeley 2001, 2004c).

Vogl (1977) hypothesized that sage scrub was an artifact of fire suppression and livestock grazing, and that its current distribution was greatly expanded due to human disturbance. This model would appear to be based on the well-known mesquite invasion of Texas grasslands, which has been clearly linked to overgrazing (Archer 1994). However, coastal sage species share little in common with mesquite, and empirical studies demonstrate sage scrub species colonize grassland sites when grazing pressure is relieved (Hobbs 1983, Freudenberger et al. 1987, Callaway and Davis 1993, McBride 1974). These patterns are more consistent with the model that sage scrub loses ground to annual grassland under frequent disturbance, although it is capable of recolonizing when disturbance frequency declines. Sage scrub also expands into chaparral sites when fire frequencies exceed the disturbance tolerance of chaparral (Cooper 1922, Wells 1962, Freudenberger et al. 1987, Callaway and Davis 1993).

Increased burning in the interior valleys, as illustrated for Riverside County (Fig. 15.3) is certainly a major stress for these

shrubs, most of which must regenerate from seed. Historical studies show that there has been a substantial type conversion of sage scrub to non-native grasslands during the twentieth century (Minnich and Dezzani 1998). It has been hypothesized that in addition to increased fire frequency, nitrogen deposition in this region of high air pollution has contributed to this shift from sage scrub to non-native grasslands (Allen et al. 2000). It is unclear to what extent this affects post-fire invasion, because soil nitrate levels normally increase by an order of magnitude in the first spring after fire (Christensen 1973). Consistent with the role of air pollution driving the invasion process is the much greater presence of non-natives during the first five post-fire years in interior sage scrub than in coastal sage scrub (Keeley et al. 2005c). However, there is also a very strong negative relationship between shrub cover and non-native presence in both the coastal and the interior sage scrub associations. Certainly a contributing factor to the greater inviability of interior sage scrub is the much slower shrub canopy recovery rate resulting from more limited resprouting and greater reliance on seedling recruitment (Fig. 15.7).

Chaparral

The primary differences in chaparral fire response are best understood by comparing responses on arid, usually south-facing slopes and ridges, with mesic, north-facing exposures. As a general rule, species that recruit seedlings after fire (Table 15.6) tend to occupy the more xeric sites, that is, low elevations and south-facing exposures (Keeley 1986, Meentemeyer and Moody 2002). Resprouting species that do not recruit after fire—for example, obligate resprouters—are usually on the more mesic slopes (Keeley 1998b). These are extremes of a gradient, and each comprises a collection of floristically different associations, not readily distinguished from one another by fire ecology or fire regime. Distribution of arid and mesic chaparral types is commonly determined by slope aspect; thus, landscapes usually comprise a mixture of different fuels and post-fire ecologies. This fine-grained distribution of different associations results in a great deal of diversity of fire behaviors and post-fire responses arising out of large fires that cover extensive portions of the landscape.

ARID SITES

Chamise is the nearly ubiquitous dominant on most arid chaparral sites. With respect to fire response, this needle-leaved shrub is a facultative seeder and often exhibits massive seedling recruitment in the first post-fire year from a dormant seed bank (Keeley 2000). There is substantial site-to-site variation in the ratio of seedlings to resprouts; on some sites regenerating almost entirely from seedling recruitment and other sites from resprouts (Keeley et al. 2005b). Fire intensity, season of burn, and level of precipitation in the first post-fire winter appear to be the primary factors determining these patterns (Moreno and Oechel 1994, Keeley and Fotheringham
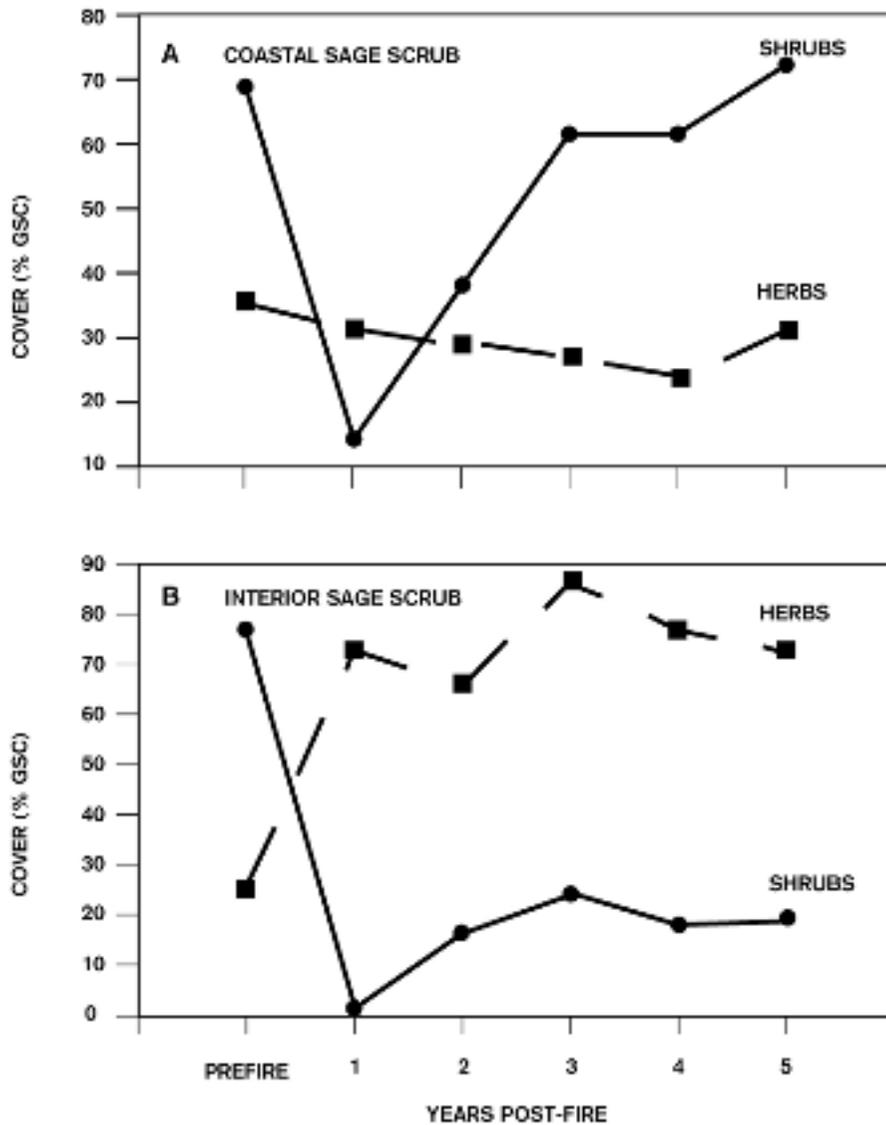
FIGURE 15.7. Foliar cover before and after fire at coastal (A) and interior (B) sage scrub sites. (Redrawn from O'Leary and Westman 1988.)

2003, Keeley et al. 2005b). Other facultative seeders include Eastwood's manzanita *(Arctostaphylos glandulosa),* chaparral whitethorn *(Ceanothus leucodermis)*, yerba santa *(Eriodictyon* spp.*),* and flannelbush *(Fremontodendron californicum)*, although these latter broad-leaved species often occupy less-arid sites.

Also at the arid end of the gradient are species that lack any ability to resprout vegetatively after fire, and their persistence is entirely a function of successful seedling recruitment from a dormant seed bank. These shrubs are termed *obligate-seeding* (Wells 1969) species, or *obligate seeders* (Keeley 1977). Chaparral, along with three of the other mediterranean-climate shrublands, is unique among woody shrublands of the world in having a large proportion of species that lack the ability to resprout following fire or other disturbance (Keeley 1986). These obligate-seeding species of manzanita and California-lilac *(Ceanothus* spp.*)* recruit heavily in the first post-fire year from dormant seed banks, and recruitment is typically nil until the next fire on the site (Keeley et al. 2005b). The bulk of the seed bank is dispersed

locally (Zedler 1995b) and with deep dormancy; thus, these species disperse more in time than in space. They are very sensitive to repeat fires and may be extirpated from a site if fires occur too frequently (Keeley 2000). Some coastal species appear to require more than 40 years without fire to establish seed banks sufficient to maintain populations (Odion and Tyler 2002).

Demography of obligate seeders is quite variable. Bush poppy *(Dendromecon rigida)* is a short-lived shrub that has massive recruitment in the first post-fire year (Bullock 1989). Shrubs die within a decade after fire and seed banks remain dormant until the next fire. On many sites, it is known that this dormant seed bank remained viable and produced a dense vigorous population after more than 125 years in the soil (Keeley et al. 2003, Keeley et al. 2005d).

