

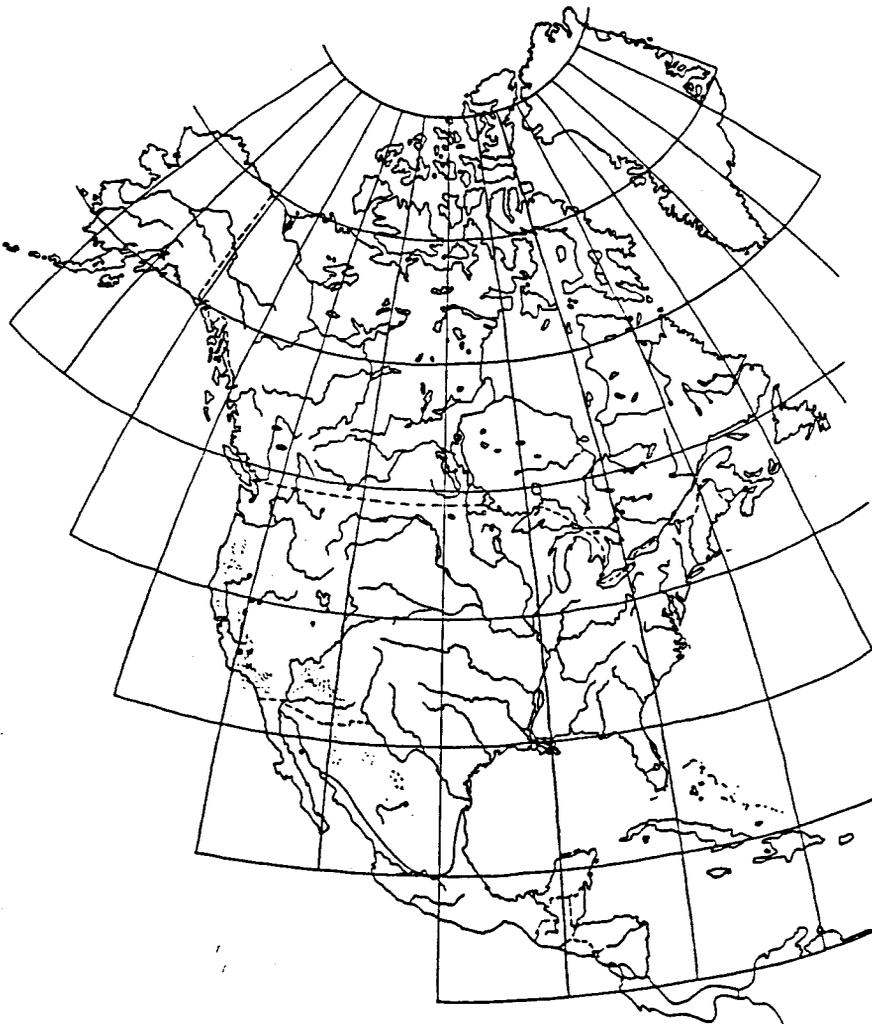
# Chapter

6

## *Chaparral*

JON E. KEELEY  
STERLING C. KEELEY

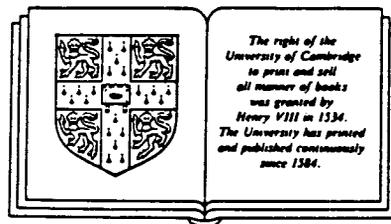
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# North American Terrestrial Vegetation

*Edited by*

*Michael G. Barbour.  
William Dwight Billings*



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## INTRODUCTION

Chaparral is the name applied to the sclerophyllous shrub vegetation of southwestern North America. This chapter concentrates on the evergreen chaparral centered in California, although related vegetation—including the interior chaparral of Arizona and northern Mexico, the winter-deciduous “petran” chaparral of the Rocky Mountains, and the West Coast summer-deciduous “soft chaparral” or coastal sage scrub—will also be discussed. For a complete bibliography of chaparral literature, see Keeley (1984a), and for reviews with a more historical perspective, see Mooney and Parsons (1973) and Hanes (1977). For in-depth comparisons of chaparral with other mediterranean-climate sclerophyllous shrub communities, see Mooney (1977b), Miller (1981), Shmida and Barbour (1982), and Kruger and associates (1983).

California chaparral dominates the foothills from the Sierra Nevada to the Pacific Ocean (Wieslander and Gleason 1954). The northern limits are the drier parts of the Rogue River watershed in Oregon (43° N latitude) (Detling 1961), and the southern limits are the San Pedro Mártir Mountains of Baja California (30° N) (Shreve 1936), and extending to 27° 30' N in isolated patches (Axelrod 1973).

Throughout this region, chaparral characteristi-

cally forms a nearly continuous cover of closely spaced shrubs 1–4 m tall, with intertwining branches (Fig. 6.1). Herbaceous vegetation is generally lacking, except after fires, which are frequent throughout the range. Chaparral occurs from sea level to 2000 m on rocky, nutrient-poor soils and is best developed on steep slopes. Because of complex patterns of topographic, edaphic, and climatic variations, chaparral may form a mosaic pattern in which patches of oak woodland, grassland, or coniferous forest appear, often in sharp juxtaposition. The fire frequency and other environmental factors play important roles in determining distribution. Chaparral is replaced by grassland in frequently burned regions, especially at low elevations, and by oak woodland on mesic slopes where fires occur infrequently.

California chaparral is distributed in a region of mediterranean climate: cool, wet winters and hot, dry summers (Fig. 6.2). Rainfall is 200–1000 mm annually, two-thirds of which falls November to April in storms of several days' duration (Miller and Hajek 1981). Because of the episodic nature of the winter rains, there may be prolonged dry spells, even during the wet season. The annual rainfall variance is significantly greater than in other regions, and extreme droughts are not uncommon (Varney 1925; Major 1977). Significant summer



Figure 6.1. View of southern California mixed chaparral.

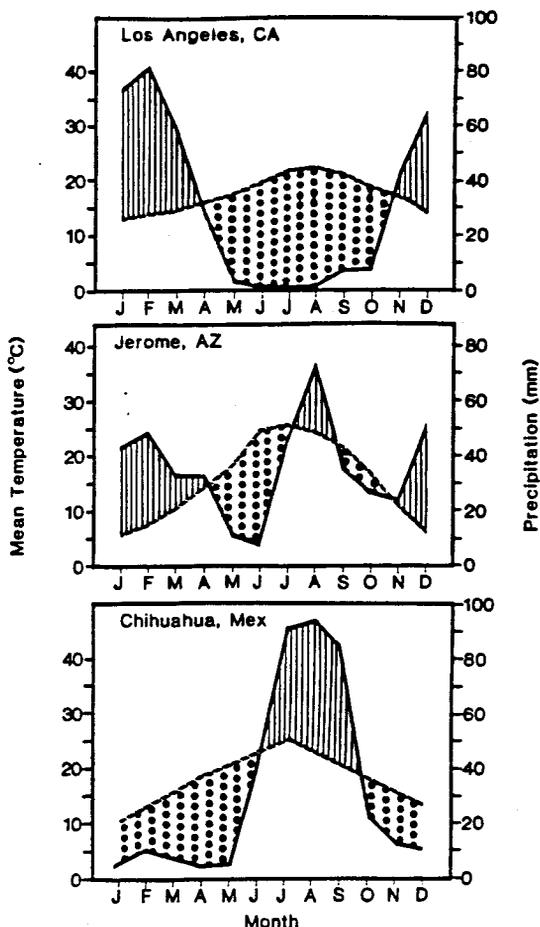


Figure 6.2. Climatic data for three chaparral sites (vertical lines, ppt > evap; dotted area, evap > ppt; solid line = precipitation, dashed line = mean temperature): Los Angeles, California (75 m; 34°05', 118°15'), Jerome, Arizona (1600 m; 34°45', 112°07'), and Chihuahua, Mexico (1350 m; 28°42', 105°57'). In addition to differences in seasonal distribution of precipitation, the annual variance in precipitation is much greater in California than interior regions. For example, 40 yr of data for Los Angeles showed 5 mo with a coefficient of variation between 220% and 350%, whereas the Arizona site had no month with more than 120% (data from U.S. Department of Commerce, *Climatic Summary of the United States*).

precipitation is rare and arises from convectonal storms in the higher elevations or tropical storms in the south. Mean winter temperatures range from less than 0°C at montane sites to greater than 10°C at lower elevations. Summer temperatures often exceed 40°C, but are more moderate along the coast and at the upper elevational limits.

The climate is dominated by the subtropical high-pressure cell that forms over the Pacific Ocean. During the summer, this air mass moves northward and blocks polar fronts from reaching land.

During the winter, this high-pressure cell moves toward the equator and allows winter storms to pass onto land. The climate is wettest in the north, where the effect of the Pacific High is least, and becomes progressively drier to the south.

Another important factor is the orographic effect. Air cools adiabatically with increasing elevation, so that temperature decreases and precipitation increases with elevation. The interior sides of mountains lie within rainshadows where it is hotter and drier than in coastal exposures at comparable elevations.

A factor of local importance in southern California is the Santa Ana wind, which is the result of a high-pressure cell in the interior of the United States driving dry desert air toward the coast. These föhn-type winds may exceed 100 km hr<sup>-1</sup> and bring high temperatures and low humidities. Santa Anas are most common in spring and fall, and some of the most catastrophic wildfires occur during these conditions.

## COMMUNITY COMPOSITION

More than 100 evergreen shrub species occur in chaparral, but only a fraction of these are widespread (Table 6.1). There may be as few as one or more than 20 species at a given site, depending on available moisture, slope aspect, slope angle, distance from the coast, elevation, latitude, and fire history. Generalizations about species preferences toward edaphic and topographic features are difficult to make in that they often change with the region. Attempts to ascribe site preferences for most species have generally produced weak correlations (Gauss 1964; Wilson and Vogl 1965; Zenan 1967; Hanes 1971; Steward and Webber 1981).

Examples of species compositions and coverage values for a range of mature chaparral stands are shown in Table 6.2. Because of the overlapping of branches, areal coverage often exceeds 100% (ground-surface cover). Typically, bare ground will be much less than 10%, but on drier desertic sites (sites VII and VIII in Table 6.2) or on serpentine soils the percentage of bare ground may be much greater. It is not uncommon to encounter stands dominated by a single species. In the absence of disturbance, species diversity is said to decrease with age, but it is clear from Table 6.2 that site factors play a major role in determining community diversity. Detailed demographic patterns for three chaparral stands are shown in Table 6.3. Sometimes a species that represents a minor part of the cover may be numerically important, as is *Cercocarpus betuloides* at site 1. This particular species often spreads over short distances by rhizomes, but

Table 6.1. Widespread dominant California evergreen chaparral shrub species

Family and species	Common name	Distribution		
		California	Interior	Non-chaparral communities
<b>Anacardiaceae</b>				
<i>Rhus integrifolia</i>	Lemonadeberry	s, B		css
<i>R. ovata</i>	Sugar bush	s, B	Az	
<i>Malosma (Rhus) laurina</i> (Young 1974)	Laurel sumac	s, B		css
<b>Ericaceae</b>				
<i>Arctostaphylos</i>	Manzanita			
* <i>A. canescens</i>		n	O	ypf
<i>A. crustacea</i>		c-n		
<i>A. glandulosa</i>		s-n, B	O	
* <i>A. glauca</i>		s-c, B		
* <i>A. manzanita</i>		c-n		ypf
<i>A. mewukka</i>		c		ypf
* <i>A. parryana</i>		s		ypf
<i>A. patula</i> (Wells 1968)		s	O, Ut	ypf
<i>A. peninsularis</i> (Wells 1972)		s?, B		
* <i>A. pringlei</i>		s, B	Az	ypf
* <i>A. pungens</i>		c-s, B	Az-Mx	owd, ypf
* <i>A. stanfordiana</i>		n	O	
<i>A. tomentosa</i>		c-n		ccf
* <i>A. viscida</i> (Wells 1968)		c-n	O	owd, ypf
<i>Comarostaphylis diversifolia</i>	Summer holly	s, B		
<i>Xylococcus bicolor</i>	Mission manzanita	s, B		
<b>Fabaceae</b>				
<i>Pickeringia montana</i>	Chaparral-pea	s-n, B		
<b>Fagaceae</b>				
<i>Quercus dumosa</i>	Scrub oak	s-n, B		
<i>Q. durata</i>		c-n		
<i>Q. turbinella</i>		s-c, B	Az-Tx	
<b>Garryaceae</b>				
<i>Garrya buxifolia</i>	Silk-tassel bush	n	O	ewd, ypf
<i>G. congdoni</i>		c-n		
<i>G. elliptica</i>		s-n	O	ewd
<i>G. flavescens</i>		s-c	Az	ypf, piw
<i>G. fremontii</i>		s-n	O-Ws	ypf, ewd,
<i>G. veatchii</i>		s-c, B		owd
<b>Papaveraceae</b>				
<i>Dendromecon rigida</i>	Tree poppy	s-n, B		
<b>Rhamnaceae</b>				
<i>Ceanothus</i>	Buckbrush, California lilac			
[Section Cerastes]				
* <i>C. crassifolius</i>		s, B		
* <i>C. cuneatus</i>		s-n, B	O	
* <i>C. greggii</i>		s-c,	Az-Mx	piw
* <i>C. jepsonii</i>		n		

Table 6.1. (Cont.)

