

Chaparral

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Introduction

Chaparral is the evergreen sclerophyllous shrubland that dominates the cismontane side of coastal mountain ranges from about San Francisco south to Ensenada in Baja, California, as well as the foothills of the Sierra Nevada (Fig. 13.1). The dense impenetrable nature of chaparral (Fig. 13.2) means that it is largely off limits to all but the more dedicated ecologists and other naturalists. It is primarily known for the spectacular crown fires that frequent chaparral and

the associated urban environments with which it is often juxtaposed. Previous reviews that include topics not covered here are in Cooper (1922), Hanes (1977), Keeley and Keeley (1988) and Keeley (2000).

Biogeographical Patterns

Chaparral is distributed from northwestern Baja, California, to south-central Oregon, with disjunct stands on mountaintops farther south in Baja, California, and arid interior slopes as far north as Washington. It reaches its greatest extent in the Transverse and Peninsular ranges of central and southern California but is also an important part of the western foothills of the interior Sierra Nevada. It continues farther east in patches on "sky islands" of desert ranges and then in a broad mid-elevation band across central and southern Arizona. Small patches of chaparral also occur in an oak and pine mosaic landscape of the Sierra Madre Occidental of mainland Mexico and in larger stands in the Sierra Madre Oriental south of Monterey, Mexico (Keeley 2000).

At a regional scale chaparral tends to dominate at elevations from 300 to 1,500 m, but under favorable maritime conditions can reach down to sea level and on south-facing slopes and ridges that extend higher into the coniferous zone. Chaparral in California ranges over nearly 10 degrees of latitude, and its elevational distribution is considerably higher at the southern than the northern end of the state. When elevations are adjusted to a reference latitude of San Diego, 40% of mapped chaparral occurs between 1,000 and 1,500 m, and 90% occurs below 2,000 m (Table 13.1).

Within this elevational zone, landscapes comprise a mosaic of different vegetation types including chaparral, sage scrub, grassland, and oak woodland. Chaparral is naturally displaced by woodlands on very mesic slopes and by sage scrub on xeric slopes. Grasslands, the vast majority of which are disturbance-dependent annual alien grasslands (Huenneke 1989), often

FIGURE 13.1 Distribution of chaparral in California.



occupy former shrublands that were displaced by frequent burning, beginning with the Native Americans (Cooper 1922; Wells 1962; Keeley 2002).

Chaparral is closely associated with the Mediterranean climate pattern of winter rain and summer drought. Within that regime it can be found under a wide range of rainfall and temperature conditions, but over 60% of the present distribution is in areas receiving between 250 and 750 mm of annual precipitation and where average January daily temperature falls between 5°C and 15°C (Table 13.2). These patterns are consistent with studies indicating that summer drought stress may limit chaparral shrub seedling establishment and that injury to adult shrubs from winter freezes may impose species-specific distributional limits (Langan, Ewers, and Davis 1997; Boorse, Ewers, and Davis 1998).

Chaparral soils tend to be shallow and rocky except near the coast where it occurs on deep Aeolian sands of marine benches and terraces. Substrates include fractured sandstones and shales, coarse-grained decomposed granitic soils, fine-grained weathered volcanics, and mafic substrates such as serpentinite and gabbros. Mafic substrates have a variety of effects on chaparral, the most obvious being the number of

endemic plant species (Kruckeberg 1984). These substrates add to the landscape diversity and have substantial effects on plant species diversity (Harrison and Inouye 2002). The lowered productivity of these soils slows the rate of fuel accumulation and reduces fire frequency, thus favoring slow growing serotinus conifer species, because of both reduced postfire competition and longer fire-free intervals (Keeley and Zedler 1998). Lower productivity maintains a more open habitat and higher plant diversity than chaparral on more fertile sites, although the postfire increase in diversity is lower (Safford and Harrison 2004).

Flora

California, like other Mediterranean climate regions, supports exceptionally high plant diversity (4,846 native vascular species) and endemism (1,693 species [35%] are confined entirely or nearly entirely to the State; Cowling et al. 1996; CalFlora 2005). These levels of species richness and endemism are lower than the Mediterranean climate regions of the Cape Region of South Africa or Southwest Australia, but on a per-area basis are still six to seven times higher than the



FIGURE 13.2 Mixed chaparral in the San Gabriel Mountains of southern California. White flowering shrub is *Ceanothus crassifolius*. Photograph by J. Keeley.

continental United States. According to the Calflora database, 1,177 (24%) of the state's native vascular species occur in chaparral communities, and 497 (42%) of these are endemics. Most of these species are also associated with several other communities. The life-form spectrum of chaparral-associated species is similar to that of the flora as a whole but is proportionally higher in annual herbs, perennial bulbs, and shrubs and lower in other perennial herbs (Table 13.3). Only 110 species, half of them shrub species, are associated solely with chaparral vegetation in the Calflora database. Notably, 76 of those chaparral-restricted species (69%) are endemic to California, and 62 (56%) are considered rare (Calflora).

Like other Mediterranean-climate regions, much of the diversity (25%) in the state is contributed by rare and localized species (Cowling et al. 1996). Chaparral leads other communities in the number of rare plant taxa, having 18% more than expected based on areal extent (Keeley 2005). Within this shrubland vegetation, rarity is not randomly distributed across growth forms. Annuals are very underrepresented on the rare plant list, whereas there are three times more rare herbaceous perennials and double the number of shrub species than expected based on the total number of species.

Landscape relations to plant species richness have been broadly studied in the California flora, and climatic variables, in particular precipitation, are the strongest predictors of diversity (Richerson and Lum 1980). In this region the marked orographic gradient results in a strong relationship between elevation and precipitation, and not surprising, elevation is also a strong predictor of plant diversity (Qi and Yang 1999). Chaparral covers a large elevational gradient, and this factor, perhaps acting through effects on precipitation, is a major determinant of diversity (Keeley, Fotheringham, and Baer-Keeley 2005b).

Ninety percent of chaparral's mapped distribution falls within 74 of 284 geographic subregions created by Harrison et al. (2000) for their analysis of serpentine species diversity patterns as encoded in the Calflora database. Contrary to patterns for the flora as a whole, the number of chaparral-associated species in these 74 units is only moderately correlated with subregion area ($r = -0.23$) or climate factors such as annual precipitation ($r = -0.27$) and is better predicted by the $\log(\text{area})$ of chaparral ($r = 0.60$) and mean ($r = -0.57$) or minimum ($r = -0.68$) latitudinally adjusted elevation in the subregion (Figs. 13.3a-c). A robust regression model accounting for chaparral area, subregion area, and minimum elevation explains 80% of the total variation in chaparral plant species richness and leaves little evidence of strong regional or latitudinal gradients in the diversity of the chaparral flora (Figs. 13.3b and 13.3c). The only systematic pattern at this scale appears to be the decreased richness in the chaparral flora with increasing elevation or decreasing winter temperatures.

The composition of the chaparral flora by geographic subregion indicates fairly steep species turnover with distance. For example, the list of species associated with chaparral in western San Diego County is 42% dissimilar to that listed for the San Bernardino Mountains and 73% dissimilar to the chaparral flora of southern Lake County (Fig. 13.4a), regions of nearly identical size and chaparral extent. Again using comparable subregions, the chaparral flora of western Calaveras County in the central Sierra Nevada is 54% dissimilar to that of central Siskiyou County to the north, and 88% dissimilar to that of the northern foot slopes of the San Gabriel and San Bernardino Mountains to the south (Fig. 13.4b).

Steep geographic turnover is found not only among chaparral-associated species but also among chaparral-restricted species and community dominants (Table 13.4). The two most diverse woody genera—*Ceanothus* and *Arctostaphylos*—both contain many narrowly endemic taxa. Of the 50 *Ceanothus* taxa (species and varieties) listed in the Calflora database, 43 (86%) are recorded in subregions totaling less than 40,000 km² (Fig. 13.5). Similarly, 71/81 *Arctostaphylos* taxa have recorded ranges less than 40,000 km² (Fig. 13.6). Cody (1986) estimated a local turnover rate of 50% of the species in these two genera within a distance of 100 to 300 km, depending on the steepness of local environmental gradients. These replacement patterns are illustrated in the distribution patterns of four closely related *Ceanothus* species in the subgenus *Cerastes* (Fig. 13.7). Similar elevational replacements have also been described by Zedler (1995a).

TABLE 13.1
Distribution of Chaparral Vegetation by Elevation

Adjusted Elevation (m)	Area in State (km ²)	Chaparral Area (km ²)	Chaparral as % State Area	% of Chaparral Area
0–500	86,430	927	1.07	3.78
500–1,000	113,703	7,856	6.91	32.05
1,000–1500	75,397	9,961	13.21	40.64
1,500–2000	47,686	3,884	8.14	15.85
2,000–2500	49,042	1,348	2.75	5.50
2,500–3000	20,826	484	2.32	1.97
3,000–3500	7,516	44	0.59	0.18
3,500–4000	3,513	5	0.14	0.02
>4,000	655	0	0.00	0.00
Total	404,768	24,509	6.06	100.00

NOTE: To adjust for the effect of increasing latitude, 0.625 m is added to elevation for every km north from the southernmost point in the state. Statewide maps of chaparral and elevation were combined to produce the statistics.

TABLE 13.2
Percentage of Chaparral Area in Different Combinations of Mean January Temperature and Total Annual Precipitation

Mean Jan temp (°C)	Mean Annual Precipitation (mm)								Total
	0–250	250–500	500–750	750–1,000	1,000–1,250	1,250–1,500	1,500–2,000	>2,000	
< –5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
–5–0	0.0	0.0	0.2	0.5	0.4	0.2	0.2	0.0	1.6
0–5	0.0	1.2	4.5	1.4	1.5	1.0	1.2	0.4	11.3
5–10	0.6	7.5	13–5	8.2	4.9	2.3	0.5	0.2	37.5
10–15	0.7	25.2	15.4	3.6	0.8	0.2	0.0	0.0	46.0
>15	0.1	3.3	0.0	0.0	0.0	0.0	0.0	0.0	3.4
Total	1.4	37.3	33.7	13–8	7.6	3.8	1.9	0.6	100.0

NOTE: Based on overlay of statewide maps of chaparral and climate data.

Relatively few dominant chaparral shrub species are widespread, the exception being *Adenostoma fasciculatum*. Perhaps most striking are the chaparral landscapes where this species is absent (Fig. 13.8). Specifically, desert borders in southern California, much of the Tehachapi Range (Bauer 1930), above 1,000 m in interior drainages of the southern Sierra Nevada, and montane chaparral and eastside chaparral of the Sierra Nevada and Cascade ranges. On the desert border and interior drainages of the southern Sierra Nevada a couple of the dominants that replace *A. fasciculatum* are *Ceanothus cuneatus* (Fig. 13.7) and *Cercocarpus betuloides*. Based on climatic analysis of their geographic ranges Westman (1991) showed that the latter two species occupied a similar precipitation range (500–750 mm) as *A. fasciculatum*,

but were more tolerant of lower January temperatures than *A. fasciculatum*. Indeed, Malanson, Westman, and Yan (1992) place the optimum growth position of *A. fasciculatum* at 9°C–12°C for the coldest month but at 0°C–3°C for *C. cuneatus*. The extreme winter temperatures on many of these interior and northern sites is likely to be the main factor limiting the distribution of *A. fasciculatum*, and this may be the primary reason it is absent from Arizona chaparral.