Obligate-seeding California-lilac varies markedly in longevity (Zedler 1995b). Some species (e.g., woolyleaf ceanothus *[Ceanothus tomentosus]*) appear to be relatively short lived, on the order of three to five decades, whereas

TABLE 15.6
Fire-response types for important species in chaparral in the South Coast bioregion

Lifeform	Type of Fire Response			Species
	Sprouting	Seeding	Individual	
Tree	None	Serotinous cones	Killed	Tecate cypress *(Cupressus forbesii)*, Cuyamaca cypress *(Cupressus arizonica),* knobcone pine *(Pinus attenuata)*
Tree	None	Variable, low level serotiny; often dependent on parent tree survival	Killed or survive	Coulter pine *(Pinus coulteri)*, Torrey pine *(Pinus torreyana)*
Subshrub or suffrutescent	None	Fire stimulated	Largely present only as dormant seed banks	California buckwheat *(Eriogonum fasciculatum)*, deerweed *(Lotus scoparius),* black sage *(Salvia mellifera)*
Shrub	None	Fire stimulated	Killed	Woolyleaf ceanothus *(Ceanothus tomentosus)*, desert ceanothus *(Ceanothus greggii)*, bigberry manzanita *(Arctostaphylos glauca)*
Shrub	Fire stimulated	Fire stimulated	Top-killed or killed	Chamise *(Adenostoma fasciculatum)*, Eastwood's manzanita *(Arctostaphylos glandulosa),* chaparral whitethorn *(Ceanothus leucodermis)*, greenbark ceanothus *(Ceanothus spinosus),* yerba santa *(Eriodictyon* spp.*)*, flannelbush *(Fremontodendrun californicum)*
Shrub	Fire stimulated	None	Top-killed or killed	Birch-leaf mountain-mahogany *(Cercocarpus betuloides),* silk tassel bush *(Garrya* spp.*)*, chaparral holly *(Heteromeles arbutifolia)*, chaparral cherry *(Prunus ilicifolia)*, scrub oak *(Quercus berberidifolia)*, California coffeeberry *(Rhamnus californica)*, spiny redberry *(Rhamnus crocea)*
Herbaceous perennials	Fire stimulated in some, in others sprouting is normal phenological stage	None	Aboveground portions of plants dead at time of fire	Sacapellote *(Acourtia microcephala)*, mariposa lily *(Calochortus* spp.*)*, soap plant *(Chlorogalum pomeridianum)*, larkspur *(Delphinium* spp.*)*, blue dicks *(Dichelostemma capitatum)*, Lomatium *(Lomatium* spp.*)*, Cucamonga man-root *(Marah macrocarpus)*, smallflower melicgrass *(Melica imperfecta)*, death camas *(Zigadenus* spp.*)*

TABLE 15.6 (continued)

| Lifeform | Type of Fire Response | | | Species |
	Sprouting	Seeding	Individual	
Annuals	None	None	Present only as a dormant seed bank	Snapdragon *(Antirrhinum* spp.*)*, red maids *(Calandrinia breweri, C.)*, common pussypaws *(Calyptridium monandrum)*, sun cup *(Camissonia* spp.*)* white pincushion *(Chaenactis artemisiifolia)*, cryptantha *(Cryptantha* spp.*)*, spotted hideseed *(Eucrypta chrysanthemifolia)*, whispering bells *(Emmenanthe penduliflora)*, gilia *(Gilia* spp.*)*, lotus *(Lotus* spp.*)*, lupine *(Lupinus* spp.*)*, San Luis blazingstar *(Mentzelia micrantha)*, fire poppy *(Papaver californicum)*, phacelia *(Phacelia* spp.*)*, manynerve catchfly *(Silene multinervia)*, chia *(Salvia columbariae)*
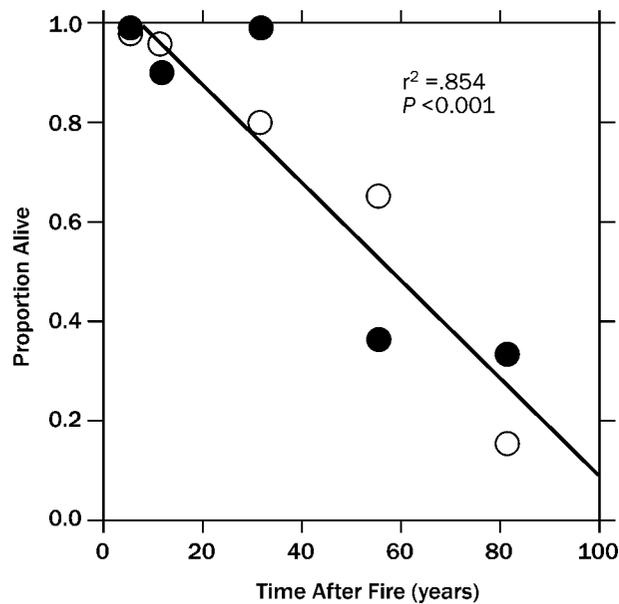
FIGURE 15.8. Mortality patterns of the obligate-seeding desert ceanothus *(Caeanothus greggii)* in different-aged chaparral stands in eastern San Diego County (from Zedler 1995). Closed circles are for north-facing exposures, and open circles are for south-facing exposures.

others persist far longer (e.g., desert ceanothus *[Ceanothus greggii]*) (Fig. 15.8). Mortality appears to be driven by competition and increases on more mesic slopes (Keeley 1992a). As stands age, there is a shifting balance in the competitive relationships resulting in a successional replacement of obligate seeders by species more competitive under long fire-free conditions. Even where populations experience complete mortality, they are highly resilient to long fire-free periods as soil-stored seed banks survive hundreds of years (Zavitokovski and Newton 1968, Franklin et al. 2001, Keeley et al. 2005b). Obligate-seeding manzanita generally have smaller seed banks, take longer to establish seed banks, recruit fewer seedlings, exhibit greater early seedling survivorship and perhaps greater longevity than California-lilac (Keeley 1977, Odion and Tyler 2002). All post-fire–seeding species exhibit structural and physiological characteristics selected to tolerate the severe conditions on open sites during the long summer-autumn drought (Davis et al. 1998, Keeley 1998b).

This community comprises a rich diversity of herbaceous species, the bulk of which form an ephemeral post-fire successional flora. Most of this flora is composed of annuals that arise from dormant seed banks, and are endemic to burned sites, and do not persist more than one or two years (Keeley et al. 2005a, b). Herbaceous perennials are almost all obligate resprouters, arising from dormant bulbs, corms, or rhizomes (Keeley 2000), although a few are short lived and are present in post-fire environments only as seedlings. Post-fire resprouts flower and disperse non-dormant seeds that readily recruit in the subsequent post-fire years. Once the canopy closes, these species may remain entirely dormant for many years (Epling and Lewis 1952) or continue to produce foliage but not flower (Tyler and Borchert 2002).

Dormant seed banks are triggered to germinate by either heat shock or chemicals from smoke or charred wood (Keeley and Fotheringham 2000). In general, species are stimulated by one or the other of these cues; however, there are a few species where both appear to play a role—for example, the nearly ubiquitous chamise is equally stimulated by either smoke or heat (Keeley, Bolton, and McGinnis unpublished data). There is a very strong phylogenetic component to germination response, with certain families responding only to heat and others only to chemicals. For example, all California-lilac species are stimulated by heat, and smoke plays no role in their germination. This pattern is typical for other fire-stimulated buckthorns, for example, *Phylica* spp. in South African fynbos (Keeley and Bond 1997). Other common families in chaparral and sage scrub with heat-stimulated germination include the legumes (Fabaceae), morning-glories (Convolvulaceae), mallows (Malvaceae), and bladdernuts (Sterculeaceae). However, the majority of species with seedling recruitment in the post-fire flora of both chaparral and sage scrub are not stimulated by heat, but rather by smoke or other chemicals produced during combustion (Keeley and Fotheringham 2000). This behavior is common in woody and herbaceous species in the sunflower (Asteraceae), borage (Boraginaceae), mustard (Brassicaceae), pink (Caryophyllaceae), waterleaf (Hydrophyllaceae), mint (Lamiaceae), evening primrose (Onagraceae), poppy (Papaveraceae), phlox (Polemoniaceae), figwort (Scrophulariaceae), and nightshade (Solanaceae) families (Keeley 1991, Keeley and Fotheringham 2000).

One factor that plays an important role in determining post-fire patterns is fire intensity. Davis et al. (1989) demonstrated that microscale patterns in post-fire regeneration resulted from spatial variation in seed banks and apparent fire intensities. Fire-intensity impacts are complex because seedling recruitment of some species is greatly inhibited by high fire intensity, whereas for others it is enhanced (Keeley et al. 2005a, b).

MESIC SITES

Broadleaved evergreen shrubs dominate these sites and include scrub oak, California coffeeberry, spiny redberry, silk tassel bush, chaparral cherry, and Christmas berry. Throughout much of the region the dominant oak is scrub oak, but in the interior ranges interior live oak dominates (Scott and Sawyer 1994). The proportion of shrubs that are killed and fail to resprout is generally very low in most of these species, and they seldom recruit seedlings except in the long absence of fire (Keeley 1992a,b). These obligate-resprouting species avoid the stressful summer drought by deep roots that gain access to water in deep rock and soil layers; however, this option is unavailable to seedlings and thus recruitment success is dependent on establishment in favorable mesic microsites (Keeley 1998b). All of these shrubs have animal-dispersed fruits and successful establishment is dependent on finding safe sites with shade and highly organic soils, usually in the understory of chaparral or woodlands. Seedlings that recruit in the understory often remain suppressed for decades; however,

they do resprout after fire, and it may be that fires are required for successful emergence into the canopy (Keeley 1992a).

