



TWENTY-FOUR

Chaparral

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Introduction

One of the most dynamic California ecosystems is chaparral. Dominated by evergreen, sclerophyllous shrubs and small trees, chaparral is the most extensive vegetation type in the state (Figure 24.1). The nearly impenetrable tangle of stiff branches of this unusual vegetation inhibits exploration, and as a consequence the public know little about its natural history and unique characteristics. This undervalued ecosystem is recognized instead by the threat of its extensive, high-intensity canopy-burning wildfires that characterize the dry summer and fall seasons of the state. Because urban areas frequently share borders or intermix with chaparral, societal interests often conflict with conservation of this ecosystem, and understanding its history and dynamics are key to appreciating its importance.

Chaparral contains numerous plants and animals found in no other habitat, and many of them are rare and threatened. A large number of environmental and biotic influences drive this diversity, but three primary ones are the protracted summer rainless period of California's Mediterranean-type climate, low-nutrient, and often shallow and rocky soils, and a fire regime that completely burns the vegetation one or more times a century. Within the widespread distribution of

chaparral, different combinations of these processes produce locally unique combinations of species, including more than one hundred evergreen shrub species across this range (Wells 1962, Keeley and Keeley 1988, Sawyer and Keeler-Wolf 1995). Many associations are named based on the dominant species, such as manzanita chaparral (*Arctostaphylos* sp.), chamise-red-shank chaparral (*Adenostoma* sp.), or mixed chaparral (Sawyer and Keeler-Wolf 1995). Others are named based on the soils, such as serpentine and dune chaparral, or based on the climatic location, such as maritime chaparral (Griffin 1978) and montane chaparral (Hanes 1977) (Figure 24.2). In all these variations the overall character and dynamics of the vegetation are directly related to strong summer droughts, low-nutrient soils, and wildfire.

The extensive spatial distribution of chaparral means that stands reflect different climatic extremes and interact with different plant assemblages. At lower elevations, for example, the vegetation includes not only the dominant shrubs, but also a postfire flora that persists only a few years after fire. These annuals and short-lived perennials arise phoenix-like after wildfires, blanketing the landscape in colorful displays and subsequently remaining dormant as seeds in soil

until the next fire. In more northerly distributions in the coast ranges, chaparral intergrades with mixed evergreen and conifer forests, sometimes as a patchwork, often as successional vegetation. Cold temperatures become important at higher elevations and in cold-air drainage basins (Ewers et al. 2003). For example, chamise drops out at high elevations in interior Sierra Nevada drainages (Westman 1991) and in Arizona chaparral (Mooney and Miller 1985). At higher elevations, especially in the Sierra Nevada and Cascades, a variant referred to as montane chaparral dominates in patches in areas above the winter snowline. While sharing dominant genera and other dynamics with chaparral of lower elevation, this mountain chaparral contains unique species and lacks familiar components like the diverse, postfire herbaceous plant response.

Besides the characteristic plants, chaparral contains numerous other organisms of which some are restricted or nearly so to chaparral. These include small rodents like woodrats (*Neotoma* sp.) and mice (e.g., *Peromyscus californicus*) as well as birds (e.g., wrentit and Bewick's wren). Animals are involved in a variety of interactions, from dispersal of seed by scatterhoarding rodents and birds to herbivory and seed predation. Animal activity can be critical for the success of some plants (e.g., Parker 2010) or shift the plant composition of areas (Quinn 1994, Moreno and Oechel 1993, Ramirez et al. 2012). Less studied are other vertebrates and insects (Andres and Connor 2003, Miller 2005) and the soil biota, even though soil nutrients are often limiting to primary production and MY ORRH AE influence vegetation dynamics (Horton et al. 1999, Dunne and Parker 1999, Treseder and Allen 2000, Egerton-Warburton et al. 2007).

In this chapter we emphasize the principal structure and dynamics of this important ecosystem. The long, summer rainless period has strong impacts on all organisms and on the fire regime that characterizes chaparral. These features make significant impacts from climate change very likely. Attempts to suppress fire also affect chaparral dynamics. Because of its dominance at lower elevations, chaparral also frequently occurs at or near the boundaries of urban developments and metropolitan centers. Conflicts between the impacts of chaparral wildfire and human activities and structures have occurred throughout California's history but have increased as development encroaches ever more into chaparral regions. Consequently, understanding of chaparral ecology is important not only because of its significance in understanding ecological evolution and ecological services provided by chaparral but also because of its direct impacts on human communities.

Geography of Chaparral

Chaparral covers much of the Peninsular, Transverse, and Coastal Ranges and portions of the Sierra Nevada and Cascade Ranges. This represents over 9% of the wildland vegetation in California, with most of it below 2,000 meters in elevation (see recent reviews by Keeley 2000, Davis, Stoms, et al. 1998, Keeley and Davis 2007) (see Figure 24.1). Chaparral is

Photo on previous page: Santa Monica Mountains (Los Angeles County); chamise and redshank (*Adenostoma fasciculatum* and *A. sparsifolium*) with big-pod ceanothus in bloom (*Ceanothus megacarpus*). Photo: R. Brandon Pratt.

particularly abundant in the mountains of southern California, which contain over a third of all chaparral found in that region (Davis, Stoms, et al. 1998), especially on the slopes of the Peninsular and Transverse Ranges (Cooper 1922, Epling and Lewis 1942). Chaparral extends south into northwest Baja California, with disjunct populations on mountainslopes as far south as 28°. Coastal mountain ranges are dominated by chaparral at most elevations in southern California but form mosaics with oak woodlands and conifer forest from central California northward.

Throughout its range, chaparral is often replaced by localized patches of grassland. This is sometimes due to moisture and edaphic characteristics but more often due to disturbance (Wells 1962) (see Figure 24.2). North of the San Francisco Bay region, chaparral dominance shifts inland and progressively diminishes to widely scattered patches on interior slopes as far north as Washington State. The foothills of the Sierra Nevada and the southern Cascades similarly are covered by chaparral at elevations generally above 300 meters, giving way to forest with increasing precipitation at higher elevations (Keeley, Baer-Keeley et al. 2005). Within the upper-elevation forest regions, chaparral appears on serpentine or other low-nutrient or shallow soils or after wildfires (Cooper 1922) (see Figure 24.2) and may persist as a consequence of self-reinforcing, high-intensity wildfires. Eastward, chaparral forms disjunct patches in mountainous areas in Arizona with particularly large chaparral landscapes above the Mogollan Rim in the middle of the state (Knipe et al. 1979). Some chaparral species form stands in areas of Arizona and Mexico with a summer rainfall regime (Vankat 1989; Bhaskar et al. 2007; Keeley, Fotheringham et al. 2012).

Stands dominated by chamise (*Adenostoma fasciculatum*) are the most abundant type of chaparral in California (Hanes 1977). Chamise often forms nearly pure stands on hot and dry slopes that are generally equatorial-facing with shallow soils. In chamise stands, other common subdominant species are manzanitas (*Arctostaphylos* spp.) and ceanothus (or California lilac; *Ceanothus* spp.) along with various sage scrub species (e.g. *Salvia* spp. and *Artemisia californica*). Coastal and montane areas may also be dominated by nearly pure stands of ceanothus or manzanita species. On more mesic slopes and in deeper soils within a site, chaparral can contain a broader range of dominant evergreen species (Hanes 1971).

Chaparral gives way to other plant associations based on water availability, temperature, soil, aspect, and elevation. At drier, low-elevation sites in nondesert areas, chaparral is replaced by sage scrub species (see Chapter 22, "Coastal Sage Scrub"). In valley bottoms with deeper soils, chaparral is replaced by oak savannas. In some cases, this transition can also be related to cold air drainage and freezing temperatures (Ewers et al. 2003, Pratt et al. 2005), animal activity (e.g., pocket gophers), or fire regime. Replacement by oak woodlands also occurs at higher elevations throughout the range of chaparral, which is generally attributed to greater rainfall. On more mesic sites, in the northern part of the state, chaparral gives way to an evergreen sclerophyllous woodland dominated by species such as tan-bark oak (*Notholithocarpus densiflorus*; formerly *Lithocarpus d.*), California bay laurel (*Umbellularia californica*), oaks, and madrone (*Arbutus menziesii*) (Cooper 1922). On desert-facing slopes, chaparral forms ecotones with Mojave desert scrub communities in the Transverse and Coast Ranges and with Sonoran desert shrub communities in the Peninsular Range and is replaced by these desert communities at more arid, lower elevations.

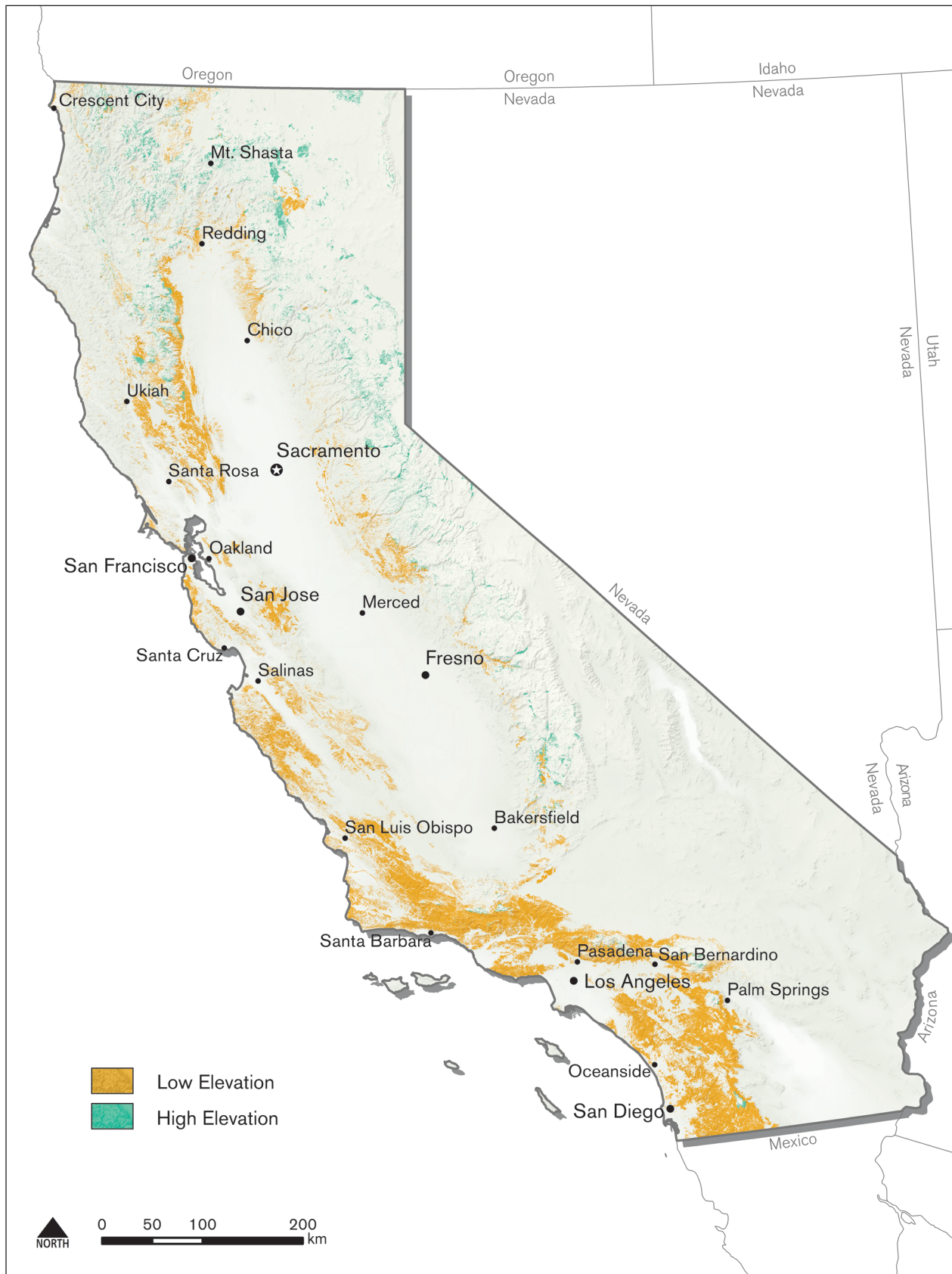


FIGURE 24.1 Distribution of chaparral vegetation in California. Data from Cal Fire, Fire Resource and Assessment Program (FRAP). Map: P. Welch, Center for Integrated Spatial Research (CISR).

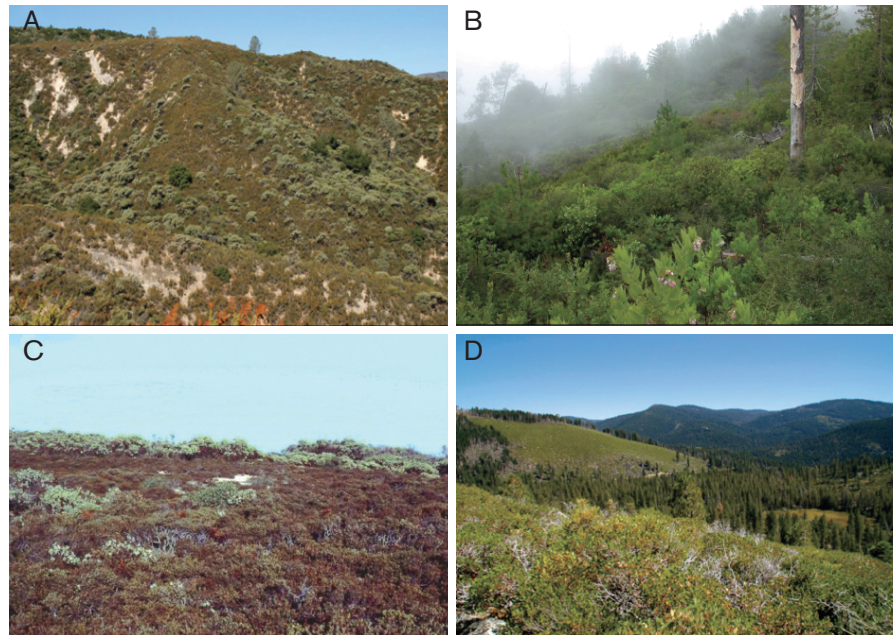


FIGURE 24.2 Examples of variation in chaparral vegetation. Photos: V. Thomas Parker.