A number of chaparral shrub species have distributions far outside the California Mediterranean climate region, yet seldom dominate chaparral in the state. These include *Garrya* spp., *Rhamnus crocea/ilicifolia* and *Rhus ovata*, all common elements in the Arizona chaparral. A few California chaparral species, *Rhamnus californica*, *Ceanothus greggii*, and

TABLE 13.3
Life-form Spectra for All California Native Vascular Plant Species, Species Associated with Chaparral,
and Species Limited to Chaparral

	<i>All Native Species</i>	<i>% All Native Species</i>	<i>Chaparral Species</i>	<i>% Chaparral Species</i>	<i>Chaparral Only Species</i>	<i>% Chaparral Only Species</i>
Life form						
Annual herb	1,443	29.78	409	34.75	27	24.55
Annual herb (aquatic)	9	0.19	2	0.17		
Annual herb (hemiparasitic)	8	0.17	2	0.17	1	0.91
Annual herb, Vine	1	0.02				
Annual herb, Vine (parasitic)	8	0.17	2	0.17		
Annual, Perennial herb	76	1.57	20	1.70	1	0.91
Annual, Perennial herb (aquatic)	2	0.04	2	0.17		
Annual, Perennial herb (rhizomatous)	1	0.02	1	0.08		
Perennial herb	2,185	45.09	389	33.05	19	17.27
Perennial herb (aquatic)	40	0.83	4	0.34		
Perennial herb (bulb)	68	1.40	29	2.46	1	0.91
Perennial herb (carnivorous)	3	0.06				
Perennial herb (hemiparasitic)	11	0.23				
Perennial herb (mosslike)	5	0.10	1	0.08		
Perennial herb (parasitic)	28	0.58	2	0.17	1	0.91
Perennial herb (rhizomatous)	162	3.34	25	2.12	2	1.82
Perennial herb (saprophytic)	6	0.12				
Perennial herb (stem succulent)	1	0.02				
Perennial herb, Shrub	10	0.21	2	0.17		
Perennial herb, Vine	14	0.29	8	0.68	1	0.91
Perennial, Biennial herb	1	0.02				
Shrub	543	11.21	219	18.61	54	49.09
Shrub (parasitic)	5	0.10				
Shrub (stem succulent)	47	0.97	9	0.76		
Shrub, Perennial herb	3	0.06				
Shrub, Tree	1	0.02				
Tree	84	1.73	22	1.87	2	1.82
Tree, Shrub	62	1.28	26	2.21	1	0.91
Vine	4	0.08				
Vine, Shrub	11	0.23	3	0.25		
Unclassified	4	0.08				
Grand Total	4,846	100.00	1,177	100	110	100.00

SOURCE: CalFlora database, December 2004.

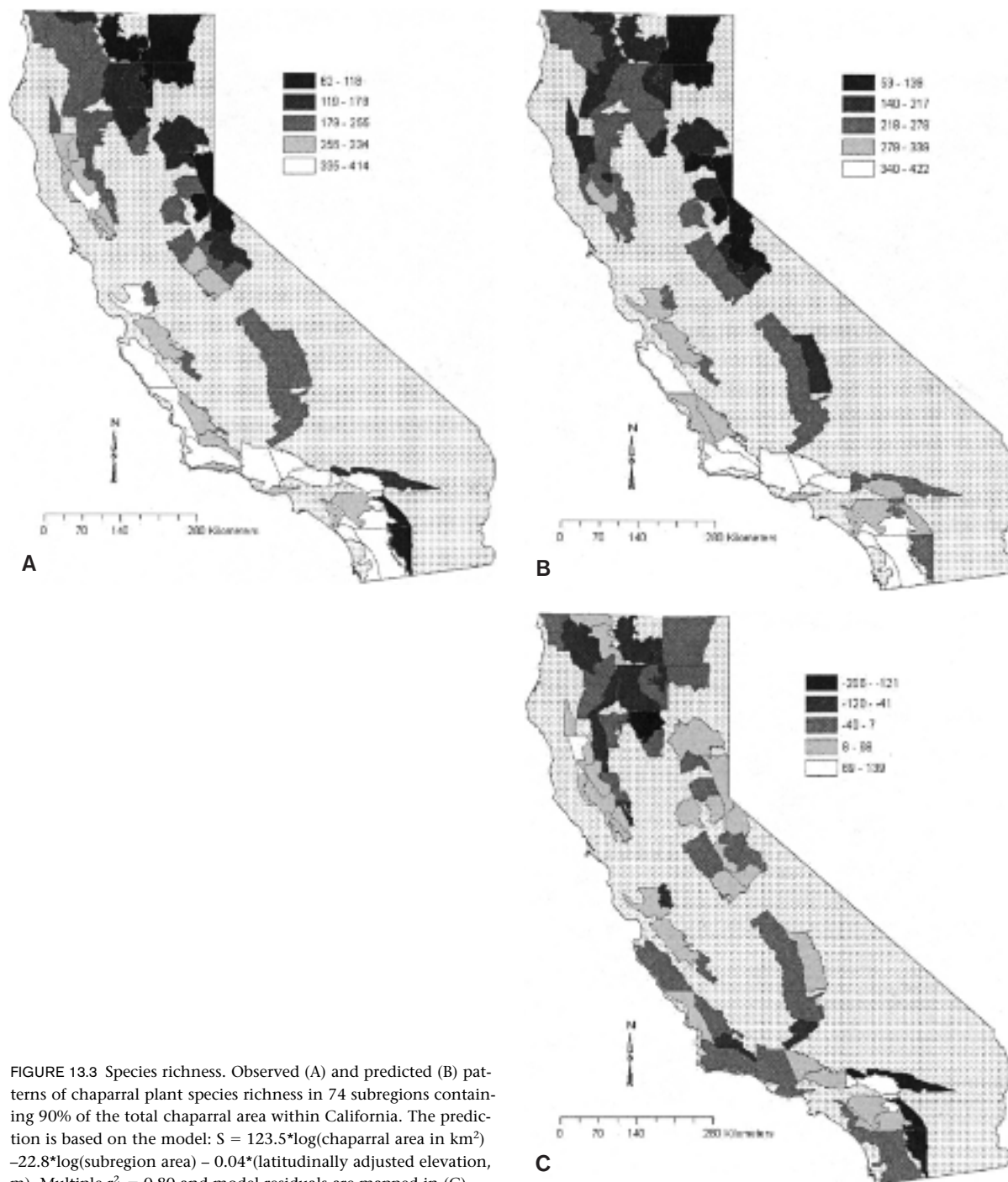


FIGURE 13.3 Species richness. Observed (A) and predicted (B) patterns of chaparral plant species richness in 74 subregions containing 90% of the total chaparral area within California. The prediction is based on the model: $S = 123.5 \cdot \log(\text{chaparral area in km}^2) - 22.8 \cdot \log(\text{subregion area}) - 0.04 \cdot (\text{latitudinally adjusted elevation, m})$. Multiple $r^2 = 0.80$ and model residuals are mapped in (C).

Arctostaphylos pungens are found in Arizona chaparral and also are important elements in the Sierra Madre Oriental chaparral of northeastern Mexico (Keeley 2000).

Community Patterns

In the absence of disturbance, communities are dominated by shrubs and subshrubs with a minor representation of other growth forms such as lianas, vines, geophytes, and annuals. Composition often changes markedly after fire

with the sprouting of dormant bulb and seed banks. With rare exceptions the prefire dominants persist after fire either as resprouts from basal buds or from dormant seed banks. On complex landscapes there is a diversity of floristically different plant associations not easily explained by any single factor (Keeley 2000).

Although *Adenostoma fasciculatum* sometimes forms nearly pure stands, more often it occurs in mixed stands with species of *Ceanothus* and *Arctostaphylos*. For example, maritime chaparral, associated with sandy substrates in

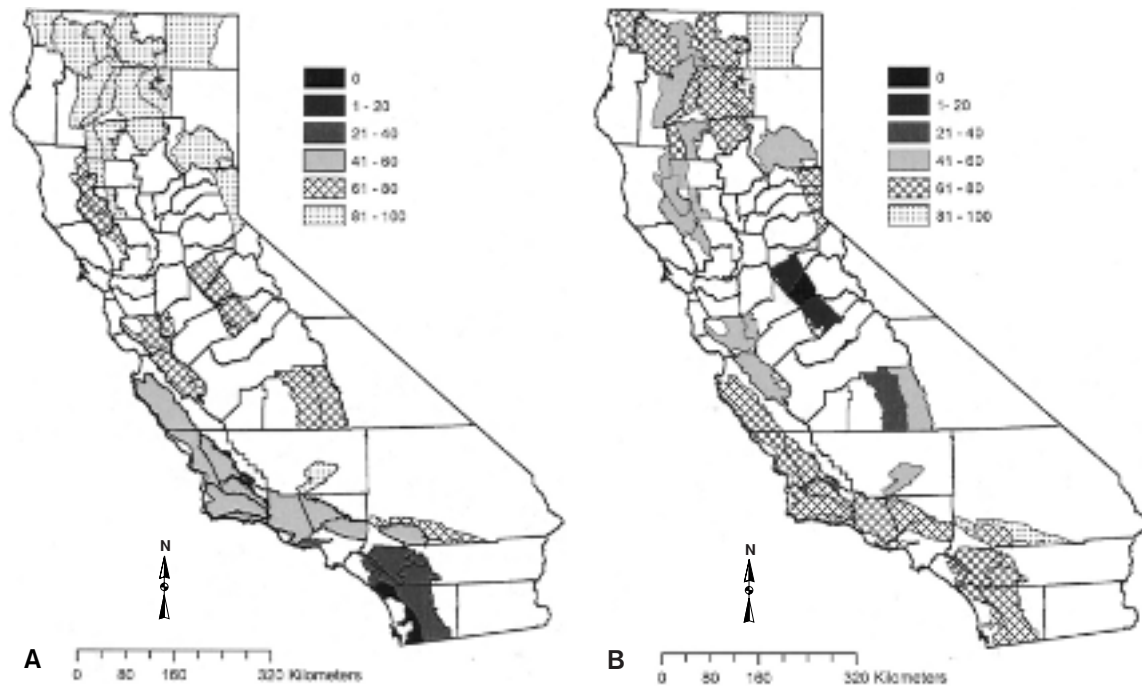


FIGURE 13.4 Sorensen percentage dissimilarity between the chaparral floras of western San Diego County (A) or western Calaveras County (B) and 47 other geographic subregion containing 75% of the current distribution of California chaparral. See Veirs et al. (2006) for description of the database used in the analysis.

level or rolling terrain within 10 to 20 km (6–12 miles) of the coast, occurs in Torrey Pines State Reserve in San Diego and is scattered along the coast from northern Santa Barbara County to Sonoma County. Although *Adenostoma fasciculatum* co-dominates maritime chaparral throughout the range of the maritime chaparral type, there is geographical replacement of rare endemic ceanothus and manzanita species from south to north; *Ceanothus verrucosus*/*A. glandulosa* ssp. *crassifolius* in San Diego, *C. impressus*/*A. rudis*/*A. purissima* in Lompoc, *C. rigidus*/*A. morroensis* near Morro Bay, and *C. cuneatus* var. *rigidus*/*A. hookeri* ssp. *hookeri*/*A. pajaroensis* near Monterey.

On highly dissected landscapes community composition is rather fine grained with communities varying between arid, usually south-facing slopes and ridges, and mesic, north-facing exposures. One of the strongest determinants of community composition is a soil moisture pattern; thus associations can be recognized as characteristic of the arid or mesic end of this gradient. Chamise (*Adenostoma fasciculatum*) is the nearly ubiquitous dominant on most arid chaparral sites. Also, well developed on arid south-facing slopes and ridges are nonsprouting species of ceanothus (*Ceanothus* spp.) (Fig. 13.2) or manzanita (*Arctostaphylos* spp). More mesic north-facing slopes often favor associations comprising broader-leaved evergreen shrubs, including scrub oak (largely *Quercus berberidifolia* but occasionally *Q. wizlizenii*), coffeeberry (*Rhamnus californica*), redberry (*R. crocea*), silk tassel (*Garrya* spp.), holly leaf cherry (*Prunus ilicifolia*), and chaparral holly (*Heteromeles arbutifolia*). Even more fine-grained

distribution patterns on individual slope faces can be related to cold air drainage patterns and freezing tolerance of different species (Davis, Pratt, and Bowen 2004).

Community Classification

Different workers have classified chaparral communities by a combination of environmental factors (e.g., maritime chaparral, serpentine chaparral, montane chaparral, semi-desert chaparral; mesic north-slope chaparral, xeric south-slope chaparral) and dominant genera (e.g., ceanothus chaparral, manzanita chaparral; e.g., Horton 1960; Hanes 1977; Mayer and Laudenslayer 1988). Holland's (1986) widely used system identified 28 chaparral communities defined by environment and dominant species. Most recently, Sawyer and Keeler-Wolf (1995) have adopted the national hierarchical vegetation classification system to California and described chaparral alliances defined by one or 2 dominant species as well as a number of associations within alliances based on quantitative plots measurements. Their list of chaparral types includes 9 "undifferentiated" chaparral scrub types and more than 60 alliances including 9 chamise alliances, 15 ceanothus alliances, 10 manzanita alliances, 18 scrub oak alliances, and 4 redshank (*Adenostoma sparsifolium*) alliances.