There are a number of facultative seeders such as greenbark ceanothus, chaparral whitethorn, and Eastwood's manzanita that often form mixed chaparral on either arid or mesic sites and their response to fire is similar to chamise, often recruiting seedlings and resprouting. Another species that seems to have a wide range of tolerances, occurring on both xeric and mesic sites, is birch-leaf mountain-mahogany, a post-fire obligate resprouter. However, unlike other obligate resprouters, it does not recruit in the understory of mature chaparral; rather, it appears to be dependent on openings created by other types of disturbance (Keeley 1992a).

Mesic sites contribute to higher fuel moisture conditions that may reduce fire intensity and fire severity; however, these mesic sites lead to higher primary production and under severe fire weather they may experience much higher fire intensity (Keeley and Fotheringham 2003). When these productive sites burn in low-intensity fires, much of the larger woody fuels are not consumed, thus putting the community on a trajectory for potentially more intense fires during the next fire.

FIRE REGIME–PLANT COMMUNITY INTERACTIONS

With rare exceptions, chaparral always burns as active crown fires. Fire-return intervals are on the order of one to several times a century, and are heavily influenced by human ignitions (Table 15.7). Complexity is commonly low to moderate, and is a function of topography, vegetation mosaic, antecedent climate, and weather. Fire intensity is generally high, but variable depending on fuels and weather.

Today, fire frequency is highest in the summer, but the bulk of the landscape burns in the fall (Keeley and Fotheringham 2003). Historically, fire frequency also would have peaked in the summer due to the timing of lightning ignitions. These summer fires spread slowly and often reached sizes of only 100 to 1,000 ha after months of burning (Minnich 1987). Fire size would have increased markedly when lightning-ignited fires persisted until the autumn Santa Ana wind season, where, within a day, these fires would have expanded to 100,000 ha and, with typical Santa Ana wind episodes lasting several days to a week, may have generated fires on the order of a million ha (Keeley et al. 2004). Today, modal fire size has greatly decreased due to habitat fragmentation and high human ignitions coupled with effective fire suppression; however, the bulk of the landscape still burns in large fires (Strauss et al. 1989) at rotation intervals of 30 to 40 years (Keeley et al. 1999). One exception to this rule is the chaparral on the Channel Islands (see Sidebar 15.2).

An alternative opinion has been expressed that large fires are a modern artifact of twentieth-century fire-suppression policy (Philpot 1974; Minnich 1995, 1998; Chou and Minnich 1997). These authors contend that fire exclusion has resulted in an unnatural fuel build-up on the southern California landscape, which is directly responsible for increasing

TABLE 15.7

Natural fire regime characteristics for chaparral in the
South Coast bioregion

Temporal	
Seasonality	Summer–fall
Fire-return interval	Moderate–long
Spatial	
Size	Moderate–large
Complexity	Low
Magnitude	
Intensity	High
Severity	Low–high
Fire type	Active crown

fire size. The hypothesis that fire suppression has excluded fire has been tested and shown to be unsupported (Moritz 1997, Conard and Weise 1998, Keeley et al. 1999, Weise et al. 2002). Indeed, during the twentieth century much of this landscape received a higher frequency of burning (30–40-year rotation intervals) than would be expected under natural conditions (Keeley and Fotheringham 2003). The role of fuel age in controlling fires is further developed in the chaparral fuels and fire sidebar (Sidebar 15.3).

Extensive chaparral dieback has the potential to cause a rapid change in fire hazard (Riggan et al. 1994). It commonly hits large patches of a single species, typically species of ceanothus in the subgenus Cerastes. This was once thought to be driven by fungal pathogens, but experimental studies demonstrate conclusively that it is a result of drought (Davis et al. 2002). These are obligate-seeding shrubs whose shallow root systems subject these plants to excessive water stress during extended droughts.

Non-native annuals frequently invade post-fire chaparral sites and may persist for several years until shrub canopies return (Keeley et al. 2005c). Invasion is largely a function of proximity of post-fire seed sources, and this is largely determined by pre-fire stand age. Mature chaparral stands generate sufficient fuels to produce fire intensities that kill seed banks of non-native grasses. However, when fires occur too frequently, shrub canopies fail to close and a substantial non-native grass flora persists (Zedler et al. 1983). These surface fuels increase the chances of another fire, and because the fuels are a mixture of shrubs and grasses, they generate lower fire intensities (Odion and Davis 2000) and greater non-native seed bank survival (Keeley 2001, 2004c).

Closed-Cone Cypress

Fire regime characteristics match that of chaparral (Table 15.7). Both Tecate *(Cupressus forbesii)* and Cuyamaca cypress *(Cupressus arizonica)* have characteristics shared by closed-

cone pines—specifically, high stand density, lack of self-pruning and thin bark, and relatively long fire-return intervals—characteristics typical of stand-replacing crown fire regimes (Keeley and Zedler 1998). These obligate-seeding trees disperse seeds shortly after fire from aerial seed banks and recruit heavily in the first post-fire spring (Table 15.6). They form monotypic even-aged stands that may require many decades of fire-free conditions in order to develop a seed bank sufficient to withstand a repeat fire (Zedler 1977). Studies of seed production show that populations younger than 30 years of age are extremely vulnerable to extinction, and seed production continues up to a century and perhaps beyond (Zedler 1995b). Canopy fuels typically produce extremely high fire intensities and sterilize the soil seed bank of competing plants. Cypress seeds are protected by cones, and following dispersal beneath the parent skeleton, seedlings are released from competition compared with microsites just outside the canopy shadow (Ne'eman et al. 1999).

Historical fire-return intervals were undoubtedly very long, perhaps once a century. Contemporary fire frequencies are much higher (Zedler 1995a), and when stands are hit with high fire frequencies they may be extirpated, though recolonization from metapopulations that survive in ravines or other fire-free refugia are likely an important means of long-term persistence (Zedler 1980). Fire frequencies greater than once or twice a century appear to be the primary threat to the persistence of these cypress populations (Zedler 1977, Reveal 1978)

Low-Elevation Pines

These pines are typically distributed in patches within a mosaic of chaparral, and thus their fire regime characteristics match that of chaparral (Table 15.7). Knobcone pine *(Pinus attenuata)* is similar to the closed-cone cypress species in its deeply serotinous cones that initiate dense monotypic stands following crown fires (Keeley and Zedler 1998, Stuart and Stephens this volume).

Coulter pine *(Pinus coulteri)* spans a range of habitats from chaparral to forests. Fire regimes vary from stand-replacing to stand-thinning fire regimes, largely dependent on associated vegetation (Dodge 1975, Minnich 1977). When associated with chaparral, cones are serotinous and recruitment is synchronized to the immediate post-fire environment, whereas on forested sites cones are not serotinous and recruitment may occur between fires (Table 15.6), and consequently stands are uneven aged (Vale 1979, Borchert 1985, Borchert et al. 2002). Torrey pine is associated with chaparral and thus naturally exposed to stand-replacing fires. Although most recruitment is tied to fire, stands comprise different age cohorts that recruit after different fire events (Wells and Getis 1999).

Both of these latter two pines share characteristics that are tied to the stand-replacing fire regime characteristic of chaparral shrublands. They typically do not self-prune lower branches, something that enhances their flammability and increases the probability of them as well as their neighbors

Eight islands ranging in size from approximately 3 to 250 km^2 lie within 100 km of the South Coast bioregion mainland (Schoenherr et al. 1999). The highest peak is 750 m and is on Santa Cruz Island. During Pleistocene glacial episodes (last one ending about 12,000 years ago), the size of islands and distance from the coast varied. At this time the four northernmost islands were connected as one island, but were still separated from the mainland by more than 4 km of ocean. Some of the earliest Native American populations were established on these islands and at the time of contact with Europeans there were sizable settlements on the larger islands (Jones 1992). Over the past 200 years, livestock, primarily goats and sheep, have expanded populations to the point of denuding vegetation from large portions of most of the islands (Schoenherr et al. 1999).

The ecosystems on these islands are broadly similar to and share a substantial number of plant species with those on the mainland. Plant communities include grassland, coastal sage scrub, chaparral, and oak woodland. The presence of fire-dependent shrubs chamise and species of ceanothus and manzanita (Minnich 1980b), fire-following annuals whispering bells and spotted hideseed (Carroll et al. 1993), and closed-cone pines (Linhart et al. 1967) are evidence that fires have historically been a predictable feature of this landscape. However, since settlement by Euro-Americans in the nineteenth century, fires have been relatively rare. During the period 1830 to 1986, only 73 fires were recorded in written records, 65% less than 10 ha and only 7% greater than 1,000 ha (Carroll et al. 1993). These numbers provide crude estimates of fire rotation intervals on the order of hundreds of years. Also, during this period only three lightning-ignited fires were recorded; however, this is likely below the historical range of variability because of greatly reduced fuels due to intense grazing pressure during the period of record.