- A Chamise-dominated chaparral (*Adenostoma fasciculatum*) with big-berry manzanita (*Arctostaphylos glauca*) as a co-dominant (Santa Lucia Mountains).
- B Maritime chaparral in the Santa Cruz Mountains dominated by *Arctostaphylos crustacea*, *A. andersonii*, *A. sensitiva*, *Ceanothus thyrsiflorus*, and *C. papillosus*.
- C Chaparral occurs on unusual soils, in this case *A. myrtifolia* and *A. viscida* on Oxisols near Lone, California.
- D Montane chaparral patches in the northern Sierra Nevada dominated by *Quercus vaccinifolia*, *Arctostaphylos patula*, *A. nevadensis*, *Chrysolepis sempervirens*, *Ceanothus cordulatus*, *C. integerrimus*, *Prunus emarginata*, and *Spiraea splendens* alternating with *Abies*-dominated forest.

Origins

Most dominant chaparral taxa date to the early Tertiary, with origins in the Eocene (Keeley, Bond et al. 2012). Assemblages with similarities to contemporary chaparral appear to have been present by the early Miocene, although the center of distribution was likely in the interior reaches of the southwestern corner of North America (Ackerly 2009; Keeley, Bond et al. 2012). By the mid-Miocene, chaparral dominants were evident in fossil floras from western Nevada and California, but the extent to which these communities resembled contemporary California chaparral is unknown. For example, contemporary chaparral in Mediterranean-climate California is markedly different from communities in summer-rain Arizona (Keeley, Fotheringham et al. 2012). Although these two different communities share many of the same shrub dominants, these climates have selected for very different post-fire herbaceous assemblages. In the Mediterranean-type climate winter annuals dominate the community, whereas in the summer rain region the herbaceous community is dominated by perennials with a substantial contribution of C₄ grasses. Thus, while shrub dominants appear to have very early Tertiary origins, the origin of contemporary California chaparral assemblages is likely tied to the origin of the Mediterranean-type climate. The timing of this event is a matter of some debate. Axelrod (1973) has long contended that the Mediterranean-type climate was late in development, dating from the Pliocene or early Pleistocene. Others argue that this summer-drought climate originated much earlier and was in

place in western Nevada and south-central California by mid-Miocene (Keeley, Bond et al. 2012; see Chapter 2, "Climate").

Evergreen sclerophyllous leaves occurred in lineages before the onset of the Mediterranean-type climate, suggesting that this feature of Mediterranean-type shrubs was not an adaptive response to that climate per se (Axelrod 1989, Verdú et al. 2003, Ackerly 2004a). Some have interpreted these sclerophyll taxa as relicts of Tertiary origins present today merely by chance avoidance of random extinctions rather than because they are adapted to contemporary environments (Herrera 1992, Valiente-Banuet et al. 2006). Others see a clear adaptive role for these taxa in the current landscape (Keeley, Pausas et al. 2012). Adaptive traits, however, are not necessarily adaptations, which are traits that have arisen via natural selection in response to a particular environmental factor such as the Mediterranean-type climate (Gould and Lewontin 1979). One view is that physiological and morphological traits in evergreen sclerophylls are adaptations to both water deficits and nutrient-poor soils, conditions present both before and after the widespread development of a Mediterranean-type climate (Keeley, Bond et al. 2012). In this model, the primary influence of the Mediterranean-type climate has not been through selection on these traits but rather has contributed to a massive expansion of suitable sites for these drought-adapted shrubs. Thus, in this view, many traits in contemporary chaparral shrubs are adaptations to contemporary conditions of periodic soil drought and nutrient-poor soils, but chaparral assemblages reflect sorting processes beginning with the origin of the Mediterranean-type climate (Ackerly 2004a).

Shrublands that resemble chaparral are also widely distributed in four other global regions: the Mediterranean basin, the Cape Region of South Africa, western and southern Australia, and central Chile—all of which share a similar Mediterranean-type climate (however, see Cowling et al. 2005). The geographical and phylogenetic distances of species inhabiting these shrublands, coupled with their similar structure, led early biogeographers to postulate that the common Mediterranean-type climate of these regions spurred convergent evolution of the evergreen sclerophyllous shrub growth form (Schimper 1903). Mooney and Dunn (1970a) extended this conclusion by providing an ecophysiological model to explain the advantage of evergreen sclerophyllous leaves in Mediterranean-type environments. Following this, extensive comparisons between chaparral and the Chilean Mediterranean-type shrublands called *matorral* generally supported the convergence hypothesis (di Castri and Mooney 1973, Miller 1981). More recent fossil evidence showing that many of the ancestral evergreen sclerophyllous species predated the Mediterranean-type climate has been interpreted to mean that the convergence hypothesis is not supported by the widespread presence of evergreen sclerophyllous species in these regions (Axelrod 1989).

Much of this debate is tied to an inordinate emphasis on similarities in the general climatic parameters of winter rain and summer drought evident across the five Mediterranean-type climate regions, rather than on differences among the regions. Evolutionary convergence is predicted when taxa evolve in similar “environments,” but each Mediterranean-type climate region exhibits subtle differences in rainfall patterns and not-so-subtle differences in soils and fire regimes that all would be expected to contribute to differences in plant traits and community assemblages (Keeley, Bond et al. 2012). Recent studies of water relations, particularly *Ψ* EM structure and function, have found California chaparral shrubs to be convergent with South African fynbos shrubs when sites were matched (Jacobsen et al. 2009). However, shrubs from the two regions also differ in life history characteristics (Pratt et al. 2012).

Principal Organisms Found in Chaparral

Plants

While many plant species can be found in chaparral, the dominant shrubs that structure of the ecosystem represent a few genera common to most sites throughout the state. Climatic patterns and soil heterogeneity sort local shrub dominance, which in turn modifies ecosystem processes like hydrology and biogeochemistry as well as animal communities. Genera with multiple species, including rare species, include manzanita, ceanothus, shrub oak, and silk tassel bush (*Garrya*) (Table 24.1). Chamise occurs throughout the range of chaparral. California red-shank, a sister taxon (*Adenostoma sparsifolium*), sporadically joins chamise from Santa Barbara County south, mostly away from the coast. Other important genera that are monotypic or have only a few species include mountain mahogany (*Cercocarpus*), cherry (*Prunus*), coffee berry (*Frangula*), sugar or lemonade bush (*Rhus*), toyon (*Heteromeles arbutifolia*), chaparral pea (*Pickeringia montana*), and laurel sumac (*Malosma laurina*).

Trees commonly associated with chaparral in some areas are usually species of pine (*Pinus*), cypress (*Hesperocyparis*),

oaks, and big-cone Douglas-fir (*Pseudotsuga macrocarpa*). The species of pines and cypress in chaparral are generally *SEROTINOUS* (e.g., knobcone pine, Sargent’s cypress) or *semiserotinous*, with slow-dispersing, heavy, thick cones (e.g., ghost, Coulter, or torrey pine). Stands of these trees are open with a dense chaparral understory or mosaic. In more mesic regions other tree species also found in adjacent mixed evergreen or coniferous forests can intergrade with chaparral. In southern California big-cone Douglas-fir is commonly found in chaparral from Santa Barbara County to San Diego County. Coast live oak (*Quercus agrifolia*) and sometimes other oaks can also invade chaparral; in some maritime associations coast live oak is a co-dominant of the chaparral.

While chaparral contains a highly diverse component of annuals and herbaceous perennials, with few exceptions older stands of chaparral lack significant herbaceous cover (Hanes 1981). This is generally because most of these species have deep seed dormancy that requires stimulation from wildfire (Sweeney 1956). For other annuals and many herbaceous perennials lacking this dormancy, growth is limited by significant herbivory from chaparral animals or by limited resources (Mooney and Dunn 1970a, Christensen and Muller 1975, Swanck and Oechel 1991). Nevertheless, post-fire stands of chaparral are often dominated by diverse herbaceous annuals and perennials for several years before shrubs regain dominance (Table 24.2).

Chaparral also contains a number of *SUFFRUTES ENT* shrubs whose presence or absence depends upon a number of factors. They are common in postfire stands because some or all of their *SEED AN S* are responsive to wildfire. However, these plants may persist long afterwards in more open conditions, such as in rockier habitats, along trails, in poor soil conditions such as in serpentine, or along the edges of drier systems like deserts or coastal scrub. While frequent or common in chaparral systems, these shrubs sometimes dominate adjacent plant communities.

Mycota and Other Microbiota

Chaparral harbors considerable diversity of fungi and microbes, but little is known about individual species or their overall ecological impacts. These organisms play key roles in decomposition, nitrogen fixation, and mineral cycling, and some are pathogens of dominant plants. Experiments indicate that they are critical in many ecosystem processes and can be affected by wildfire (Horton et al. 1998, Stoll 1998, Baar et al. 1999, Peay et al. 2009) and increased atmospheric CO₂ (Allen et al. 2005).

Surveys of *MY OTA* and DNA fingerprinting indicate that chaparral stands can have a high diversity of mycota (Bradford 1998, Blair 1999). Over 134 taxa of fungi in 33 families and 17 orders were found beneath stands of manzanita (Blair 1999); 5 fungal families had the highest representation, including 2 familiar as boletes or amanitas. Almost all of these species are thought to form mycorrhizal relationships with plant hosts. In another study that sampled manzanita root tips, diversity of mycorrhizal fungi was extremely high (Bradford 1998). Within chaparral, species of pines, manzanitas, and shrub oaks all associate with *E TOMY ORRH AE* and as a consequence might facilitate successional dynamics from shrub- to forest-dominated sites (Amaranthus and Perry 1994, Horton et al. 1999, Dunne and Parker 1999, Bode 1999). Other plant genera associate with *AR US U ARMY ORRH AE*, usually with taxa in the

TABLE 24.1
Common plants in California chaparral

Species	Common name	Notes	Occurrence and distribution	Life history
TREES				
<i>Pinus</i>	Pine	Especially <i>P. attenuata</i> , <i>P. radiata</i> , <i>P. muricata</i> , <i>P. sabiniana</i>		Serotinous or slow seed dispersal (semiserotinous)
<i>Hesperocyparis</i> (formerly <i>Cupressus</i>)	Cypress	Especially <i>H. sargentii</i> , <i>H. macnabiana</i>		Serotinous
<i>Quercus agrifolia</i>	Coast live oak	Most common oak found in chaparral	Coast ranges from San Francisco Bay region south	Obligate sprouter
<i>Pseudotsuga macrocarpa</i>	Big-cone Douglas-fir		Occasional in southern California mountains	Obligate sprouter
SHRUBS				
<i>Adenostoma</i> sp.	Chamise	Especially <i>A. fasciculatum</i>	Common and widespread	Facultative seeder
<i>Arctostaphylos</i> sp.	Manzanita	96 taxa in California; many rare	Common and widespread, especially in more mesic ranges	Facultative seeder or obligate seeder
<i>Ceanothus</i> sp.	California lilac; buckbrush; etc.	60 taxa in California; many rare	Common and widespread, mostly chaparral	Facultative seeder or obligate seeder
<i>Quercus</i> sp.	Scrub oak	Especially <i>Q. berberidifolia</i> , <i>Q. durata</i> , <i>Q. vaccinifolia</i> , <i>Q. wislizenii</i> var. <i>frutescens</i>	Common and widespread	Obligate sprouter
<i>Heteromeles arbutifolia</i>	Toyon		Common and widespread	Obligate sprouter
<i>Pickeringia montana</i>	Chaparral pea			Obligate sprouter
<i>Garrya</i> sp.	Silk tassel	Especially <i>G. elliptica</i> , <i>G. fremontii</i> , <i>G. veatchii</i>	Frequent	Obligate sprouter
<i>Prunus</i> sp.	Holly-leaved cherry	Especially <i>P. ilicifolia</i> , <i>P. emarginata</i> , <i>P. subcordata</i>	Frequent, southern California to southern North Coast ranges, deciduous species at high elevation	Obligate sprouter
<i>Frangula</i> sp. (formerly <i>Rhamnus</i>)	Coffee berry	Especially <i>F. californica</i> , <i>F. rubra</i>	Widespread and frequent	Obligate sprouter
<i>Cercocarpus</i> sp.	Mountain mahogany	Especially <i>C. betuloides</i>	Widespread	Obligate sprouter
<i>Rhus</i> sp.	Sugar berry, Lemonade bush	Especially <i>R. ovata</i> , <i>R. integrifolia</i>	Mostly southern California	Obligate sprouter or facultative seeder
<i>Malosma laurina</i>			Southern California	Obligate sprouter

SOURCE: Sweeney 1956, Keeley and Keeley 1988, Soule et al. 1988, Keeley, Fotherington, and Baer-Keeley 2005.

fungal genera *Acaulospora*, *Glomus*, *Gigaspora*, or *Scutellospora* (Allen et al. 1999). Chamise, in the rose family, appears to associate with mycorrhizae that are usually arbuscular; it has also been observed associating with ectomycorrhizae that include seven different mushrooms or cup fungi (Allen et al. 1999). Other members of the rose family appear to also produce both types of mycorrhizae (Smith and Read 1997).