Although this floristically based system has advantages as a naming system for some resource management purposes, it is of more limited value to ecologists interested in community structure and function (Zedler 1997), the primary limitation being the independent nature of species

TABLE 13.4

Common Shrubs in Chaparral and their Regeneration Characteristics in the First Postfire Year

<i>Scientific Family/Species Name</i>	<i>Common Name</i>	<i>Seedling Recruitment^a</i>	<i>Basal Sprouting^b</i>
Anacardiaceae			
<i>Malosma laurina</i>	laurel sumac	postfire	yes
<i>Rhus ovata</i>	sugar bush	postfire	yes
Ericaceae			
<i>Arctostaphylos glauca</i>	big-berry manzanita	postfire	no
<i>A. glandulosa</i>	Eastwood manzanita	postfire	yes, burl ^c
<i>A. hookeri</i>	Hooker manzanita	postfire	no
<i>A. manzanita</i> ssp. <i>roofii</i>	Common manzanita	postfire	yes, burl ^d
<i>A. parryana</i> ssp. <i>parryana</i>	Parry's manzanita	postfire	no
<i>A. parryana</i> ssp. <i>tuberescens</i>	Parry's manzanita	postfire	yes, burl ^d
<i>A. rainbowensis</i>	Rainbow manzanita	postfire	yes, burl
<i>A. rudis</i>	sand mesa m.	postfire	no/yes, burl ^e
<i>A. stanfordiana</i>	Stanford's manzanita	postfire	no
<i>A. tomentosus</i>	woolly-leaf manzanita	postfire	yes, burl
<i>A. viscida</i>	white-leaf manzanita	postfire	no
<i>Xylococcus bicolor</i>	mission manzanita	unknown (rare)	yes, burl
Fabaceae			
<i>Pickeringia montana</i>	chaparral pea	unknown	yes
<i>Prunus ilicifolia</i>	holly-leaved cherry	older stands	yes
<i>Quercus berberidifolia</i>	scrub oak	older stands	yes
<i>Q. durata</i>	leather oak	older stands	yes
<i>Q. garryana</i> var. <i>breweri</i>	Brewer's oak	older stands	yes
<i>Q. wizlizenii</i>	shrub live oak	older stands	yes
Garryaceae			
<i>Garrya</i> spp.	silk tassel	postfire	yes, burl
Rhamnaceae			
<i>Ceanothus crassifolius</i>	hoaryleaf ceanothus	postfire	no
<i>C. cuneatus</i>	buck brush	postfire	no
<i>C. greggii</i>	cupleaf ceanothus	postfire	no
<i>C. impressus</i>	Santa Barbara ceanothus	postfire	no
<i>C. leucodermis</i>	chaparral whitethorn	postfire	yes, burl
<i>C. megacarpus</i>	bigpod ceanothus	postfire	no
<i>C. oliganthus</i>	hairy ceanothus	postfire	no
<i>C. spinosus</i>	greenbark ceanothus	postfire	yes, burl
<i>C. tomentosus</i>	woolly-leaf ceanothus	postfire	

TABLE 13.4 (continued)

Scientific Family/Species Name	Common Name	Seedling Recruitment ^a	Basal Sprouting ^b
<i>var. tomentosus</i>			yes ^f
<i>var. olivaceous</i>			no
<i>C. verrucosus</i>	wart-stemmed ceanothus	postfire	no
<i>Rhamnus californica</i>	coffeeberry	older stands	yes
<i>R. crocea</i>	redberry	older stands	yes
Rosaceae			
<i>Adenostoma fasciculatum</i>	chamise	postfire	yes, burl
<i>A. sparsifolium</i>	red shank	unknown	yes, burl
<i>Cercocarpus betuloides</i>	mountain mahogany	various disturbances	yes, base and rhizomes
<i>Heteromeles arbutifolia</i>	chaparral holly	woodland gaps	yes
Sterculiaceae			
<i>Fremontodendron</i> spp.	flannel bush	postfire	yes

NOTE: Postfire obligate seeders are non-sprouting species with postfire seedling recruitment. Postfire facultative seeders are sprouters with postfire seedling recruitment. Postfire obligate resprouters resprout but do not recruit seedlings in the postfire environment.

^a Seedling recruitment is largely unknown in a few species.

^b Not all species that resprout will form burls or lignotubers as a normal ontogenetic developmental stage. In some cases, such as *Quercus* spp. swollen burl-like structures will form as a type of "coppicing" effect.

^c Although a vigorous resprouter distributed from Baja California to Oregon, a single non-burl forming population, unable to resprout after fire, is known from northern Baja California (J. Keeley, Vasey, and Parker in press).

^d *Arctostaphylos manzanita* and *A. parrayana* have non-burl forming subspecies in open woodland habitats and burl forming subspecies in chaparral (Keeley, Boykin, and Massihi 1997).

^e *Arctostaphylos rudis* has burl-forming and non-burl-forming plants in the same population such as Nipoma Mesa.

^f *Ceanothus tomentosus* populations from the central Sierra Nevada are resprouters and the southern California populations are non-sprouters.

distribution on most chaparral landscapes (Ackerly 2003). For example, overlaying maps of 19 chaparral shrub species in a 60,000-ha area of the Santa Monica Mountains in southern California produced 220 unique combinations of locally dominant species that could be construed as alliances (Syphard, Franklin, and Keeley 2006). Additional quantitative phytosociological studies are needed to establish general chaparral types that are both useful for inventory and management and ecologically meaningful.

Local Diversity Patterns

Community level plant diversity in California shrublands has long been known to follow a marked temporal pattern with the greatest richness concentrated in the early postfire years (Sampson 1944; Horton and Kraebel 1955; Keeley et al. 1981; Davis, Hickson, and Odion 1988; Guo 2001). In early successional stands plant richness may range from 0 to 30 species per m² (average ~ 10) and 25 to 80 or more per 0.1 ha (average ~ 50; Keeley and Fotheringham 2003a). These values are quite similar to those reported for the very species rich South African fynbos or Western Australian heathlands. Thus,

although these latter mediterranean climate shrublands may have substantially higher regional plant species diversity, they are quite comparable at the community level to postfire Californian chaparral. The primary difference between California and these Southern Hemisphere shrublands is that in chaparral, high species richness is a transient postfire condition, and as shrub canopies close in, diversity drops.

Diversity in chaparral is made up of a large number of relatively minor species and this is illustrated by dominance-diversity curves (Fig. 13.9) that tend to fit a geometric series in early succession and even more accentuated in later succession (Keeley and Fotheringham 2003a). Communities fitting this geometric curve are thought to be driven by the niche-preemption model, which describes communities where a single species dominates a substantial fraction of resources and subordinate species in sequence occupy a similar fraction of the remaining resources (Whittaker 1972). Dominance in chaparral is driven by the fact that a substantial portion of postfire resources are immediately occupied by resprouts from large root crowns and lignotubers, even though these resprouters comprise only about a quarter of the flora (Keeley 1998). Additionally, some of these same species recruit

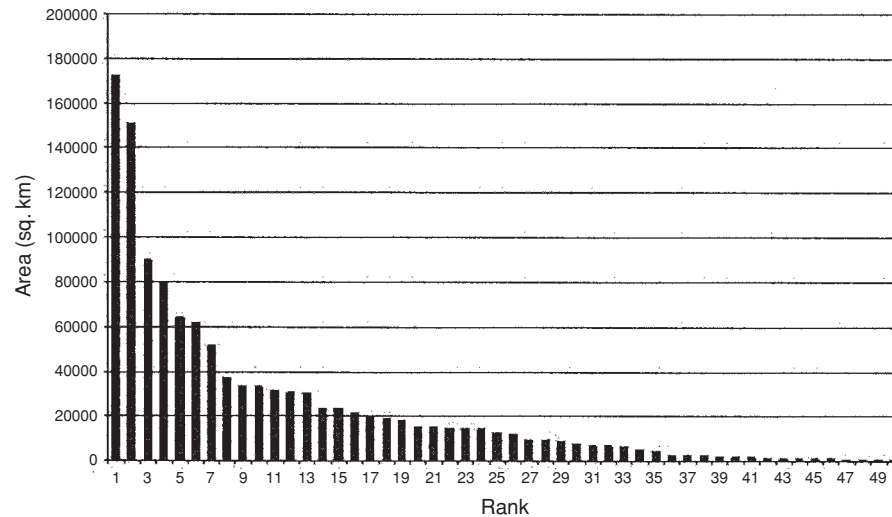


FIGURE 13.5 Rank ordering of range sizes (km²) for 50 *Ceanothus* taxa based on documented occurrence in the CalFlora database within 284 geographic subregions in California.

from fire-stimulated seed banks and thus are poised for expanding dominance with age. The annual life history results in unstable competitive boundaries that are continually readjusted each year, eventually being all but completely crowded out as the shrub canopy closes.

Fire

Chaparral fires are nearly always active crown fires in which living and dead fuels in the canopy carry fire, and surface fuels play little or no role. Fire behavior is most strongly controlled by wind and in the absence of significant winds is controlled by the proportion of living and dead canopy biomass and topography (Keeley and Fotheringham 2003b). When strong winds are present, fires often burn large

swaths of landscape on the order of thousands of hectares and occasionally much larger areas.

Recovery is rapid (Fig. 13.10) because it largely involves residual species regenerating by resprouts from vegetative structures or germinating from dormant soil-stored seed banks. Colonization is of relatively limited importance in terms of biomass but may significantly affect diversity. In a southern California postfire study it was found that of the species present in tenth hectare plots during the first 5 years, only about 50% to 60% were present in the first year (Keeley, Fotheringham, and Baer-Keeley 2005a). However, in Year 5 those species present since the first year comprised about 90% of the cover. Very few species are long-distance dispersers, and colonization is largely from localized populations in adjacent burned areas that expand following fire

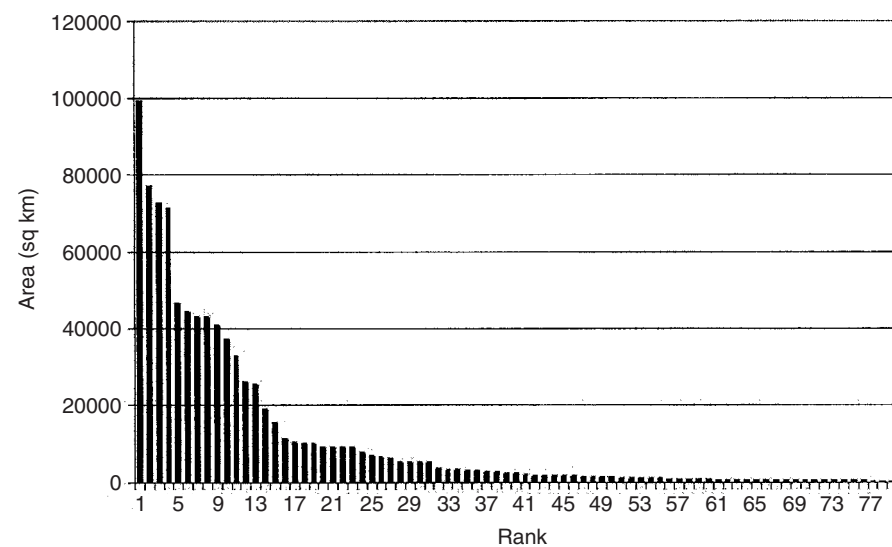


FIGURE 13.6 Rank ordering of range sizes (km²) for 81 *Arctostaphylos* taxa based on documented occurrence in the CalFlora database within 284 geographic subregions in California.

FIGURE 13.7 General distribution of four *Ceanothus* species in southern California. Data source: California Gap Analysis Project. http://www.biogeog.ucsb.edu/projects/gap/gap_home.html.