Prior to the exploitation of these islands with over-grazing, there is evidence that communities such as chaparral and coastal sage scrub formed more contiguous vegetation capable of carrying fire (Minnich 1982). The presence of Native American settlements for the last 10,000 years, coupled with their use of fire as a land management tool (Keeley 2002a), makes it seem likely that fires were a regular feature of some of these islands. Prior to Indian occupation, lightning was an occasional source of ignition and it need not have been frequent to maintain fire-type species on the islands. The high frequency of winds on the islands (Yoho et al. 1999) would have contributed to the drying of fine fuels, as well as ensuring fire spread. Fire spread would also have been enhanced during Pleistocene glacial episodes when some of the islands were connected.

In chaparral, the limited fire activity over the historical period since Euro-American settlement appears to have reduced the extent of fire-dependent shrubs such as chamise and species of ceanothus and manzanita, and favored species capable of regenerating in fire-free periods such as species of cherry, Christmas berry, oak, coffeeberry and redberry, and lauril sumac (Minnich 1980b, Landis 2000). Although some of the fire-dependent species still retain fire-stimulated germination, some produce a smaller proportion of dormant seeds than mainland taxa (Carroll et al. 1993). In the absence of fire, closed-cone pines exhibit a low level of seed release and seedling recruitment and an uneven age structure (Linhart et al. 1967, Walter and Taha 1999).

Several lines of evidence cast doubt on the strict control of fires by fuel age in these crown fire regimes. For example, large fires (>5,000 ha) in the westernmost portion of the Transverse Range are fueled primarily by shrublands that are less than 20 years of age (Keeley et al. 1999). In addition, across all of Los Angeles County there is no statistically significant change in probability of burning after approximately 20 to 25 years (Schoenberg et al. 2003). A thorough analysis of the role of fuel age by Moritz et al. (2004) included ten chaparral landscapes from Baja California to Monterey, a span of 500 km, with each data set representing tens of thousands of hectares and hundreds of fires over an 85-year period (in most cases). For nine of the ten landscapes they observed a near constant probability of burning with age. Hazard functions calculated with the Weibull function indicated that the rate of fire hazard did not change over time, ranging from 2%–4% in year 20 and 4%–7% in year 60. Collectively, these data refute the hypothesis that large fires are determined by a build-up of dead fuels. Indeed, several lines of evidence suggest the primary determinant of fire size is the coincidence of ignitions and Santa Ana winds (Davis and Michaelsen 1995; Conard and Weise 1998; Keeley and Fotheringham 2001a, 2001b; Moritz 2003).

This does not mean that fuel age has no effect on chaparral fires. In general it appears that fuel age is primarily a controlling factor under moderate weather conditions, and relatively unimportant under severe weather conditions accompanying Santa Ana winds (Keeley et al. 2004). However, Zedler and Seiger (2000) contend that it is unlikely that fuel age alone has ever maintained a landscape pattern of small fires. Their modeling studies demonstrate that it would take only a single large Santa Ana fire to set the landscape to the same age class, and thus, if subsequent fires were controlled by fuel age, the landscape would be forever doomed to burn in large fires.

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not surviving fires (Keeley and Zedler 1998, Schwilk and Ackerly 1999, Schwilk and Kerr 2002, Schwilk 2003). Chaparral populations of Coulter pine are strongly serotinous (Borchert 1985), but Torrey pine *(Pinus torreyana)* is not, although some seeds persist in the cones for years after seed maturity (McMaster and Zedler 1981). This delayed seed dispersal is thought by McMaster and Zedler (1981) to result from selection in an environment where large crown fires occur at long and unpredictable intervals, often longer than one generation. Such relaxed serotiny is also found in other closed-cone pines when distributed in coastal environments where natural lightning-ignited fires are rare (e.g., Millar 1986). These coastal pines also have a very subtle form of serotiny in that seeds dispersed in the year of maturity typically disperse months later than most pine species, thus dispersing seeds in winter, following the autumn fire season (Keeley and Zedler 1998).

Both of these pines have large seeds and exhibit far less capacity for wind dispersal than montane pines such as ponderosa pine (Johnson et al. 2002). Localized dispersal in these

chaparral-associated pines has likely been selected for because large stand-replacing fires generate suitable habitat close to the now-dead parent tree. In contrast, low-severity surface fire or mixed-severity fire regimes typical of ponderosa pine forests present fewer safe sites for recruitment, thus selection for the ability to disperse into gaps produced by the patchiness of mixed-severity fires (see yellow pine forest section).

Big-Cone Douglas-Fir

Big-cone Douglas-fir *(Pseudotsuga macrocarpa)* is one of only three conifers in California capable of resprouting after fire (Pacific yew *[Taxus brevifolia]* and coast redwood *[Sequoia sempervirens]* also resprout), but unlike the other two, big-cone Douglas-fir typically does not resprout from the base, rather from epicormic buds present throughout the length of the bole and branches (Fig. 15.9). Trees less than 10 cm dbh fail to resprout (Bolton and Vogl 1966); however, Minnich (1980a) reported that sprouting success appeared to be dependent primarily on fire severity rather than on tree size (Table 15.8).

FIGURE 15.9. Big-cone Douglas-fir *(Pseudotsuga macrocarpa)* tree in the early stages of resprouting from epicormic buds following wildfire in the San Gabriel Mountains. (Photo by J. Keeley.)

Minnich (1974) hypothesized that resprouting ability was not an adaptation to fire; rather, it evolved in response to mechanical damage from strong winds and excess snow. This seems improbable since most other Northern Hemisphere conifers are exposed to wind and snow, yet very few resprout. Also, big-cone Douglas-fir has one of the highest wood densities of any conifer (McDonald 1990), which should reduce mechanical damage relative to many other conifers. In this regard, pines provides a useful study in that in this large genus, the few species that resprout exist in stand-replacing fire regimes conducive to vegetative regeneration (Keeley and Zedler 1998), as is the case with big-cone Douglas-fir.

Seedling recruitment occurs sporadically during fire-free periods often under chaparral or oak woodland (Bolton and Vogl 1969, McDonald and Litterell 1976). Seedlings and saplings are very sensitive to burning, and thus successful establishment requires extended fire-free periods of at least two decades (Minnich 1980a). Unless recruitment occurs in a very sheltered environment, a further hiatus in burning for many more decades is apparently required for successful establishment of mature trees (Bolton and Vogl 1969). Seedling recruitment is uncommon on south-facing exposures, and it seems likely that the more mesic conditions on north-facing slopes, coupled with longer fire-free intervals

TABLE 15.8

Fire-response types for important species in big-cone Douglas-fir forests in the South Coast bioregion

Lifeform	Type of Fire Response			Species
	Sprouting	Seeding	Individual	
Tree	Fire stimulated, only epicormic	None	Top-killed or survive	Big-cone Douglas-fir *(Pseudotsuga macrocarpa)*
Tree	Fire stimulated basal or epicormic	None	Top-killed or survive	Canyon live oak *(Quercus chrysolepis)*

due to higher fuel moisture, are factors contributing to greater seedling recruitment on those slopes.

Aspects of this species' life history seem anomalous. Adult trees survive and resprout after fires only if fires are of low to moderate intensity. The habitat of this tree includes chaparral and oak woodlands, and low-intensity fires in these fuels are most likely if they occur frequently. However, seedling and sapling recruitment is eliminated under frequent fires of any intensity, and successful emergence into a canopy-level tree may require 50 to 100 years of fire-free conditions. In short, frequent fires favor adult persistence and infrequent fires favor population expansion.

FIRE REGIME–PLANT COMMUNITY INTERACTIONS

Fire regimes in big-cone Douglas-fir forests vary spatially and temporally (Table 15.9). Historically, higher-elevation groves associated with conifer forests likely experienced fires on decadal time scales, but lower elevations more on the scale of once or twice a century. Fires can burn as surface fires, but burn mostly as crown fires; thus complexity is high, being heavily influenced by topography and associated vegetation.

Big-cone Douglas-fir forests are typically restricted to ravines and steep slopes, comprising groves of a few trees to thousands of trees. There is the widespread belief that this species has become more restricted with Euro-American and Mexican settlement due to increased fire frequency or more severe fires due to ignition during severe fire weather (Leiberg 1900b, Horton 1960, Gause 1966). Groves that occur amidst chaparral are particularly vulnerable to high-severity fire that results in substantial mortality, whereas forests in more sheltered ravines and steep slopes are often immune to destruction (Minnich 1988). In the San Bernardino Mountains between 1938 and 1975, Minnich (1980a) reported 25% mortality of this species and that survivorship increased with increasing slope inclination, from 37% on slopes less than 20° to greater than 90% on slopes exceeding 40°. In a study of big-cone Douglas-fir mortality on two different aspects following a lightning-ignited wildfire in the San Gabriel Mountains (Keeley et al. unpublished data), it was found that pop-

TABLE 15.9

Natural fire regime characteristics for big-cone Douglas-fir in the South Coast bioregion

Temporal	
Seasonality	Late summer–fall
Fire-return interval	Moderate–long
Spatial	
Size	Small–moderate
Complexity	High
Magnitude	
Intensity	Mix of low and high
Severity	Low–high
Fire type	Surface, active or passive crown

ulations on relatively level terrain suffered 100% mortality, whereas a population on a steep north-facing slope had substantial survivorship, but only of large trees (Fig. 15.10A, B).