Family and species	Common name	Distribution		
		California	Interior	Non-chaparral communities
* <i>C. jepsonii</i>		n		
* <i>C. megacarpus</i>		s-c		
* <i>C. pumilus</i>		n	O	
* <i>C. ramulosus</i>		c-n		
* <i>C. verrucosus</i>		s, B		
[Section <i>Euceanothus</i> ]				
<i>C. cordulatus</i>		s-n, B	O, Nv	ypf
<i>C. dentatus</i>		c		ccf, ewd
<i>C. intergerrimus</i>		s-n	O-Ws, Az	ypf, ewd
<i>C. leucodermis</i>		s-n, B		
<i>C. oliganthus</i>		s-c		
<i>C. palmeri</i>		s-n, B		ypf
<i>C. papillosum</i>		s-c		ewd
<i>C. parryi</i>		n		
<i>C. soledatus</i>		s-n		owd, ewd
<i>C. spinosus</i>		s-c, B		css
<i>C. thyrsiflorus</i>		s-n	O	ypf
<i>C. tomentosus</i>		s-c, B		
<i>C. velutinus</i>		c-n	O-BC-Co	ypf, ewd
<i>Rhamnus crocea</i>	Redberry	s-n, B	Az	owd, ypf
<i>R. californica</i>	Coffee berry	s-n, B	O, AZ-NM	css, ewd, owd, ypf
Rosaceae				
<i>Adenostoma fasciculatum</i>	Chamise	s-n, B		
<i>A. sparsifolium</i>	Red shanks	s-c, B		
<i>Cercocarpus betuloides</i>	Mountain mahogany	s-n, B	O, Az	owd
<i>C. ledifolius</i>		s-n, B	O-Ws-Co-A	pjw, sbs
<i>Heteromeles arbutifolia</i>	Chaparral holly	s-n, B		owd
<i>Prunus ilicifolia</i>	Chaparral cherry	s-n, B		owd
Sterculiaceae				
<i>Fremontia [Fremontodendron]</i>	Flannel bush			
<i>F. californica</i>		s-n	Az	
<i>F. mexicana</i>		s, B		

Note: s = southern, c = central, n = northern, B = Baja California, O = Oregon, Az = Arizona, BC = British Columbia, Co = Colorado, Mx = Mexico, Nv = Nevada, NM = New Mexico, Tx = Texas, Ut = Utah, Ws = Washington. Non-chaparral communities: ccf = closed-cone forest, css = coastal sage scrub, ewd = evergreen woodland, owd = oak woodland, pjw = pinyon-juniper woodland, sbs = sagebrush scrub, ypf = yellow pine forest.

\*Indicates obligate-seeding species (i.e., taxa without the ability to regenerate after tops are killed), with exceptions: *Ceanothus cuneatus* is a very weak sprouter in certain high-elevation Sierra Nevada sites; *C. greggii* is reported to have weak sprouting ability in Arizona; various *Arctostaphylos* taxa show subspecific variation in this regard (Wells 1968, 1972).  
Source: Nomenclature according to Munz (1959) except where indicated otherwise.

Table 6.2. Areal coverage values for 11 selected stands (I–XI) of mature chaparral throughout the range

Species	Percentage ground surface cover										
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
<i>Adenostoma fasciculatum</i>	138	49	80	7		5			33	9	5
<i>Arctostaphylos auriculata</i>										64	
<i>A. glandulosa</i>						2			58		
<i>A. glauca</i>			33				17	19			
<i>A. pajaroensis</i>											50
<i>Ceanothus cuneatus</i>										10	
<i>C. greggii</i>		22					9		7		
<i>C. megacarpus</i>				79							
<i>C. spinosus</i>					136						
<i>Cercocarpus betuloides</i>				26	3	11	5				
<i>Heteromeles arbutifolia</i>					5	10					12
<i>Quercus dumosa</i>		8				93					
Other species	3		1	13	10	12	18	42	5		16
Bare ground (%)	—	—	7	7	3	5	>47	>37	—	12	16
Species diversity (H')	0.068	1.531	0.793	1.827	1.958	2.964	—	—	1.913	—	—
Years since last fire	35	22	95	55	55	>115	—	—	>45	—	—

## Notes:

- I. Parsons (1976): south-facing slope at 800 m in the southern Sierra Nevada.
- II. Keeley and Johnson (1977): east-facing slope at 1000 m in the interior Peninsular Range.
- III. J. Keeley (unpublished data): south-facing slope at 1100 m in the southern Sierra Nevada.
- IV. J. Keeley (unpublished data): west-facing slope at 400 m in the coastal Transverse Ranges.
- V. J. Keeley (unpublished data): north-facing slope at 300 m in the coastal Transverse Ranges.
- VI. J. Keeley (unpublished data): north-facing slope at 1000 m in the coastal Peninsular Ranges.
- VII. Vasek and Clovis (1976): east-facing slope at 1100 m in the interior Transverse Ranges.
- VIII. Vasek and Clovis (1976): a level site at 1300 m in the interior Transverse Ranges.
- IX. Schorr (1970): southeast-facing slope at 1000 m in the interior Peninsular Ranges.
- X. Davis (1972): south-facing slope at 400 m in the northern Central Coast Ranges.
- XI. Davis (1972): south-facing slope at 100 m in the northern Central Coast Ranges.

this is atypical for most species. Sprouting shrubs such as *Adenostoma fasciculatum* commonly produce three to four stems per plant, although on more open sites the number may be much higher. Non-sprouting species of *Ceanothus* and *Arctostaphylos* usually have a single stem per shrub. Species in the latter genus may reach tree-like proportions and dominate a site, despite being numerically less important than other species (site 2 in Table 6.3).

The most widely distributed chaparral shrub is *Adenostoma fasciculatum* (Fig. 6.3). This species is found from Baja to northern California in pure stands (chamise chaparral) or mixed stands with other shrub species. It often dominates at low elevations and on xeric south-facing slopes, with 60–90% cover. The short needle-like leaves produce a sparse foliage, and soil litter layers are poorly developed. Along its lower elevational limits, *A. fasciculatum* intergrades with subligneous coastal sage subshrubs, particularly *Salvia mellifera*, *S. apiana*, and *Eriogonum fasciculatum*.

*Adenostoma fasciculatum* is often codominant with one or more species of *Arctostaphylos* or *Ceanothus*. Two such mixed chaparral stands are shown in

Table 6.3. Site 1 is a low-elevation coastal stand dominated by a species of *Ceanothus*; as is commonly the case in chaparral along the lower elevational border, subshrubs form a significant part of the cover. Site 2 is a south-facing site dominated by *Arctostaphylos glauca*. Species of *Ceanothus* and *Arctostaphylos* predominate in mixed chaparral from middle to high elevations and also can occur in pure stands (manzanita chaparral or *Ceanothus* chaparral). There are more than 60 species in each of these two genera. Some are highly restricted, whereas others are nearly as widespread as *Adenostoma*. Most species are endemic to the California chaparral and show specific suites of characters that make them well adapted to this community. Both genera contain species that respond to fire by resprouting, as well as species that have no capacity for vegetative regeneration but require fire scarification of seeds (Table 6.1). The nonsprouting (obligate-seedling) species tend to be more abundant on south-facing slopes, ridge tops, and desert exposures. Sprouting species are more important on mesic slopes and at higher elevations (Keeley 1977b).

*Adenostoma*, *Arctostaphylos*, and *Ceanothus* spe-



Figure 6.3. The needle-leaved *Adenostoma fasciculatum* (chamise) is the most widely distributed of all California chaparral shrubs, but it is absent from Arizona chaparral.

cies predominate in the drier areas of chaparral, but as conditions become more mesic, other broad-leaved sclerophyllous shrubs become important (site 3 in Table 6.3). This association, sometimes referred to as broad-sclerophyll chaparral, is more diverse and includes *Quercus dumosa* (Fig. 6.4), *Heteromeles arbutifolia*, *Prunus ilicifolia*, *Cercocarpus betuloides*, *Rhamnus* species, *Garrya* species, *Rhus* species, and *Malosma laurina*. Shrubs are generally taller in this chaparral, 3–6+ m, and because of overlapping canopies, areal coverage often exceeds 100%. Light levels below the canopy are often quite low, and soil temperatures seldom approach levels found in more open stands. These stands commonly have a well-developed soil litter layer. Some of the species in this association are long-lived and, if left undisturbed, are capable of becoming small trees; for example, *Heteromeles* and *Prunus* can reach 11 m or more (J. Keeley, pers. observ.), and *Malosma* was considered to be one of the dominant arboreal species of southern California (Hall 1903). Most of these species are common components of other communities such as oak woodland.

In moist ravines, many of these broad-sclerophyll species coexist with small winter-deciduous trees such as *Sambucus* species and *Fraxinus dipetala*.

Montane chaparral at the upper elevational limits has a somewhat different physiognomy. The evergreen shrubs have a more rounded, compact shape, with foliage to the ground surface. Some sites may be covered by snow for many months. The association is dominated by vigorous sprouting species capable of dense coppice growth after fire, resulting in nearly impenetrable thickets with more than 100% cover (Wilson and Vogl 1965; Conard and Radosevich 1982). Often montane chaparral is dominated by species that are more typically found as understory or gap-phase coniferous forest shrubs (e.g., *Castanopsis sempervirens*, *Quercus vaccinifolia*, prostrate species of *Arctostaphylos* and *Ceanothus*, and winter-deciduous shrubs such as species of *Prunus*, *Ribes*, *Amelanchier*, and *Symphoricarpos*).

### Regional Composition

Evergreen chaparral is best developed at middle elevations (300–1500 m) in southern California. This area, sometimes described as the South Coast Region (Sampson 1944), includes the Transverse and Peninsular ranges, which extend from Ventura County to northern Baja California. Here chamise chaparral forms a blanket-like cover over large areas from the coast to the mesas and foothills and into the mountains. Near the coast, chaparral commonly gives way to the summer-deciduous coastal sage scrub, although the evergreen sclerophylls *Rhus integrifolia* and *Malosma laurina* are often associated with coastal sage vegetation. In parts of this region, *Adenostoma fasciculatum* is replaced by *A. sparsifolium*. This latter shrub is distributed from the southern part of the south Coast Ranges through the coastal section of the Transverse Ranges and the interior parts of the Peninsular Ranges (Marion 1943); it appears to replace *A. fasciculatum* on more mesic and fertile sites (Beatty 1984). The species coexist on some sites, and Hanes (1965) suggested that phenological and physiological differences are important in promoting coexistence, although Beatty (1984) contended that even within the same stand of chaparral these congeners are distributed in different soil microhabitats. Epling and Lewis (1942) considered this South Coast Region to hold special significance because of the occurrence of numerous chaparral shrubs that are endemic or reach their most northern distribution here. Throughout this region, chaparral occurs on a variety of soils and substrates, including Jurassic, Upper Cretaceous, and Eocene sedimentary rocks and

Table 6.3. Demographic structures of three older stands of chaparral in southern California

Species	Post-fire regeneration	Density		m <sup>2</sup> basal stem per hectare	
		Individuals ha <sup>-1</sup>	Stems ha <sup>-1</sup>		
Site 1. West-facing slope (30–35°) in Santa Monica Mountains (400 m), 55 yr old					
<i>Ceanothus megacarpus</i>	(OS) <sup>a</sup>	Alive	2,530	2,970	34.9
		Dead	950	1,110	5.0
<i>Adenostoma fasciculatum</i>	(FR)	Alive	1,140	4,140	4.8
		Dead	1,170	5,420	2.7
<i>Rhamnus crocea</i>	(OR)	Alive	190	330	0.5
		Dead	110	280	0.6
<i>Cercocarpus betuloides</i>	(OR)	Alive	610	34,190	2.1
		Dead	500	5,920	0.6
Four other shrub species	(OR)	Alive	140	2,330	4.1
		Dead	80	830	1.0
Six subshrub species	(FR & OR)	Alive	3,170	7,000	10.1
		Dead	1,750	5,640	6.7
Three woody vine species	(OR)	Alive	250	2,250	<0.1
		Dead	110	220	<0.1
Site 2. Southeast-facing slope (25–30°) in San Gabriel Mountains (1000 m), 88 yr old					
<i>Arctostaphylos glauca</i>	(OS)	Alive	2,000	5,300	41.8
		Dead	1,700	5,400	8.1
<i>Adenostoma fasciculatum</i>	(FR)	Alive	5,200	17,800	21.9
		Dead	4,900	18,000	9.7
<i>Ceanothus crassifolius</i>	(OS)	Alive	1,400	2,400	17.3
		Dead	2,800	5,600	16.6
<i>Quercus dumosa</i>	(OR)	Alive	200	1,300	2.3
		Dead	30	30	<0.1
Two other shrub species & one subshrub species	(OR)	Alive	150	260	<0.1
		Dead	90	300	<0.1
Site 3. North-facing slope (35–40°) in San Gabriel Mountains (900 m), 65 yr old					
<i>Adenostoma fasciculatum</i>	(FR)	Alive	1,100	3,900	16.0
		Dead	1,100	5,300	21.2
<i>Heteromeles arbutifolia</i>	(OR)	Alive	300	7,400	12.3
		Dead	0	2,700	3.5
<i>Prunus ilicifolia</i>	(OR)	Alive	300	5,900	10.3
		Dead	30	3,000	5.7
		Seedlings	4,528	4,528	0.7
<i>Quercus dumosa</i>	(OR)	Alive	800	5,200	8.8
		Dead	0	900	1.2
		Seedlings	80	80	<0.1
<i>Garrya veatchii</i>	(OR)	Alive	400	1,900	7.4
		Dead	30	1,700	5.7
<i>Ceanothus crassifolius</i>	(OS)	Alive	200	250	0.8
		Dead	700	1,000	4.9
<i>Arctostaphylos glauca</i>	(OS)	Alive	200	200	0.6
		Dead	30	200	1.0
Four other shrub species	(OR)	Alive	310	6,590	5.5
		Dead	80	910	1.3
Two subshrub species	(FR & OR)	Alive	110	2,390	3.6
		Dead	0	410	1.3
One woody vine species	(OR)	Alive	60	170	<0.1
		Dead	0	0	

<sup>a</sup>OS = obligate-seeder (no capability for resprouting); FR = facultative-resprouter (resprouts and establishes seedlings); OR = obligate-resprouter (typically does not establish seedlings after fire).

Source: J. Keeley and T. Montygiard-Loyba (unpublished data).



Figure 6.4. *Quercus dumosa* is a broad-sclerophyll species commonly forming nearly pure stands known as scrub oak chaparral. This species is replaced in Arizona by the very closely related (if not conspecific) *Q. turbinella*, which is one of the most widely distributed of the interior chaparral species.

Tertiary volcanics in coastal ranges, and granitic substrates of Precenozoic metamorphic and metavolcanic rock on interior ranges (Minnich and Howard 1984).