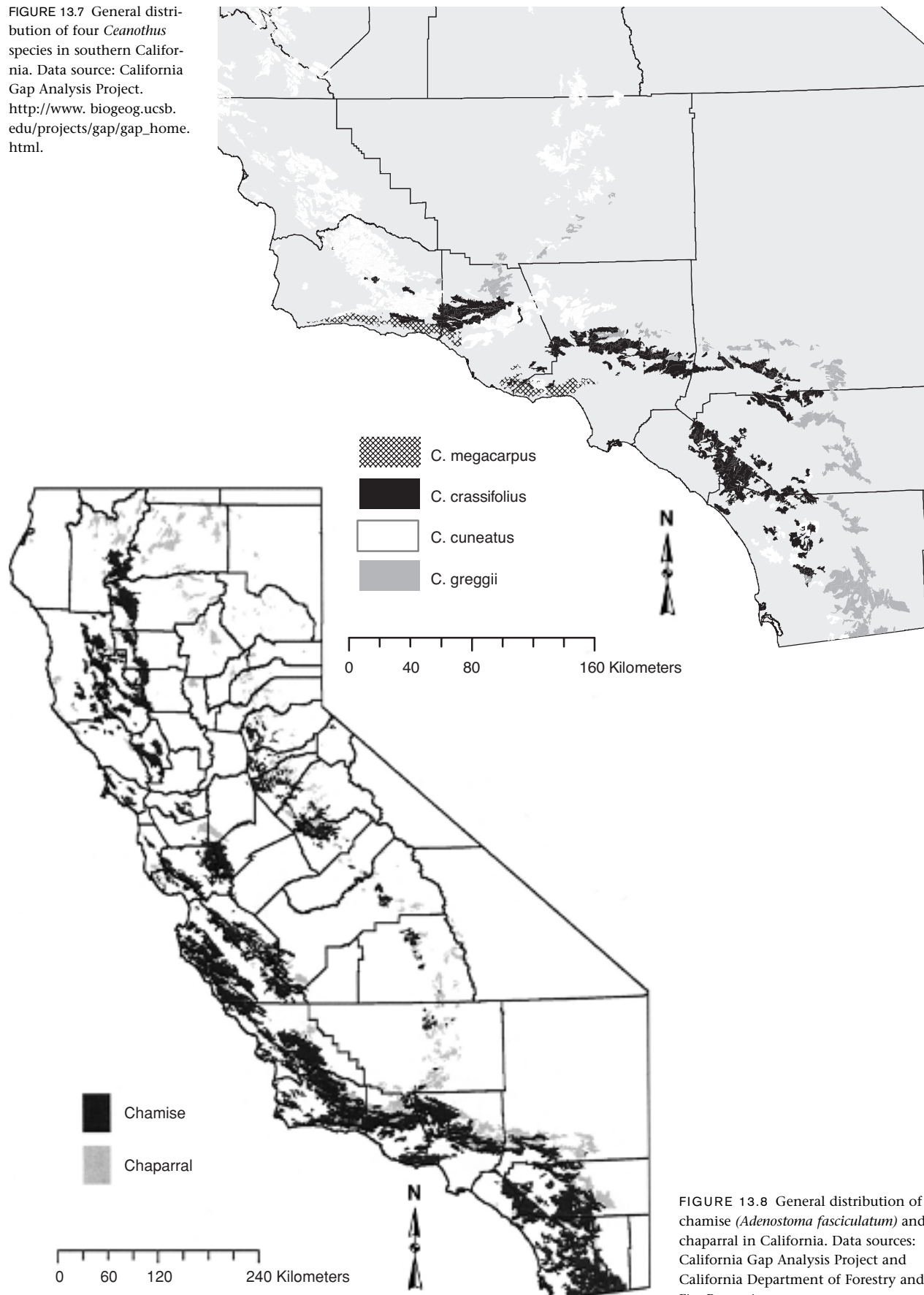
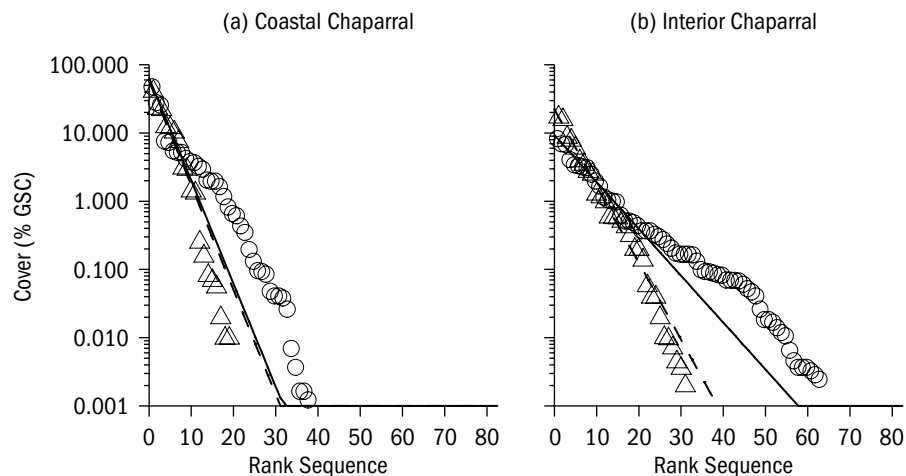


FIGURE 13.8 General distribution of chamise (*Adenostoma fasciculatum*) and chaparral in California. Data sources: California Gap Analysis Project and California Department of Forestry and Fire Protection.

FIGURE 13.9 Dominance-diversity curves for coastal (a) and interior (b) chaparral in southern California for the first postfire year (circles) and the fourth postfire year (triangles). Data taken from Keeley and Fotheringham (2003a).



(Keeley, Fotheringham, and Baer-Keeley 2006). Rates of shrub recovery are affected by a number of environmental parameters, e.g., it is generally slower on interior slopes (Fig. 13.11a).

Demographic Patterns of Woody Dominants

Shrubs differ in their exploitation of the postfire environment for seedling recruitment. Many taxa, *Adenostoma fasciculatum*, all chaparral species of *Arctostaphylos* and *Ceanothus*, *Fremontodendron* spp., *Malosma laurina*, and *Rhus ovata* have seedling recruitment largely restricted to the immediate postfire environment. Although these species flower and set seed on an annual or biennial basis (Keeley 2000), the bulk of this seed pool is dormant and they accumulate in the soil until germination is triggered by heat or smoke (Keeley 1991). These are termed “fire dependent” because seedling recruitment is practically nil after the first postfire year. Many of the *Arctostaphylos* and *Ceanothus* species lack the capacity to regenerate vegetatively, and these are termed “postfire obligate seeders.” Other species in these two genera, as well as the rest of the postfire seedling recruiters also resprout from the stem base and are termed “postfire facultative seeders.”

Typically the postfire seedling/parent ratio for shrubs is between 50 and 100 or more (Keeley, Fotheringham, and Baer-Keeley 2006). However, there is marked spatial variation, and some stands have very depauperate seedling recruitment after fire, sometimes resulting in local extirpation (e.g., *C. crassifolius* in Horton and Kraebel 1955; or *C. megacarpus*, Fig. 6.15 in Keeley 2000; and Jacobsen, Davis, and Babritius 2004). One of the major factors is what Zedler (1995) termed “immaturity risk,” where populations of obligate seeders are at risk of extirpation from short fire-return intervals because of insufficient time for establishing an adequate soil seed bank. Establishing this lower limit is not a simple function of age of maturity because seed production per se is not the only factor. A population must establish a critical mass of seeds in the soil prior to fire and we know

too little about the dynamics of soil seed banks to establish precise bounds. As a rough generalization it is very likely that most postfire obligate seeding *Ceanothus* species would be threatened by fire-return intervals of less than 10 years, and most would have sustainable populations with 20-year or greater fire-return intervals. Obligate seeding *Arctostaphylos* require much longer fire-return intervals, and fires in 20-year-old stands often fail to establish replacement-level seedling populations. In some species the lower limit is quite high; for example, in *A. morroensis*, fire in 40-year-old stands failed to generate replacement-level seedling populations (Odion and Tyler 2002). Age effects on seed production capability is likely one of the primary factors involved (Keeley and Keeley 1978).

Seed production of course is just one of a plethora of factors that control postfire shrub seedling recruitment patterns. Factors such as fire intensity, drought, herbivory, and competition all control the size of seedling populations (Davis, Borchert, and Odion 1989; Moreno and Oechel 1991; Tyler 1995, 1996; Tyler and D’Antonio 1995; Odion and Davis 2000).



FIGURE 13.10 Vegetative growth of shrubs and herbs in the first growing season postfire. Photograph by J. Keeley.

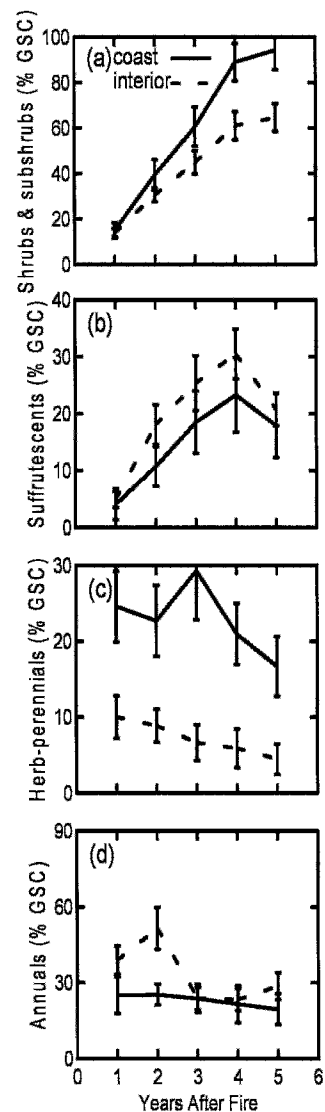


FIGURE 13.11 Postfire changes in cover for different life forms in chaparral. From Keeley, Fotheringham, and Baer-Keeley (2005a).

Species specialized for seedling recruitment in the postfire environment face an additional problem described as “senescence risk” (Zedler 1995b). Specifically, if the length of the fire cycle exceeds the life span of both the existing population and the seed bank, then the population faces some risk of extirpation. However, seed banks in century-old chaparral appear to retain more than enough viable seed to ensure postfire regeneration (Keeley 1977, 1987; Parker and Kelly 1989; Zammit and Zedler 1988; Keeley, Lubin, and Fotheringham 2003; Keeley, Pfaff, and Safford 2005). Thus, these obligate seeding species appear to be rather resilient to long fire-return intervals but poorly resilient to short ones.

Other shrubs such as *Cercocarpus betuloides*, *Heteromeles arbutifolia*, *Quercus* spp., *Prunus ilicifolia*, *Rhamnus californica*, and *R. crocea* produce short-lived seeds that form a transient seed bank. When fires occur there is essentially no seedling

recruitment, and these species persist because of their ability to resprout and are termed “postfire obligate resprouters.” Seedling recruitment of these species occurs sporadically during the fire-free interval (Keeley 1992b).

Fire-caused mortality of resprouting species is highly variable. Most obligate resprouters suffer 0% to 5% mortality, whereas facultative seeders such as *Adenostoma fasciculatum* may have substantially higher mortality after some fires (e.g., Stohlgren 1985). Resprouting success is a function of both innate characteristics of each species as well as environmental variation during and after fire. Physiological status of storage carbohydrates has been implicated in seasonal differences in resprouting behavior (Radosevich and Conard 1980; Rundel et al. 1987). Low fire intensity (Moreno and Oechel 1991; Borchert and Odion 1995) and older aged plants (Vesk, Warton, and Westoby 2004) are traits found to be associated with increased resprouting ability, but opposite results have been reported in some studies (Keeley 2006a). Site differences also play a critical role as illustrated by the postfire resprouting success of *A. fasciculatum* after a massive wildfire event in southern California; percentage of shrubs-resprouting was negatively correlated with annual solar radiation calculated from latitude, slope aspect, and incline ($r = -.46$, $P < 0.01$, $n = 45$ sites; Keeley unpublished data).