Bolton and Vogl (1969) observed that big-cone Douglas-fir could invade chaparral on gentler slopes only in the absence of fire, usually during a series of wet years following a severe fire that had destroyed the existing vegetation. These invasions were most often terminated with fire, unless the trees had grown large enough in the fire-free period to become fire resistant. Dense chaparral on shallow slopes is generally free of big-cone Douglas-fir because of frequent high-severity fires (e.g., Fig. 15.10B).

Minnich (1988) suggested that infrequent high-severity fires in these forests are an artifact of fire suppression, and under natural conditions, low-intensity fires would burn at frequent intervals under more moderate summer weather conditions. As a consequence, fire intensity would be less and tree mortality would be limited. While this model would ensure survival of existing big-cone Douglas-fir, frequent fires greatly restrict population expansion since recruitment of seedlings and saplings is dependent on long fire-free periods.
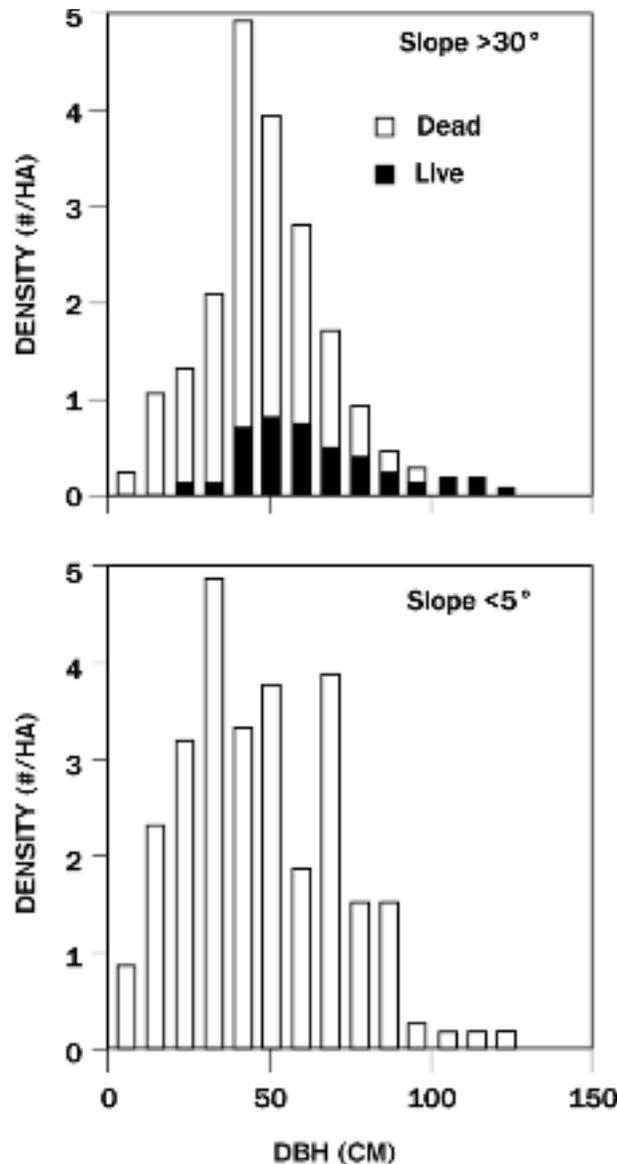
FIGURE 15.10. Live and dead big-cone Douglas-fir trees 13 years after a wildfire in the San Gabriel Mountains on sites of different incline. Approximate elevations were: site A, 1,700 m, and site B, 1,500 m. Sites burned in the Sage Fire of 1979 and were sampled in autumn of 1992. (Data from Keeley, Crandell, and Calderon, unpublished data.)

Long-term dynamics of this chaparral conifer are best explained by a metapopulation model involving fire-free refugia. This "fire refugia model" is based on the premise that frequent fires will be conducive to maintaining static adult populations, but a dynamic population capable of expansion would require extended fire-free conditions. During extreme fire events, such as illustrated in Figure 15.10B, populations would retreat to steep fire-resistant slopes that act as refugia (Fig. 15.10A). From these refugia, the species disperses back into more hazardous habitats during extended fire-free conditions. Subsequent fires on these sites will eliminate all of the younger trees and the extent to which mature trees survive will be dependent on fuels and severity of the fire weather. Thus,

understanding the dynamics of big-cone Douglas-fir requires an understanding of the long-term role of metapopulations and not the short-term effects of fires on individual populations. This model is based on a similar idea proposed by Zedler (1981) who highlighted the importance of refugia to the long-term persistence of closed-cone cypress, particularly in the face of increased anthropogenic fires. The general dynamic of population contraction and expansion under altering fire regimes possibly applies to other chaparral conifers such as Coulter pine and the more northerly gray pine.

Riparian Woodland and Shrublands

Response to fire is uniform, as nearly all are vigorous resprouters, either from rootcrowns or rhizomes (Davis et al. 1989). None of the riparian species are post-fire seeders, because all have transient seed banks; indeed, most have extraordinarily short-lived seeds measured on the order of days or weeks (Table 15.10). A number of factors account for the lack of selection for post-fire seedling recruitment: (1) the unpredictability of fire penetrating riparian woodlands, (2) the ready water source favors rapid and dense vegetative regrowth that results in intense competition for seedings, and (3) the severe surface scour resulting from annual winter flooding, which carries away any soil stored seed banks. Differences in species response to fire are largely unexplored, although these differences are to be expected based on species differences in distribution along disturbance gradients (Harris 1987, Bendix 1994).

FIRE REGIME–PLANT COMMUNITY INTERACTIONS

Riparian zones maintain communities that, relative to upland species, have higher fuel moistures during severe fire weather. As a consequence, they potentially pose an important barrier to fire spread, and thus play a role in determining landscape patterns of burning (Dwire and Kauffman 2003). The deciduous habit of dominant species, coupled with increased water availability during winter to summer, greatly limits the fire season, except during severe droughts (Table 15.11). Although most fires burn as crown fires with high intensity, fire severity is generally low due to the predominance of vigorous sprouting species.

Riparian areas are of particular ecological concern because of their disproportionate share of biodiversity and propensity to non-native invasion (Rundel and Sturmer 1998). A major threat to southern California riparian communities is the highly aggressive non-native grass known as giant reed *(Arundo donax)* or bamboo, which has displaced substantial portions of the native vegetation in southern California riparian ecosystems (Rieger and Kreager 1989). It has invaded thousands of hectares of riparian habitat, including all major drainages from Ventura to San Diego counties (Bell 1997). It is extremely flammable and can change green riparian corridors that are barriers to fire spread into highly combustible fire conduits. Giant reed is a very vigorous resprouter capable of dominating riparian sites far more quickly than the native species.

TABLE 15.10

Fire-response types for important species in riparian woodland-shrubland in the South Coast bioregion

Lifeform	Type of Fire Response			Species
	Sprouting	Seeding	Individual	
Tree	Fire stimulated	None	Top-killed or survive	White alder *(Alnus rhombifolia)*, western sycamore *(Platanus racemosa)*, Fremont cottonwood *(Populus fremontii)*, willow *(Salix* spp.*)*
Shrub	Fire stimulated	None	Top-killed or survive	Mule fat *(Baccharis salicifolia)*, black-berry *(Rubus* spp.*)*, poison oak *(Toxicodendron diversilobum)*

TABLE 15.11

Natural fire regime characteristics for riparian woodland and shrublands in the South Coast bioregion

Temporal	
Seasonality	Fall
Fire-return interval	Moderate–long
Spatial	
Size	Moderate
Complexity	Low
Magnitude	
Intensity	Moderate–high
Severity	Low
Fire type	Active crown

Oak and Walnut Woodlands

The dominant oaks in this association have thick bark and are quite resistant to frequent fires. Based on bark thickness and mortality following fires (Table 15.12), it appears that Engelmann oak *(Quercus engelmannii)* is more fire resistant than coast live oak *(Quercus agrifolia)* (Lawson 1993). Where understory fuels have accumulated, fires may carry into the canopy, producing lethal crown fires, since these older trees seldom resprout from the base when top-killed. They have long juvenile periods and thus frequent fires may inhibit successful establishment (Plumb 1980, Lawson 1993). Seedlings and saplings often resprout from the base after fire, but if fires are frequent enough they remain suppressed for many decades. They apparently require an extended fire-free period to emerge to a size capable of withstanding fires, a pattern typical of recruitment in many savanna trees (e.g., Bond et al. 2001). For these southern California oaks, Lawson (1993) reported a negative relationship between fire frequency and density of both saplings and mature trees.

In walnut *(Juglans californica)* woodlands, all of the dominant species are vigorous basal resprouters after fire. There is no information on how burning during the growing versus dormant season affects resprouting of this winter-deciduous tree. Seedling recruitment is limited following fires, but in the long absence of fire, walnut seedling recruitment is abundant, and successful establishment generates an uneven age structure that appears to form a stable age distribution (Keeley 1990a). Also in the absence of fire, mesic-type chaparral shrubs persist as "gap-phase" species capable of seedling recruitment into openings in the walnut canopy, as well as gaps in other woodland associations (Campbell 1980).