The roles of microbes in chaparral, though relatively poorly understood, undoubtedly play a critical role in a number of

ecosystem functions. For example, mycorrhizae can produce extensive hyphal networks that can link multiple individual plants. While mycorrhizae generally are the principal pathway for mineral uptake, these networks also have been implicated in the survival of seedlings through summer drought (Horton et al. 1999, Dunne and Parker 1999, Egerton-Warburton et al. 2003, Egerton-Warburton et al. 2007, Plamboeck et al. 2007). Nitrogen cycling within vegetation is regulated largely by microbial communities, both bacterial and fungal

TABLE 24.2

Representative plants found in postfire chaparral areas in California

Species	Family	Range
COMMON POSTFIRE ANNUALS		
<i>Chaenactis artemisiifolia</i>	Asteraceae	Common, southern California
<i>Emmenanthe penduliflora</i>	Boraginaceae	Common
<i>Phacelia brachyloba</i>	Boraginaceae	Frequent
<i>Phacelia parryi</i>	Boraginaceae	Common, southern California
<i>Phacelia grandiflora</i>	Boraginaceae	Common, southern California
<i>Phacelia cicutaria</i>	Boraginaceae	Common, southern California
<i>Phacelia minor</i>	Boraginaceae	Common, southern California
<i>Phacelia suaveolens</i>	Boraginaceae	Common, northern California
<i>Eucrypta chrysanthemifolia</i>	Boraginaceae	Frequent
<i>Cryptantha microstachys</i>	Boraginaceae	Common
<i>Silene coniflora</i>	Caryophyllaceae	Frequent
<i>Lupinus succulentus</i>	Fabaceae	Occasional
<i>Lupinus bicolor</i>	Fabaceae	Common
<i>Acmispon maritimus</i>	Fabaceae	Occasional
<i>Salvia apiana</i>	Lamiaceae	Frequent, central, southern California
<i>Salvia columbariae</i>	Lamiaceae	Common
<i>Calandrinia ciliata</i>	Montiaceae	Common
<i>Calyptidium monandrum</i>	Montiaceae	Common, central, southern California
<i>Eulobus californicus (Camissonia)</i>	Onagraceae	Common, central, southern California
<i>Ehrendorferia chrysantha (Dicentra)</i>	Papaveraceae	Common, northern California
<i>Ehrendorferia ochroleuca (Dicentra)</i>	Papaveraceae	Common, southern California
<i>Papaver californicum</i>	Papaveraceae	Occasional
<i>Romneya coutleri</i>	Papaveraceae	Occasional, southern California
<i>Antirrhinum coulterianum</i>	Plantaginaceae	Common, southern California
<i>Allophylllum glutinosum</i>	Polemoniaceae	Frequent, central, southern California
<i>Gilia capitata</i>	Polemoniaceae	Common
<i>Saltugilia australis (Gilia)</i>	Polemoniaceae	Frequent, southern California
<i>Chorizanthe fimbriata</i>	Polygonaceae	Frequent, southern California
COMMON SUFFRUTESCENTS		
<i>Artemisia californicum</i>	Asteraceae	Common
<i>Baccharis pilularis</i>	Asteraceae	Common, esp. northern California
<i>Ericameria arborescens</i>	Asteraceae	Common, northern California
<i>Eriodictyon californicum</i>	Boraginaceae	Common, central, northern California
<i>Eriodictyon crassifolium</i>	Boraginaceae	Common, southern California
<i>Helianthemum scoparium</i>	Cistaceae	Common
<i>Acmispon glaber (Lotus scoparius)</i>	Fabaceae	Common
<i>Lepichinia calycina</i>	Lamiaceae	Common, northern California

(continued)

TABLE 24.2 (continued)

Species	Family	Range
COMMON SUFFRUTESCENTS		
<i>Salvia mellifera</i>	Lamiaceae	Common, southern California
<i>Mimulus aurantiacus</i>	Phrymaceae	Common
<i>Eriogonum fasciculatum</i>	Polygonaceae	Common, southern California

SOURCES: Sweeney 1956, Keeley and Keeley 1988, Soule et al. 1988, Keeley, Fotherington, and Baer-Keeley 2005.

(Grogan et al. 2000). Increases in atmospheric CO₂ concentrations appear to increase the importance of microbial regulation of nitrogen (Allen et al. 2005), as elevated CO₂ increases nitrogen deficiency in chaparral soils.

Chaparral Animals

Invertebrate diversity in chaparral is thought to be considerable, but relatively few studies have been conducted at the community level. Invertebrates are a key component of ecosystem processes of mineral and energy flow as DETRITORES and FOSSILES. Also, most chaparral plants are pollinated by a diversity of insects (Mosquin 1971, Fulton and Carpenter 1979). Other invertebrates are key members of food webs as parasitoids and predators and in other trophic roles. One study of a single montane chaparral species, green-leaf manzanita, found over 500 arthropod taxa from 169 different families in 19 orders (Valenti et al. 1997). About 80% of these species were herbivores, predators, or parasitoids. Another study investigated insects associated with leaves and branches of 26 coastal manzanita species and found over 209 insect taxa, with over 85% of them folivores (Andres and Connor 2003). They found a density of approximately 350 individuals m⁻² for just leaf miners, leaf galls, sap-suckers, and chewing insects. These studies indicate the importance of small insects and other arthropods in energy and mineral cycling of chaparral food webs. Chaparral also is a habitat in which many insect lineages have evolved (Miller and Crespi 2003). For example, one aphid genus (*Tamallia*) has radiated on species of manzanita (Miller 1998a, 1998b).

Chaparral also harbors a large number of vertebrates, from mammals like woodrats, chipmunks, and harvest mice (Table 24.3) and birds (Table 24.4) like Bewick's wren and the wren-tit to a variety of common reptiles like the western fence lizard (*Sclerophorus occidentalis*) and the Pacific rattlesnake (*Crotalus viridis*). These animals are generally granivores (seed eaters), herbivores, insectivores, or other types of predators that modify and extend the food web found within chaparral. Because of their size and density, such animals can significantly influence the dominance and frequency of certain plants (Quinn 1994, Mills 1983, Frazer and Davis 1988). For example, grazing by deer or rodents in the first several years after fire tends to differentially impact certain plant species, shifting their dominance (Mills 1983, Quinn 1994, Frazer and Davis 1988, Ramirez et al. 2012). Seed predators can limit seed input to seed banks (Keeley and Hays 1976, Kelly and Parker 1990, Quinn 1994, O'Neil and Parker 2005, Warzecha and Parker 2014). On the other hand, scatter-hoarding rodents may be critical in the burial

of seed for many PERSISTENT SEED BANK species, burying them deep enough to permit survival of high temperature wildfires (Parker 2010).

Life Histories and Wildfire

Fires are a natural and critical ecosystem process in chaparral. Chaparral dynamics correspond to cycles of wildfire, postfire recovery, and stand maturation. Chaparral is resilient to fires at 30 to 150+ year intervals, and within this range communities quickly return to prefire conditions. This occurs because all components of the prefire state are present after fire and because colonization plays a limited role in reestablishing vegetation (Hanes 1971). Of critical importance is that chaparral is adapted to a particular fire regime of a range of frequency, intensity, and timing (see Chapter 3, "Fire as an Ecosystem Process"). A departure from the natural fire regime, either by excluding fire or adding too much fire, reduces the sustainability of this ecosystem (Zedler et al. 1983, Parker 1990, Zedler 1995, Parker and Pickett 1998, Jacobsen et al. 2004, Keeley et al. 2005a, Keeley et al. 2005b).

Postfire plant regeneration involves dormant seed banks that germinate after fire and resprouting from persistent stem bases and lignotubers (Parker and Kelly 1989). Consequently, fire size often does not affect community recovery. Rather, an appropriate fire regime that allows stands to recover and begin reproduction is critical. Because canopy fires typify chaparral, intensity and heat penetration into the soil vary with temperature, wind, soil, and fuel moisture prior to the fire, as well as aspect, exposure, and other characteristics. Heat penetration into the soil critically influences outcomes because many plant species recover from seed in the soil that must survive heat pulses (e.g., Odion and Davis 2000, Odion and Tyler 2002).

Different types of seed banks can be found among chaparral plants. They illustrate a range of adaptations based on the type and degree of seed dormancy. Species with seeds that lack any type of long-term dormancy and germinate within a year are described as having TRANSIENT SEED BANKS. For these species a period of time exists when no seed reserve is found in the soil. Should a wildfire occur during that time period, the population will be eliminated unless some other life history stage can survive the fire. Species with more extensive seed dormancy, barring predation, always have seeds present in the soil. These are referred to as having persistent seed banks, whose crucial characteristic is that a reserve of seed is typically available. Trees found in chaparral often have serotinous cones, considered a persistent canopy or aerial seed bank.

TABLE 24.3
Common mammals found in chaparral areas in California

Species	Common name	Taxonomic subgroups	Occurrence in chaparral
LARGE MAMMALS			
<i>Puma concolor</i>	Mountain lion		Occasional
<i>Lynx rufus</i>	Bobcat		Common
<i>Odocoileus hemionus</i>	Mule deer		Common, esp. postfire
<i>Canis latrans</i>	Coyote		Common
<i>Taxidea taxus</i>	Badger		Occasional postfire
<i>Procyron lotor</i>	Raccoon		Occasional postfire
<i>Urocyron cinereoargenteus</i>	Gray fox		Occasional
SMALL MAMMALS			
<i>Tamias</i> sp.	Chipmunks	Especially <i>T. merriami</i> , <i>T. sonomae</i> <i>T. quadrimaculatus</i> ,	Frequent, common at higher elevations
<i>Spermophilus</i> sp.	Ground squirrel	Especially <i>S. lateralis</i> , <i>S. beecheyi</i>	
<i>Sylvilagus</i> sp.	Brush rabbit	Especially <i>S. bachmanii</i> and <i>S. audobonii</i>	Common
<i>Lepus</i> sp.	Jackrabbit	<i>L. californicus</i>	Common
<i>Chaetodipus</i> sp.	Pocket mouse	Especially <i>C. californicus</i> and <i>C. fallax</i>	Frequent, especially in southern California
<i>Dipodomys</i> sp.	Kangaroo rat	<i>D. venustus</i> , <i>D. agilis</i> , <i>D. heermanni</i>	Coastal Ranges
<i>Neotoma</i> sp.	Woodrats	Especially <i>N. fuscipes</i> , <i>N. lepida</i>	Common
<i>Peromyscus</i> sp.	Deer mouse	Especially <i>P. maniculatus</i> , <i>P. boylii</i> , <i>P. californicus</i>	Common
<i>Reithrodontomys</i> sp.	Harvest mouse	Especially <i>R. megalotis</i>	Frequent
<i>Perognathus californicus</i>			
<i>Microtus</i> sp.	Vole	Especially <i>M. californicus</i>	Frequent postfire

SOURCES: Based on Lawrence 1966, Fellers 1994, Price et al. 1995, Schwilk and Keeley 1998, Laakkonen 2003.

Characteristic postfire annuals (or PYRO ENDEMS and suffrutescents usually produce a wholly or partially dormant, persistent soil seed bank that responds to wildfire by losing dormancy and germinating in the next growing season (Sweeney 1956, Hanes 1977, Keeley 1991). Dormant seed banks of these species are triggered by either intense heat shock or combustion products from smoke or charred wood (e.g., Keeley 1991, Keeley and Fotheringham 2000). Their relative dominance depends on site history and the rainfall and temperature pattern of the initial postfire year, but generally their cover is significant and they continue to expand their populations into the second year. Consequently, chaparral typically has the highest plant diversity in the first and second years after fire (Sweeney 1956, Keeley et al. 2005a). Plant diversity declines in later years, although this trend may be reversed by very high rainfall in early seral stages (Keeley et al. 2005b). While annuals decline, suffrutescents remain until overtopped by reestablishing sclerophyllous shrubs or trees. Within chaparral, some annuals and suffrutescents typically establish in gaps and tolerate drought and other envi-

ronmental conditions found in postfire habitats. The substantial restriction of these widespread native annuals and suffrutescents to postfire stands evinces the long history of wildfire shaping plant community dynamics in the Mediterranean-type climate.

Woody plants can be grouped into three general, postfire life history categories based on combinations of seed dormancy and postfire resprouting (Keeley 1987; Keeley, Bond et al. 2012; Parker and Kelly 1989). One cluster of species survives fire as adults; their aboveground stems are killed, but they resprout from stem or root crowns afterwards. Because of their transient seed banks, these species have no postfire seedling recruitment; consequently these types of plants are considered OBLIGATE RESPROUTERS. The seeds and seedling establishment patterns of obligate resprouters reflect no specific response to fire and are similar in reproductive characteristics and patterns to close relatives in other vegetation types. Two groups of plants, however, produce seeds that are dormant at maturity and create persistent soil or aerial canopy seed banks. Their seeds are wholly or principally stimu-

TABLE 24.4
Common birds found in chaparral areas in California

Species	Common name	Occurrence in chaparral
COMMON CHAPARRAL BIRDS		
<i>Callipepla californica</i>	California quail	Common
<i>Thryomanes bewickii</i>	Bewick's wren	Common
<i>Chamaea fasciata</i>	Wrentit	Common
<i>Toxostoma redivivum</i>	California thrasher	Common
<i>Psaltriparus minimus</i>	Bushtit	Frequent
<i>Aphelocoma californica</i>	Western scrub jay	Common
<i>Pipilo maculatus</i>	Spotted towhee	Common
<i>Passerina amoena</i>	Lazuli bunting	Occasional
<i>Melospiza crissalis</i>	California towhee	Common
<i>Melospiza fuscus</i>	Canyon towhee	Frequent
<i>Poliophtila californica</i>	California gnatcatcher	Occasional in southern California
<i>Geococcyx californianus</i>	Road runner	Occasional
<i>Calypte costae</i>	Costa's hummingbird	Occasional
<i>Calypte anna</i>	Anna's hummingbird	Occasional
<i>Artemisiospiza belli</i>	Sage sparrow	Occasional
<i>Aimophila ruficeps</i>	Rufous-crowned sparrow	Occasional
<i>Spizella atrogularis</i>	Black-chinned sparrow	Occasional
<i>Zenada macroura</i>	Mourning-dove	Occasional, especially postfire
<i>Columba livia</i>	Rock dove	Occasional, especially postfire
COMMON POSTFIRE PREDATORS		
<i>Buteo jamaicensis</i>	Red-tailed hawk	Occasional postfire
<i>Accipiter cooperii</i>	Cooper's hawk	Occasional postfire
<i>Accipiter striatus</i>	Sharp-shinned hawk	Occasional postfire
<i>Falco sparverius</i>	American kestrel	Occasional postfire
<i>Bubo virginianus</i>	Great horned owl	Occasional postfire
<i>Corvus corax</i>	Raven	Occasional postfire

SOURCES: Based on Lawrence 1966, Soule et al. 1988.

lated by wildfire and they germinate and establish in post-fire stands. Of these plants, many can also resprout after fire and are considered **FA U T A T E S E E D E R S**, reflecting the survival of the adults and the postfire potential for a flush of new recruits. Finally, a third group of species does not resprout after fire, and their adults are killed by fire. Their populations persist exclusively through seed banks and seedling recruitment to reestablish their populations. These types of plants are called **O B L I G A T E S E E D E R S** and in California are made up primarily by manzanitas and ceanothus among the shrubs and by pines and cypresses among the trees.