Demographic Patterns of the Ephemeral Flora

In the immediate postfire environment, the bulk of plant cover is usually made up of species present prior to the fire only as a dormant seed bank or underground vegetative structures. This postfire community comprises a rich diversity of herbaceous and weakly woody species, the bulk of which form an ephemeral postfire successional flora. Typically 60% or more of the species are annuals (Keeley, Fotheringham, and Keeley 2005a), comprising 25% to 50% ground surface cover in the first couple of postfire years (see Fig. 13.11d).

This annual flora includes a rich diversity of demographic patterns (Fig. 13.12). Truly unique is the collection of several dozen species that are restricted to recently burned sites; being present in the first postfire year and typically gone by the third postfire year (Table 13.5). These postfire endemics arise from dormant seed banks that were generated after the previous fire and typically spend 95% or more of their life span as dormant seeds (Fig. 13.12a-c). Circumstantial evidence suggests these postfire endemics retain viable seed banks for more than a century without fire until germination is triggered by heat or smoke (Keeley 1991; Keeley, McGinnis, and Bollens 2005). A much larger flora of annuals exhibit similar patterns except they are less closely tied to immediate postfire conditions. Postfire specialists peak soon after fire but persist during early succession (Fig. 13.12d-f), and opportunists are annuals that persist until the canopy closes in and eliminates them from the site (Fig. 13.12g-i). A few, rather uncommon species increase with time since fire (Fig. 13.12j-l). Many of these species persist in gaps in mature chaparral, and their

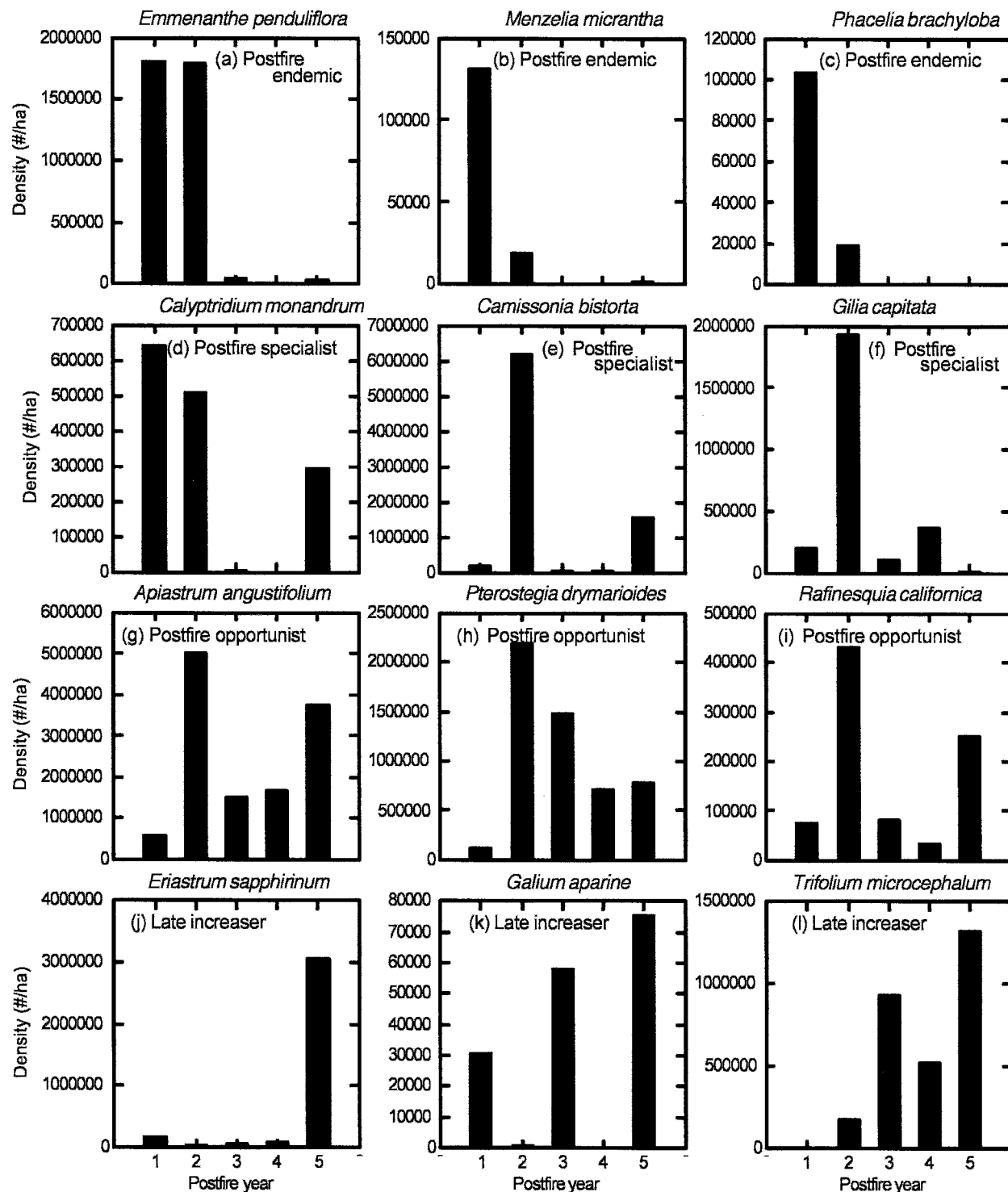


FIGURE 13.12 Postfire changes in abundance of annuals that (a-c) are strict postfire endemics, (d-f) fire specialists that persist during early succession, (g-i) opportunistic species that expand after fire but persist in gaps fluctuating with annual precipitation patterns, and (j-l) species that increase later in succession. From Keeley, Fotheringham, and Baer-Keeley (2006).

persistence is controlled by a number of factors including herbivory, nutrients, and soil moisture (Swank and Oechel 1991; Zammit and Zedler 1994).

Many of these annuals, even some species that in chaparral are postfire endemics, are important components of other open habitats such as grasslands or desert scrub,

where they do not exhibit a close relationship to fire. For example, *Emmenanthe penduliflora* is largely restricted to postfire conditions in chaparral and remains for many decades as a dormant seedbank until the next chaparral fire. However, it also occurs in desert scrub where fires are rare and its presence appears to be more a function of winter

TABLE 13.5
Examples of Postfire Annual Flora

<i>Species</i>	<i>Family</i>	<i>Germination Trigger</i>
Native Postfire Endemics (Restricted to the First 1–2 Postfire Years)		
<i>Allophyllum glutinosum</i>	Polemoniaceae	Smoke or charred wood
<i>Calandrinia ciliata</i>	Portulacaceae	Smoke or charred wood
<i>Caulanthus heterophyllus</i>	Brassicaceae	Smoke or charred wood
<i>Emmenanthe penduliflora</i>	Hydrophyllaceae	Smoke or charred wood
<i>Lotus salsuginosus</i>	Fabaceae	Heat shock
<i>Lupinus succulentus</i>	Fabaceae	Heat shock
<i>Menzelia micrantha</i>	Loasaceae	Smoke or charred wood
<i>Nicotiana attenuata</i>	Solanaceae	Smoke or charred wood
<i>Papaver californicum</i>	Papaveraceae	Smoke or charred wood
<i>Phacelia brachyloba</i>	Hydrophyllaceae	Smoke or charred wood
<i>P. grandiflora</i>	Hydrophyllaceae	Smoke or charred wood
<i>Silene multinervia</i>	Caryophyllaceae	Smoke or charred wood
Native Postfire Specialists (Most Abundant in the First 1–2 Postfire Years and Persisting During Early Succession)		
<i>Antirrhinum coulterianum</i>	Scrophulariaceae	Smoke or charred wood
<i>Calyptridium monandrum</i>	Portulacaceae	Smoke or charred wood
<i>Camissonia californica</i>	Onagraceae	Smoke or charred wood
<i>Chaenactis artemisiifolia</i>	Asteraceae	Smoke or charred wood
<i>Chorizanthe fimbriata</i>	Polygonaceae	?
<i>Cryptantha microstachys</i>	Boraginaceae	Smoke or charred wood
<i>Eucrypta chrysanthemifolia</i>	Hydrophyllaceae	Smoke or charred wood
<i>Gilia capitata</i>	Polemoniaceae	Smoke or charred wood
<i>Linaria canadensis</i>	Schrophulariaceae	?
<i>Lupinus bicolor</i>	Fabaceae	Heat shock
<i>Malacothrix clevelandii</i>	Asteraceae	Smoke or charred wood
<i>Nemacladus ramosissimus</i>	Caprifoliaceae	Smoke or charred wood
<i>Phacelia cicutaria</i>	Hydrophyllaceae	Smoke, charred wood, or heat
<i>Salvia columbariae</i>	Lamiaceae	Smoke, charred wood, or heat
<i>Silene antirrhinia</i>	Caryophyllaceae	Smoke or charred wood
<i>Trifolium wildenovii</i>	Fabaceae	Heat shock
Native Postfire Opportunists (Abundant During Early Succession but Persisting at Lower Density in Openings in Mature Chaparral)		
<i>Amsinckia menziesii</i>	Boraginaceae	Mostly transient seed banks
<i>Antirrhinum kelloggii</i>	Scrophulariaceae	Mostly transient seed banks
<i>Apiastrum angustifolium</i>	Apiaceae	Mostly transient seed banks
<i>Conyza bonariensis</i>	Asteraceae	Mostly transient seed banks

(continued)

TABLE 13.5 (continued)

<i>Species</i>	<i>Family</i>	<i>Germination Trigger</i>
<i>Cryptantha muricata</i>	Boraginaceae	Mostly transient seed banks
<i>Daucus pusillus</i>	Apiaceae	Mostly transient seed banks
<i>Filago californica</i>	Asteraceae	Mostly transient seed banks
<i>Gnaphalium californicum</i>	Asteraceae	Mostly transient seed banks
<i>Pterostegia drymarioides</i>	Polygonaceae	Mostly transient seed banks
<i>Rafinesquia californica</i>	Asteraceae	Mostly transient seed banks
<i>Stephanomeria virgata</i>	Asteraceae	Mostly transient seed banks
<i>Uropappus lindleyi</i>	Asteraceae	Mostly transient seed banks
Native Late Successional Increasers (More Common in Mature Chaparral)		
<i>Claytonia perfoliata</i>	Portulacaceae	Mostly transient seed banks
<i>Collinsia parryi</i>	Scrophulariaceae	Mostly transient seed banks
<i>Crassula connata</i>	Crassifloiaceae	Mostly transient seed banks
<i>Eriastrum sapphirinum</i>	Polemoniaceae	Mostly transient seed banks
<i>Galium aparine</i>	Rubiaceae	Mostly transient seed banks
<i>Githopsis diffusa</i>	Campanulaceae	Mostly transient seed banks

NOTE: Species endemic to burned sites refers to their behavior in chaparral as some of these species occur in other vegetation types where they do not exhibit a strict adherence to postfire environments. From Keeley (1991, 2000) and Keeley, Fotheringham, and Baer-Keeley 2005a.

rainfall. Another example is *Lupinus succulentus*, which in chaparral has deeply dormant seed banks that are triggered to germinate by fire; however, it also occurs in grassland habitats where its presence is unrelated to fire. These and other patterns suggest there is much ecotypic variation that has yet to be explored for a lot of this postfire flora.

Herbaceous perennials commonly comprise 20% of the postfire flora (Keeley and Fotheringham 2003a) and 10% to 25% of the cover (Keeley, Fotheringham, and Baer-Keeley 2005a). There are marked gradients with this life form declining from the coast to the interior. Nearly all are obligate resprouters, arising from dormant bulbs, corms, or rhizomes and typically flowering in unison in the first postfire year (Keeley 2000; Borchert 2004). Very few produce fire-dependent seeds; consequently seedling recruitment tends to be heavy in the second and subsequent postfire years (Borchert 1989; Keeley 1991; Keeley, Fotheringham, and Baer-Keeley 2006). Once the shrub canopy closes in, they may remain entirely dormant for many years (Epling and Lewis 1952) or continue to produce foliage but not flower (Stone 1951; Tyler and Borchert 2002). Thus, although being postfire obligate resprouters, reproduction by herbaceous perennials is indirectly tied to fire.