FIRE REGIME–PLANT COMMUNITY INTERACTIONS

Fire regimes in oak and walnut woodlands are variable depending on moisture status, woodland density, and location in the landscape (Table 15.13). Fire-return intervals occur on the order of one to several times a century. On mesic sites, the higher fuel moisture, coupled with the closed canopy, which reduces drying of surface fuels, act in concert to reduce fire frequency. On these sites, fire complexity can be high with patches of crown fire and surface fire interspersed with unburned patches. At the xeric end of the gradient, more-open woodlands today support surface fuels of annual grasses, which increase fire frequency, but reduce fire intensity and complexity. The rapid growth rates of understory subshrubs and herbs make it likely that historically the primary limitation to fires was ignitions. Thus, it is to be expected that fire-return intervals varied along a gradient from the coast to the interior in conjunction with the distribution of summer lightning storms. Due to the mosaic distribution of woodlands, fires typically burn into them from adjacent shrublands.

With the mid-Holocene shift of Native American diets to emphasize acorns and other seeds (Erlandson and Glassow 1997), settlements centered around oak woodlands increased fire frequency, both to maintain herbaceous understories and reduce pathogens (Anderson 1993). Wells (1962) hypothesized

TABLE 15.12

Fire-response types for important species in oak and walnut woodlands in the South Coast bioregion

	Type of Fire Response			
Lifeform	Sprouting	Seeding	Individual	*Species*
Tree	Fire stimulated, basal when young, epicormic in mature trees	None	Top-killed or survive	Coast live oak *(Quercus agrifolia)*, Engelmann oak *(Quercus engelmannii)*
Tree	Fire stimulated	None	Top-killed	California black walnut *(Quercus kelloggii)*

TABLE 15.13

Natural fire regime characteristics for southern oak woodland in the South Coast bioregion

Temporal
    Seasonality   Summer–fall
    Fire-return interval   Moderate–long

Spatial
    Size   Moderate–large
    Complexity   Low–high

Magnitude
    Intensity   Low–moderate
    Severity   Low–high
    Fire type   Surface–passive crown

that prior to extensive Native American burning, oak woodlands in coastal California supported subshrub understories, which would have contributed to a greater incidence of high-severity fire. He contended that throughout the region, Native American burning converted oak woodland sage scrub associations to oak savannas (Cooper 1922, Wells 1962), although remnants of this woodland sage scrub association are still evident in the central coast. Historical studies of oak woodlands indicate that twentieth-century fire regimes have had no discernable impact on woodland cover in San Diego County (Scheidlinger and Zedler 1980).

Black Oak Woodlands

At higher elevations, black oak *(Quercus kelloggii)* woodland often interfaces between the crown-fire chaparral ecosystem below and the surface-fire yellow pine forests above. Although little specific information is available, this community likely had a mixed fire regime such that surface fires burning downslope from pine forests were low-intensity surface fires and those burning upslope from chaparral were high-intensity crown fires. Considering the elevational distribution of lightning fires it seems likely that fires more

often burned in from higher-elevation conifer forests. Thick bark would have contributed to surviving surface fires, although these trees would succumb to high-intensity crown fires. Fire-free conditions in adjacent yellow pine forests are said to promote invasion by black oak (Laven 1978).

Yellow Pine Forests

The dominant pines are adapted to a mix of low-severity surface fires and high-intensity crown fires. Thick bark and self-pruning of dead branches ensure survival of the larger trees under low-intensity surface fires (Keeley and Zedler 1998), but a mix of high and low fire severity patches is requisite for reproduction (Table 15.14). Seedling recruitment requires gaps produced by localized high-severity fire, which exposes mineral soil by removing surface duff, and opens the canopy to sunlight. Critically important is the size of these gaps, because recruitment is dependent on survival of parent seed trees in adjacent patches of forest that are either unburned or burned by low-severity surface fire. The high-severity crown fires are also critical because by opening the canopy these microhabitats accumulate fuels at a slower rate and inhibit subsequent fires from burning in and destroying recruitment cohorts (Keeley and Stephenson 2000).

Understory species have received limited attention in these forests, although many of the patterns observed in Sierra Nevada forests following fires of different severities (Keeley et al. 2003) likely hold here as well. The dominant species are typically greenleaf manzanita *(Arctostaphylos patula)* and deer brush *(Ceanothus intergerrimus)* that often germinate *en masse* after fire from soil seed banks. Recruitment, however, is not restricted to burned sites, and these species often recruit into gaps caused by other disturbances. Herbaceous species are mostly perennials that resprout after fire, and it is to be expected that seedling recruitment would follow in subsequent years.

FIRE REGIME–PLANT COMMUNITY INTERACTIONS

Fire history studies in the San Bernardino Mountains show that the pre-settlement fire return intervals were slightly longer than for Sierra Nevada forests, with estimates of 10 to 14 years

TABLE 15.14

Fire-response types for important species in montane coniferous forests in the South Coast bioregion and includes yellow pine forests on drier sites and white fir–dominated mixed conifer forests on more mesic sites

Lifeform	Type of Fire Response			Species
	Sprouting	Seeding	Individual	
Tree	None	Recruitment from seeds dispersed by parent trees that survive fire, in first year or later	Survive or killed	White fir *(Abies concolor)*, incense-cedar *(Calocedrus decurrens)*, Jeffrey pine *(Pinus jeffreyi)*, sugar pine *(Pinus lanbertiana)*, ponderosa pine *(Pinus ponderosa)*
Shrub	None	Fire stimulated	Killed	Greenleaf manzanita *(Arctostaphylos patula)*
Shrub	Fire stimulated	Fire stimulated	Top-killed	Mountain whitethorn *(Ceanothus cordulatus)*, deer brush *(Ceanothus intergerrimus)*
Shrub	Fire stimulated	None	Top-killed	Bush chinquapin *(Chrysolepis sempervirens)*, bitter cherry *(Prunus emarginata)*, currant *(Ribes* spp.*)*, snowberry *(Symphoricarpos* spp.*)*
Herbaceous perennial	Yes, as a normal phenological response, not fire stimulated	None	Top-killed	Rock cress *(Arabis* spp.*)*, Indian paintbrush *(Castilleja* spp.*)*, squirreltail *(Elymus elymoides)*, imbricate phacelia *(Phacelia imbricata)*, Lemmon's catchfly *(Silene lemmonii)*, violet *(Viola* spp.*)*
Annual	None	A few fire stimulated, mostly transient seed banks that escape high-intensity fire	Killed or dead at time of fire	Groundsmoke *(Gayophytum* spp.*)*, lotus *(Lotus* spp.*)*, blazing star *(Mentzelia* spp.*)*, monkeyflower *(Mimulus* spp.*)*.

for ponderosa pine forests (Table 15.15) and longer intervals for the drier Jeffrey pine forests (McBride and Laven 1976, McBride and Jacobs 1980). Historically, fires were primarily from summer lightning storms and were predominately surface fires with patches of passive crown fire (Minnich 1974). Due to the short fire season and low-intensity surface fires, humans have been very effective at suppressing fires, and as a consequence the contemporary fire-return interval is much longer and far outside the historical range of variability (Table 15.1; Figure 15.6). As with other parts of the western United States, during the twentieth century much of this landscape has escaped fire entirely (Stephenson and Calcarone 1999).

Evidence of the impacts of management practices on forest structure in the eastern Transverse Ranges is presented by Minnich et al. (1995). They utilized VTM (Vegetation Type Map) plot data from 1932 as a baseline for measuring historical changes in these forests by comparing with contem-

porary samples. Their study showed increased in-growth of white fir and incense cedar into yellow pine forests over the 60 years of study, reflecting the impact of fire suppression. This generalization primarily applies to ponderosa forests as Jeffrey pine forests have had far less white fir in-growth under long fire-free periods (Laven 1978, Minnich et al. 1995). These ponderosa pine forests present a greater fire hazard for crown fires than would be expected under natural fire regimes, though it is worth noting that stand densities of 200 to 300 per hectare (Minnich et al. 1995) are substantially lower than those commonly observed in contemporary Sierra Nevada forests (Rundel et al. 1977).

Other historical changes in mixed conifer forest structure reported by Minnich et al. (1995) include 79% mortality of all ponderosa pine greater than 30 cm dbh during the 60 years between the 1930s VTM plots and their samples, attributed to ozone pollution. However, other studies have not reported

TABLE 15.15

Natural fire regime characteristics for the montane conifer-
ous forests in the South Coast bioregion.

Temporal	
Seasonality	Summer–fall
Fire-return interval	Short–moderate
Spatial	
Size	Small–moderate
Complexity	Moderate–high
Magnitude	
Intensity	Mix of low to high
Severity	Low–high
Fire type	Surface and passive crown, rarely active crown

twentieth-century mortality levels anywhere near these val-
ues (McBride and Laven 1999), and some of this estimated
mortality may be tied to errors associated with use of VTM
plots (Bouldin 1999, Keeley 2004b). However, this level of
ponderosa pine mortality has been observed in the early years
of the twenty-first century, and is attributed to severe drought
and associated beetle damage (USDA Forest Service 2004).