Common obligate resprouters are toyon and shrub oak

species (see Table 24.1). Toyon produces fleshy, bright-red, bird-dispersed fruit that mature in early winter. Once deposited in the droppings of birds, toyon seeds generally germinate quickly. The seedlings tolerate the shaded conditions in the understory of a mature chaparral canopy. Similarly, oak acorns mature in the fall and are dispersed by scatter-hoarding birds or rodents; acorns not buried shortly after falling from shrubs dry out and lose viability over a few weeks. The seeds lack complex dormancy mechanisms and germinate following initial fall rains or after **S T R A T E G I C A T I O N**, resulting in yearly germination under chaparral canopies. Obligate resprouters thus build up small to extensive seedling banks in

the understory of older-growth chaparral (e.g., Keeley 1992) and to some extent depend on longer fire-free intervals in chaparral to provide the occasional and necessary canopy gap for seedling emergence.

Facultative and obligate seeders both produce persistent soil seed banks. Such seed banks derive from PHYSIOLOGICAL DORMANCY mechanisms (manzanitas), have thick seed coats that prevent the entry of water until modified by heat pulses (PHYSIOLOGICAL DORMANCY; ceanothus species), have combinations of physical and physiological dormancy mechanisms (chamise), or retain seeds in thick woody cones that remained closed until opened by age or wildfire (pines and cypresses). In each of these ways, recruitment is restricted to the first year following wildfire. Fire opens canopies, increasing available light energy and soil surface temperature; ashes organic matter, making minerals available; and limits leaf area, reducing overall water loss from the soil by transpiration. These conditions are relatively ideal for seedling establishment in these genera, although the overall success of establishment then depends on survival of summer drought and herbivory.

Woody plants that fall into these seed bank categories predictably reflect other sets of adaptive characteristics. Surveys of chaparral over large regions indicate that chaparral is dominated by species with persistent soil seed banks (facultative and obligate seeders) (Parker and Kelly 1989). Shrubs with persistent seed banks average over 80% cover across both coastal and interior conditions (Vasey et al. 2014). Patterns occur within sites. Obligate resprouters, for example, are often more mesophytic (moisture loving) and tend to dominate more mesic sites like north-facing slopes or ravines. Obligate seeders and some facultative seeders are more xerophytic (adapted to dry conditions) in structure and dominate drier sites such as ridgelines and south-facing aspects. These persistent seed bank species might also be seen as occupying a gradient of population dynamic responses to fire, from species with adults surviving most wildfires, to species losing a considerable number of adults in fires, to obligate seeders that lose all adults that burn. The trade-offs in retaining some adults vegetatively versus sexually reproducing a cohort of seedlings after a fire lead reflect complex combinations of allocational trade-offs, history, site productivity, spatial and temporal environmental variability at a site, and the frequency with which fire returns.

Organisms besides plants also have to survive wildfire. Wildfires undoubtedly have substantial impacts on microbial communities (Kaminsky 1981), but soils tend to buffer them except in the uppermost levels (Taylor and Bruns 1999). Like many chaparral plants, microbes have resistant stages. For example, fungi build up spore banks containing dormant spores and sclerotia in the soil (Taylor and Bruns 1999, Baar et al. 1999). The heat and ash from wildfires can influence the dominance of particular microbial species in postfire stands, sometimes favoring particular groups of fungi (e.g., Ascomycetes, Stoll 1998) but differentially sorting microbial species based on their ability to tolerate heat and ash (Baar et al. 1999, Izzo et al. 2006, Peay et al. 2009, 2010). Reviews of the roles of soil microbes in ecosystem processes and the influence of wildfire on those soil communities can be found in Neary et al. (1999) and Cairney and Bastias (2007). Animal recovery following fire differs profoundly from plant responses. Most plant taxa regenerate endogenously from dormant seed banks and/or resprouting and are relatively insensitive to fire inten-

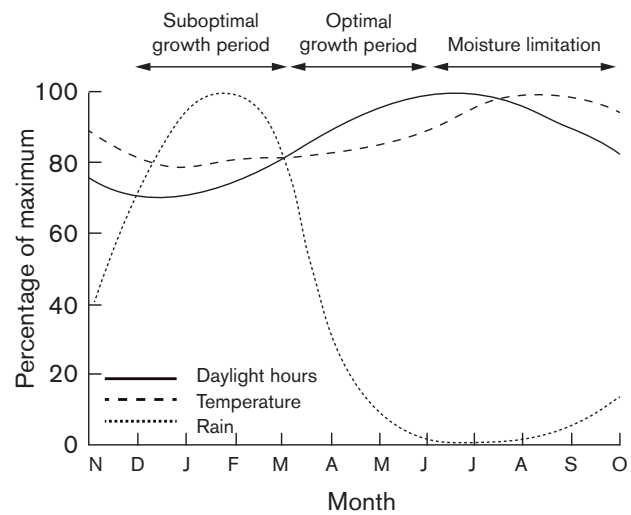


FIGURE 24.3 Seasonality of the Mediterranean-type climate. Seasonal maxima of three key factors are illustrated: daylight hours, temperature, and rain. At top, suboptimal and optimal growth periods for plant growth are represented, followed by the season in which moisture limitation restricts growth potential. Source: Data calculated from long-term average monthly means at the Los Angeles Civic Center (NOAA).

sity and fire size (Keeley et al. 2005a). In contrast, many chaparral fauna are far more sensitive to fire behavior characteristics, including fire severity and fire size, as well as the extent to which land management practices have fragmented metapopulations and altered corridors (see Chapter 3, “Fire as an Ecosystem Process”).

Physiology of Chaparral Shrubs

In the past fifty years, the physiology of evergreen chaparral shrubs has been more intensively studied than that of perhaps any other plant community. Many excellent reviews have been written of chaparral shrub physiology (Mooney and Parsons 1973, Mooney et al. 1977, Miller and Hajek 1981, Mooney and Miller 1985, Carlquist 1989, Field and Davis 1989, Davis, Kolb, and Barton 1988, Keeley 2000). Chaparral shrub physiology is strongly shaped by the seasonality of the Mediterranean-type climate. Winter and spring rains recharge soil moisture, with most of the rain falling when temperatures are cool and days are short. This is the time when growth and photosynthesis of shrubs and ecosystem processes are most active (Figure 24.3). The evolutionary implications of this have not been well explored. Much of the interest in evolution of chaparral taxa has focused on the summer dry season, but many traits (particularly reproductive ones) are tied to winter rains, which likely have been present far longer than dry summers (Keeley, Bond et al. 2012). A second factor affecting chaparral physiology is the recurrent crown fires that occur during the summer or fall. These fires open space for seedlings of obligate seeders, gap specialists with a suite of life history and physiological characters linked to the postfire regeneration niche, to recruit (Figure 24.4). Obligate resprouters, in contrast, recruit seedlings during fire-free intervals and resprout after fire, and their physiology and life history traits diverge from the obligate seeders.



FIGURE 24.4 Abundant seedlings of (left) *Ceanothus megacarpus*, a postfire obligate seeder, and (right) resprouts of chamise (*Adenostoma fasciculatum*). Photos: R. Brandon Pratt.

Growth and Photosynthesis

Vegetative growth of chaparral shrubs is affected by temperature, by photoperiod, and most strongly by available soil moisture (Miller and Hajek 1981, Miller 1983). During the wettest winter months, temperatures and photoperiod are at their lowest, producing suboptimal growth conditions (see Figure 24.3). The peak growing season for most shrubs is in spring, when temperatures and photoperiod rise and soils are still moist (Mooney et al. 1975, Mooney et al. 1977). During the dry summer and autumn months, growth is limited by low soil moisture availability (Davis and Mooney 1986). Timing of flowering diverges among shrubs, with some species flowering in the winter (e.g., big-berry manzanita and big-pod ceanothus), some in the spring (e.g., sugar bush and scrub oak), and still others during the summer and autumn (e.g., chamise and toyon) (Bauer 1936). Winter- and spring-flowering species tend to produce flower buds in the prior year and thus flower on old growth prior to current-year leaf production, whereas summer-flowering species flower on new growth following leaf production.

The evergreen leaves of chaparral shrubs can photosynthesize year-round, but rates are moderate in the winter and early spring and increase in early summer (Figure 24.5). The chief factors affecting photosynthesis, ordered from most to least important, are available soil moisture, photoperiod, and temperature (Mooney et al. 1975). During the winter-growing season, chaparral species are able to photosynthesize at near-maximum rates over a broad range of temperatures (85% of maximum rates can be achieved between approximately 10°C and 30°C) (Mooney et al. 1975, Oechel et al. 1981). This broad temperature response is adaptive because daily and seasonally temperatures can fluctuate broadly. During the summer and autumn months, shrubs restrict stomatal apertures to conserve water and avoid desiccation, which limits diffusion of CO₂ to chloroplasts. The cool and short days during growing season favor C3 photosynthesis and C4 species virtually absent from chaparral communities (Sage et al. 1999).

Evergreen and deciduous leaf habits represent two different strategies for photosynthetic carbon assimilation. Longer-lived evergreen leaves have lower maximum photosynthetic rates than shorter-lived deciduous ones (Table 24.5). For evergreen chaparral leaves, net carbon gain accrues more slowly

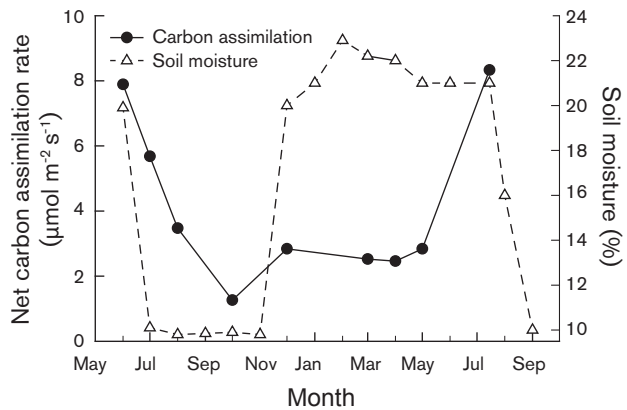


FIGURE 24.5 Seasonal patterns of soil moisture and maximum photosynthesis (carbon assimilation) for a typical chaparral shrub. Unpublished data from a southern California site are for *Rhus ovata* and soil moisture content at 2 meter depth. Source: Modified from Mooney and Dunn 1970b.

over a longer period, whereas deciduous leaves have a faster return rate over a shorter period (Mooney and Dunn 1970b, Harrison et al. 1971, Orrians and Solbrig 1977, Field et al. 1983, Field and Mooney 1986, Ackerly 2004b, Wright et al. 2004). Evergreen leaves have lower SPE F EAF AREA and are more sclerophyllous and mechanically stronger and stiffer, providing a more protected and durable leaf with greater longevity than deciduous leaves (Mooney and Dunn 1970b, Balsamo et al. 2003, Wright et al. 2004). In addition, deciduous leaves tend to have higher nitrogen levels and greater SLA (because they are less sclerophyllous) than evergreen leaves.

In more arid sites evergreen chaparral gives way to sage scrub and desert scrub communities dominated by deciduous species. This pattern has been explained in the context of leaf economics (Mooney and Dunn 1970b, Mooney 1989). Because stomatal closure limits evergreen photosynthesis during the dry season, the costs of long-lived evergreen leaves exceed the return they can achieve at sites with more protracted dry seasons such as desert ecotones and coastal areas (Poole and Miller 1981, Mooney 1989). In these more arid sites the net carbon gain of deciduous leaves exceeds evergreens, giving the former a competitive advantage.

TABLE 24.5
Leaf function of deciduous (n=6) and evergreen (n=6) chaparral shrubs grown in a common garden

Leaf habit	Anet area ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Anet mass ($\mu\text{mol kg}^{-1} \text{s}^{-1}$)	Nitrogen (%)	Specific leaf area (m^2/kg)	Tensile strength ^A (N/mm^2)
Deciduous	31.5 (3.6)	414.1 (69.1)	4.16 (0.40)	12.71 (0.80)	0.72 (0.15)
Evergreen	23.6 (4.1)	191.5 (3.5)	2.61 (0.16)	8.88 (1.30)	1.45 (0.24)

SOURCE: Pratt, unpublished data.

NOTE: Data are means with 1SE in parentheses.