One factor that plays an important role in determining postfire patterns is fire intensity. Davis, Borchert, and Odion

(1989) and Odion and Davis (2000) demonstrated that microscale patterns in postfire regeneration resulted from spatial variation in seed banks and apparent fire intensities. In a large postfire study, surrogate measures of fire intensity (best termed fire severity) specifically, twig diameter and height of shrub skeletons, were negatively correlated with diversity and cover (Keeley, Fotheringham, and Baer-Keeley 2005a). However, 5 years after fire there was no relationship between fire-severity measures and ecosystem recovery. These and other studies also show that fire-severity impacts on ecosystem recovery are complex, because although seedling recruitment of some species is inhibited by high fire severity, it is enhanced for others (Keeley, Pfaff, and Safford 2005).

Suffrutescents are weakly woody species with dormant buds aboveground. Unless a repeat fire occurs in a young stand, none of these species resprouts; rather, they all arise from dormant seed banks. They are relatively short-lived, perhaps 5 to 10 years depending on site conditions.

Subshrubs are relatively short-lived weakly woody diminutive species that are present mainly as dormant seed banks at the time of fire. For example, bush poppy (*Dendromecon rigida*) is a short-lived shrub that has massive recruitment in the first postfire year (Bullock 1989). Shrubs usually die within a decade after fire and seed banks remain

dormant until the next fire. On one site it is known that this dormant seed bank remained viable and produced a dense vigorous population after roughly 115 years in the soil (Keeley, Lubin, and Fotheringham 2003).

Regional Variation in Fire Regime

California chaparral exhibits marked regional variation in contemporary burning patterns, and there is good reason to believe historical patterns were different as well (Keeley and Fotheringham 2003b). Winds are an important factor in these regional differences. In many respects the southern California landscape is a bit of an anomaly with annual occurrence of severe fire weather, known locally as Santa Anas. Every autumn the region experiences 5 to 10 days of strong offshore flow that accompanies winds of 100 kph or more. These winds result from a high-pressure system in the interior West, and as the air descends it dries adiabatically so that relative humidity at the surface often is below 10%. These severe weather conditions follow the annual drought of 6 months or more and represent the worst fire climate in North America (Schroeder et al. 1964). Under these conditions fuel age appears to be of limited importance to the ultimate fire size (Keeley, Fotheringham, and Moritz 2004; Moritz et al. 2004). One consequence of these conditions, coupled with high frequency of human ignitions, is that probably only a few percent of the landscape has escaped fire during the last century, and much of the lower elevation chaparral is burned at a very high frequency. This landscape has a fire-return interval that is at the low end, and in many lowland coastal areas is clearly outside the historical range of variability. Thus, in southern California there is very little evidence that twentieth-century fire suppression activities have reduced burning over natural levels (Keeley, Fotheringham, and Morais 1999), which is at odds with the hypothesis that fire suppression successes during the past century explain differences in fire size north and south of the United States (Minnich 1983).

In contrast, the southern Sierra Nevada chaparral landscapes are not exposed to these Santa Ana winds, nor are they exposed to the heavy load of human ignitions as in southern California. As a consequence of these conditions, coupled with relatively effective fire-suppression activities, approximately 45% of the landscape has never had a recorded fire (Keeley, Pfaff, and Safford 2005). This landscape is very likely at the high end of the historical range of variability, although perhaps not outside the historical range of variability. These older stands of chaparral appear to maintain natural ecosystem processes and exhibit no sign of dying out or replacement by other vegetation types. This is particularly evident following fires in these ancient stands of chaparral that exhibit recovery in cover and diversity indistinguishable from postfire recovery in younger stands.

Other evidence of regional variation is apparent from studies of fire-hazard functions, where estimates of how the

probability of burning changes with age are compared across chaparral from the central coast (Moritz et al. 2004). The front side of the Santa Ynez Mountains above the city of Santa Barbara exhibits a very different pattern that indicates fuel age may be an important determinant of burning. This appears to be the result of much more limited Santa Ana wind activity in this part of California, although local winds known as "sundowners" have been associated with several catastrophic fires (Blier 1998).

Community and Ecosystem Processes

Successional Changes

There is very little evidence that even after a century without fire, chaparral is replaced by other vegetation types (Hedrick 1951; Keeley 1992a; Callaway and Davis 1993). Most changes are the result of changing dominance patterns within the shrub flora. Obligate-seeding *Ceanothus* vary markedly in longevity (Zedler 1995b). Some species, for example, *C. tomentosus*, appear to be relatively short-lived, on the order of 3 to 5 decades, whereas others persist far longer, for example, *C. greggii* (Keeley 1975; Zammit and Zedler 1992). These post-fire-seeding species exhibit structural and physiological characteristics selected to tolerate the severe conditions on open sites during the long summer-autumn drought (Davis, Kolb, and Barton 1998; Keeley 1998b). As a consequence of their adaptation to high light environments they tend to be shade intolerant (Mahall and Schlesinger 1982). Thus, in older stands, mortality appears to be driven by competition, and there is a shifting balance in the competitive relationships resulting in a successional replacement of obligate seeding *Ceanothus* species by various sprouting species that are more competitive under long fire-free conditions (Keeley 1992a; Keeley Pfaff, and Safford 2005c). However, even where populations experience complete mortality, they are likely to be highly resilient to long fire-free periods as soil-stored seed banks of *Ceanothus* species appear to survive hundreds of years of soil storage (Zavitkovski and Newton 1968). Some obligate seeders such as species of *Arctostaphylos* are much longer lived and persist for a century or more (Keeley and Zedler 1978).

Shrub Life History Syndromes

Both woody and herbaceous life forms in chaparral can be subdivided into fire-dependent and non-fire-dependent species for completion of their life cycle, although timing of dependence and degree of independence are complex (Table 13.6). Species with clearly fire-dependent recruitment (see Fire section) are recognized by seedling recruitment entirely restricted to the immediate postfire environment due to fire-stimulated germination of dormant seed banks. Others such as herbaceous perennials lack immediate postfire seedling recruitment, but ultimately it is dependent on fire-stimulated flowering. However, for all of the postfire obligate

resprouting shrub species, seedling recruitment is independent of fire (Keeley 1998). Recruitment is sporadic and most commonly observed in the understory of older stands of chaparral with a thick litter layer (Keeley 1992b). Some species such as *Rhamnus crocea* establish seedlings in the mature shrub understory, and these grow rapidly and recruit into the canopy. *Quercus berberidifolia* on the other hand may exhibit successful recruitment of seedlings that persist for decades as stunted saplings in the understory. These saplings are heavily browsed and often will produce swollen burl-like structures that continually sprout new shoots. These serve as a sapling bank that is capable of resprouting after fire and exhibit a growth release that enhances their chances of recruiting into the mature canopy during early succession. Thus, in some sense these shrubs may be indirectly fire dependent for completion of their life cycle.

Some shrubs appear to recruit rarely in chaparral. For example, although a few instances of seedlings of *Heteromeles* are known from chaparral, the greatest concentration of recruitment by this species is observed in woodland habitats where it commonly acts as a sort of gap-phase species (Keeley 1990a). *Xylococcus bicolor* is of particular interest because it produces copious fruits; yet despite many directed searches, one of the authors (J. Keeley) has never observed a seedling of this species, in burned or unburned stands.

Shrubs exhibit diversified flowering behavior in terms of morphology, phenology, and periodicity. *Arctostaphylos*, *Ceanothus* and *Garrya* flower on old growth from preformed buds produced the previous growing season and this likely contributes to them being the earliest flowering shrubs, typically from winter to early spring. *Adenostoma fasciculatum*, *Heteromeles arbutifolia*, and *Malosma laurina* flower on new growth near the end of the growing season and as a consequence flower later in summer.

The later flowering shrubs tend to be annual producers that disperse seeds annually. On the other hand the early flowering shrubs seldom flower annually and are biennial bearers under good conditions, but more often seed production is sporadic with occasional "mast" years of seed production (Keeley 1987a; Keeley and Keeley 1988).

In terms of seed dispersal, shrubs can be divided between those with temporal dispersal versus those with strong spatial dispersal. The former are the fire-dependent species that accumulate dormant seed banks, which in essence disperse these shrubs in time, from one fire cycle to the next. Within this group there is variable spatial dispersal. *Ceanothus* have explosive capsules that shoot seeds several meters from the parent shrub (Davey 1982). It is doubtful these heavy, smooth coated seeds are dispersed much farther before burial. *Arctostaphylos* have dry drupes that are attractive to a limited number of dispersers, most prominently coyotes and bears. It is apparent that some seeds are distributed rather long distances; however, on most sites it appears the bulk of the seed production is dispersed passively and

not far from the parent plant (J. Keeley personal observations). *Adenostoma fasciculatum* produces small light achenes that potentially could be widely dispersed but we know very little about dispersal curves for this or any chaparral species.

Species that exhibit fire-free (non-fire-dependent) recruitment such as *Heteromeles arbutifolia*, *Prunus ilicifolia*, *Quercus* spp., *Rhamnus* spp., and *Rhus integrifolia* have fruits highly attractive to birds and mammals, and the bulk of the seed crop appears to be dispersed by these vectors (Keeley 1991; Lloret and Zedler 1991). Seedling recruitment is sensitive to desiccation (Keeley 1998); thus it is of some significance that one of the main dispersers of these fruits, the scrub jay (*Aphelocoma californica*), preferentially caches seeds in the shade (Dally, Emery, and Clayton 2004).

Suffrutescents are short-lived semi-woody species that generally do not survive beyond the first decade after fire and if alive at the time of fire do not resprout because dormant buds are aboveground on weakly woody structures. Although they generally produce deeply dormant seed banks that germinate after fire, there is some level of polymorphism, for example, *Lotus scoparius* shows low levels of seedling recruitment after exceptional rainfall years at least 5 years after fire (Keeley, Fotheringham, and Baer-Keelay 2006). Other similar species are *Eriophyllum confertiflorum* and *Helianthemum scoparium*.

On arid sites, subshrubs commonly fill in arid gaps in chaparral. They comprise the same species as found in the lower stature sage scrub vegetation (Rundel this volume) where these species are commonly facultative seeders. However, higher intensity fires in chaparral make resprouting unlikely in most stands; thus these species generally are present after fire as seedlings. In postfire environments they often are rather widespread and short-lived where overtopped by shrubs.

Chaparral has a number of lianas in genera such as *Lonicera* and *Keckiella*. These lianas overtop the canopy of the shrubs and flower on an annual or near-annual frequency. The former produces fleshy animal-dispersed fruits; and the latter, dry capsules with light seeds that may be wind borne. Both have weak seed dormancy and transient seed banks and often establish seedlings in the understory.

Flowering and Dispersal in Herbs

Annuals exhibit extraordinary fluctuations in population size and persistence after fire. Postfire endemics are highly restricted to the immediate postfire conditions and, if the second year has sufficient precipitation, will persist beyond the first year (Fig. 13.12a-c). These produce copious seed banks that are largely dispersed in time rather than in space. Most do not have characteristics suggestive of widespread dispersal. For example, the fire-following *Emmenanthe penduliflora* derives its common name, whispering bells, because the flowers and fruits are pendulous and drop seeds directly beneath the parent plant. Asteraceae postfire species, for

TABLE 13.6
Shrub Life History Syndromes in Chaparral with Fire-dependent or Fire-free Seedling Recruitment

	<i>Fire-dependent</i>	<i>Fire-free</i>
Examples	<i>Adenostoma fasciculatum</i> , <i>Arctostaphylos</i> spp., and <i>Ceanothus</i> spp.	<i>Prunus ilicifolia</i> , <i>Quercus</i> spp., <i>Rhamnus</i> spp.
Seedling recruitment	Strictly first postfire year	Irregular, generally long fire-free periods
Gaps	Gap species	Gap avoider
Resprouting	Mostly obligate seeders Facultative seeders do not often suffer high mortality.	High resprouting success
Seed dormancy	Innate dormancy	Weak or no dormancy
Seed banks	Long-term seed banks	Transient seed banks (<1 yr)
Germination	Germination of all or most of the seed pool dependent on fire; heat shock or chemicals from smoke or charred wood. May require cold.	Germination may require brief Cold
Dispersal strategy	Temporal	Spatial
Mode	Passive	Animal
Shadow	Narrow	Wide
Season	Spring–summer	Fall–winter
Seed size	Small	Large
Water stress mode	Tolerators	Avoider
Water potential with 50% embolism	>–10 Mb	<–3 Mb
Mechanism	Physiological Anatomical	Morphological
Drought-induced mortality		
Adults	Moderate (increasing with age)	Very low
Seedlings	Moderate	Very high
Flammability	Retain dead wood	Self-pruning Higher fuel moisture

NOTE: Based on Keeley (1998). Sources for trait assignment reviewed in Keeley and Keeley (1998), Keeley (2000), Davis et al. (1998), Ackerly (2003, 2004a, 2004b), and Schwilk (2003).

example, *Malacothrix clevelandii* or *Chaenactis artemisiifolia* have deciduous pappus suggestive of weak dispersal.