In the central coastal regions of California, the chaparral is less continuous and is part of a mosaic with grassland, coastal sage scrub, and broadleaf and coniferous forest (Shreve 1927). Fire is believed to be the determining factor in this mosaic distribution because no consistent pattern of edaphic or topographic factors coincides with the distribution of chaparral (Wells 1962). A noteworthy feature of this region is the large number of endemic species of *Arctostaphylos* and *Ceanothus*, many of which are restricted to particular substrates (Wells 1962) or coastal areas under marine influences (Griffin 1978). Davis (1972) described the distribution of six species in the *Arctostaphylos andersonii* complex in the Santa Cruz Mountains. He suggested that the group had its origin on forested sites and radiated

into chaparral, with each species occupying a habitat characterized by a distinct combination of soil conditions, including water-holding capacity, texture, pH, depth, root penetrability, and fertility. Both *Arctostaphylos* and *Ceanothus* have endemic species on the Channel Islands. Here the chaparral has a more open, woodland aspect (Bjornalden 1978), apparently because of less frequent fires and more intensive grazing by feral animals (Minnich 1980a).

In the north coastal region, chaparral becomes a less important component of the landscape and is restricted to the driest sites (Clark 1937). *Adenostoma fasciculatum* is common in the drier interior valleys, whereas broad-sclerophyll species are more important on the coastal slopes, where some (such as *Prunus ilicifolia*) form small tree-like communities (Oberlander 1953). Throughout this region, localized outcrops of serpentine substrate produce a more open vegetation referred to as serpentine chaparral. Low levels of Ca and high levels of Mg, plus potentially toxic levels of Ni and Cr, in these soils (Koenigs et al. 1982) restrict the distribution of many species (Whittaker 1960; Kruckeberg 1969). Serpentine endemics include shrubs such as *Q. durata*, *Garrya congdoni*, *Ceanothus jepsonii*, *C. ferrisae*, various subspecific taxa of *Arctostaphylos*, and herbaceous species. There is good evidence that other more widespread species have evolved serpentine ecotypes. Mechanisms for tolerating serpentine soils vary with the species; for example, White (1971) found that *Arctostaphylos nevadensis* was able to selectively take up Ca over Mg, whereas *Ceanothus pumilus* was not able to do so, but it could regulate Mg, Ni, and Cr uptake. The exclusion of serpentine endemics from other sites has been attributed to competition (Kruckeberg 1954), although Tadros (1957) and Wicklow (1964) found that in the case of the fire-following annual *Emmenanthe rosea*, restriction to serpentine sites was due to an inability to establish on more fertile soils that supported greater microbial growth.

Chaparral is absent from the Central Valley of California; however, some claim that this is an artifact of human disturbance (Cooper 1922; Bauer 1930). Above 500 m in the Sierra Nevada foothills, grasslands or xeric woodlands of *Pinus sabiniana* and *Aesculus californica* intergrade into mixed chaparral or nearly pure stands of *Ceanothus cuneatus* or *Adenostoma fasciculatum* (Graves 1932; Rundel and Parsons 1979; Vankat 1982). Above 1000 m, montane chaparral occurs, eventually giving way to coniferous forest above 2000 m. This upper border is dynamic and strongly influenced by fire frequency (Wilken 1967).

On the interior side of the Sierra Nevada, mon-

tane chaparral forms a mosaic with coniferous forest, pinyon-juniper woodlands, or scrub vegetation with Great Basin affinities (Skau et al. 1970). On these sites montane chaparral may replace coniferous forest after wildfires and remain for 50+ yr (Townsend 1966). In the northern Sierra Nevada and Cascade ranges, extending as far north as Bend, Oregon (W. D. Billings, pers. commun.), montane chaparral becomes more restricted and forms a mosaic with ponderosa pine forest and a variety of other, more mesic vegetation. It often forms associations with winter-deciduous shrubs, especially on the eastern slopes of the Sierra Nevada and adjacent ranges.

### Community Response to Wildfire

Wildfires are a dominant part of the environment. At present, the fire frequency averages once every two to three decades, but this may be more frequent than in the historical past (Byrne et al. 1977, unpublished data). Lightning strikes are the natural source of fire ignition, but today humans are responsible for most wildfires (Keeley 1977b). Lightning-ignited fires increase with elevation, latitude, and distance from the coast, whereas human-ignited fires show the opposite pattern and peak in different months (Parsons 1981; Keeley 1982). Throughout much of its range, chaparral forms a continuous cover over great distances, and as a result, huge wildfires that cover tens of thousands of hectares are not uncommon, particularly during Santa Ana wind conditions. Minnich (1983) suggested that fires of this size are an artifact due to modern-day fire suppression that results in unnaturally large accumulations of fuel. In support of this, he reported that large wildfires are relatively unknown from northern Baja California. Although Santa Ana winds are less common in this region, the difference is probably largely due to the fact that fire prevention is not encouraged, nor is fire suppression practiced, in Baja California. Consequently, fires are three times more common (largely ignited by humans), and this higher burning frequency keeps the vegetation more open and also produces a mosaic of different fuel conditions. Minnich (1983) argued that this represents the more "natural" situation for chaparral; however, this assumes that the fire-recurrence interval for a stand of chaparral is entirely a function of fuel load and, under primeval conditions, is not limited by sources of ignition. In the central Coast Ranges, Greenlee and Langenheim (1980) did a careful survey of the distribution of lightning-caused fires in conjunction with known patterns of fire behavior. They concluded that the "natural fire cycle" for the

inland reaches of Santa Cruz County may have ranged upward to 100 yr and was probably far longer in the coastal and lower-elevation areas.

Fires typically kill all aboveground biomass, although much of the belowground shrub biomass on sprouting species remains alive. In the first year after fire, there is an abundant growth of herbaceous and suffrutescent vegetation (Fig. 6.5), the extent of which varies with site and year (Sampson 1944; Horton and Kraebel 1955; Sweeney 1956; Stocking 1966; Ammirati 1967; Keeley 1977c; Keeley et al. 1981). This "temporary" vegetation is relatively short-lived, and by the fourth year shrubs commonly dominate the site (Fig. 6.6). The rate of shrub recovery, however, varies with elevation, with slope aspect and inclination, and with coastal versus desert sites (Hanes 1971).

The herbaceous flora arising after fire is dominated by annuals, and species diversity is typically greatest the first year after fire. Sweeney (1956) studied 10 chaparral burns in northern California and reported 214 herbaceous species, two-thirds



Figure 6.5. This lush herbaceous growth the first spring after wildfire is in marked contrast to the depauperate herbaceous vegetation under the mature-chaparral shrub canopy.

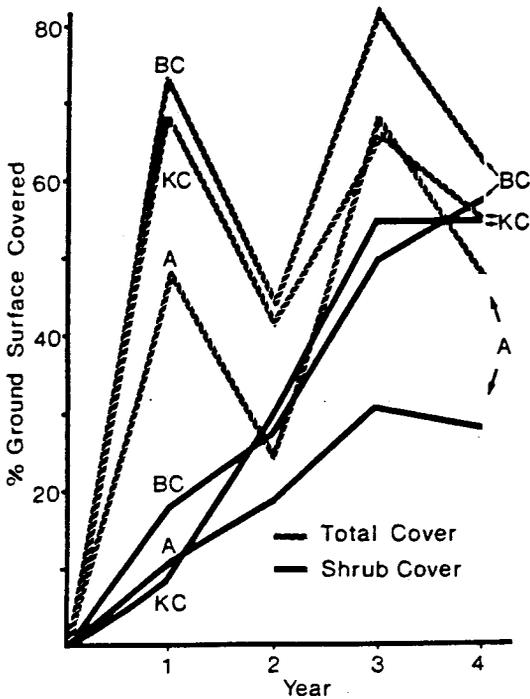


Figure 6.6. Changes in shrub cover and total cover (shrubs + "temporary" species) after fire at three sites at 560 m (A), 1000 m (BC), and 1670 m (KC) in southern California (from Keeley and Keeley 1981). The first-year increase total cover is largely due to herbaceous species, but by the fourth year after fire, shrubs account for nearly all of the cover except at the lowest elevation. The drop in total cover in the second post-fire year was apparently due to low rainfall (Keeley 1977c).

of which were annual species. Few of these were widespread, and nearly one-third of the herb species were found on only a single burn. Annuals dominated most sites the first year after fire, but in subsequent years herbaceous perennials became a more prominent part of the herb flora. Ammirati (1967) noted that herbaceous perennials were more important than annuals on the more mesic coastal slopes of ranges in northern California. In southern California, Keeley and associates (1981) studied sites at three elevations burned in the same month (same sites as in Fig. 6.6) and found 99 herb and suffrutescent species, of which two-thirds were annuals. At all sites the number of herb species was greatest in the first year after fire. The number of herb species ranged from 19 to 38 on different slopes at the lowest-elevation site, and from 12 to 19 at the highest elevation. Annuals accounted for 87–97% of the herb coverage in the first year, but only 20–28% by the fourth year.

Recovery of shrub biomass is from basal resprouts (Fig. 6.7) and seedlings. After a spring or early summer burn, sprouts may arise within a few



Figure 6.7. Resprout from lignotuber of *Adenostoma fasciculatum* in the first spring after fire.

weeks, whereas after a fall burn, sprout production may be delayed until winter (Biswell 1974). Seed germination, on the other hand, is delayed until the following spring. After the first year, shrub seedling establishment is uncommon.

Fire-caused mortality of potentially resprouting shrubs is variable, depending on species, site, and fire characteristics. Some, such as *Quercus dumosa*, *Heteromeles arbutifolia*, and *Malosma laurina*, are seldom killed, whereas others, such as *Adenostoma fasciculatum* and various *Ceanothus* species, sometimes suffer extensive mortality (Keeley 1977b). Factors that may be involved include season of burn, elevation, soil moisture, plant size, and physiological condition (Laude et al. 1961; Plumb 1961; Keeley and Zedler 1978; Tratz 1978; Baker et al. 1982a; Stohlgren et al. 1984). Comparisons of pre-fire soil seed pools with post-fire seedling densities suggest that vast numbers of seeds are killed (Keeley 1977a; Bullock 1982; Davey 1982). Generalizations about the temperatures that shrub bases or seeds are exposed to during fires are difficult to make, because temperatures vary greatly

with depth of burial, stand age and composition, weather conditions, and burning patterns (Sampson 1944; Bentley and Fenner 1958; DeBano et al. 1977; Anfuso 1982). For example, surface temperatures may remain higher than 500°C for more than 5 min during some fires, but not exceed 250°C in others. Temperatures at 2.5 cm depth are more commonly in the range of 50–200°C, but often persist for half an hour or longer.

Seedling mortality is generally high during the first year and is concentrated in the spring (Bullock 1982; Mills 1983). Seedlings are strikingly smaller than resprouts (Sampson 1944; Horton and Kraebel 1955; Keeley and Keeley 1981) and are most successful in gaps between the resprouting shrubs. Herbivory of seedlings and resprouts is important at this time (Davis 1967; Howe 1982; Mills 1983) and remains a factor in mature chaparral (Bartholomew 1970; Christensen and Muller 1975b; Schlising 1976).

Agencies concerned with managing chaparral lands often seed recently burned sites with non-native herbs, *Lolium perenne* (ryegrass) in particular. Such artificial seeding has been carried out for two purposes: "Type-conversion" programs may seed in order to produce fuel loads sufficient for repeat burns in successive years, that will replace chaparral with grassland (Sampson 1944). More commonly, the justification for seeding is that species such as *L. perenne* are thought to establish a better plant cover and reduce soil erosion. There is evidence that this practice is having negative effects on the natural regeneration of chaparral (Schultz et al. 1955; Corbett and Green 1965; Gautier 1981; Keeley et al. 1981; Griffin 1982).

It has been hypothesized that in the absence of fire, chaparral would be replaced by other types of vegetation. Sampson (1944) suggested that in northern California, grassland would eventually replace chaparral. Hedrick (1951), however, found no evidence of this in San Benito County chaparral free from fire for more than 90 yr. He commented that "the most striking feature of this old chamise stand is the lack of evidence that it is dying out or being replaced by herbaceous vegetation. It is true that old plants become defoliated and many stems die but these seem to be replaced by additional crown sprouts." This notion of resprouting shrubs rejuvenating themselves in the absence of fire is at odds with much published dogma on chaparral, but recent work suggests that it may be more important than previously thought, as discussed in the next section. In addition to Hedrick's study, other investigations have shown no evidence of old chaparral being replaced (sites III and VI in Table 6.2, sites 2 and 3 in Table 6.3) (Keeley and Zedler

1978), and it appears to be resilient to fire-recurrence intervals of 100+ yr (Keeley 1981, 1986). However, for most, but not all shrub species, mortality in old stands of chaparral is not accompanied by seedling establishment (Table 6.3). When there are unusually long intervals between fires, chaparral may be replaced by sclerophyllous woodland (Cooper 1922; Wells 1962). This will be a function of available seed sources, site factors, and particularly the life-history characteristics of the shrub species already established.

## PLANT LIFE HISTORIES

Chaparral has a rich diversity of species with a variety of life histories closely linked to fire (Table 6.4).

### Shrubs

Shrub species form a continuum in terms of mode of post-fire regeneration, ranging from species entirely dependent on seedling recruitment to sprouting species that rarely establish seedlings after fire.

Obligate-seeding species establish seedlings in the first year after fire, but seedling recruitment is almost nonexistent in subsequent years. Consequently, populations are usually even-aged (Schlesinger and Gill 1978). Post-fire seedlings of obligate seeders arise from a long-lived seed pool that lies dormant in the soil (Keeley 1977a; Davey 1982) until germination is cued either by intense heat (Quick 1935; Hadley 1961; Quick and Quick 1961) or by chemical stimulus from charred wood (Keeley 1987).

Sprouting species of *Arctostaphylos* and *Ceanothus* and *Adenostoma fasciculatum* often establish many seedlings after fire, although the proportion of resprouting shrubs to seedlings is variable with the species, site, and fire (Keeley 1977b). As with obligate-seeding species, seedling establishment by these facultative resprouters is confined to the first post-fire year, cued by heat or charred wood. *Adenostoma fasciculatum* is reported to produce two types of seeds: those that germinate readily at maturity, and a portion that require intense heat shock (Stone and Juhren 1951, 1953). Thus, the former seed type could germinate in the absence of fire. Although successful seedling establishment under the shrub canopy is in fact nonexistent, such seeds do contribute to colonization of other types of disturbance.