A. This is the modulus of rupture, or maximum force before breaking per unit leaf cross-sectional area of leaf.

TABLE 24.6
Leaf stress traits: Adaptive leaf traits for coping with the stressful summer and autumn dry season typical of a Mediterranean-type climate

Leaf traits	Function	References
Sclerophyllous leaves	Structural support when turgor is lost and prevention of cell implosion; durability	Oertli et al. 1990, Brodribb and Holbrook 2005, Balsamo et al. 2003
Xeromorphic leaves	Aid in water retention	Cooper 1992
Stomatal response to drying soils	Reduce transpiration	Poole and Miller 1975, Jacobsen et al. 2008
Leaf angling during dry season	Reduce interception of solar radiation; thermal balance; reduced transpiration and photoinhibition	Comstock and Mahall 1985, Ehleringer and Comstock 1989, Valladares and Pearcy 1997, Valiente-Banuet et al. 2010
Heat shock proteins	Aid in stress tolerance	Knight 2010
Xanthophyll cycling and carotenoid accumulation	Protect photosynthetic pigments	Stylinski et al. 2002

Water Stress

The protracted summer/fall rainless season creates hot, dry, and stressful conditions. South-facing slopes are often more arid and dominated by drought-tolerant species such as ceanothus, manzanitas, and chamise. North-facing slopes experience lower evaporation; however, north-facing slopes may dry out more rapidly and to a greater degree than south-facing slopes in mature stands because of a higher leaf area index and stand transpiration (Ng and Miller 1980). The effect of aspect may be especially important after fire when sensitive seedlings and resprouts are in the early establishment stage. Fog along the coast can help to mitigate the summer dry season (Vasey et al. 2012) because fog reduces evapotranspiration, and in some coastal areas because fog drip can lead to significant soil inputs of precipitation (Corbin et al. 2005). In southern California's coastal areas fog inputs to the soil apparently do not provide a significant water source for shrubs (Evola and Sandquist 2010). Chaparral shrubs must cope during the protracted summer and fall rainless season with water stress, high temperature stress, and solar radiation that exceeds photosynthetic needs. The leaves of chaparral shrubs have a host of traits that equip them to manage these stressful conditions (Table 24.6).

Shrubs can be categorized along a continuum by the degree of water stress they experience during an average dry season, which is measured as the minimum seasonal WATER POTENTIAL (Bhaskar and Ackerly 2006). At one end of the continuum are water stress tolerators that experience low water potentials during the dry season because they are relatively shallowly rooted (e.g., some ceanothus and manzanita species) (Hellmers, Horton et al. 1955; Poole and Miller 1975; Miller and Poole 1979; Poole and Miller 1981; Thomas and Davis 1989; Ackerly 2004b; Jacobsen et al. 2007a). At the other end of the continuum are deeply rooted water stress avoiders that experience a narrower range of water potential declines seasonally. This group is exemplified by Anacardiaceae including laurel sumac, sugar bush, lemonade bush (Miller and Poole 1979, Poole and Miller 1981, Thomas and Davis 1989, Jacobsen et al. 2007a). Most species experience water potentials in between the tolerators and avoiders, indicating that they have intermediate rooting depths or those varying from intermediate to deep depending on local edaphic conditions (e.g., chamise, ceanothus, toyon, scrub oak). Even water stress avoiders with deep roots experience a drop in water potential during the dry season, because all shrubs have some roots in shallow soil layers to acquire nutrients (Kummerow, Krause et al. 1978; Marion and Black 1988).

TABLE 24.7
Tolerator/avoider strategies for coping with water stress

Traits	Stress tolerators	Intermediate	Stress avoiders	References
	<i>Ceanothus</i> spp. subgenus <i>Cerastes</i> ^A	<i>Heteromeles</i> <i>arbutifolia</i>	<i>Malosma</i> <i>laurina</i>	
Maximum rooting depth (m)	2.4	n/a	>13.2	1
Minimum seasonal water potential (MPa)	-6.9	-4.3	-1.8	2, 3
Stem cavitation resistance (MPa) ^B	-9.1	-6.2	-1.6	2, 3
Water potential at stomatal closure (MPa)	-5.5	-3.5	-2.2	4
Turgor loss point (MPa)	-5.6	-4.0	-2.3	5, 6, 7
Density of stem xylem (kg/m ³)	674	611	462	2, 8
Stem mechanical Strength (N mm ⁻²)	251	238	168	2, 3
Stem xylem starch storage (%)	2.9	3.0	4.8	9
Vessel implosion resistance (t/b) _h ²	0.041	0.035	0.019	2, 8
Vessel density (#/mm ²)	244	182	129	10
Vessel diameter (μm)	25	26	53	2, 8
Stem hydraulic efficiency ^C	1.5	2.3	5.7	2

SOURCES: 1. Thomas and Davis 1989; 2. Jacobsen, Pratt, Ewers et al. 2007; 3. Pratt, Jacobsen, Ewers et al. 2007; 4. Poole and Miller 1975; 5. Pratt et al. 2005; 6. Roberts 1982; 7. Calkin and Percy 1984; 8. Pratt et al. 2008; 9. Pratt, unpublished data; 10. Anna Jacobsen, unpublished data.

A. Data are from *Ceanothus crassifolius*, *C. cuneatus*, *C. gregii*, or *C. megacarpus*. Data taken from references 2, 3, and 8 reported multiple species and data reported here are means.

B. This is water stress–induced cavitation estimated as the water potential causing 50% loss in hydraulic conductivity.

C. This is the maximum stem hydraulic conductivity (in the absence of emboli) divided by the sapwood area (xylem specific conductivity).

Stress tolerators diverge from the avoiders in a suite of traits that allow them to maintain a broader range of physiological function at more negative water potentials (Table 24.7). Key among these is greater resistance to water stress–induced xylem cavitation (Kolb and Davis 1994, Davis, Kolb, and Barton 1988, Davis et al. 2002). Cavitation describes the process by which air is pulled into xylem conduits and displaces water with air emboli (Tyree and Sperry 1989). When this happens, emboli reduce flow (hydraulic conductivity) through the vascular system. If emboli occur in many conduits, a positive feedback loop can ensue, leading to runaway cavitation and desiccation of leaves, dieback of branches, or whole plant mortality (Davis et al. 2002, Paddock et al. 2013, Pratt et al. 2008). Species that experience more negative minimum seasonal water potentials have greater cavitation resistance (Davis, Kolb, and Barton 1988; Davis, Ewers et al. 1999; Bhaskar et al. 2007; Jacobsen et al. 2007a; Pratt, Jacobsen, Ewers et al. 2007) (Figure 24.6). Moreover, greater cavitation resistance is correlated with greater survival of drought in chaparral seedlings (Pratt et al. 2008). In mixed stands, co-occurring species often have widely divergent cavitation resistances that reflect differences in access to soil moisture during the dry season and selection that occurs at the seedling stage and during episodic drought (Thomas and Davis 1989, Davis, Kolb, and Barton 1988, Jacobsen et al. 2008).

The only way for plants to recover hydraulic conductivity following cavitation is to refill conduits or regrow new xylem, both of which cannot occur during the protracted dry season when water potentials are low (Kolb and Davis 1994, Williams et al. 1997). Thus, avoiding cavitation by resisting it is the most effective strategy for evergreen shrubs whose leaves

require a sustained water supply. Evergreen chaparral shrubs do have greater cavitation resistance of stems than deciduous shrubs that occur in the chaparral community (Figure 24.7). However, deciduous species are not necessarily strict drought avoiders (Gill and Mahall 1986, Jacobsen et al. 2008).

Cavitation and reduced hydraulic conductivity can occur in roots, stems, or leaves, and a process similar to xylem cavitation can occur in the rhizosphere. Among stress tolerators, the rhizosphere's hydraulic conductivity may be most limiting during the dry season because of the high resistance of stems and roots (Davis et al. 2002; Pratt, Jacobsen, Golgotiu et al. 2007). This allows stress tolerators to extract the maximum amount of water from a limited volume of drying soil and also to rapidly resume water and nutrient uptake when winter rain falls (Poole and Miller 1975; Mooney and Rundel 1979; Gill and Mahall 1986; Pratt, Jacobsen, Golgotiu et al. 2007). At least two other traits are important for stress tolerators to maintain physiological function. The leaves of stress tolerators close their stomata at more negative water potentials than the stress avoiders, allowing them to continue to photosynthesize at greater water deficits (Poole and Miller 1975, Miller and Poole 1979, Oechel et al. 1981, Jacobsen et al. 2008). They also have lower turgor loss points than stress avoiders (Roberts 1982). In spite of a lower turgor loss point, stress tolerators lose turgor during the dry season, so it is not avoidance of turgor loss that is important but maintenance of turgor at more negative water potentials and tolerance of turgor loss (Saruwatari and Davis 1989).

Additional traits are associated with the stress-tolerator strategy (see Table 24.7). Stem vascular tissue is denser and mechanically stronger (Wagner et al. 1998, Jacobsen et al.

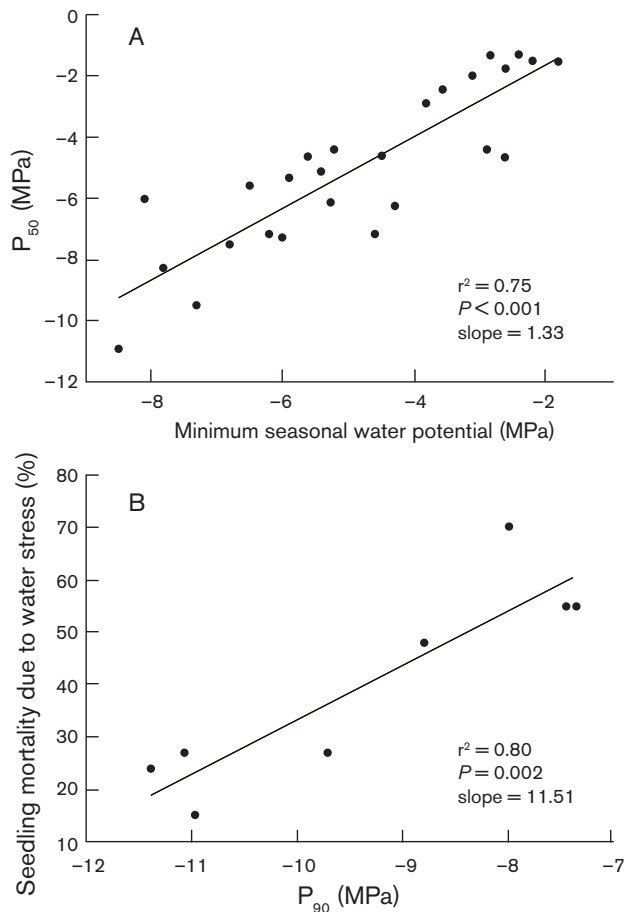


FIGURE 24.6 Species that experience more negative minimum seasonal water potentials have greater cavitation resistance. Source: Data modified from Jacobsen et al. 2007a and Pratt et al. 2008.

- A Stem xylem cavitation resistance estimated as the water potential at 50% loss of hydraulic conductivity (P_{50}) plotted against the seasonal low in water potential measured during the peak of the summer rainless period for adult chaparral shrubs.
- B Greater cavitation resistance is associated with lower levels of mortality due to water stress for seedlings.

2005, Jacobsen et al. 2007a). The vessels of stress tolerators are more resistant to implosion when the xylem is under tension (Jacobsen et al. 2007a; Pratt, Jacobsen, Ewers et al. 2007) and have narrower diameter vessels (Jacobsen et al. 2007a). Shoots of tolerators have lower leaf area per unit sapwood area of their branches (Ackerly 2004b). Finally, the stem xylem of stress tolerators store less carbohydrate than the stress avoiders during the dry season (see Table 24.7). This is hypothesized to be due to the ability of stress tolerators to photosynthesize at more negative water potentials and rely less on stored carbohydrates than stress avoiders (McDowell et al. 2008).

Species dominating the more arid sage scrub and Mojave Desert communities are less resistant to water stress-induced xylem cavitation than chaparral communities (Jacobsen et al. 2007b), even though species in these communities do not differ in minimum seasonal water potential they experience (Jacobsen et al. 2008). The costs associated with greater cavitation resistance may limit cavitation resistance in these species (Pratt, Jacobsen, Ewers et al. 2007). Leaf shedding during

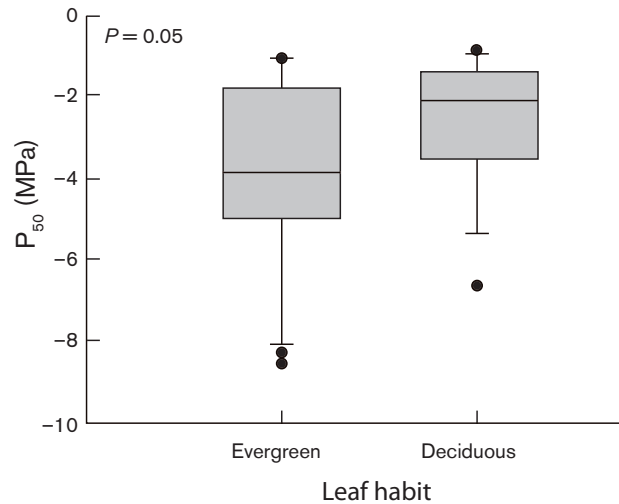


FIGURE 24.7 Stem resistance to cavitation estimated as the water potential at which 50% of conductivity is lost (P_{50} , $n=16$ for deciduous and $n=18$ for evergreen). Data are from chaparral shrubs growing at four field sites located in the San Gabriel, Santa Monica, San Bernardino, and the San Jacinto Mountains. Source: R. Brandon Pratt, unpublished data.

dry periods, common among species in the more arid communities, may mitigate water stress compared to evergreen chaparral. However, drought-deciduous species are not necessarily water stress avoiders (Gill and Mahall 1986, Kolb and Davis 1994, Jacobsen et al. 2008). At a Sonoran Desert/chaparral ecotone, some desert species—for example, jujube (*Ziziphus parryi*)—are fully deciduous, quite vulnerable to cavitation, have low water-storage capacity, and experience highly negative water potentials during the dry season, suggesting that their roots remain in contact with dry soils. Perhaps species with this trait combination are able respond to seasonal rains or rain pulses by rapidly refilling xylem conduits and growing new high SLA leaves.