Opportunistic annuals typically reach their peak population sizes in the postfire years (Fig. 13.12g-i), but persist at low levels into mature chaparral. They produce polymorphic seed pools with both deeply dormant and nondor-

mant seeds. These species fluctuate in relation to annual precipitation patterns, often not appearing at all in dry years (Keeley, Fotheringham, and Baer-Keeley 2006). Many of these species have fruits adapted to wider distribution, for example, winged mericarps in *Apiastrum angustifolium*, stiff hairs in *Daucus pusillus* or *Cryptantha muricata* or fine

pappus in *Conyza bonariensis*, *Rafinesquia californica*, or *Stephanomeria virgata*.

Herbaceous perennials are highly variable, some sprouting every spring and growing vegetatively in the understory of mature chaparral, but flowering only after fire. Others remain entirely dormant for many years but sprout and flower in unison after fire such as *Zigadenus fremontii* (Tyler and Borchert 2002). *Calochortus* is a genus of geophytes that also appears to focus flowering and subsequent seedling recruitment on the rather narrow window of opportunity following fires. This undoubtedly has contributed to limited dispersal opportunities, which is thought to have been a major factor leading to high endemism in the group (Patterson and Givnish 2003). Growth form plays a significant role here. *Marah macrocarpus* is a vine that sprouts most years and grows into the shrub canopy where it flowers frequently, particularly abundantly in high rainfall years. Seeds are short-lived and die if not successful in germinating following the first fall rains. Seedlings can establish successfully in the understory (Schlising 1966), but *Marah* also resprouts vigorously after fire, and fruit production is copious in early post-fire succession. Most seeds fall close to the parent plant, but a significant fraction are dispersed locally by rodents (Borchert 2004). Others such as *Paeonia californica* never reach the canopy but can successfully reproduce in gaps within the mature chaparral canopy (Schlising 1976).

Yucca whipplei is a fibrous herbaceous species that persists as an aboveground rosette of evergreen leaves. It survives fire because it exists on open rocky sites with limited fuels, and typically only the outside leaves are scorched, and they protect the central meristem. This species flowers prolifically after fire, although it is unclear whether flowering is more common than in the intervening years between fires. Seeds lack dormancy (Keeley and Tufenkian 1984), and recruitment occurs sporadically on open sites.

Seed Germination

Fire-dependent species produce dormant seeds that require a stimulus from fire for germination, including either heat shock or chemicals from smoke or charred wood (Keeley and Fotheringham 2000). In many cases dormancy is only broken by clear fire-type signals, and in the absence of fire there is no germination. In other species polymorphic seed pools are produced, and a portion can germinate in the absence of fire. The widespread *Adenostoma fasciculatum* is illustrative of this latter pattern, where a small portion of freshly dispersed seeds germinate readily in the understory of mature chaparral (Stone and Juhren 1953). These seedlings succumb to the shade and predation and do not survive long under these conditions, but if these nondormant seeds land on open sites there is some chance they will be successful. The bulk of the seed bank, however, is dormant, and this dormancy is broken by fire.

Germination of many postfire species has been studied, and it is clear that although germination of a few species is

triggered by heat shock, the vast majority respond to chemicals generated by biomass combustion—received as either smoke, adsorbed onto the seed coat or soil particles, and transferred by dissolving in solution (Fig. 13.13). There is evidence that a variety of chemicals in smoke and charred wood may be responsible for stimulating germination of postfire species, and both inorganic (Keeley and Fotheringham 1997) and organic compounds may be involved (Flematti et al. 2004). It is apparent that germination behaviors are complex, and the triggers in smoke would appear to vary among species and in the mechanisms responsible (Keeley and Fotheringham 1998).

In general, species are stimulated by either heat of the fire or chemicals produced during biomass combustion (e.g., Table 13.5). There is a very strong phylogenetic component to germination response, with certain families responding only to heat and others only to chemicals. For example, all *Ceanothus* species are stimulated by heat, and smoke plays no role in their germination. This pattern is typical for other fire-stimulated Rhamnaceae, for example, *Phyllica* in South African fynbos (Keeley and Bond 1997) or *Trevoa* in Chile (Keeley unpublished data). Other common families in chaparral and sage scrub with heat-stimulated germination include the Fabaceae, Convolvulaceae, Malvaceae, and Sterculiaceae. However, the majority of species with seedling recruitment in the postfire flora of both chaparral and sage scrub are not stimulated by heat, but by smoke or other chemicals produced during combustion (Keeley and Fotheringham 2000). Included here are the plant families Hydrophyllaceae, Lamiaceae, Polemoniaceae, and Scrophulariaceae (Table 13.5). Some species (e.g., *Adenostoma fasciculatum*) exhibit enhanced germination with heat treatments, but the bulk of the dormant seed bank is stimulated by chemicals from smoke or charred wood (Odion 2000; Keeley, McGinnis, and Bollens 2005). In germination trials with *Arctostaphylos morroensis*, a rare endemic of maritime chaparral, 40% of viable seed germinated with no fire cues. Neither heat shock nor charate alone enhanced germination, but when combined these treatments resulted in highest germination rates (Tyler and Odion unpublished).

Seeds of many species have a requirement for cold temperatures (<5°C), which is interpreted as a seasonal cue (Keeley 1991). In these Mediterranean-climate species it appears that this requirement is not like the cold stratification requirement of many species from colder climates, where the seeds require a certain duration of cold in order to prevent winter germination. In California species even a short burst of cold will trigger germination, interpreted not as a cue that winter is over but rather that winter is here, which is consistent with the winter germination behavior of many natives.

Allelopathy

The striking contrast between the depauperate herb growth under and adjacent to mature chaparral (Fig. 13.14), and the

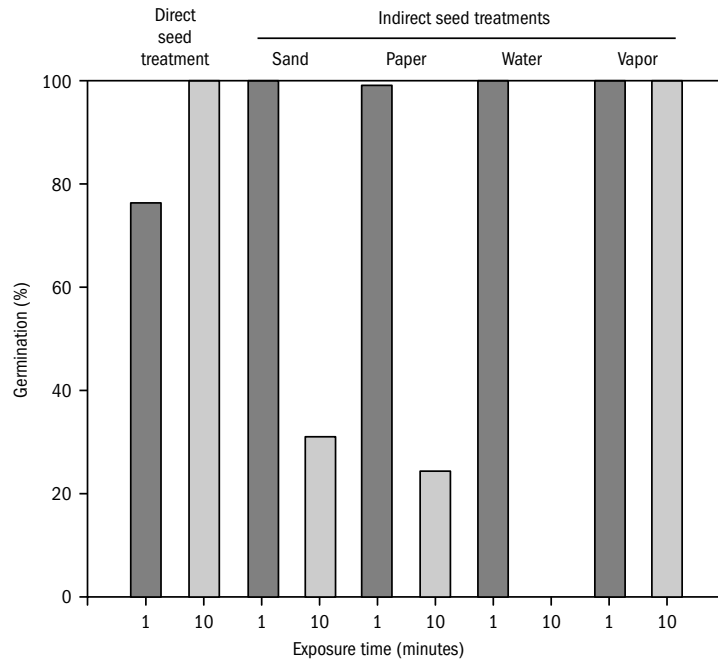


FIGURE 13.13 Germination of postfire endemic annual *Emmenanthe penduliflora* illustrating deep dormancy of control seeds, complete germination with direct smoke treatment of seeds or high germination with indirect exposure of seeds to smoke by sowing seeds on smoke-treated sand or filter paper or watering seeds with smoke-treated water or exposing untreated seeds to vapors emitted from smoke treated sand. The control for exposure time is zero minutes. From Keeley and Fotheringham (1997).

flush of herbs after fire (see Fig. 13.10) has been hypothesized to be due to allelopathic suppression of germination by the overstory shrubs. There is a rich history behind the development of allelopathy theory well reviewed by Halsey (2004).

After field and laboratory studies, McPherson and Muller (1969) concluded: "nearly all seeds in the soil of mature *A. fasciculatum* stands are prevented from germinating by the toxin (leached from the shrub overstory) which is most abundantly present during the normal germination period." Fire consumes the shrubs and destroys the toxin, thus releasing the herb seeds from inhibition. Some investigators have questioned this conclusion (Christensen and Muller 1975a, 1975b; Keeley and Keeley 1989).

One of the primary shortcomings of the theory of allelopathic control of the postfire ephemeral flora is that it cannot account for the fact that the vast majority of

species produce innately dormant seeds with fire-stimulated germination. It has been hypothesized that the poor conditions of low light, limited water, insufficient nutrients, high predation, and possibly allelopathic toxins have selected for seed dormancy broken by fire-related cues (Keeley and Keeley 1989). This applies to the many species that are strictly tied to fire, although it may not apply to other opportunistic species that colonize gaps in mature chaparral (Swank and Oechel 1991; Zammit and Zedler 1994). It has been hypothesized that the nonrefractory seeds of such species have evolved a sensitivity to allelopathic compounds leached from the overstory canopy as a means of inducing secondary dormancy until conditions are more suitable for germination and establishment (Keeley 1991).

Alien Plants

In California shrublands, natural successional processes are dominated by native residual species that are derived from either dormant seed banks or resprouts from dormant bud banks on tubers. Despite this, there is a substantial number of plant species that colonize burned sites during the early postfire years (Keeley, Fotheringham, and Baer-Keeley 2005a). Alien annual grasses and forbs are a significant part of this colonizing flora, and under some conditions these species may become aggressive invaders that dominate the site for extended periods (Freudenberger, Fish, and Keeley 1987; Keeley 1990b; Minnich and Dezzani 1998; Stylinski and Allen 1999). For many decades land management agencies seeded burned areas with alien mustards (*Brassica* spp.) or alien annual grasses (e.g., *Lolium multiflorum*, *Vulpia myuros*) to reduce soil erosion. Evidence that such seeding reduces soil erosion is mixed at best, but it is clear that it can



FIGURE 13.14 Bare zone typical of the ecotone between chaparral and grassland. Photograph by J. Keeley.

significantly reduce cover and diversity of native species (reviewed by Beyers 2004).

Degradation and type conversion of native shrublands to alien-dominated grasslands has been noted by numerous investigators, some of whom contend that increased frequency of disturbance is the primary factor that favors alien annuals over woody native species (Cooper 1922; Wells 1962; Zedler, Gautier, and McMaster 1983; O'Leary and Westman 1988; Keeley 1990b, 2002), whereas others maintain it is driven by pollution effects arising from ozone that is more toxic to native shrubs (Westman 1979) or nitrogen deposition that favors alien annuals (Allen et al. 2000).

The role of these factors has been evaluated for young postfire stands in chaparral and sage scrub using a type of path analysis known as structural equation modeling (Keeley, Baer-Keeley, and Fotheringham 2005). Models that included nitrogen deposition and distance from the coast were not significant, but with those variables removed, the remaining model gave an $R^2 = 0.60$ for the response variable of fifth-year alien dominance. According to this model the most critical factor influencing aliens is the rapid return of the shrub and subshrub canopy. Thus, in these communities a single functional type (woody plants) appears to be the most critical element controlling alien invasion and persistence. Fire history is an important indirect factor because it affects both prefire stand structure and postfire alien seed banks. Despite being fire-prone ecosystems, these shrublands are not adapted to fire *per se*, rather to a particular fire regime. Alterations in the fire regime produce a very different selective environment and high fire frequency changes the selective regime to favor aliens. This study does not support the widely held belief that prescription burning is a viable management practice for controlling alien species on semiarid landscapes.