Obligate resprouters such as *Heteromeles arbutifolia*, *Quercus dumosa*, *Prunus ilicifolia*, *Cercocarpus betuloides*, and *Rhamnus* species seldom establish seedlings after fire. In mature chaparral, these shrubs do produce substantial seed crops that are

Table 6.4. Life-history modes in chaparral, including only native higher vascular plants and not meant to be an exhaustive list

Evergreen sclerophyllous shrubs (see Table 6.1)	
Obligate-seeders	
Sprouters with post-fire seedling recruitment	
Sprouters without significant post-fire seedling recruitment	
Evergreen sclerophyllous trees	
Cupressaceae	<i>Cupressus</i> spp.
Pinaceae	<i>Pinus</i> spp. <i>Pseudotsuga macrocarpa</i>
Ericaceae	<i>Arbutus menziesii</i>
Fagaceae	<i>Quercus</i> spp.
Lauraceae	<i>Umbellularia californica</i>
Semi-deciduous subshrubs	
Anacardiaceae	<i>Rhus trilobata</i>
Asteraceae	<i>Artemisia californica</i> <i>Cutierrezia sarothrae</i> <i>Haplopappus squarrosus</i>
Hydrophyllaceae	<i>Eriodictyon</i> spp.
Lamiaceae	<i>Salvia</i> spp. <i>Lepechinia</i> spp. <i>Trichostema lanatum</i> , <i>T. parishii</i>
Malvaceae	<i>Malacothamnus fasciculatus</i> , <i>M. fremontii</i>
Polygonaceae	<i>Eriogonum fasciculatum</i>
Saxifragaceae	<i>Ribes</i> spp.
Scrophulariaceae	<i>Mimulus aurantiacus</i> , <i>M. longiflorus</i> , <i>M. puniceus</i>
Suffrutescents	
Asteraceae	<i>Eriophyllum confertiflorum</i>
Cistaceae	<i>Helianthemum scoparium</i>
Fabaceae	<i>Lotus scoparius</i>
Fumariaceae	<i>Dicentra chrysantha</i> , <i>D. ochroleuca</i>
Hydrophyllaceae	<i>Turricula parryi</i>
Papaveraceae	<i>Romneya coulteri</i> , <i>R. trichocalyx</i>
Scrophulariaceae	<i>Penstemon centranthifolius</i> , <i>P. heterophyllus</i> , <i>P. spectabilis</i>
Agavaceae	<i>Yucca whipplei</i>
Woody vines	
Anacardiaceae	<i>Toxicodendron (Rhus) diversiloba</i> (Munz 1974)
Caprifoliaceae	<i>Lonicera interrupta</i> , <i>L. subspicata</i>
Ranunculaceae	<i>Clematis lasiantha</i> , <i>C. ligusticifolia</i> , <i>C. pauciflora</i>
Rubiaceae	<i>Galium</i> spp.
Scrophulariaceae	<i>Keckiella (Penstemon) cordifolia</i> , <i>K. ternata</i> (Munz 1974)
Herbaceous vines	
Convolvulaceae	<i>Convolvulus</i> spp.
Cucurbitaceae	<i>Marah fabaceus</i> , <i>M. macrocarpus</i>
Cuscutaceae	<i>Cuscuta</i> spp.
Fabaceae	<i>Lathyrus laetiflorus</i> , <i>L. splendens</i> , <i>L. vestitus</i>
Perennial herbs	
Apiaceae	<i>Lomatium</i> spp. <i>Sanicula</i> spp.
Asteraceae	<i>Helianthus gracilentus</i> <i>Perezia microcephala</i>
Caryophyllaceae	<i>Silene californica</i> , <i>S. laciniata</i>
Lamiaceae	<i>Salvia sonomensis</i>
Paeoniaceae	<i>Paeonia californica</i>
Ranunculaceae	<i>Delphinium</i> spp.
Scrophulariaceae	<i>Scrophularia californica</i>
Solanaceae	<i>Solanum</i> spp.
Amaryllidaceae	<i>Allium</i> spp. <i>Bloomeria crocea</i> , <i>B. clevelandii</i> <i>Brodiaea</i> spp.

(Cont.)

Table 6.4. (Cont.)

Iridaceae	<i>Sisyrinchium bellum</i>
Liliaceae	<i>Calochortus</i> spp. <i>Chlorogalum pomeridianum</i>
Poaceae	<i>Elymus condensatus</i> <i>Melica imperfecta</i> <i>Stipa</i> spp. <i>Zigadenus fremontii</i> , <i>Z. micranthus</i>
Annuals	
Apiaceae	<i>Apiastrum angustifolium</i> <i>Daucus pusillus</i>
Asteraceae	<i>Chaenactis</i> spp. <i>Filago arizonica</i> , <i>F. californica</i> <i>Gnaphalium</i> spp. (biennials) <i>Heterotheca grandiflora</i> <i>Malacothrix clevelandii</i> <i>Rafinesquia californica</i> <i>Stephanomeria virgata</i>
Boraginaceae	<i>Cryptantha</i> spp. <i>Plagiobothrys</i> spp.
Brassicaceae	<i>Caulanthus</i> spp. <i>Descurainia pinnata</i> <i>Lepidium nitidum</i> <i>Streptanthus</i> spp.
Caryophyllaceae	<i>Silene multinervia</i>
Fabaceae	<i>Lotus salsuginosus</i> , <i>L. strigosus</i> <i>Lupinus</i> spp.
Hydrophyllaceae	<i>Eucrypta chrysanthemifolia</i> <i>Phacelia</i> spp.
Lamiaceae	<i>Salvia columbariae</i>
Onagraceae	<i>Camissonia</i> spp. (Munz 1974) <i>Clarkia</i> spp.
Papaveraceae	<i>Eschscholzia</i> spp. <i>Papaver californicum</i>
Polemoniaceae	<i>Allophyllum</i> spp. <i>Gilia</i> spp. <i>Linanthus</i> spp. <i>Navarretia</i> spp.
Polygonaceae	<i>Chorizanthe</i> spp. <i>Pterostegia drymarioides</i>
Portulacaceae	<i>Calandrinia breweri</i> <i>Calyptridium monandrum</i> <i>Montia perfoliata</i>
Scrophulariaceae	<i>Antirrhinum</i> spp. <i>Collinsia parryi</i> <i>Cordylanthus</i> spp. <i>Mimulus</i> spp.
Poaceae	<i>Festuca</i> spp.

Source: Nomenclature according to Munz (1959) except where indicated otherwise.

widely dispersed (Bullock 1978; Hom 1984); the seeds, however, are short-lived and germinate readily with adequate moisture, and thus a dormant seed pool does not build up in the soil (Keeley 1987). This, coupled with the observation that these seeds are easily killed by intense heat, accounts for the failure to establish seedlings after fire.

On recently burned sites, obligate-seeding species typically have very high seedling densities, but low coverage relative to sprouting species

(Sampson 1944; Horton and Kraebel 1955; Vogl and Schorr 1972; Keeley and Zedler 1978; Keeley and Keeley 1981). These obligate-seeding species require 5–15 yr before substantial seed crops are produced, and thus fires at intervals more frequent than this can produce localized extinctions (Zedler et al. 1983). In the absence of fire, these species produce seed crops that are largely deposited in the soil around the parent plant and lie dormant until the next fire. Despite relatively large seed crops by

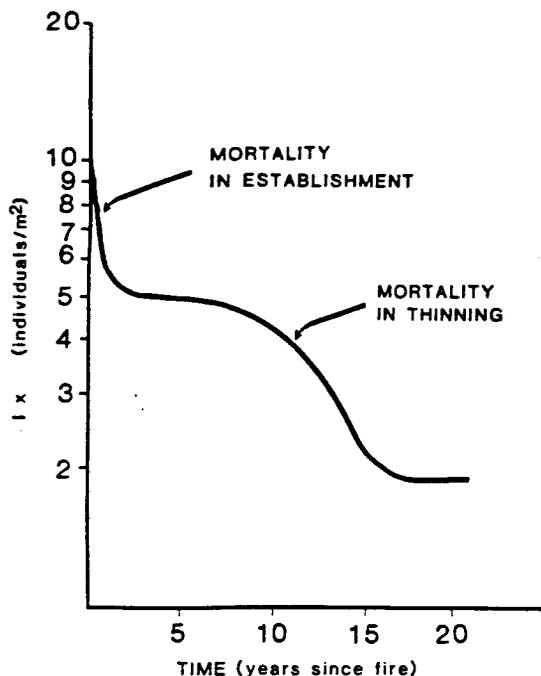


Figure 6.8. Generalized survivorship ( $I_x$ ) curve for individuals in pure even-aged stands of *Ceanothus megacarpus* in the south Coast Range (redrawn with permission from Botanical Review 48: 86 1982, Schlesinger et al. and The New York Botanical Garden). Not shown are variance/mean ratios calculated for living stems per plot, which showed a drop with thinning, suggesting that shrubs are becoming less clumped as the stand ages.

these species, accumulation in the soil appears to be relatively slow because a large portion of the seed crop is removed from the soil by predators (Keeley and Hays 1976; Davey 1982). In one study, two *Arctostaphylos* species were found to produce more seeds in a single year than were present in the soil seed pool (Keeley 1977a). A follow-up study 10 yr later showed no statistically significant changes in the sizes of the soil seed pools (J. Keeley, unpublished data).

As stands age and the canopy closes, there is intense competition and density-dependent thinning, resulting in high mortality (Fig. 6.8). In stands older than 50 yr, the fate of obligate-seeding species varies with the species and site. On mesic slopes, these shrubs are commonly outlived ("out-competed"?) by sprouting species, as illustrated by the ratio live : dead plants on the north-facing slope (site 3) in Table 6.3. On drier sites (site 2 in Table 6.3), obligate-seeding shrubs are dominant for much longer, although certain species such as *Arctostaphylos glauca* are capable of great size (>9 m) and readily shade out *Ceanothus* species (site 2) (Keeley

Table 6.5. North- versus south-facing slope comparison for *Ceanothus crassifolius* populations in the San Gabriel Mountains (800 m) of southern California

Parameter	North	South	<i>p</i>
Total plant cover (% ground surface)	>100%	<80%	—
<i>C. crassifolius</i>			
Height (m)	2.6	2.6	n.s.
Areal coverage, individual ( $m^2$ )	2.6	5.6	<0.01
Mortality over 6 yr (% per yr)	2.9	0	<0.01
Fruit production over 6 yr (fruits per $m^2$ areal coverage)	254	481	<0.01

Note: Each slope aspect represents 15 shrubs on two different slopes ( $N = 30$ ). Shrubs were 24 yr old at the end of the study. Source: J. Keeley (unpublished data).

and Zedler 1978). On the most xeric sites, non-sprouting *Ceanothus* species may still dominate the stand even after 50 yr (e.g., *C. megacarpus*, site 1 in Table 6.3). In general, obligate-seeding species increase in abundance, diversity, and longevity with increasing aridity (Keeley 1975, 1986). Even within a site, obligate-seeding species often do much better on drier south-facing slopes than on adjacent north-facing slopes (Table 6.5). Not surprisingly, there is evidence that seedlings of these species are more tolerant to drought than seedlings of associated sprouters (Musick 1972; Jacks 1984).

Sprouting shrubs are distinctly different from obligate-seeding species in that the aboveground stems are not even-aged. All sprouting species continually produce new shoots from the root crown throughout their life spans (Fig. 6.9). Figure 6.10 illustrates that the demographic pattern of stem recruitment is not the same in all such species.

The timing of seedling recruitment is not well documented for those obligate-resprouting species that fail to establish seedlings after fire. In general, establishment appears to be restricted to older, more mesic stands of chaparral, although seldom are seedlings of these species very abundant. Successful reproduction does occur under some conditions, as illustrated by the age distributions of *Quercus dumosa* and *Rhamnus crocea* seedlings in one very old chaparral stand (Fig. 6.11); some individuals do survive from most cohorts, and thus recruitment into the adult population seems likely. Seedlings in mature chaparral have also been noted for *Cercocarpus betuloides*, *Prunus ilicifolia*, and *Heteromeles arbutifolia* (Gibbens and Schultz 1963; Patric and Hanes 1964; Zedler 1982).



Figure 6.9. Multistemmed *Adenostoma fasciculatum* shrub with various-aged shoots arising from a common root crown. The distribution of stem ages for this individual is shown in Fig. 6.10.

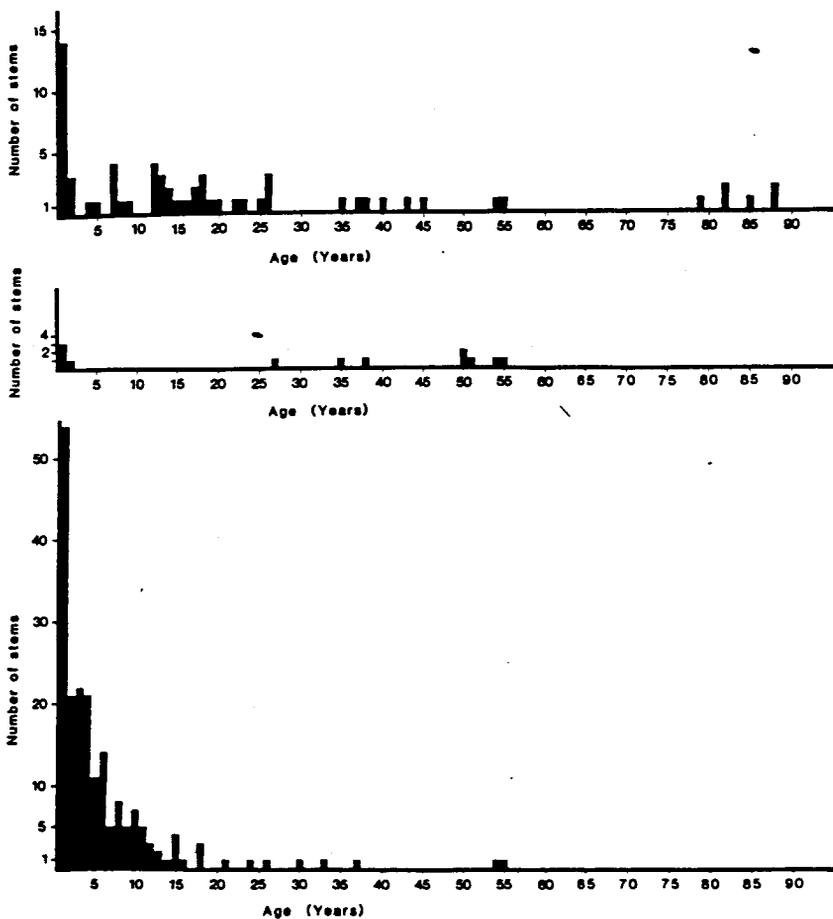


Figure 6.10. Age histograms for all stems on one individual each of *Adenostoma fasciculatum* (top), *Ceanothus spinosus* (middle) and *Heteromeles arbutifolia* (bottom) from different

sites in southern California (J. Keeley and T. Montygiard-Loyba, unpublished data).