Freezing and Distribution

Freezing temperatures can limit the distribution of frost-sensitive species at higher elevations and at low-elevation basins that fill with cold air. The coldest air temperatures are commonly caused by radiation frosts on calm and clear nights in the months of December and January (Davis et al. 2007). At freezing ecotones, species turnover can be abrupt and the turnover occurs where the minimum air temperatures drop to levels that cause damage to sensitive species (Ewers et al. 2003, Davis et al. 2007). In the Santa Monica Mountains of southern California, laurel sumac and ceanothus species dominate on coastal exposures and warmer sites outside cold air drainage zones. On the lower slopes and the valley floors these species are replaced by other more frost-tolerant species: sugar bush and other species of ceanothus (Davis et al. 2007).

Some cold-sensitive species like laurel sumac suffer direct damage to their living leaf cells by freezing temperatures (Boorse et al. 1998, Pratt et al. 2005) and suffer freeze/thaw-induced cavitation (Langan et al. 1997). The mechanism of cavitation caused by freeze/thaw-induced cavitation is different from that caused by water stress (Jarbeau et al. 1995), but they both result in emboli that reduce xylem hydraulic conductivity. The emboli typically form in the distal branches

and can lead to desiccation of leaves in the days and weeks that follow the frost (Langan et al. 1997, Pratt et al. 2005, Davis et al. 2007). Overnight freezing temperatures are frequently followed by warm sunny days, thus the combination of evergreen leaves and a highly embolized vascular system can lead to dieback of branches even during the moist winter (Davis et al. 2005). For a plant under water stress, freeze/thaw-induced cavitation leads to more extensive formation of emboli, dieback, and plant mortality (Langan et al. 1997, Davis et al. 2005, Davis et al. 2007). Species with larger-diameter vessels are more vulnerable to freeze/thaw-induced embolism (Davis, Sperry et al. 1999).

The Link between Life History Type and Physiology

Recurring crown fires are important for understanding the physiology of chaparral shrubs, particularly at the critical seedling stage. An important framework for understanding the nexus between fire and physiology is to consider the different chaparral life history types. The three different life history types recruit seedlings in different environments, and that recruitment environment selects for different physiologies (Keeley 1998, Pratt et al. 2012). This coupled with physiological and allocation trade-offs leads to divergence in the suite of functional traits of the different life history types. Obligate seeders recruit seedlings in the most arid and open canopy microsites. Consistent with this, obligate seeders are more water stress tolerant and the least shade tolerant than the other life history types (Pratt et al. 2008). Facultative seeders recruit seedlings in open environments, but have greater survival in shadier or moister microsites where stress is ameliorated (Pratt et al. 2008). Accordingly, these facultative seeders have lower water stress tolerance and greater mortality of seedlings during the first dry season following fire (Thomas and Davis 1989). Obligate resprouter seedlings recruit during fire-free intervals in the shady understory of mature chaparral canopies (Keeley 1992). These species have the highest degree of shade tolerance, and they are of similar or greater water stress tolerance to the facultative seeders, which may be related to competition for water in a mature chaparral stand (Pratt et al. 2008).

This divergence in seedling recruitment environments (Figure 24.8) is linked to other characteristics as well, such as differences in rooting patterns (Thomas and Davis 1989, Keeley 1998). Obligate seeders are commonly shallow-rooted, whereas facultative seeders are variable and some are relatively shallow-rooted (e.g., some populations of chamise and manzanita), yet others are among the most deeply rooted (e.g., laurel sumac). Instructively, the more shallowly rooted facultative seeders tend to be the ones that recruit more seedlings after fire and often resprout more weakly (e.g., some chamise populations)—that is, they trend towards the obligate seeder end of the spectrum. Successful seedling recruitment in gaps after fire is achieved by both the ability to rapidly acquire resources when they are abundant after fire and by greater levels of stress tolerance when water is limiting. Evolving this ability and the associated necessary traits appears to compromise resprouting ability (Pratt et al. 2014).

Stress tolerators have trait combinations that include both stress-tolerance traits and rapid-resource acquisition traits such as high net carbon assimilation rates per unit leaf area (Ackerly 2004b, Pratt et al. 2012), transpiration rates (Parker 1984), and hydraulic efficiency at the whole plant level (Pratt

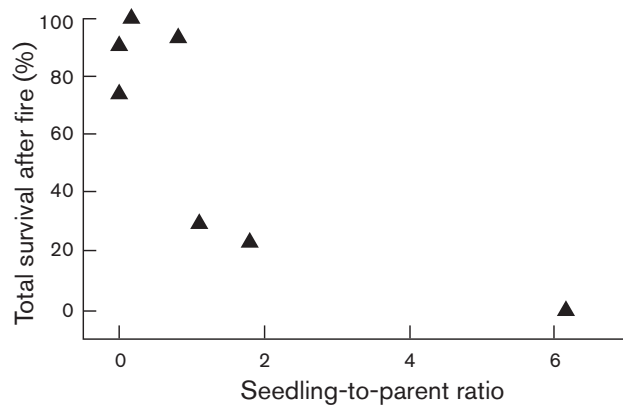


FIGURE 24.8 Greater seedling production (seedling-to-parent ratio) is significantly associated with lower levels of resprout survival two years after fire ($r = -0.81$; $P = 0.03$). All species co-occurred at a Santa Monica Mountains site. Source: Pratt et al. 2014.

et al. 2010). This is likely because during the wet season in the postfire environment, water and nutrients are readily available and seedlings must compete for these resources with other seedlings, including those of herbaceous fire-followers, and resprouting shrubs (McPherson and Muller 1967). At this time, they also must grow fast enough to establish a root system that will prevent them from desiccating during the hot and dry summer and fall. Once the summer and fall season arrives, seedlings experience considerable stress and mortality is often high at this time (Thomas and Davis 1989). These circumstances select for seedlings to rapidly grow and acquire resources when they are available and also to tolerate low levels of resources as they become scarce (Keeley 1998).

Chaparral in the Long Absence of Fire

Because chaparral ranges from arid southern California to more mesic maritime regions and northern California mountain ranges, chaparral dynamics similarly can vary. Thus the phrase “the long absence of fire” has to be defined in the local climatic context. We can reiterate that climate, topography, soils, and wildfire are the principal determinants of the distribution of chaparral across the California landscape. As these principal influences vary among sites and when the between-fire period increases, chaparral dynamics might be expected to change. Earlier studies of chaparral in southern California led to a paradigm that little succession occurred in chaparral and that stands older than sixty years were decadent (Hanes 1971). The idea was that stands reached some age at which plants began to senesce, productivity dropped, and no seedling establishment occurred (Hanes 1971, Hanes 1977, Vogl 1977, Reid and Oechel 1984). *Ceanothus* species, especially from subsection *Cerastes*, were thought to live only thirty-five to fifty years at best. Succession was seen as the eclipsing of coastal sage scrub species by evergreen sclerophyllous species in the first few decades. While some thought that woodland might eventually invade and convert the site if fire was excluded (Horton and Kraebel 1955, Horton 1960, Wells 1962), others thought no further succession would occur (Hanes 1971).

More detailed studies shifted the concepts of chaparral dynamics in the long absence of fire. Old-growth stands of big-pod ceanothus were found to have dead individuals

within them, but the larger living plants were still growing and mortality patterns suggested little change in the stand as it aged (Montygierd-Loyba and Keeley 1987). When a large number of sites were compared along an age gradient, species diversity was found to be stable although some composition change occurs as stands age (Keeley 1992). The greatest mortality rates were among species that fail to grow tall fast enough as they age, such as nonsprouting ceanothus species; other evergreen species showed almost no mortality across a diverse latitudinal and elevation gradient (Keeley 1992). One significant difference between these studies and the earlier paradigm was the evidence that obligate resprouters were establishing seedling banks in the understory of these older stands at fairly high densities (0.1-3.7 m⁻²). This work confirmed and extended earlier studies reporting the establishment of obligate resprouter seedlings in chaparral understory (P. H. Zedler 1981, P. A. Zedler 1982, Parker and Kelly 1989, Lloret and Zedler 1991).

These seedling patterns in southern California chaparral tend to reinforce the life history categories found among the woody plants, those with persistent seed banks recruiting new individuals in the year or two after fire (obligate seeders, facultative seeders), while obligate resprouters require longer time intervals for their shade-adapted seedlings to establish in the understory of chaparral. Succession beyond these demographic shifts depends upon the proximity of other vegetation to old-growth chaparral. Conifers have limited dispersal ranges, and if chaparral stands are quite extensive, initially they have little ability to invade beyond the edges. Similarly, oaks and other hardwoods may benefit from animal dispersal in terms of farther potential dispersal distances, but establishment patterns remain low because of the low productivity and resource limitations of chaparral in this part of the state.

Moving toward central and northern California or shifting to higher elevations into montane chaparral yields a different pattern. In these regions chaparral forms mosaics with forests with the sizes of each type of vegetation patch depending on local climate, topography, soils, and wildfire history. In areas near urban sites or where forest timber is economically critical, fire suppression has generally been the practice for the past century. As a consequence, chaparral stands often are invaded by conifers or other trees and the extent of chaparral may be quite reduced (Vankat and Major 1978, Conard and Radosovich 1982, Nagel and Taylor 2005, Collins and Stephens 2010, van Wagtenonk et al. 2012). One study in the Sierra reported that over the past sixty to seventy years, comparisons of aerial photographs reveal a loss of chaparral spatial coverage by over 60% (Nagel and Taylor 2005). Conifer invasion of chaparral does not always require long-term lack of fire in northern California, however, where, if conditions are appropriate, conifers may invade immediately after fire (Sparling 1994, Horton et al. 1998). For example, following a 1945 wildfire, one chaparral stand adjacent to a forest was invaded the first growing season after the fire, followed by pulses of invasion over the next thirty years (Sparling 1994, Horton et al. 1998).

The conifer forest-montane chaparral mosaics have received considerable attention because of the economic importance of the forests. Studies indicate that forest and chaparral burn at different time intervals and at substantially different fire intensities; forests burn at relatively low intensities while chaparral fires are high intensity. Early researchers considered forest and chaparral patches as alternative vegetation states across the landscape, each maintaining itself due

to their different interactions with fire (Leiberg 1902, Show and Kotok 1924, Wilken 1967). Similar patterns are found in other Mediterranean-climate systems (Mount 1964, Jackson 1968). The differential distribution of these two vegetation types contributes to the self-reinforcing nature of their interaction with fire. High-intensity wildfires tend to occur on steeper or more south-facing aspects in the northern part of the state (Weatherspoon and Skinner 1995, Taylor and Skinner 1998, Alexander et al. 2006). The abiotic conditions combined with further resource limitations imposed by chaparral reduce the rate of conifer invasion and productivity. The cumulative effects of multiple high-intensity fires reduces soil carbon and site productivity, further slowing tree growth rates (Waring and Schlesinger 1985).

Such differential impacts by chaparral and forest were modeled by Odion et al. (2010) to test the concept of alternative vegetation states. Their models supported co-occurring but different stands of vegetation due to different self-reinforcing relationships with fire. Chaparral vegetation burned at higher intensity, particularly on steep or equatorial-facing slopes, and its fire regime kept soil productivity from increasing through time. Forests maintain themselves in sites with gentler slopes and greater soil depth and tend to dominate polar-facing slopes. Their conclusion was that conifer invasion of chaparral sites resulted in conifers being in a "fire trap." Chaparral sites burned at high enough intensity to remove conifers that had established since the last fire. This pattern has been found frequently in the western United States (e.g., Thompson et al. 2007, Holden et al. 2010). Focusing on the central Sierra Nevada, van Wagtenonk et al. (2012) found that these different vegetation patches were maintained as long as fire intensities were low to moderate; high fire intensities resulted in dominance of montane chaparral regardless of the prior vegetation.

Another aspect to the dynamics between chaparral and forest patches is that some types of chaparral create conditions favorable to the facilitation of forest establishment. For example, most conifer seedlings benefit from chaparral canopies providing shade and higher levels of moisture, even though their growth rates may be restricted by resource competition (Conard and Radosovich 1982, Dunne and Parker 1999). Coast live oak, for example, is facilitated by chaparral and coastal scrub (Callaway and D'Antonio 1991) and populations differentially expand within shrub-dominated areas in central California (Callaway and Davis 1998). Furthermore, in the more mesic regions of chaparral distributions in which chaparral exists in mosaics with forests, the dominants of chaparral tend to be species of manzanita or shrub oak, both of which have mycorrhizal mutualisms with fungal species that are shared with conifers in the Pinaceae (Horton et al. 1998). The mycelial networks of fungal mutualists facilitate the establishment of conifer seedlings in conditions that otherwise prevent establishment (Dunne and Parker 1999, Horton et al. 1998). A study testing this idea randomly sampled chaparral stands from northern and central California that were adjacent to forests; chaparral was invaded by conifers in those stands at a rate and density proportional to the percentage of ectomycorrhizal species in the chaparral stand (Bode 1999).