Although the success of fire-suppression activities is cer-
tainly a factor in driving these structural changes, past logging
practices have perhaps created a bigger problem. Data from
Minnich et al. (1995) show that stand density was 51% higher
on logged, as opposed to unlogged sites. This is important in
light of the fact that over a 30-year period beginning in 1950,
roughly 350 million board feet were removed from the rather
limited conifer forests of the Transverse Ranges (McKelvey and
Johnston 1992). In-growth from this cutting has greatly added
to the contemporary fire hazard in these forests.

The high fire hazard in these forests has contributed to
some significant crown fire damage. For example, crown fires
with tree mortality of 90% or more in ponderosa and Jeffrey
pine forests have been reported for several twentieth- and
twenty-first-century fires in the Peninsular Ranges (Dodge
1975, Halsey 2004), and similar fires have occurred in the
eastern Transverse Ranges (Minnich 1988). However, it is
unclear how far outside the natural range of variation such
fires are because historical records show large high-intensity
fires did occur in these forests during the nineteenth century
(Minnich 1978, p. 134). Also, evidence of former conifer forests
now occupied by chaparral indicates high-intensity crown
fires prior to the twentieth century (Minnich 1999).

Mixed Conifer Forests

These are white fir–dominated forests with incense-cedar
(Calocedrus decurrens), sugar pine *(Pinus lambertiana)*, and Jef-
frey pine *(Pinus jeffreyi)* as co-dominants. They are more mesic
than yellow pine forests and occur either at higher elevations

or lower on north-facing slopes. Productivity, and thus fuel
loads, are typically higher and largely comprise needles and
branches, with relatively little of the fuel load from herba-
ceous fuels as in the drier ponderosa type.

Both white fir and incense cedar can persist and recruit
seedlings and saplings in the absence of fire. This characteris-
tic allows them to expand into drier yellow pine forests when
fires are excluded. Under a mixed fire regime, both white fir
and incense cedar are also capable of taking advantage of fire-
induced gaps and recruiting into them. These species have
thick fire-resistant bark and are tolerant of surface fires,
although less tolerant than associated yellow pines. Although
both white fir and incense cedar can recruit after fire, unlike
the yellow pines, recruitment is not fire dependent. Sugar pine
is very long lived, capable of surviving low-intensity surface
fires, and recruiting both after and between fires.

Associated shrubs that are typically restricted to perma-
nent or temporary gaps in the forest canopy include bush
chinquapin *(Chrysolepis sempervirens)*, huckleberry oak *(Quer-
cus vaccinifolia)*, bitter cherry *(Prunus emarginata)*, and moun-
tain whitethorn *(Ceanothus cordulatus)*. All of these are vig-
orous resprouters after fires or other disturbances, and the
last species recruits seedlings after fire.

FIRE REGIME–PLANT COMMUNITY INTERACTIONS

Fire return intervals historically were frequent—10 to 30
years—but since the turn of the century fires have been
excluded from much of the higher-elevation mixed conifer
landscape (McBride and Laven 1976, Everett 2003). It has
been suggested that north-facing slopes in these forests have
historically had a higher fire frequency (Minnich et al. 1995).
This is based on the higher productivity of these slopes and
more rapid fuel production. However, that model assumes
fuel load is the only determinant of fire return interval. His-
torical studies of fire return intervals in mixed conifer forests
of the Sierra Nevada show that north-facing slopes have had
longer fire return intervals, presumably because high fuel
moisture levels inhibit ignition more often than on south-
facing slopes (Tony Caprio, Sequoia National Park, unpub-
lished data; Fites-Kaufman 1997). The importance of fuel
moisture is suggested by the observation that in the eastern
Transverse Ranges, severe fires consistently burn a greater per-
centage of the landscape on south-facing than on north-
facing slopes (Minnich 1999).

Savage (1994) examined patterns of mortality in forest
dieback in the San Jacinto Mountains and recorded that the
bulk of the mortality occurred in the older age classes of pon-
derosa and Jeffrey pines, with relatively few trees older than 60
years surviving. Roughly half of the white fir older than 40
years died, whereas sugar pine and incense cedar suffered lit-
tle or no mortality. Of particular interest to understanding fire-
suppression impacts is the fact that stand density did not dif-
fer between high-mortality and low-mortality plots; thus,
in-growth from fire suppression does not appear to have been
a major contributing factor to dieback. Periodic severe drought

followed by bark beetle attack seems to be the primary factors affecting pine survival. These mortality events may be a natural part of this system and would contribute sufficient fuels to produce high-intensity crown fires resulting in a burning mosaic of gaps, suggesting that mixed fire regimes of low and high severity are likely within the range of natural variation.

In summary, a fire suppression appears to have excluded natural fires over much of the mixed conifer landscape (Fig. 15.6D, E, F), it is not clear how much structural change in these forests can be specifically attributed to fire management policy. The natural fire regime included substantial surface fire burning, but the natural range of variation in high-severity crown fires, their frequency and size, are unknown.

Lodgepole Pine Forests

In this bioregion, lodgepole pine *(Pinus contorta* var. *murrayana)* forests are at the highest end of the elevational gradient for forests exposed to fire on any regular basis. Lodgepole pine has thin bark and is not highly tolerant of even moderately intense surface fires. Recruitment is not tied to fire and stands tend to be uneven aged (Keeley and Zedler 1998).

FIRE REGIME–PLANT COMMUNITY INTERACTIONS

These forests are characterized by a shorter growing season, lower fuel accumulation, more infrequent droughts, and lower lightning fire incidence than characterize lower-elevation forest types (Sheppard and Lassoie 1998). As is common in other high-elevation pines, lodgepole pine is quite long lived (more than 600 yrs, Fowells 1965). Periodic seedling recruitment is restricted to gaps created by wind-thrown trees or to meadows experiencing a drop in water table, or seedlings may initiate primary succession on granitic outcrops (Rundel 1975). Lodgepole pine forests are not replaced by more shade-tolerant species, perhaps due to the shallow granitic soils (Rundel et al. 1977). Where this species comes together with more stress-tolerant taxa (e.g., Jeffrey pine), forests appear to result from a lottery-type coexistence, which derives from infrequent, species-specific pulses of seedling recruitment in response to differing sets of environmental conditions.

These high-elevation forests receive a frequent bombardment of lightning strikes but ignitions are limited by fuels and fuel moisture. The porous soils in combination with the mediterranean-climate summer drought are not conducive to herbaceous growth sufficient to form a cover that will carry fire. Fuels are primarily short needles and woody litter, and in forests that have experienced a century of fire suppression, fuel loads are 15 to 19 Mg/ha (Hanawalt and Whittaker 1976, Sheppard and Lassoie 1998). Low productivity in these high-elevation forests and the lack of continuity of fuels are important limitations to fire spread. Fires in this type generally are low-severity surface fires that usually are rather localized and spread slowly, often being contained by lack of fuel continuity to areas on the scale of hectares or less. Minnich (1988) reviewed a number of historical accounts that reported crown fires on the scale of hundreds to thousands of hectares. It appears that on a frequency of perhaps once a century, the surface fire regime may be punctuated by larger high-intensity fires that cover thousands of hectares (Sheppard and Lassoie 1998). The impact of these high-intensity fire events on forest structure is apparently highly variable. Sheppard and Lassoie (1998) report that such fire events reduce the smaller size classes but have little impact on the larger trees.

Management Issues

Fire regimes vary markedly between the crown fire regimes of the foothill zone and the mixed surface and crown fire regimes of the montane zone, and fire suppression policy has played a very different role in each.

Montane environments have experienced an unnaturally low level of fires this past century, and there is reason to believe fire exclusion has resulted from both fire-suppression policy and the loss of herbaceous surface fuels due to livestock grazing (Minnich et al. 1995). Fire hazard is currently higher than was likely the case historically and is largely the result of increased surface fuels and increased in-growth of saplings (Everett 2003, USDA Forest Service 2004). Although higher fuel loads are often blamed on fire exclusion, an equally important factor is past logging practices that promoted recruitment of young trees induced by the removal of overstory canopy trees (Minnich 1980a, Everett 2003). Severe drought during the years 2002 to 2003 has resulted in substantial pine mortality in southern California forests, potentially exacerbating the fire hazard situation (USDA Forest Service 2004). The bulk of mortality occurred in ponderosa pine, which is at the southernmost limits of its distribution on the West Coast, and it is unclear how much of this is natural mortality to be expected at the limits of a species' range or is the result of increased competition for water due to increased forest density during the twentieth century (Keeley et al. 2004).

These forests require some form of fuel manipulation to reduce the fire hazard for human safety and diminish negative ecosystem impacts. Prescription burning is a viable option in parts of these ranges but not widely applicable in areas highly fragmented by private in-holdings. In addition, atmospheric circulation in most of these ranges is closely linked with foothills and valleys, and as a consequence, air quality constraints greatly limit the window of opportunity for prescription burning. Mechanical thinning is perhaps the only viable option in many of these forests; however, it is costly, particularly if the prescriptions focus just on removing those size cohorts most responsible for fire hazard. Thinning projects can pay for themselves, but usually only if larger trees are taken. This creates a dilemma because removing large trees promotes further in-growth and exacerbates the fire hazard problem, requiring future mechanical thinning at shorter intervals. It is unknown if this required reentry interval is long enough to allow sufficient growth to regenerate larger, commercially acceptable trees needed to fund these operations.