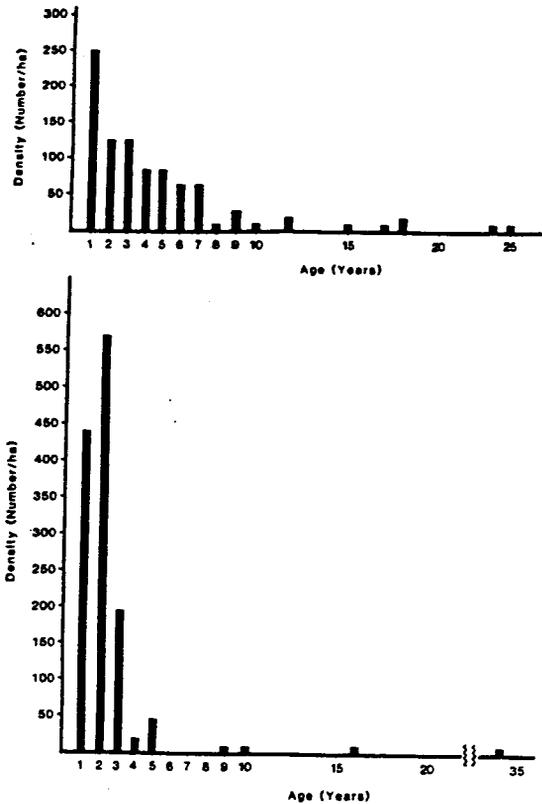


Figure 6.11. Age histograms for seedling populations of *Rhamnus crocea* (top) and *Quercus dumosa* (bottom) in a north-facing broad-sclerophyll chaparral stand at 900 m in the Santa Ana Mountains of southern California unburned for more than 115 yr (site VI in Table 6.2). Mature shrub densities were  $3420 \text{ ha}^{-1}$  and  $40 \text{ ha}^{-1}$  for *Quercus* and *Rhamnus*, respectively (J. Keeley and T. Montygiard-Loyba, unpublished data).

## Trees

Evergreen coniferous trees, such as species of *Cupressus*, *Pinus attenuata*, and *P. muricata*, often form dense even-aged stands surrounded by a matrix of chaparral (Vogel et al. 1977; Zedler 1977, 1981), commonly on serpentine or other unusual substrates (McMillan 1956; Koenigs et al. 1982). These species do not resprout after fire, and seedling establishment is in the first post-fire year from a dormant seed pool. In this case, seeds are released after fire from serotinous cones held on the trees for many years prior to the fire. *Cupressus abramsii* in the Santa Cruz Mountains commonly exceeds 100 yr of age, and cones with viable seeds are known to survive intact for more than 40 yr (H. Kuhlmann, pers. commun.).

*Pinus coulteri*, *P. sabiniana*, and *P. torreyana* are, typically, nonserotinous species associated with chaparral in certain regions, but seldom in dense stands. Populations of *P. coulteri* are polymorphic

with respect to cone serotiny, with this characteristic increasing toward the drier, chaparral-dominated end of its distribution (Borchert 1985). For all three species, seedling recruitment following fire is most abundant from seeds retained in previously opened cones, from the current crop of cones that commonly are unopened at the time of most fires, or from "seed trees" that survive the fire (Vale 1979; Minnich 1980b; McMaster and Zedler 1981). *Pseudotsuga macrocarpa* is the only conifer in chaparral capable of resprouting after fire. Sprouts arise from epicormic buds along the trunk and main branches. Seedling recruitment occurs under the chaparral or oak woodland canopy during fire-free periods (Bolton and Vogl 1969; McDonald and Litterell 1976), and thus populations of big-cone spruce are uneven-aged.

There is evidence that for most of these species, ranges have become more restricted in modern times because of increased fire frequency (Shantz 1947; Horton 1960; Gause 1966; Zedler 1977). In the case of *Cupressus forbesii*, Zedler (1981) has shown that reproductive success increases with the length of interval between fires. This obligate-seeding serotinous species starts producing cones at an early age, and cones accumulate on the trees. As a result, post-fire seedling establishment is an order of magnitude greater in stands over 50 yr of age at the time of burning than in stands 30 yr of age (Table 6.6). Long fire-free periods are also apparently necessary for successful seedling establishment by *Pseudotsuga macrocarpa* (Minnich 1980b).

Hardwood trees, in particular evergreen sclerophylls such as *Quercus agrifolia*, *Q. wislizenii*, *Q. chrysolepis*, *Arbutus menziesii*, and *Umbellularia californica*, occasionally occur within chaparral vegetation. These species are best developed in ravines and mesic north-facing slopes. Because of the higher moisture content of the fuels, such sites often escape complete destruction by wildfires. Depending on the severity of the fire, these species may resprout from epicormic buds beneath the bark of stems or from the root crown. Seedling establishment after fire is rare because of the lack of a dormant seed pool stored in the soil or on the plant; the seeds are short-lived and germinate readily at maturity (Keeley 1987). These tree species more commonly form woodland or riparian communities, often in association with a variety of winter-deciduous tree species.

## Subshrubs

These summer-deciduous species are dominants in the lower-elevation coastal sage scrub vegetation, and in chaparral they are most important along the xeric borders (Hanes 1971). They are readily shaded

Table 6.6. Parameters related to recovery of burned *Cupressus forbesii* stands (Tecate cypress) in southern California

Site	Age at time of fire (yr)	Pre-burn trees (m <sup>-2</sup> )	Cones per pre-burn trees	Seedlings per cone	Seedlings per Pre-burn trees	Seedlings (m <sup>-2</sup> )
Tecate A	10	0.05	0.8	0.33	0.28	0.02
Tecate B	32	8.90	3.7	0.25	0.07	0.60
Otay Mocado	33	1.70	9.9	0.03	0.33	0.57
Tecate C	52	1.21	21.7	0.22	4.25	5.15
Tecate D	52	0.36	29.9	0.51	15.30	5.51
Tecate E	95	0.44	33.5	0.13	4.25	1.87

Source: Zedler (1981).

out by the evergreen chaparral species (McPherson and Muller 1967; Gray 1983) and thus occupy gaps in the chaparral canopy. Most have light, readily dispersed seeds (Wells 1962) and are capable of recruiting new individuals into gaps, as well as establishing after fire from a dormant seed pool. The relatively complex germination behavior of the subshrub *Salvia mellifera* (Table 6.7) may represent a response to this environmental pressure (seeds exposed to light germinate readily without other stimuli, increasing under a variable diurnal temperature regime such as might occur near the soil surface on open sites; buried seeds that are in the dark require the presence of charred wood for germination).

### Suffrutescents

These species are abundant in the first year after fire, germinating from seeds in the soil. The germination cue may be heat for some and charred wood for others (Table 6.8). Depending on the site, one of these species may dominate a burned area in the

second or third year after a fire, but as the shrub cover increases, suffrutescent species are eliminated or restricted to gaps (Horton and Kraebel 1955; Keeley et al. 1981).

On open rocky sites from central California southward, the rosette-forming *Yucca whipplei* is a conspicuous element. Seeds germinate readily with adequate moisture, and populations are various-aged (Keeley and Tufenkian 1984). In southern California chaparral, this species is monocarpic: The rosette grows for a decade or more before flowering and dying. Not all populations, however, are monocarpic (Haines 1941). On the desert slopes of the Transverse Ranges, plants produce up to 100 rosettes during the vegetative phase, and flowering may be spread over many decades; in the central Coast Ranges, *Y. whipplei* populations are capable of vegetative spread by rhizomes.

### Vines and Perennial Herbs

Both woody and herbaceous vines are frequent in older stands of broad-sclerophyll chaparral. They

Table 6.7. Seed germination for the subshrub *Salvia mellifera* collected from a chaparral site after heat treatment or placed with charred wood

Condition	Percentage germination				Charred wood	p
	Control	70°C (1 hr)	70°C (5 hr)	120°C (5 min)		
Constant 23°C incubation						
Dark	1	2	5	0	24	<0.01
Light	23	24	17	25	25	>0.05
23°C/13°C diurnal incubation						
Dark	4	5	9	3	37	<0.01
Light	50	54	55	50	55	>0.05

Note: N = 3 dishes of 50 seeds each.  
Source: Keeley (in press).

Table 6.8. Seed germination for suffrutescent species after heat treatment or with charred wood or with potentially allelopathic leachate from *Adenostoma fasciculatum foliage*

Condition	Percentage germination				p
	Control	80°C (2 hr)	120°C (5 min)	150° (5 min)	
<i>Helianthemum scoparium</i>					
Control	23	15	43	3	<0.01
Leachate	29	17	50	11	<0.01
Charred wood	23	16	37	4	<0.01
C + L	25	17	40	9	<0.01
p	>0.05	>0.05	>0.05	>0.05	
<i>Eriophyllum confertiflorum</i>					
Control	4	6	4	1	<0.05
Leachate	8	6	6	1	>0.05
Charred wood	52	58	66	2	<0.01
C + L	58	63	65	3	<0.01
p	<0.01	<0.01	<0.01	>0.05	

Note: C + L = charred wood + leachate; N = 8 dishes of 50 seeds each; similar variation is evident in other suffrutescent species; e.g., *Lotus scoparius* is stimulated by heat, whereas *Romneya* species and *Penstemon* species are stimulated by charred wood.  
Source: Keeley et al. (1987); Keeley (1987).

grow into the shrub canopy and flower prolifically in wet years. Seeds of most of these species germinate readily, and seedlings are often produced under the shrub canopy. After fire, all of these species resprout from rootstocks, and seedling recruitment is uncommon at this time.

Perennial herbs are most conspicuous in the first spring after fire, and their presence is due to re-sprouting from bulbs or other buried parts. As the shrub canopy returns, these species persist, but they produce very depauperate growth in most years. Because of low light levels, they seldom flower under the canopy (Stone 1951). The timing of seedling recruitment is unknown, although it is clear that most of these species have seeds that germinate readily without treatment other than cold stratification (Sweeney 1956; Keeley et al. 1985; Keeley and Keeley in press).

### Annuals

Annuals make up the most diverse component of the chaparral flora. They are most abundant in disturbed areas and produce spectacular floral displays in the first spring after fire. Some of these species, such as *Phacelia* species, *Emmenanthe penduliflora*, and *Papaver californica*, have been referred to as "fire annuals" or "pyrophyte endemics" because of the fact that they may dominate a site in the first year after fire and then disappear until the next fire. These species do not have well-developed dispersal characteristics; hence, the long-lived seeds

(Went 1969) simply wait in the soil for disturbance to come to them. Germination is apparently not stimulated by heat (Sweeney 1956; Keeley et al. 1985) but rather is dependent on the presence of charred wood (Wicklowsky 1977; Jones and Schlesinger 1980; Keeley and Keeley 1982); germination is stimulated by a water-soluble organic compound leached from charred, but not ashed, wood (Keeley and Nitzberg 1984; Keeley et al. 1985). The compound is apparently a breakdown product of lignin and hemicellulose from any species of wood and is produced at temperatures greater than 175°C (Keeley and Pizzorno 1986).

Other native annuals are quite opportunistic in that they are most abundant on burned sites, but persist within gaps in the chaparral canopy. Some of these species have polymorphic seed pools in which a portion of the seeds germinate readily and another portion is refractory, requiring the stimulus of intense heat or charred wood for germination (Table 6.9). The mechanisms by which these factors stimulate germination probably are different. Species with heat-stimulated germination typically have seed coats with a water-impermeable cuticle that appears to crack under heat treatment (Keeley and Kelley in press). None of the species stimulated by charred wood has an obvious cuticle, and it is known, at least for *Emmenanthe penduliflora*, that the seed coat is freely permeable to water (Sweeney 1956).

Some native annuals are typically most abundant in gaps in mature chaparral, and their seeds

Table 6.9. Seed germination for native annuals after heat treatment or with charred wood

	Percentage germination			p
	Control	120°C (5 min)	Charred wood	
<i>Antirrhinum coulerianum</i>	2	3	42	<0.01
<i>A. kelloggii</i>	40	45	63	<0.01
<i>A. nuttallianum</i>	69	56	58	>0.05
<i>Camissonia californica</i>	3	6	48	<0.01
<i>C. hirtella</i>	30	66	26	<0.01
<i>Chorizanthe fimbriata</i>	37	43	45	>0.05
<i>Clarkia purpurea</i>	40	40	72	<0.01
<i>Collinsia parryi</i>	24	12	77	<0.01
<i>Cordylanthus filifolius</i>	57	27	62	<0.01
<i>Cryptantha muricata</i>	24	37	67	<0.01
<i>Gilia australis</i>	31	32	80	<0.01
<i>G. capitata</i>				
Burn	20	25	69	<0.01
Mature*	15	27	67	<0.01
<i>Lotus salsuginosus</i>	24	40	20	<0.01
<i>Malacothrix clevelandii</i>	9	10	35	<0.01
<i>Rafinesquia californica</i>	4	3	55	<0.01
<i>Silene multinervia</i>	36	43	83	<0.01

\*Seeds from a recent burned site and adjacent mature chaparral; see also Grant (1949).  
Source: Keeley and Keeley (in press).

germinate readily without special treatment (*Cordylanthus filifolius* in Table 6.9). Such species, as well as those with polymorphic seed pools, increase in abundance in more open communities, arising from repeated disturbances or along xeric margins. On such sites, very closely related species may have quite different microsite requirements. For example, Shimida and Whittaker (1981) reported that *Cryptantha muricata* and *Lotus strigosus* were restricted to the open, whereas the congeners *C. intermedia* and *L. salsuginosus* increased nearer to clumps of *Adenostoma fasciculatum*.