Nonnative annual grasses and forbs are found throughout chaparral regions. Under a regime of frequent fires, they readily displace the native herb flora if fires are frequent enough, converting chaparral to annual grassland (Cooper 1922; Sampson 1944; Arnold et al. 1951; Wells 1962; Haidinger and Keeley 1993). In the absence of fire, seeds of nonnatives have a low residence time in the soil; thus the presence of these species on burned sites is more often due to colonization after fire. Most, such as species of *Bromus*, *Erodium*, and *Centaurea*, disperse prior to the summer fire season and consequently are less common in first-year burns, but may be present in subsequent years (Sampson 1944; Horton and Kraebel 1955; Keeley et al. 1981). Fall-fruiting species such as *Lactuca serriola* and *Conyza bonariensis* are likely to be more common on first-year burns.

The most aggressive and widespread aliens are grasses and most alien species are not specific to either chaparral or sage scrub (Keeley, Baer-Keeley, and Fotheringham 2005). Although several species of *Bromus* are very widespread, the most abundant, both in density and breadth of distribution, is *B. madritensis*.

Evolutionary and Geological History

Shrub Life History Syndromes

Chaparral shrub life history has been interpreted in the context of trait syndromes that reflect the coordinated evolution of structure and function (Keeley 1991, 1998; Zedler 1995b; Davis, Hickson, and Odion 1988; Ackerly 2003, 2004a; Schwilk 2003). Fundamental to this discussion is the recognition that although fire has been an important selective force in the evolution of some chaparral species it has not played an obvious role in shaping life histories of other species. We recognize two distinct modes, those species with strict fire-dependent seedling recruitment and those that recruit only in the absence of fire. These modes of recruitment co-vary with a combination of morphological, physiological, and other reproductive traits (Table 13.6). These correlated traits arise because of inevitable tradeoffs and can only be understood in the context of the syndrome of plant characteristics that comprise the structural and functional attributes of the whole plant. The trait associations are well documented (Table 13.6), and we hypothesize the following causal pathway of evolution.

Species selected to capitalize on the rich resources of light, water, and nutrients available after fire by restricting seedling recruitment to the first postfire growing season have had to make adjustments. Evolution of seed dormancy that results in a viable seed bank poised to take advantage of these conditions required mechanical and physiological mechanisms that could be overcome by firetype cues. Because fires are always large stand-replacing crown fires, there has been little selection for traits that enhance spatial dispersal. Seedling establishment on open burned sites in drought-prone environments necessitates rapid growth rates and physiological changes that can endure these severe conditions. As a result of anatomical and osmotic adjustments these species are better able to tolerate severe drought conditions than other chaparral dominants (Davis, Kolb, and Parton 1998; Ackerly 2004a). Selection for rapid growth and early flowering in postfire settings may be factors selecting for loss of the basal lignotuber in the obligate seeder taxa with fire-dependent seedling recruitment (Schwilk and Ackerly 2005). Bond and Midgley (1995) and Schwilk and Kerr (2002) have proposed mechanisms, whereby flammability characteristics may enhance inclusive fitness of fire-dependent recruiting species, and increased flammability and potential for differential effects on reproduction in chaparral seeders has been demonstrated by Schwilk (2003).

Non-fire-dependent seedling recruitment is coupled with a very different mode of dealing with drought. These taxa do not tolerate severe soil drought and survive by deep root systems capable of exploiting more of the soil water resource. In a fire-prone environment, this mode of avoiding drought stress requires resprouting ability that maintains long-lived root systems. However, this mode of drought avoidance poses major problems for seedling recruitment because avoiding drought by tapping water with deep roots is not an option for

seedlings. As a consequence, these species recruit successfully in more mesic conditions, typically in the shade of the mature canopy. All of these species have animal-dispersed propagules selected because safe sites for seedling establishment are widely scattered on these drought-prone landscapes.

These life histories have placed constraints on landscape patterns of distribution. Postfire seeding species typify arid slopes and ridges, and non-fire-recruiting species dominate more mesic aspects. Wells (1969) and Raven (1973) hypothesized that the higher number of sexually reproduced generations by postfire seeders has increased the ability of these taxa to track environmental changes. A possible example of this is the greater trait specialization by obligate seeding *Ceanothus* species for tolerating summer drought, relative to congeneric facultative seeding species (Davis, Kolb, and Barton 1998). If such putative adaptive responses were the only factor driving community assembly, it would suggest that the non-fire-dependent seeding species (i.e., postfire obligate resprouters) have been pushed to the more mesic parts of the landscape due to their failure to adapt to changing conditions. Alternatively, we could view the reproductive niche of these non-fire-adapted taxa as one that specializes on widely scattered mesic microhabitats prone to long fire-free periods, embedded within an arid, fire-prone landscape. Other examples of such ecological specialization to a restricted subset of conditions that persists despite changing ecological conditions have been described for other functional groups (Ricklefs and Latham 1992).

Chaparral Origins

Evergreen shrubs are likely a rather ancient functional type that specialized on arid habitats and severe substrates. Such conditions are poorly documented from the fossil record, but it must be recognized that the fossil record is not an unbiased sample of past environments; indeed fossils are least likely to be deposited under arid conditions. Analogous habitats of "chaparral-like" vegetation that were exposed to periodic fires have been described from as far back as the early Cretaceous (Insole and Hutt 1994). The earliest homologous communities with modern taxa date to the mid-Tertiary; one of the earliest is the Oligocene Creede Flora (27 Ma) of southern Colorado (Axelrod 1987). Chaparral taxa included *Cercocarpus*, *Mahonia*, *Prunus*, and *Ribes*, and it included *Chamaebatiaria* (the closest extant relative to *Adenostoma*; Potter et al. 2002). Mixtures of these shrub fossils with forest and woodland fossils led Axelrod to conclude that there was no chaparral association; rather these occurred as forest understory species. Wolfe and Schorn (1989), however, disagree and contend that this flora represents climate-driven alterations between chaparral and forest communities, and chaparral was most prominent during periods of warm-season drought and winter precipitation. Thus, it would appear that the essential features of a Mediterranean climate are potentially very old, and the primary effect of the synoptic climatic patterns of the contemporary

Mediterranean climate is to create a landscape where such conditions dominate. Consequently, apparent niche conservatism (Ackerly 2004b) may be the result of niche conditions that have persisted through time rather than the result of a failure to adapt to changing conditions.

Fossils with close affinities to modern fire-dependent seeding taxa, *Ceanothus* and *Arctostaphylos*, first appear in the mid-Miocene and became increasingly more common in late Miocene deposits (Axelrod 1989). Postfire seeding species (Table 13.4) in the Mulholland flora (6–7 Ma) include *Arctostaphylos*, *Ceanothus*, *Dendromecon*, *Fremontodendron*, *Malosma*, and *Rhus* (*Schmaltzia*). Axelrod contends that these were merely seral species in otherwise woodland habitats; but the evidence for this view is rather weak (e.g., Wolf and Schorn 1989), and we find little reason to discount the likelihood that chaparral as a vegetation type was present by late Miocene. Indeed, there is some evidence that the genus *Arctostaphylos* was rather diverse with several lineages present by this time (Edwards 2004). Thus, there is reason to believe fire-type vegetation dates back to at least the late Miocene. This timing would be consistent with a global increase in fire activity at that time, driven by increasing seasonality that produced favorable growing conditions for high fuel production, followed by a season of drying that favored fire (Keeley and Rundel 2005). Also consistent with a late-Tertiary or even earlier origin for fire responses is the demonstration that in many clades, postfire annuals with smoke-stimulated germination are often basal in their clades (Fotheringham unpublished data).

In contrast to Axelrod (1989), who believed fire played relatively little role in the evolution of chaparral taxa, we believe that postfire seeding species illustrate an important evolutionary role for fire. It is difficult to imagine that fire has played no role in selecting for the highly synchronized postfire seed germination triggered by heat shock and smoke, not only for the fire-dependent recruiting shrubs but also for the very diverse fire endemic flora (Table 13.5 and Fig. 13.13). Another fire-selected trait is the basal lignotuber that is produced as a normal ontogenetic stage, as opposed to swellings that result from coppicing (Keeley 1981). Although all non-fire-dependent recruiting species in chaparral resprout, it is only the few resprouting species of the fire-dependent recruiting mode that produce such lignotubers. Coalesced fruits in *Arctostaphylos* have also been suggested as a fire-selected trait (Keeley 2000).

The present distribution of chaparral is a result of Holocene climatic drying. Prior to this, chaparral was displaced farther south and to lower elevations. For example, the Vizcaino Desert at 27° N in central Baja, California, had chamise (*Adenostoma fasciculatum*) chaparral only 10,200 years BP (Rhode 2002). At comparable elevations (780 m) the present southern boundary of chamise chaparral is more than 500 km north of this Pleistocene population. Farther north in Baja, California, at 30° N, Wells (2000) reported a diverse chaparral assembly at 550 to 600 m elevation between 10,000 and 17,000 years BP; presently chaparral

is displaced 400 m higher. In southern California, late Pleistocene floras were distributed 800 to 900 m lower (Anderson et al. 2002).

Areas for Future Research

Roughly 55% of chaparral is managed by the federal government, primarily for watershed conservation or military operations. Another 40% is privately owned and managed for livestock grazing or open space. Only 15% of chaparral is in formally designated parks and wilderness areas, but the inaccessibility of the majority of chaparral means that most other public lands see similar use patterns as designated reserves. Most chaparral conservation efforts have focused on localized often edaphically restricted communities such as maritime chaparral, serpentine chaparral, gabbroic chaparral, and lone chaparral, where housing development, mining, and other activities threaten rare and endemic species, promote invasive exotics, and make it difficult to manage fire in remaining chaparral fragments (Kruckeberg 1980; Davis, Hickson, and Odion 1988; Harrison 1997; D'Antonio, Odion, and Tyler 1993; Holl et al. 2000; Odion and Tyler 2002).

Fire management is one of the most critical concerns in chaparral. Historical studies show that large high-intensity crown fires are a natural part of this ecosystem, and there is little reason to believe there will not be more such fires in the future. Critical study of fire management on chaparral landscapes exposed to severe fire weather such as Santa Ana or Diablo winds suggest that fuel manipulations are unlikely to turn the tide from a regular cycle of catastrophic wildfires (Keeley, Fotheringham, and Moritz 2004). Californians need to embrace a different model of how to view fires on these landscapes. Our response needs to be tempered by the realization that these are natural events that cannot be eliminated from the southern California landscape. In this respect we can learn much from the science of earthquake or other natural disaster management. No one pretends they can stop them; rather they engineer infrastructure to minimize impacts, and in this respect there is much that can be done at the level of land planning.

The dominant influence of shrub and subshrub canopy recovery on controlling alien invasions also raises serious issues about the use of prescription burning and other fuel manipulations in these shrubland ecosystems. These landscapes currently experience an unnaturally high frequency of fire; thus much of it is at risk for alien invasion. Fire managers need to consider this risk (Halsey 2005) and the potential effects of prescription burning and other prefire fuel manipulations, which decrease woody plant cover and expose sites to alien invasion. In managing these landscapes, it might be helpful to consider the fact that the vast majority of alien species in California are opportunistic species that capitalize on disturbance. Adding additional disturbance through prescription burning (or grazing) will only exacerbate the alien problem.

Projected rapid climate change and associated change in atmospheric CO₂, operating in tandem with a steady increase in California's human population and land development, are likely to make chaparral management even more challenging. Recent scenarios predict an increase in wildfire hazard (Lenihan et al. 2003; Fried and Torn 2004) and expansion of grassland into many chaparral areas (Lenihan et al.; Syphard, Franklin, and Keeley 2006). Limited dispersal of a majority of chaparral species suggests that this rich and endemic biota might be especially sensitive to rapid climate shifts. Increased atmospheric CO₂ affects fundamental ecosystem processes such as plant water use efficiency, carbon cycling, and microbial processes (Treseder et al. 2003). Although we can only speculate about the more distant future of chaparral landscapes, the climate change research to date underlines the need for more information on dispersal traits and bioclimatic responses of chaparral species, closer monitoring of chaparral species' distributions and abundances, and a precautionary perspective when designing fire management and biodiversity conservation solutions in chaparral landscapes.

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