In the long absence of fire, chaparral begins to shift demographically; early successional species including those that may be prominent in coastal or sage scrub vegetation tend to disappear in the first few years to the first decade. As individuals increase in size, compositional shifts or proportions

TABLE 24.8
Adaptive traits for nutrient-poor soils

Traits	Function	References
Root nodules ^A	Symbioses with bacteria that fix atmospheric nitrogen	Pratt, Jacobsen, Ewers, et al. 2007 Kummerow, Alexander, et al. 1978
Long-lived leaves	Greater nitrogen use efficiency	Aerts and Van der Peijl 1993
Evergreen sclerophyllous leaves	Storage compartment for nutrients captured during nutrient pulse following first fall rains	Mooney and Rundel 1979, Shaver 1981
Luxury consumption	Consume nutrients beyond immediate need and store for later use	Rundel and Parsons 1980, Gray 1983
Mycorrhizae	Aid in phosphorous extraction and uptake	Allen et al. 1999

A. Examples include *Ceanothus* spp., *Cercocarpus betuloides*, and legumes such as *Acmispon glaber* (formerly *Lotus scoparius*).

of dominance also change. In the southern ranges of chaparral, fire usually returns prior to any further shifts; however, in more mesic regions, chaparral dynamics involve adjacent vegetation. Some chaparral species, for example, may facilitate forest invasion because of their shared mutualisms with mycorrhizal fungi and the modification of environmental extremes that chaparral canopies may provide. Wildfires balance this process. Chaparral sites burn at an intensity too high for conifers or most forest species to survive, creating fire traps that provide maintenance of chaparral stands over the long term. These changes in chaparral result from differences among chaparral species in their rates of growth, height, or other aspects. While shared mutualisms with forest species may facilitate invasion of chaparral, wildfire, climate, topography, and soil conditions generate the conditions that retain chaparral as a dominant vegetation type in California.

Biogeochemical and Hydrological Dynamics

Carbon Exchange

Community productivity indicates the amount of energy captured and converted to biomass and has important implications for trophic interactions and biotic diversity. At the community scale, chaparral stands can be quite productive annually. For example, stands dominated by big-pod ceanothus have productivity rates of 850 g m⁻² yr⁻¹ (Schlesinger and Gill 1980) and have been reported to be as high as 1,056 g m⁻² yr⁻¹ (Gray 1982). The higher value is comparable to some temperate forest communities and is generally higher than nearby coastal sage communities (Schlesinger and Gill 1980, Gray 1982). Other studies have documented productivity values somewhat lower to much lower at more arid chaparral sites where chamise is abundant (Rundel and Parsons 1979, Vourlitis et al. 2009). Productivity broadly varies on an annual basis depending on temperature and seasonal rainfall (Hellmers, Bonner et al. 1955; Li et al. 2006; Vourlitis et al. 2009).

The net ecosystem exchange of CO₂ of old-growth chaparral stands indicates that they can be substantial carbon sinks (Luo et al. 2007). This suggests that gross primary productivity can remain high in these communities and does not support the idea that the productivity of chaparral stands declines as they age (Hanes 1971). The amount of CO₂ that old-growth stands accumulate or give off annually depends

on current and previous year precipitation and environmental conditions (Luo et al. 2007) and the interaction between the time since the last fire and available nutrients (see “Mineral Nutrition,” below).

Mineral Nutrition

Unburned chaparral soils are poor in available nutrients, and chaparral shrubs have a host of traits that are adaptive in this context (Table 24.8). Nitrogen, and in some cases phosphorous, are in limiting supply, leading to reduced levels of productivity, whereas exchangeable cations are of secondary importance (Rundel 1983). When long unburned plots are fertilized with nitrogen, growth of plants is generally stimulated, which demonstrates the influence of nitrogen on productivity (Hellmers, Bonner et al. 1955; McMaster et al. 1982; Vourlitis 2012). At the system level, most of the nitrogen exists in unavailable standing biomass and litter (Rundel 1983). This reservoir is converted by periodic crown fires and results in a pulse of available nitrogen to the soil (Christensen 1973, Christensen and Muller 1975, Rundel and Parsons 1980, Vourlitis et al. 2009). Immediately after fire, the ammonium significantly increases in the upper soil layers, whereas nitrate is little affected (DeBano, Eberlein et al. 1979; Rundel 1983; Fenn et al. 1993). In the months after fire, the soil pH increases towards neutral and this stimulates nitrogen fixation, leading to an increase in soil nitrate (Dunn et al. 1979, Rundel 1983).

Although fires greatly increase available forms of nitrogen in the soil, nitrogen is volatilized by fire, resulting in significant losses from the system (DeBano and Conrad 1978; DeBano, Eberlein et al. 1979; Rundel 1983). The intensity of the fire is an important determinant of how much nitrogen is volatilized (DeBano, Rice et al. 1979; Marion et al. 1991). Other postfire losses include leaching, surface runoff, dry erosion, and biogenic emissions (Christensen 1973, DeBano and Conrad 1978, Rundel and Parsons 1980, Gray and Schlesinger 1981, DeBano and Dunn 1982, Rundel 1983, Mooney et al. 1987). Losses would be greater if nutrients were not immobilized by a dense growth of fire-following annual herbs and short-lived shrubs such as deer weed (*Acmispon glaber*, formerly *Lotus scoparius*) (Nilsen and Schlesinger 1981).

After successive fires, chaparral soils would eventually be depleted of nitrogen without new inputs. Atmospheric nitro-

gen fixation by microorganisms that are free-living and symbiotic with plants are an important new nitrogen input that offsets some losses (Kummerow, Alexander et al. 1978; Dunn et al. 1979; Ellis and Kummerow 1989; Ulery et al. 1995). Other smaller nitrogen inputs come from precipitation and dry deposition of nutrients on leaves, which reach the soil in solution as a pulse following the first fall rains (Christensen 1973, Schlesinger and Hasey 1980). These atmospheric inputs have increased due to pollution caused by the burning of fossil fuels (see below).

Decomposition converts complex organic substances into simpler forms, and it affects nitrogen availability in between fires. Decomposition by soil animals and microorganisms occurs primarily during the wet season and at a much lower level during the summer dry season (Quideau et al. 2005, Li et al. 2006). Rates are also affected by local conditions such as soil texture and type, slope, and elevation, and rates differ under different evergreen species (Quideau et al. 1998, Quideau et al. 2005). The chief litter input is from leaves, thus their nutrient content and turnover rate are dominant factors in nutrient cycling and are key reasons why the litter of a given species affects decomposition. Much of the nitrogen and phosphorous of leaves are reabsorbed prior to abscission, thus the nutrient quality of the litter in chaparral stands is poor (Mooney and Rundel 1979, Schlesinger 1985, Quideau et al. 2005). The poor quality of the litter (high C:N and C:P ratios) slows decomposition (Schlesinger 1985). Moreover, decomposition is slowed by the high levels of carbon forms that are resistant to decomposition, such as lignin, cutin, and phenolics, which are typically higher in evergreen sclerophylls than deciduous species (Schlesinger 1985, Aerts 1997).

Decomposition of leaves occurs in three phases: first is the leaching of soluble components (K, Mg, carbohydrates, phenolics) during rainstorms (Schlesinger and Hasey 1981). This phase is rapid (greater than one year) and is determined by the amount of soluble components in the litter. The second phase is slower (approximately one to five years) and results from litter fragmentation and slow release initially of non-soluble components (e.g., N, P, Ca, and lignin) upon breakdown by soil microbes. Turnover rates of litter organic matter during this phase ranges from 2.8 to 7.7 years, with litter bag studies tending to yield higher values than mass balance methods (Schlesinger 1985). A three-year study found that the nitrogen and phosphorous becomes immobilized in the litter layer, making it unavailable over this time period (Schlesinger 1985). A third, slower decomposition phase occurs when organic matter is mixed with mineral soil and chemically altered and breakdown products are leached (Chapin et al. 2002). Studies of this phase are lacking, but there have been studies of nutrients across chronosequences that provide some insight. Total nitrogen and potentially mineralizable nitrogen decline in stands older than fifty years (Marion and Black 1988). In some systems, nitrogen is immobilized in microbial products; however, this does not appear to be the case in chaparral topsoil (Fenn et al. 1993). The decline of available soil nitrogen as stands age occurs because the amount sequestered into biomass and recalcitrant soil compounds is greater than inputs. The tendency for stands to become nutrient poor in the decades following fire, particularly in nitrogen, has been suggested to lead to declines in productivity and senescence of plants in old stands (Rundel and Parsons 1980, Marion and Black 1988; however, see Fenn et al. 1993) (Figure 24.9).

Many aspects of decomposition are poorly understood in the chaparral. One in particular is phase three dynamics

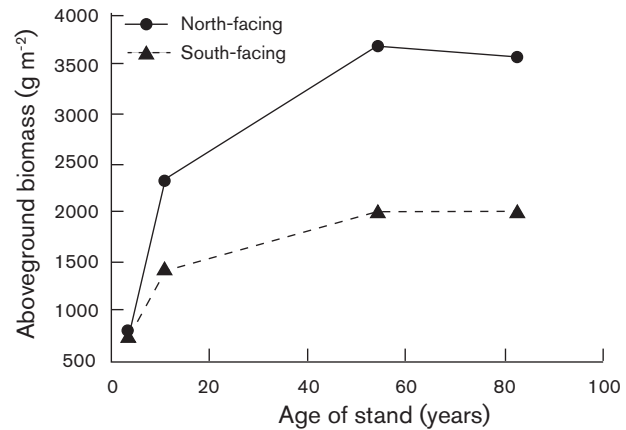


FIGURE 24.9 Relationship between aboveground biomass of shrubs on north- and south-facing slopes and age of chaparral. Source: Data modified from Table 24.1 in Marion and Black 1988. To simplify chronosequence, same-age sites are averaged.

and the controls over longer-term decomposition processes. Another area that is little studied is decomposition in the rhizosphere. Fine root mass has significant turnover in the top 10 to 20 centimeters of soil on a seasonal basis (Kummerow, Krause et al. 1978). Many fine roots in these shallow soil layers die during the summer dry season and then presumably decompose during the following wet season (Kummerow, Krause et al. 1978).

Phosphorous may be a limiting nutrient for some species in long unburned stands as suggested by fertilization studies (Hellmers, Bonner et al. 1955; McMaster et al. 1982). In particular, species that form symbioses with nitrogen-fixing bacteria may have adequate nitrogen but may become phosphorous-limited (Schlesinger and Gill 1980, McMaster et al. 1982, Schlesinger 1985). The majority of phosphorous in chaparral systems is in unavailable forms in the soil (DeBano and Conrad 1978, Rundel 1983). Like nitrogen, but to a lesser degree, available phosphorous increases following fire (Christensen and Muller 1975, Marion and Black 1988). Unlike nitrogen, little phosphorous is lost from the system after fire (DeBano and Conrad 1978, Marion and Black 1988). Phosphorous inputs are from weathering, inorganic solutes in precipitation, dry deposition, and, to a lesser degree, decomposition (Marion and Black 1988). Available phosphorous in older stands (older than fifty years since the last fire) is low and availability is determined by absorption and desorption reactions between soluble phosphorous and soil surfaces (Marion and Black 1988). Chaparral species form associations with mycorrhizal fungi that likely aids in extraction of phosphorous from soils (Allen et al. 1999).

Burning of fossil fuels has led to the production of numerous air pollutants that contain nitrogen (Bytnerowicz and Fenn 1996). Some of these pollutants are dry deposited on chaparral canopies and are then leached to the soil during rains. Areas that have fog may also experience significant wet deposits of nitrogen. An area especially affected is the Los Angeles Air Basin. Because chaparral communities are nitrogen-limited, deposition can lead to higher rates of net productivity (Vourlitis 2012). In areas of high and chronic deposition, the system may become nitrogen-saturated, as has been documented in the portions of the San Gabriel and San Bernardino Mountains (Fenn et al. 1998). Compared to unsaturated systems, nitrogen-saturated systems have elevated leaf

and tissue nitrogen content, nitrate losses from streams, NO loss from the soil, N mineralization and litter decomposition, and lowered pH and base saturation of soils (Fenn et al. 1996, Vourlitis and Fernandez 2012).

Hydrology

Studies have examined the precipitation inputs and losses of chaparral watersheds at the San Dimas Experimental forest in the San Gabriel Mountains in Los Angeles County and at Echo Valley in San Diego (Hamilton and Rowe 1949, Rowe and Colman 1951, Poole et al. 1981). The chief input of precipitation is about seven to fifteen rainstorms during the winter wet season (Cowling et al. 2005). About 78% to 80% of precipitation reaches the soil as throughfall, which falls directly to the soil or drips off the canopy to the soil (Hamilton and Rowe 1949, Poole et al. 1981), and another fraction of water reaches the soil by flowing down stems (Poole et al. 1981). Stemflow is affected by canopy architecture, and species with erect branches and smooth bark have greater stemflow (Hamilton and Rowe 1949). In one study, chamise had greater stemflows than other co-occurring chaparral shrubs (Poole et al. 1981).

Losses of precipitation occur via canopy interception, surface runoff, evaporation from the soil, and $TRANSPIRATION$. Water may be lost through subsurface drainage into fractures in the soil depending on site, and such losses are greater in heavier rainfall years (Rowe and Colman 1951, Hill 1963, Ng and Miller 1980, Poole et al. 1981). Some precipitation intercepted by the canopy evaporates from plant surfaces. The amount of loss from the canopy is determined by the number of rainfall events, the intensity of storms, and the canopy architecture (Poole et al. 1981). Previous studies have found that 5–41% of precipitation is lost due to canopy interception with average losses higher in southern California (Hill 1963, Hill and Rice 1963, Poole et al. 1981). Greater losses may occur when a storm occurs in the warm summer, when canopies have higher levels of leaf area, and when precipitation falls as snow (Poole et al. 1981). Greater numbers of smaller storms leads to greater losses from the canopy (Hamilton and Rowe 1949). With needle leaves and erect branches, chamise has low levels of canopy interception (Poole et al. 1981), whereas species with more leaf surface area intercept more precipitation (Poole et al. 1981).