In the lower coastal valley and foothill zone, fire suppression has not reduced the natural fire frequency (Table 15.1). Currently there are many more fires than historically, but fire-suppression policy has kept many of these in check so that, although fire rotation intervals are shorter, most stands burn within the range of natural variability, albeit at the lower end of the range. However, landscapes surrounding urban areas fires have been of sufficient frequency to affect widespread type conversion to non-native grasslands (Keeley and Fotheringham 2003). During severe fire weather, a small percentage of fires escape containment and account for the bulk of the landscape that burns in this region (Minnich and Chou 1997, Moritz 1997). The limited number of lightning ignitions in this zone, coupled with historical accounts of relatively little area burned by these summer fires (Minnich 1987), suggests they were not responsible for most of the area burned. However, the infrequent occurrence of lightning-ignited fires persisting until the Santa Ana wind season (Fig. 15.1) would readily account for massive fires capable of burning huge fragments of the landscape in a matter of days (Keeley and Fotheringham 2003).

Maintaining this historical fire regime creates a major management dilemma because chaparral and sage scrub share this landscape with people in an ever-expanding urban sprawl. On these landscapes, fire is as much a social and political problem as it is a fire management problem (Rodrigue 1993). The primary driver of large fires that are often catastrophic to humans is the coincidence of fire ignitions and Santa Ana winds (Davis and Michaelsen 1995; Moritz 1997, 2003; Moritz et al. 2004; Conard and Weise 1998). Under these severe fire weather conditions, fuel age is ineffective as a barrier to fire spread, which limits the value of pre-fire fuel manipulations (Keeley and Fotheringham 2001b, 2003; Keeley et al. 2004).

The important management implication of these conclusions is that landscape scale prescription burning on a rotational basis is a questionable management strategy in this bioregion. The notion that a mosaic of age classes will act as a barrier to the spread of Santa Ana wind–driven fires is not supported (Dunn 1989, Keeley 2002b, Keeley and Fotheringham 2003). Illustrative of this are the massive wildfires that burned more than 300,000 ha in the last week of October 2003 (Halsey 2004). Within the perimeters of these large fires were substantial areas that had burned by either prescription burns or wildfires within the previous 10 years (Keeley et al. 2004). Fires either burned through or skipped over or around these younger age classes. The San Diego County Cedar fire, which was larger than any other fire recorded for the twentieth century in California, burned through extensive areas of young fuels that spanned nearly the entire width of the fire in two separate areas. On its southern boundary the Cedar fire burned through three-year-old chaparral (with fuel loads of 10 to 20 metric tons/ha; Keeley and Halsey, unpublished data) and then proceeded to skip over a six-lane freeway. North of this fire was the Piru fire that burned substantial areas of sage scrub that had previously burned in 1997. At the southern end of the bioregion,

the Otay fire burned through thousands of hectares of chaparral that previously had burned in 1996, and then continued to burn across the Mexican border until halted by the Tijuana River and a change in weather that brought rain.

This does not suggest that prescription burning has no place in the chaparral management arsenal, only that it needs to be used strategically with a clear understanding of its limitations. Even during severe fire weather, young fuels do reduce fire intensity and thus provide defensible space for fighting fires. This argues for the use of prescription burning and other fuel manipulations in strategic sites that could be utilized during extreme fire events. Fuel treatments in the backcountry, far removed from the urban interface, have limited value because of the extreme danger of frontal attacks on Santa Ana wind-driven fires when firefighters are completely surrounded by shrubland fuels. In addition, these fires move at such a rapid pace that by the time firefighting resources can be mobilized, the fires are already threatening homes and lives at the wildland-urban interface (Rohde 2002). As this interface zone expands and increases in complexity, an increasingly greater proportion of firefighter resources will be diverted to protecting homes, and fewer resources will be available for directly attacking these potentially catastrophic fires. These considerations argue for greater diversion of pre-fire fuel manipulations from the backcountry to the wildland-urban interface (Keeley et al. 2004).

Broader application of fuel manipulations may be warranted for managing fires that occur under mild weather conditions and are not wind-driven events. These so-called plume-dominated fires differ because the flame is nearly vertical and fuels ahead of the fire front are not preheated by hot gases (Morvan and Dupuy 2004). Under these conditions, age mosaics of young chaparral fuels can provide barriers to fire spread as suggested by anecdotal observations (Philpot 1974). Age mosaics also may control burning patterns south of the U.S.-Mexico border where wildfires are generally fanned by mild on-shore breezes, and are seldom under Santa Ana conditions (Minnich 1989, 1998; Minnich and Everett 2002). In southern California, fires that ignite under mild weather are seldom responsible for major property damage or loss of lives (Halsey 2004). Thus, the critical question about the widespread use of prescription burning to inhibit the spread of these fires is whether or not it is cost effective; further research on this question is needed. This is particularly important when considering the high cost of burning in crown fire ecosystems, which is often increased in southern California due to temporal restrictions imposed by air quality constraints (Conard and Weise 1998).

Costs of prescription burning also need to be evaluated in terms of impacts on resources. The lower-elevation chaparral and sage scrub in this region are already stressed with unnaturally high fire frequencies that threaten to replace much of this landscape with non-native annual plants (Keeley 2001, 2004c; USDA Forest Service 2004b). The primary concern with prescription burning is that it makes these stands vulnerable to type conversion by reburning due to the high frequency of anthropogenic fires. Other suggested

benefits of prescription burning include the effects of mosaic age classes on reducing post-fire flooding and mudflows (Loomis et al. 2003); however, winter precipitation is a far greater factor, and high-frequency fires increase the chances of fire being followed by a winter of high rainfall (Keeley et al. 2004).

This analysis suggests that the appropriate currency for successful prescription burning is not "total acres burned," as is commonly employed, but rather strategic placement of fuel manipulation projects. For much of southern California, this represents a major paradigm shift from the widely accepted model of landscape scale rotational burning. Some agencies appear to be making this paradigm shift. For example, the recent fire management plan for the Santa Monica Mountains has proposed a major switch from the former rotational burning model to one that uses more limited and strategic application of fuel management practices (USDI National Park Service 2004). Similar ideas have been included as alternatives in southern California forest plans (USDA Forest Service 2004a).

It is important to recognize that there is much intra-regional variation in fire regimes, evident in different levels of fire hazard (Moritz 2003, Moritz et al. 2004) and different fire seasons (Keeley and Fotheringham 2003) throughout central and southern California chaparral. The lack of fire-suppression impacts on chaparral in this region is not necessarily shared throughout the state. For example, marked fire exclusion is documented for chaparral in the southern Sierra Nevada (Keeley et al. 2005d), which suggests a need for different approaches to fire management in different regions.

A problem that is likely to capture more and more attention in the future is the impact of fire management practices on invasive species problems. One illustration is the widespread use of black mustard *(Brassica nigra)* and shortpod mustard *(Hirschfeldia incana)* for post-fire rehabilitation projects in the 1940s and 1950s. These seed sources were abandoned long ago because of their aggressive invasive tendencies, particularly into economically important citrus orchards. However, we still see the ghost of past seedings because these species produce dormant seed banks that are fire stimulated; thus, after fire many shrublands are rapidly invaded from within. Most of the data to date do not support use of these or any other non-native species for post-fire management, both because they are not particularly effective and because they have serious negative ecosystem impacts (Conard et al. 1995).

Another area in serious need of consideration is the impact of fuel breaks on invasive species (Keeley 2004a). By removing the native shrub and tree cover these sites act as sources for non-native species to further spread into wildlands. The fact that fuel breaks typically form long corridors makes them ideal mechanisms for transporting non-native species into remote wildlands. When sites are burned, the non-native seed banks in shrubland vegetation are generally killed by the high fire intensities, but are not killed by lower fire intensities in the fuel breaks, and thus provide a ready seed source for invasion of burns. Co-locating fuelbreaks with roadways may be one way to minimize the non-native invasion of wildland areas.

What about planning for the future? Anticipated climate changes include an approximately 25% greater winter rainfall, coupled with a 1°C–3°C increase in temperature, and these have been used to predict higher primary productivity, higher fuel loads, and thus a worsening of the current fire hazard problems (Davis and Michaelsen 1995, Field et al. 1999). That scenario is not likely to be borne out in chaparral shrublands since contemporary fire problems are not closely linked to fuel level, and antecedent climate seems to have minimal impact on large fires (Keeley 2004a). These predicted climate changes, however, might increase the fire hazard in montane forests where fuel load does appear to be an important determinant of fire hazard. However, predictions are complicated, and the present modeling effort falls short of including all of the important ecosystem processes. For example, because the primary fuels in conifer forests are dead material on the surface, increased decomposition due to the expected higher temperatures and moisture could act to reduce fuels. On the other hand, the greater mineralization and release of nutrients could, through increased productivity, have the opposite impact. Regardless of how climate affects fuels, based on current patterns of burning it appears that throughout this region the primary threat to future fire regimes is more tied to future patterns of human demography than to climate.

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