The striking contrast between the depauperate herb growth under mature chaparral and the flush of herbs after fire has been hypothesized to be due to allelopathic suppression of germination by the overstory shrubs. After field and laboratory studies, McPherson and Muller (1969) concluded that "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. Their theory is widely cited in textbooks and other sources, although as a note of caution we suggest that the following points should be considered: (1) The majority of their work focused on the effects of leached inhibitors on growth of non-native seedlings, not on germination of native herbs. (2) Leachate from *Adenostoma foliage* may inhibit the germination of some species, but apparently has no

effect on many others (Table 6.8) (McPherson and Muller 1969; Christensen and Muller 1975a; Keeley et al. 1985). (3) Temperatures applied to the soils that resulted in enhanced germination were far lower than the temperatures needed to degrade the suspected toxins (Chou and Muller 1972). (4) The concentration of toxins McPherson and associates (1971) found necessary for inhibition were much higher than those in the soil (Kaminsky 1981). (5) Christensen and Muller (1975a) found that the concentrations of suspected allelopathic toxins were greatest in soils from recently burned sites. (6) Seeds in soil that had been heat-treated and then returned to beneath the shrub canopy (and exposure to the putatively allelopathic leachate) showed high germination (Christensen and Muller 1975b). (7) Seeds of many chaparral herbs fail to germinate even if they are never exposed to so-called allelopathic toxins.

Kaminsky (1981) hypothesized that toxins produced by soil microbes are responsible for inhibiting herb germination under chaparral, and he demonstrated such an inhibitory effect with lettuce seeds. Pack (1987), however, could not duplicate this effect with seeds of native species. Also, it appears that the potential for microbial inhibition of germination is greater in soils from burned sites (Keeley 1984b), which is consistent with the fact that fungal and bacterial populations in soils increase after fire (Christensen and Muller 1975a).

Field studies suggest that any seedlings that do establish under mature chaparral are consumed by

small animals. In all studies in which animals were excluded from plots beneath chaparral, there were highly significant increases in herb densities, although they were not comparable in species composition or density to those observed after fire (McPherson and Muller 1969; Christensen and Muller 1975b; Quinn 1986).

In summary, it appears that in response to the poor conditions of low light, limited water, insufficient nutrients, and high predation under the shrub canopy, many species of annuals have evolved mechanisms that ensure seed dormancy until the canopy is removed. A germination requirement for intense heat or charred wood cues establishment to the post-fire environment. Opportunistic annuals colonize gaps in the chaparral canopy with a portion of their seed pool that is nonrefractory. Such a system of germination cues could be fine-tuned if these seeds were sensitive to "allelopathic" compounds, using such chemicals as cues to inhibit germination when under the canopy (Koller 1972); however, this remains to be demonstrated.

Non-native annual grasses and forbs are found throughout chaparral regions. Under a regime of frequent fires, they readily displace the native herb flora, and if fires are frequent enough, chaparral can be converted to grasslands dominated by these non-native species (Cooper 1922; Sampson 1944; Arnold et al. 1951; Hedrick 1951; Wells 1962). In the absence of fire, seeds of non-natives have a low residence time in the soil, and thus the presence of these species on burned sites is due to colonization after fire. Most, such as *Bromus* species, *Erodium* species, and *Centaurea melitensis*, disperse prior to the summer fire season and consequently are uncommon in first-year burns, but are common in the second and third years (Sampson 1944; Horton and Kraebel 1955; Keeley et al. 1981). Fall-fruiting species such as *Lactuca serriola* and *Conyza canadensis* are often present in first-year burns.

## SHRUB MORPHOLOGY AND PHENOLOGY

### Leaves

The dominant shrubs are evergreen, with small, sclerified, heavily cutinized leaves (Cooper 1922). The widespread *Adenostoma fasciculatum* has a linear-terete isofacial leaf less than 1 cm in length (0.06 cm<sup>2</sup>) that is markedly smaller than leaves of other chaparral shrubs (Fishbeck and Kummerow 1977). These leaves are produced individually on new growth and in short-shoot fascicles on old growth (Jow et al. 1980). Leaves on seedlings and fire-

induced basal resprouts (but not on basal sprouts from mature shrubs) are bifacial and deeply lobed (compare Figs. 6.3 and 6.7). Similar juvenile-type leaves occur on mature plants under abnormally mesic conditions. Other shrub species have broad-sclerophyll leaves remarkably convergent in size, shape, and anatomy. Most are simple (<5 cm in length and 1–5 cm<sup>2</sup>), with average leaf thickness ~300 μ, plus 5–10 μ cuticles on upper and lower surfaces (Cooper 1922; Fishbeck and Kummerow 1977). Many species have sharply serrated leaves (Fig. 6.4). Most *Arctostaphylos* species and *Dendromecon rigida* have isofacial leaves with an upper and lower palisade and stomata on both surfaces. In *Arctostaphylos*, such leaf types are largely restricted to interior species, whereas coastal taxa have stomata restricted to the lower leaf surface, and some have bifacial leaves (Howell 1945). Species in other genera have stomata restricted to the lower leaf surface. Sunken stomata are not uncommon, ranging from slightly sunken stomata in *Heteromeles arbutifolia* to the extreme case in certain *Ceanothus* species with stomatal crypts that are invaginated to over half the width of the leaf. These stomatal crypts are characteristic of the subgenus *Cerastes* (except in the seedling stage) and are absent in *Euceanothus* (Nobs 1963). Species of *Cerastes* also have markedly thicker leaves, higher leaf specific weights, and thicker cuticles than *Euceanothus* species (Barnes 1979).

Leaf orientation is variable among shrub species and depends on environmental conditions. Nearly vertical leaves are prominent in *Dendromecon rigida* and *Arctostaphylos* species, and many other species have leaf angles greater than 50° (Kummerow et al. 1981). In *Arctostaphylos* species, the leaf angle increases with aridity (Shaver 1978), and in *H. arbutifolia*, sun leaves have significantly steeper angles that shade leaves (H. A. Mooney, unpublished data). Other leaf characteristics are also highly modifiable, depending on the microenvironment (Cooper 1922; Mortenson 1973; Krause and Kummerow 1977; Hochberg 1980; Ball et al. 1983).

### Stems and Growth Forms

Chaparral shrubs show a remarkable degree of convergence in growth form. Across areas of similar topography, shrubs are of similar heights and give the impression of a smooth blanket of vegetation. Detailed studies of plant structure show similar degrees of convergence in distribution of leaves and stems among unrelated taxa (Mooney et al. 1977; Kummerow et al. 1981). Growth forms vary with environment, as on north- versus south-facing slopes (Table 6.5) or on coastal versus desert

sites (Vasek and Clovis 1976). Growth forms may also change temporally, as in *Arctostaphylos* and *Ceanothus* species, which in older stands grow horizontally to "escape" shading by adjacent plants. Often such branches will root and spread vegetatively by layering, often forming large clones (James 1984).

Fires affect growth form in that many species capable of tree-like proportions resprout after fire, giving rise to a multistemmed shrubby growth form. Resprouting ability is found in all chaparral shrub species, with the obvious exception of obligate-seeding *Ceanothus* and *Arctostaphylos* taxa (Table 6.1). The mode of sprouting, however, is variable. *Adenostoma fasciculatum* and sprouting taxa of *Ceanothus* and *Arctostaphylos* initiate a basal lignotuber or burl as a normal part of seedling development (Wieslander and Schreiber 1939), although populations of seedlings with and without lignotubers are known for *A. fasciculatum* on mesas north of San Diego and for *Arctostaphylos rudis* on mesas east of Lompoc (J. Keeley, unpublished data). Some species, such as *Heteromeles arbutifolia* and *Quercus dumosa*, may have large lignotuberous structures that are induced by repeated coppice growth after fires. Others, such as *Cercocarpus betuloides*, sprout from rhizomes a meter or more distal to the main shoot system (Site 1 in Table 6.3).

Lignotubers are uncommon in shrubs outside of mediterranean ecosystems (Keeley 1981). These "burls" are often large and commonly exceed the aboveground biomass (Kummerow and Mangan 1981). They differ anatomically among species (Anfuso 1982; Lopez 1983; James 1984), but in all cases they proliferate adventitious buds that are suppressed to various degrees by the dominant stems. After fire, new shoots are initiated from these burls, fed by carbohydrate stores in the burls (Lopez 1983) and roots (Jones and Laude 1960; Laude et al. 1961). Reserves appear sufficient to sustain the roots for more than 1 yr (Kummerow et al. 1977). Storage of inorganic nutrients may also be an important function of lignotubers. After fire, sprouts from burls are more robust because of a much larger pith (Watkins 1939), and often such sprouts will branch and proliferate multiple shoots at the ground level. Sprout production continues in the absence of fire, replacing stems that die (Figs. 6.9 and 6.10).

Stems of most species are ring-porous, with well-developed annual rings, but stems tend toward diffuse-porous, with poorly defined rings, in such others, as *Prunus ilicifolia* and *Malosma laurina* (Webber 1936; Watkins 1939; Young 1974; Carlquist 1980). Wood storage products such as tannins and

calcium oxalate are abundant in many species. Older stems of some species (e.g., *Adenostoma fasciculatum*) tend to rot, whereas others (e.g., *Quercus dumosa*) remain resistant for much longer periods.

Stem development in species of *Arctostaphylos* and *Ceanothus* (*Cerastes*) follows a peculiar pattern (Fig. 6.12). In *Arctostaphylos*, large stripes of bark die, leaving behind only a ribbon of living tissue (Adams 1934). In *Ceanothus* species, living tissues grow around these dead stripes, producing a flanged appearance called "longitudinal fissioning" by Jepson (1928). These stripes of dead stem tissue are connected to shaded branches or roots in unfavorable microsites and are often produced during severe droughts (Parsons et al. 1981). This characteristic of allowing selected strands of vascular tissue to die may have evolved as a way of decreasing the amount of stem cortical surface needed to maintain productive parts of the canopy or root system, and this apparently increases the longevity of these nonsprouting species (Davis 1973; Keeley 1975).



Figure 6.12 Stems showing patterning described as bark striping in *Arctostaphylos* (far left stem) or longitudinal fissioning in *Ceanothus* (far right stem).

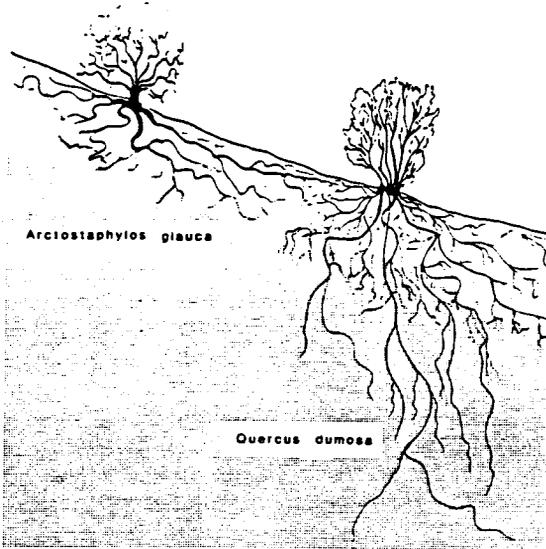


Figure 6.13. Root distribution of the nonsprouting *Arctostaphylos glauca* and the sprouting *Quercus dumosa* (redrawn from Hellmers et al. 1955b by T. Montygierd-Loyba).

## Roots

Root systems vary with species and soil depth. Sprouting shrub species tend to have more deeply penetrating roots than nonsprouting species (Fig. 6.13) (Cooper 1922; Hellmers et al. 1955b). Soil depth limits root penetration, but in highly fractured substrates, roots may penetrate bedrock to 9 m or more (Hellmers et al. 1955b). Deep roots may not be a prerequisite for surviving summer drought. Kummerow and associates (1977) excavated a site in southern California on shallow soil overlying bedrock and found that *Adenostoma fasciculatum* roots penetrated to less than 60 cm, and over two-thirds of all root biomass was in the top 20 cm of the soil profile. At another site on deeper soil, roots were distributed deeper for sprouting species *A. fasciculatum* and *Quercus dumosa*, but not for the nonsprouting *Ceanothus greggii* (Kummerow and Mangan 1981). In northern California, Davis (1972) excavated nonsprouting *Arctostaphylos* species and found much of the root mass concentrated in the upper 20 cm of the soil profile. Popenoe (1974) found that soil depth was positively correlated with plant height for shrub species in mixed chaparral.

Fine roots (defined as <0.25 cm in diameter) tend to be concentrated below the canopy; however,

there is a great deal of overlap in the distribution of these feeder roots between adjacent plants (Fig. 6.14), suggesting the potential for direct competition for water and nutrients. David (1972) reported that on sites with a well-developed litter layer, *Arctostaphylos* species proliferate feeder roots near the soil surface, and these roots penetrate the decomposing litter mat. In general, for most shrubs, the radial spread of roots is several times greater than the canopy, although root : shoot biomass ratios are less than 1 (Kummerow 1981). Despite the fact that sprouting species maintain their major roots between fires, root : shoot ratios are similar between sprouting and nonsprouting species.