Surface runoff is the difference between precipitation inputs, soil storage, and $EVAPOTRANSPIRATION$. The amount of precipitation that makes it into the soil storage is dependent on frequency and size of rainfall events, slope, postfire factors, as well as soil structure and chemistry. Soil structure is partially affected by species composition, as is stemflow, thus species-level effects can influence infiltration of precipitation. Surface runoff is generally low but can be high during high rainfall years (Rowe and Colman 1951, Meixner and Wohlgemuth 2003). At a site in San Diego County, surface runoff in average and low rainfall years was low (0–4%) with the greater runoff on north-facing slopes (Ng and Miller 1980, Poole et al. 1981). Farther north in Los Angeles County, runoff of a chaparral watershed has been estimated by streamflow, and the fifteen-year average of streamflow yield was 11% of the total rainfall input (Hill and Rice 1963). During the wettest year, streamflow yield was higher at 21% and during the driest year streamflow yield was trace. More direct smaller-scale measurements of runoff have been made at this site in large

YS METER studies (Patric 1961), which found about 14.5% of precipitation inputs was lost as runoff averaged across five consecutive dry years, and 40% was lost during a wet year (Hill and Rice 1963). Over the short-term, crown fire leads to large increases in surface runoff and streamflow (Meixner and Wohlgemuth 2003). This effect is due to a decline in evapotranspiration and the formation of hydrophobic soils after fire (DeBano et al. 1977, Valeron and Meixner 2010).

The chief loss of water is due to evapotranspiration. In lysimeter studies virtually all of the water that enters the soil is lost to evapotranspiration during below-average rainfall years, and more than 80% of it is lost during years when rainfall is substantially above average (Patric 1961). A chamise-dominated south-facing slope can show 80% loss due to evapotranspiration, whereas a north-facing slope of mixed chaparral with greater leaf area can lose virtually all of the precipitation input to evapotranspiration (Ng and Miller 1980). Estimates of the separate contribution of evaporation and transpiration have been made in a chamise-dominated stand, in which the amount of water transpired is about equal to the amount evaporated (Poole et al. 1981). However, in mixed chaparral stands with greater canopy cover, transpiration is about three times greater than evaporation (Poole et al. 1981). Hydraulic redistribution refers to the movement of water by plant roots from one soil compartment to another down a water potential gradient. Such water fluxes may be an important factor affecting the hydrology of chaparral sites, particularly in its effects on evapotranspiration. Studies of hydraulic redistribution are currently lacking for chaparral sites.

Ecosystem Services

Ecosystem services describe the ways that ecosystems benefit people. Such services can be categorized as regulating (e.g., climate, flooding), provisioning (e.g., food, fuel, fresh water), supporting (e.g., nutrient cycling and carbon sequestration), and cultural (e.g., aesthetic, educational, recreation) (Millennium Ecosystem Assessment 2005). Chaparral provides services in each of these categories. For regulating services, chaparral vegetation absorbs sunlight and transpires water—both of which help to regulate temperature during the hot summer months compared to highly urbanized areas that experience the “heat island effect” (LaDochy et al. 2007). The growth of shrublands on steep hillsides helps to reduce flooding, erosion, and mudslides that can occur during heavy rains that commonly occur each winter (Gabet and Dunne 2002). This service is especially apparent after chaparral has been removed by fire, and heavy winter rains cause costly and lethal mudslides (Ren et al. 2011).

Provisioning services of chaparral includes filtration of rainwater, which helps to maintain fresh drinking water in aquifers and reduce $EUTROPHICATION$ in the ocean and reservoirs that receive runoff. This is important in some areas where nitrogen deposition is high and nitrogen pollutants such as nitrate might be more prone to leach into groundwater supplies and collect in downstream bodies of water. Areas that were formerly chaparral that have been converted to grassland are not as effective at filtering water and they yield greater nitrate runoff (Riggan et al. 1985). In areas where nitrogen pollution is the most severe, such as some watersheds in the San Bernardino and San Gabriel Mountains northeast of Los Angeles, runoff of nitrate is among the highest in the United States (Fenn and Poth 1999).

Supporting services include carbon sequestration with stands of chaparral, even very old ones, acting as carbon sinks (Luo et al. 2007). The pollination services provided by native bees are associated with the amount of nearby natural habitat (including chaparral) where these bees reside (Kremen et al. 2004). As discussed already, chaparral vegetation has a substantial impact on the hydrology of a watershed. Studies conducted in the Transverse mountain range at the San Dimas Experimental Station manipulated the vegetation in an effort to increase usable water. Chaparral and riparian vegetation was removed from a portion of the watershed and this increased water yield from the watershed (Hill and Rice 1963, Meixner and Wohlgenuth 2003). This result confirms many studies that removing chaparral or any vegetation type that is deeply rooted reduces transpiration of the system. Increases in water yield by removing chaparral are likely to come at the expense of water quality, a reduction in temperature regulation services, and a loss in cultural services.

Cultural services provided by chaparral systems are high. Chaparral systems are located in some of the largest metropolitan areas in North America such as Los Angeles. This ensures that there are many millions of visitors to these shrublands for recreation activities such as hiking, biking, horse riding, and camping. The presence of chaparral on the low-elevation slopes beautifies the landscape. The educational impact of chaparral is high due to the large numbers of parks, colleges and universities, and organizations that operate near chaparral systems. For example, the Santa Monica Mountains National Recreation Area is a park in southern California that receives about thirty-five million visitors annually with outreach and educational programs that target people of all ages.

The Future of Chaparral

Predictions are that the climate in California will be increasingly warmer and drier in the coming decades (Hayhoe et al. 2004); however, there is uncertainty in this prediction because rainfall may increase in some regions of California (Neelin et al. 2013). The water deficits for chaparral shrublands will depend on interplay between temperature, the amount and timing of rainfall, and local soil water storage dynamics. Of paramount importance will be how the changing climate affects extreme weather patterns (maximum and minimum temperatures and drought intensity) and wildfire (Westerling et al. 2006). Extreme events such as the record droughts since 2012 and heat waves will likely have direct impacts on chaparral communities. These effects are already evident at the arid ecotones where chaparral mixes with desert scrub communities and some adult chaparral species have experienced significant levels of mortality (Paddock et al. 2013). Increases in minimum nighttime temperature (Crimmins et al. 2011) will affect species whose current distributions are limited by subzero temperatures (Ewers et al. 2003, Davis et al. 2005, Davis et al. 2007). Higher nighttime temperatures may lead to greater rates of respiration with implications for carbon balance. Climate will likely interact with fire to drive change. For example, a recent study found that postfire resprouts of some species suffered high levels of mortality in the first year after a fire during an intense drought, whereas adjacent unburned plants did not suffer mortality (Pratt et al. 2014).

One of the most immediate and devastating affects to chaparral communities is alteration of the fire regime. Chaparral

stands are generally not resilient to short fire-return intervals less than about fifteen to twenty years (Zedler et al. 1983, Jacobsen et al. 2004, Keeley et al. 2005b). Such short return intervals have become more common due to anthropogenic ignitions and the abundant fine fuels produced by annual alien grasses in disturbed areas (Brooks et al. 2004). If short fire-return interval fires continue or increase in the future, increasing areas of chaparral communities will be converted into homogenous savannahs where only the most vigorous resprouters persist (e.g., laurel sumac in southern California).

Other aspects of climate change, such as increasing CO₂, may increase water-use efficiency and alter patterns of fuel moisture in ways that potentially could offset increasing fire ignition hazard due to warmer temperatures (Oechel et al. 1995); however, CO₂ may also stimulate biomass accumulation and lead to an increase in fuels and high-intensity fires. Increased CO₂ will also subtly shift the importance of the less well-known microbial communities as already low levels of nutrients may become more limiting and cascade along food webs (Oechel et al. 1995). Because of its presence at or near the boundaries of urban developments and metropolitan centers, conflicts between the impacts of chaparral wildfire and human life and structures likely will increase without intelligent regional development policies. Historically the primary management focus on chaparral has been one of fuels and fire hazard (Parker 1987, 1990; see Chapter 3, "Fire as an Ecosystem Process"); indeed that was the primary motivation for the development of the vegetation-type mapping project begun in the late 1920s (Keeley 2004). Today fire hazard and watershed hydrology are the primary foci of management, and the maintenance of chaparral cover for its critical role in hydrology will increase in importance in a future with potentially less precipitation and warmer temperatures.

Summary

Chaparral shrublands are biotically diverse and the most abundant vegetation type in the state. These shrublands are dominated by evergreen species and occur in areas with hot, dry summers and cool, moist winters. The species that inhabit the chaparral are adapted to a Mediterranean-type climate. Chaparral is a dynamic ecosystem, and wildfires (see Chapter 3, "Fire as an Ecosystem Process") facilitated by the summer rainless period are more predictable than in many other fire-prone landscapes; this is reflected in many evolutionary responses to fire. While diverse in microbes and animals, the dominant plants exhibit characteristics explicitly selected by wildfire in their development of persistent soil or canopy seed banks. Chaparral ecosystems provide many services, such as the stabilization of steep slopes, filtration of drinking water, and myriad recreational opportunities. They also beautify the landscape for many millions of California inhabitants and visitors. Increasingly, chaparral is being managed for its intrinsic value to resource conservation and even community restoration programs. There are many threats to chaparral ecosystems from climate change, altered fire regimes, development, non-indigenous invasive species, and poor management practices.

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Glossary

- ARBUSCULAR MYCORRHIZAE** Mycorrhizae are mutualistic associations between higher fungi and vascular plants. In arbuscular mycorrhizae the fungus forms hyphae that penetrate the cell walls of plant roots, where they form structures (arbuscules) with large surface areas that facilitate the exchange of minerals and carbohydrates. The fungi involved in arbuscular mycorrhizae are from a lineage in the Zygomycetes.
- CATIONS** A positively charged atom or molecule such as potassium and calcium.
- CAVITATION** The breaking of the water column in vessels or tracheids whereupon liquid water changes to water vapor ultimately leading to emboli. Plants differ in their susceptibility to cavitation, but it is common in the vascular tissues when water content of the soil is low or during episodes of freezing and thawing.
- DETRITIVORES** These heterotrophic organisms consume detritus (which is decomposing plant and animal parts) to obtain energy and minerals, and consequently they contribute to decomposition and the nutrient cycles.
- ECTOMYCORRHIZAE** These mycorrhizae (mutualistic associations between higher fungi and vascular plants) are characterized by the presence of a fungal mantle covering the plant host roots with some fungal hyphae penetrating between root cells (called a Hartig net). The fungi are usually from two fungal groups, Basidiomycetes and Ascomycetes.
- EMBOLI (SING. EMBOLUS)** These gas bubbles form following cavitation in the water and transport cells (vessels or tracheids) within plant vascular tissue.
- EUTROPHICATION** The response of an aquatic system to pollutants contained in runoff. In the case of nitrogen pollutants, this response is often a bloom of algal growth that can choke waterways and lead to the reduction in oxygen levels to levels lethal to some species.
- EVAPOTRANSPIRATION** The sum of the water lost via evaporation and transpiration.
- FACULTATIVE SEEDERS** Shrubs or trees that survive wildfire and sprout new shoots after the fire. These types of plants also have persistent soil seed banks that fire stimulates, and they recruit new individuals from seedlings that successfully establish in the postfire environment.
- FOLIVORE** An herbivore that specializes in eating leaves.
- LYSIMETER** A device used to measure the evapotranspiration from plant/soil systems as the difference between precipitation inputs and water lost through the soil.
- MYCORRHIZA (PL.: MYCORRHIZAE)** A symbiotic, mutualistic (but occasionally weakly pathogenic) association between a fungus and the roots of a vascular plant. Mycorrhizae are critical in bringing water and minerals to their host plant, which in turn provides carbon energy to the fungus.
- MYCOTA** Refers to species from the kingdom Fungi.
- NITRIFICATION** The oxidation of ammonia into nitrate by microorganisms.
- OBLIGATE RESPROUTER** Shrubs or trees that can survive wildfire and sprout new shoots after the fire. Generally no seedlings are recruited in the postfire environment.
- OBLIGATE SEEDERS** Shrubs or trees that are killed by wildfire and persist in the habitat because they have persistent soil seed banks that fire stimulates. Obligate seeders recruit new individuals after wildfire from the seed bank and establish new populations in the postfire environment.
- PERSISTENT SEED BANK** Refers to viable seed constantly being found in the soil unless stimulated by a strong environmental event such as a wildfire.
- PHYSICAL DORMANCY** When referring to seeds, this generally means that there is a thick seed coat or other structure that does not allow water or gasses to enter a seed, keeping the seed in a dormant state.
- PHYSIOLOGICAL DORMANCY** When referring to seeds, this generally means that there are physiological processes that have to be met before normal metabolism will stimulate germination; examples are light, temperatures, and chemicals from smoke.
- PYRO-ENDEMIC** Refers to annual or short-lived plants that are only found in postfire stands of vegetation.
- SCLEROPHYLLOUS** Refers to plants or to a vegetation indicating plants have generally small tough leaves with thick cuticles; usually an adaptation to low water availability and nutrient-poor soils.
- SEED BANK** Viable plant seed stored in the soil or in serotinous cones or woody fruit in the canopy of a tree or shrub.
- SEROTINOUS** Having seed held in woody cones or fruit rather than releasing at seed maturation. Release occurs in response to an environmental trigger, usually fire, or death of the stem.
- SPECIFIC LEAF AREA (SLA)** The fresh leaf area divided by the oven-dry mass; SLA is an index of sclerophylly with lower values being more sclerophyllous.
- STRATIFICATION** Some seeds require a chilling period (generally several degrees above freezing) that lasts a minimum time period (weeks to months) before dormancy is broken and germination can occur; the chilling is called stratification.
- SUFFRUTESCENT** A small shrub having a stem that is woody only at the base or some of the main stems; generally the wood is light.
- TRANSIENT SEED BANK** Refers to all seed germinating or losing viability within a year such that there is a fraction of the year with no seed stored in the soil.
- TRANSPIRATION** Loss of water through the tiny pores (stomata) of plant leaves.
- WATER POTENTIAL** The potential energy of water relative to pure water. It is used as a measure of plant water status

with more negative values indicating that tissues are more dehydrated.

XYLEM The vascular system of plants that conducts water. Cells are usually dead and hollow at maturity.

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