Root nodules with symbiotic nitrogen-fixing actinomycetes are known for species of *Cercocarpus* (Vlamis et al. 1964) and *Ceanothus*, but their presence is dependent on various site factors (Vlamis et al. 1958; Furman 1959; Hellmers and Kelleher 1959; White 1967; Youngberg and Wollum 1976; Kummerow et al. 1978). Ectomycorrhizal associations are common with *Quercus dumosa* and *Arctostaphylos glauca*, and vesicular-arbuscular mycorrhizae with *Adenostoma fasciculatum*, *Ceanothus greggii*, and *Rhus ovata* (Kummerow 1981). Root grafting is apparently not common, although it has been observed in *Q. dumosa* (Hellmers et al. 1955b) and *Prunus ilicifolia* (Bullock 1981).

## Vegetative Phenology

Rates of development and growth are controlled by the interaction of low temperatures and irradiance in winter, and low soil moisture and high temperatures in summer. After winter rains have replenished soil moisture, growth initiation is dependent on the onset of higher temperatures. In general, phenological events begin and end later on north-facing exposures and are delayed with increasing elevation and latitude. Even at the same site, phenological events are not synchronized. In southern California, mean dates of stem elongation range from March to June, depending on the species, and the growing season ranges from 2 mo for *Adenostoma fasciculatum* to 1 mo for *Rhus ovata* (Kummerow et al. 1981). Such patterns also vary spatially; Bedell and Heady (1959) noted a 3-mo growing season for *A. fasciculatum* in northern California. Some species, such as *Malosma laurina* (Watkins and DeForest 1941) and *Adenostoma sparsifolium* (Hanes 1965), may continue growth during the summer months. In years of severe drought, there may be no new leaf production or stem elongation (Harvey and Mooney 1964).

Leaf longevity averages 1.5 yr in *Ceanothus mega-*

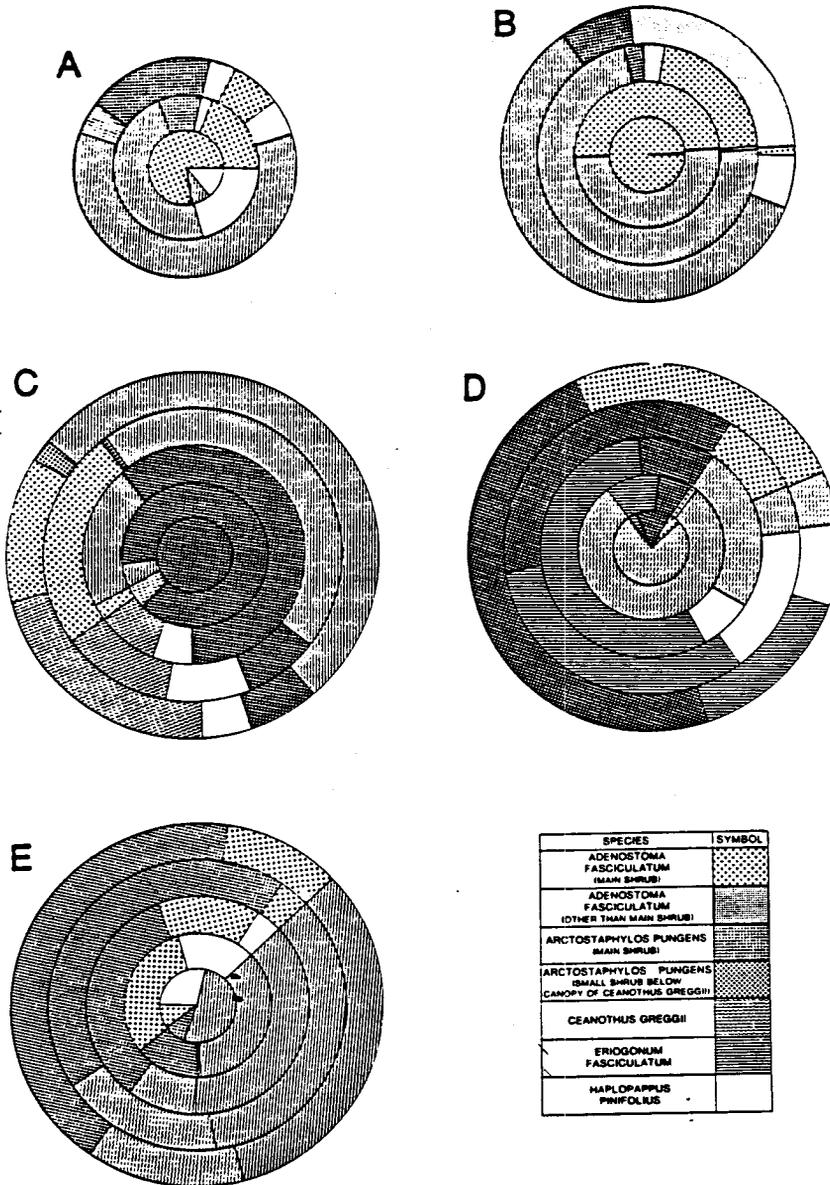


Figure 6.14. Graphic representation of fine-root distribution around the root crowns of five chaparral shrubs in southern California. Each ring represents a width of 1 m. The fine-root amount is expressed as a percentage of the total fine-root mass in the indicated area. The central core of each diagram represents one "soil unit" (= 0.6 m<sup>2</sup>) containing the root

crown of the respective shrub. The first ring represents 8, the second 16, the third 24, and the fifth 32 soil units. A: *Adenostoma fasciculatum*, main shrub. B: *A. fasciculatum*, stump sprout. C: *Arctostaphylos pungens*. D: *Ceanothus greggii*. E: *Haplopappus pinifolius* (from Kummerow et al. 1977).

*carpus* (Gray 1982) and 2 yr in *Adenostoma fasciculatum* (Jow et al. 1980). *Heteromeles arbutifolia* leaves average 2 yr (maximum 3 yr) in full sunlight and 3 yr (7 yr maximum) in shade (H. A. Mooney, unpublished data). Litter fall peaks following the completion of primary growth in most species (Mooney et al. 1977). It is almost entirely composed

of leaves, as most shrubs have a marked tendency to retain dead twigs and branches.

Secondary stem growth begins earlier and extends later into the season than primary growth (Avila et al. 1975); in *Rhus* species and *Malosma laurina* it may occur year-round. The width of growth rings is significantly lower in drought years

(Gray 1982) and was shown to be sensitive to the level of late winter and spring precipitation (Guntle 1974).

Fine root growth follows a pattern of growth similar to aboveground growth, with peak biomass levels in midsummer and a massive die-off as soil moisture is depleted (Kummerow et al. 1978).

## Reproductive Phenology

Flowers of most shrub species are small and are borne in large showy clusters, but few of the flowers produce mature fruits. Most species are largely self-incompatible (Raven 1973; Moldenke 1975). Fulton and Carpenter (1979) reported self-compatibility in *Arctostaphylos pringlei*, but Brum (1975) found this species to be entirely self-incompatible.

Most species are insect-pollinated, and this may have selected for the markedly asynchronous nature of flowering phenology in different species (Mooney 1977b). *Arctostaphylos* and *Garrya* species flower earliest in the season, prior to the initiation of vegetative growth, followed by *Ceanothus* and *Rhus* species. Early flowering in these four genera may be related to the fact that they flower on old growth, from floral buds initiated during the previous year's growing season (J. Keeley, unpublished data). *Adenostoma fasciculatum*, *Heteromeles arbutifolia*, and *Malosma laurina* flower later, on new growth after stem elongation is completed (Bauer 1936; Kummerow et al. 1981), and *Adenostoma sparsifolium*, with stem growth extending well into summer, is one of the latest flowering species, typically not beginning until August (Hanes 1965).

Annual flower and fruit production patterns are variable. Some species (e.g., *Heteromeles* and *Malosma*) tend to flower (and fruit) more or less annually, whereas others, such as *Arctostaphylos* and *Ceanothus* species, are typically biennial bearers.

## PHYSIOLOGY AND PRODUCTIVITY

### Water Relations

Chaparral shrubs vary in water-relations characteristics largely in accordance with species-specific differences in rooting habit (Poole et al. 1981). Shallow-rooted species are able to respond to elevated soil moisture levels early in the rainy season. During the summer, shallow-rooted nonsprouting species of *Arctostaphylos* and *Ceanothus* (section *Cerastes*) are exposed to extremely negative soil water potentials. At this time they commonly have pre-dawn stem xylem water potentials of  $-6.5$  to  $-8$  MPa versus  $-3$  to  $-4$  MPa during the summer drought for deeper-rooted shrubs such as *Rhus*

*ovata*, *R. integrifolia*, *Malosma laurina*, *Heteromeles arbutifolia*, sprouting species of *Arctostaphylos* and *Ceanothus* (section *Euceanothus*), *Prunus ilicifolia*, and *Rhamnus californica* (Poole and Miller 1975, 1981; Dunn et al. 1976; Burk 1978; Barnes 1979; Miller and Poole 1979; Schlesinger and Gill 1980; Parsons et al. 1981).

Stem water potentials are more negative during summers following low-rainfall seasons (Poole and Miller 1981), although the monthly distribution of rainfall may be as influential as the seasonal total (Gill 1985). In a study by R. Macdonald (unpublished data) in northern California, water potentials in *Adenostoma fasciculatum* and *Ceanothus cuneatus* fell from  $-2$  to  $-5$  MPa during July to October of a normal-rainfall year (1974), whereas in a drought year (1979) these species fell an additional  $-1.5$  to  $-3.5$  MPa; species in other communities showed less reduction, with the magnitude decreasing in the order savanna > woodland > alluvial forest, and with riparian trees showing little change from 1974. During a severe drought in the Sierra Nevada foothills in 1977, the shallow-rooted *Arctostaphylos viscida* reached pre-dawn potentials of  $-7$  MPa and showed very little diurnal variation, whereas the following summer, after a very wet winter, the lowest pre-dawn potentials were  $-4$  MPa, and there was a large diurnal change (Parsons et al. 1981). For most species, water potentials are more negative at their lower elevational and southern latitudinal limits than in the center of their distribution (Poole and Miller 1975; Mooney et al. 1977).

New resprouts may have stem water potentials one-third as negative as mature shrubs, but any differences disappear by the second year after fire (Radosevich and Conard 1980; Oechel and Hastings 1983). Seedlings of *Adenostoma fasciculatum* and *Ceanothus greggii* in recent burns may have water potentials below  $-6$  MPa during the summer (Barro 1982). Schlesinger and Gill (1980) showed that water potentials for the shallow-rooted *C. megacarpus* changed markedly as the stand developed after fire. Comparing stands 6, 13, and 22 yr old, they found that throughout the year, values were always more negative for plants in the youngest-aged stands. Within the 6-yr-old stand, smaller plants suffered more severe water stress during the summer drought than did larger plants; there was a significant correlation ( $r = 0.68$ ) between stem diameter and xylem pressure potential, and one small stem had an amazing pre-dawn water potential of  $-12$  MPa (Schlesinger et al. 1982). They contended that water stress is a major factor in stand thinning.

The relationship between xylem water potential and leaf conductance (Fig. 6.15) shows that most

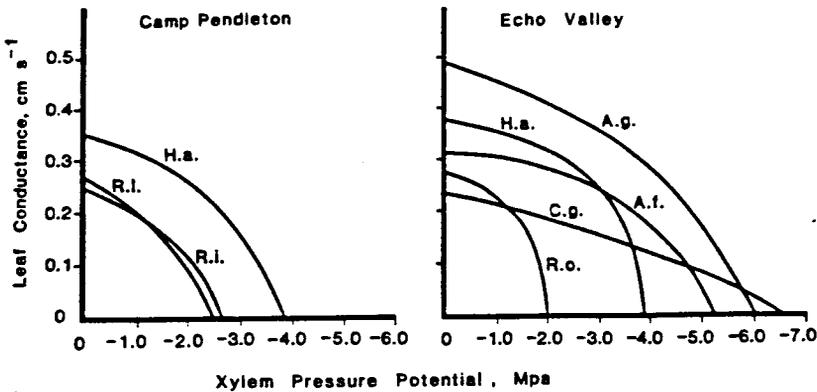


Figure 6.15. Relation between leaf conductance and xylem pressure potential in evergreen chaparral shrubs in southern California: Echo Valley, an interior site at 1000 m, and Camp Pendleton, a coastal site at 100 m. Species are *Heteromeles*

*arbutifolia* (Ha.), *Malosma* (*Rhus*) *laurina* (Rl.), *Rhus integrifolia* (Ri.), *Arctostaphylos glauca* (Ag.), *Adenostoma fasciculatum* (Af.), *Ceanothus greggii* (Cg.), and *Rhus ovata* (Ro.) (redrawn from Poole et al. 1981).

deep-rooted species exhibit stomatal closure at far lower water stress than shallow-rooted species. A similar pattern was observed by Barnes (1979) for shallow-rooted nonsprouting *Ceanothus* species in section *Cerastes* versus deeper-rooted species in section *Euceanthus*. The coastal and inland populations of *Heteromeles arbutifolia* illustrated in Fig. 6.15, as well as comparisons of northern and southern California plants (Harrison 1971), show that the relationship between stomatal conductance and xylem water potential is relatively constant for a species.

Stomatal conductances during the winter remain high throughout the day for most shrubs, although the absolute levels are typically twice as high for shallow-rooted species as for deeper-rooted species (Poole et al. 1981). Stomatal conductances of  $0.5 \text{ cm sec}^{-1}$  observed for the shallow-rooted *Arctostaphylos glauca* and *Ceanothus greggii* are among the highest for chaparral evergreen shrubs, but they are only about half as high as conductances recorded for other associated-life-history types, such as subshrubs and herbs.

During the growing season, there is a midday depression in stomatal conductance that begins earlier in the day as the season progresses. Shallow-rooted *Arctostaphylos* and *Ceanothus* species are likely to maintain more active photosynthesis longer into the drought than many deep-rooted shrubs. On the other hand, by late summer, these shallow-rooted species may show complete stomatal closure for a month or more, whereas deeper-rooted species commonly have a brief period of stomatal conductance each day. There is some evidence that these patterns may be the result of seasonal and diurnal osmotic adjustments (Roberts 1982; Calkin and Pearcy 1984).

These water-relations characteristics produce distinctive species-specific patterns of annual transpiration that vary with elevation and slope exposure and predict different patterns of productivity for these species. Poole and Miller (1981) hypothesized that chaparral communities on different sites should converge at maturity in terms of transpiration per unit of leaf area, and they put that figure at  $150\text{--}200 \text{ mm yr}^{-1}$ . Parker (1984) found that maximum transpiration rates are consistently higher for shallow-rooted obligate-seeding species of *Arctostaphylos* and *Ceanothus* than for deeper-rooted sprouting shrub species. He hypothesized that this characteristic results in more rapid seedling growth rates and hence a better potential for establishment in comparison with seedlings of resprouting species.

### Nutrients

Enhanced vegetative and reproductive growth after fertilizer application suggests that chaparral shrubs are nutrient-limited (Hellmers et al. 1955a; Vlamis et al. 1958; Christensen and Muller 1975a; McMaster et al. 1982; Gray and Schlesinger 1983). *Adenostoma fasciculatum* is clearly nitrogen-limited, whereas others such as *Ceanothus megacarpus* and *C. greggii* apparently are not, although the latter species does respond to phosphorus addition. *Ceanothus* species are nitrogen-fixers, and there is some evidence that such species are capable of enhancing the nitrogen status in soils surrounding them (Quick 1944; Hellmers and Kelleher 1959; Vlamis et al. 1964; Kummerow et al. 1978). Asymbiotic nitrogen fixation may also be important (Ellis 1982; Poth 1982).

Foliar leaching of nitrate with the first fall rains may result in a pulse of nitrogen input to the soil

(Christensen 1973). Schlesinger and Hasey (1980) found that this was largely from atmospheric deposition, and this, plus foliar-leached ammonium, could exceed the input by symbiotic nitrogen fixation. Quantitatively, litter fall is the most important means of returning nutrients to the soil (Gray and Schlesinger 1981). Litter fall is concentrated in summer, and decomposition is relatively rapid (Schlesinger and Hasey 1981). The highest concentrations of soil nutrients tend to be in the upper soil layers (Christensen and Muller 1975a), thus, shallow-rooted shrub species may have a competitive advantage. In *Adenostoma fasciculatum*, most of the nitrogen and phosphorus uptake occurs in winter, prior to growth, and Mooney and Rundel (1979) suggested that this may reduce leaching losses from the soil. These winter uptake patterns, however, are not typical of all species (Shaver 1981; Gray 1983).

Fire has a marked effect on the nutrient status of chaparral soils. By recycling nutrients tied up in plant matter, soil levels of most nutrients increase after fire (Sampson 1944; Christensen and Muller 1975a; Gray and Schlesinger 1981). Fires, however, result in substantial ecosystem losses of K and N through volatilization and runoff (DeBano and Conrad 1978) that may require 60–100 yr to replace (Schlesinger and Gray 1982). The first year after fire, the foliage concentrations of important nutrients are very high, although by the second or third year, nutrient levels may be comparable to levels observed for mature vegetation (Sampson 1944; Rundel and Parsons 1980, 1984). On some sites, the post-fire proliferation of suffrutescent and annual legumes may add nitrogen through their symbioses with nitrogen-fixing *Rhizobium* bacteria (Poth 1982).

### Productivity

Chaparral shrubs are all  $C_3$  plants (Mooney et al. 1974b) and have the capacity to fix carbon year-round. Maximum photosynthetic rates range from 5 to 15 mg  $CO_2$   $dm^{-2}$   $hr^{-1}$  (Mooney 1981). These relatively low rates result from internal limitations inherent in the sclerophyllous leaf structure (Dunn 1975) and strategies of nitrogen use efficiency (Field et al. 1983). For most species there is a broad temperature optimum range for photosynthesis between 10°C and 30°C, and there is apparently little capacity for temperature acclimation (Oechel et al. 1981). Some species are light-limited at less than one-third full sunlight (e.g., *Heteromeles arbutifolia*) (Harrison 1971), whereas others, such as *Ceanothus greggii*, are not saturated at two-thirds full sunlight (Oechel 1982). In general, sprouting species such as *H. arbutifolia*, *Quercus dumosa*,

*Prunus ilicifolia*, and *Rhus* species are reasonably shade-tolerant, but nonsprouting species seldom survive under the canopy of adjacent plants. Part of the explanation may lie in the observation that although leaves of *Ceanothus megacarpus* in low-light environments show a net carbon gain, they have lower water use efficiency than leaves under higher irradiances (Mahall and Schlesinger 1982). Field and associates (1983) reported that for five species of evergreens in northern California, photosynthetic capacity was highly correlated with stomatal conductance, and water use efficiency was highest in species commonly found in the driest habitats and lowest in the species common in the wettest habitats. However, species from the wetter habitats had the highest photosynthesis per unit of leaf nitrogen, and this is consistent with a similar finding by Rundel (1982).

The thermal insensitivity of photosynthesis suggests that low temperatures are likely to play a minor role in limiting wintertime carbon gain. Mooney and associates (1975) calculated photosynthetic rates for one evergreen shrub under typical seasonal limitations of light, temperature, and water. Their simulation suggests that wintertime depression of photosynthesis is largely a result of limited irradiance. Peak photosynthetic rates are typically observed only during the spring growing season, and as the season progresses, water availability becomes the major limiting factor for photosynthesis. Oechel (1982) suggested that xylem water potentials of -4 to -4.5 MPa mark the point of zero daily carbon uptake for *Adenostoma fasciculatum* and *Arctostaphylos glauca*. Because tissue water stress, through its effect on stomatal conductance, limits daily  $CO_2$  uptake, carbon-gain patterns vary between species and years. Dunn and associates (1976) showed that the carbon balance for a summer-fall season following a wet winter was several times greater than for a summer following a dry winter for *Heteromeles arbutifolia*, *Rhus ovata*, and *Prunus ilicifolia* (but *A. fasciculatum* was little affected). Similar results have been observed between natural and irrigated plants (Gigon 1979).

After fire, there is a rapid increase in above-ground shrub biomass that continues for several decades (Fig. 6.16). The estimated annual biomass production ranges from 840 to 1750  $kg\ ha^{-1}$ , with the lower values being from southern California (Ehleringer and Mooney 1983). After the first 20 yr, primary production slows, although the living biomass remains stable for 60 yr or more (Fig. 6.16). These older stands may be nutrient-limited, but this idea has been questioned (Schlesinger et al. 1982). Old stands of chaparral are frequently described as "decadent," "senescent," or "senile,"

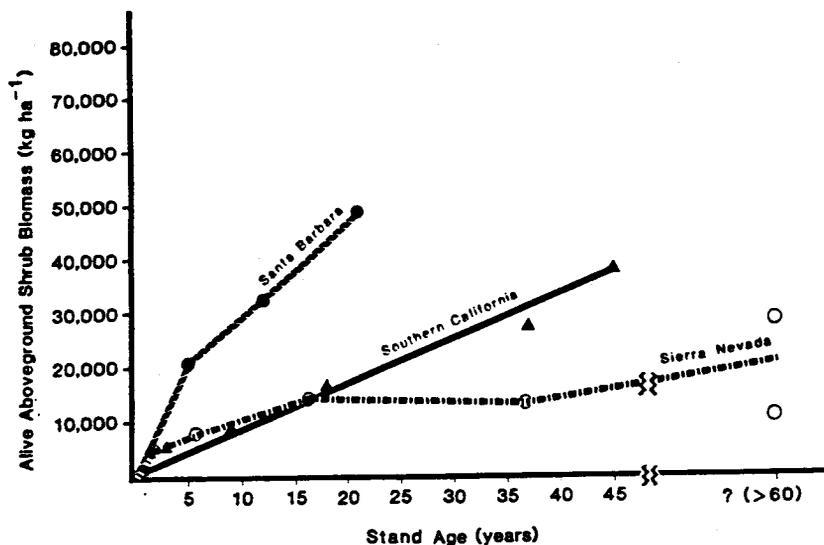


Figure 6.16. Standing living biomass in chaparral stands as a function of age since last fire: southern California mixed chaparral at San Dimas Forest from Specht (1969) (last datum point from Conrad and DeBano 1974); Santa Barbara Ceano-

thus megacarpus chaparral from Schlesinger and Gill (1980); Sierra Nevada foothills chamise chaparral from Rundel and Parsons (1979), Stohlgren et al. (1984), and Stohlgren (pers. commun.).

terms that lack clear definition and are based on little more than anecdotal observations. These terms apparently derive from the fact that as chaparral matures, there is a natural thinning of shrub density (Fig. 6.8), and dead stems accumulate and give the impression that the stands are "trashy" (Hanes 1971). Dead stems, however, are continually replaced by new basal sprouts in sprouting shrub species (Figs. 6.9 and 6.10), and surviving shrubs often remain quite healthy. For example, Rundel and Parsons (1979 and unpublished erratum) found that *Adenostoma fasciculatum* shrubs older than 60 yr had more live biomass than 40-yr-old shrubs. Nonsprouting species clearly are unable to replace older stems from basal sprouts, and this lack may account for the evolution of peculiar stem morphologies that appear to increase longevity (Fig. 6.12). Vigorous populations of nonsprouting *Arctostaphylos* and *Ceanothus* unburned for half a century or more are not uncommon (Table 6.3).

Chaparral stands older than 60 yr have been described as unproductive, with little annual growth (Hanes 1977), an idea apparently derived from measurements of browse production for wildlife (Biswell et al. 1952; Hiehle 1961; Gibbens and Schultz 1963). These studies showed that older chaparral produces very little deer browse. However, those were not valid measures of productivity, because production above 1.5 m, which is normally unavailable to deer, was not included;

most new growth in older stands occurs higher than 2 m. There is evidence, in fact, that older chaparral shrubs are capable of considerable annual growth. In a 1-yr study, *Arctostaphylos glauca* and *A. glandulosa* shrubs unburned for 90 yr produced as much or more terminal shoot growth and fruits (per unit of areal coverage) as individuals of the same species in a younger 23-yr-old chaparral stand (Keeley and Keeley 1977). A similar pattern has been recorded for *Adenostoma fasciculatum* in the same stands (J. Keeley and S. Keeley, unpublished data).

## RELATED PLANT COMMUNITIES

### California Coastal Sage Scrub

Often called "soft chaparral," this summer-deciduous vegetation tolerates more xeric conditions than evergreen chaparral (Mooney 1977a). The name derives from its Coastal Range distribution, where it occurs on both coastal and interior slopes. Coastal sage is most common at lower elevations below chaparral, but patches occur at higher elevations on outcroppings of shallow or fine-textured soils or on excessively disturbed sites. The dominants include all of the subshrubs and suffrutescent species that often are associated with chaparral, in gaps or after fires (Table 6.4), plus more restricted species such as *Encelia californica*, *Baccharis pilularis*, *Viguera laciniata*, and *Lepidospar-*

*tum squamatum*. Coastal sage scrub is lower (<1.5 m) and more open than chaparral and frequently has some herbaceous understory (Westman 1981a). Various associations have been delineated on the basis of latitudinal changes in species composition from Baja to northern California (Axelrod 1978; Kirkpatrick and Hutchinson 1980; Westman 1983) and show alliances with the northern coastal scrub (Heady et al. 1977). Succulents in the Crassulaceae and Cactaceae are important components near the coast and at the southern limits (Mooney and Harrison 1972). Oftentimes, evergreen sclerophyllous shrubs, such as *Malosma laurina* and *Rhus integrifolia*, will be distributed singly at various intervals throughout coastal sage stands, apparently exploiting infrequent favorable soil microsites.

Most dominants have nonsclerified malacophyllous leaves (3–6 cm<sup>2</sup>) that abscise and are replaced during the drought by a few smaller leaves surrounding terminal buds (Harrison et al. 1971; Gray and Schlesinger 1981; Westman 1981b), and these two leaf types may differ physiologically (Gigon 1979; Gulmon 1983). In *Salvia* species, a portion of the leaves may curl up during the summer drought, but then expand during the following growing season, making these plants technically evergreen (Mahall 1985). During the spring growing season, maximum leaf conductances, transpiration rates, and photosynthetic rates may be more than double those observed for sclerophyllous shrubs (Harrison et al. 1971; Oechel et al. 1981; Poole et al. 1981). These shallow-rooted subshrubs avoid drought by losing their foliage; however, they respond to summer or fall precipitation very rapidly and can initiate meristematic activity within a week of such events. Vigorous growth begins in early winter and extends until soil moisture, temperature, and photoperiod induce leaf abscission (Nilsen and Muller 1981; Gray 1982). Flowering is on new growth and thus is delayed until summer or fall (Mooney 1977a).

Volatilization of aromatic compounds from leaves is a notable feature of the coastal sage dominants *Artemisia californica*, *Salvia mellifera*, and *S. leucophylla*. Muller and associates (1964) showed that these compounds were potentially allelopathic to herb growth and suggested that this accounted for the typical "bare zone" of a meter or more that forms between coastal sage and grasslands. Such bare zones also occur between grassland and nonaromatic vegetation such as chamise and scrub oak chaparral. Enclosure experiments in both vegetation types, however, have shown small mammals are a major factor in bare-zone formation because of their propensity to forage on grassland species as close to the protective shrub canopy as possible

(Bartholomew 1970; Halligan 1974; Bradford 1976). Allelopathy still may play some role. The facts that coastal sage aromatics represent a substantial carbon drain on the plant (Tyson et al. 1974) and are potentially toxic (Muller and del Moral 1966; Muller and Hague 1967; Halligan 1975) argue strongly for an adaptive role; however, antitranspirant or antitherbivore functions have not been explored.

Coastal sage scrub is intermediate between grassland and chaparral in its resilience following frequent fires (Wells 1962; Kirkpatrick and Hutchinson 1980; Keeley 1981). Fire-recurrence intervals of 5–10 yr may result in chaparral being replaced with coastal sage scrub. More frequent fires, however, will eliminate sage, leaving such sites dominated by non-native grasses. The mode of post-fire recovery of coastal sage scrub is distinctly different from that of the dominant chaparral shrubs. Most sage scrub dominants establish few seedlings in the first year after fire; however, all are capable of resprouting and flowering vigorously in the first year (Westman et al. 1981; Malanson and O'Leary 1982; Keeley and Keeley 1984). These seed crops result in a huge pulse of seedling establishment in the second year after fire, because the seeds of most species (*Artemisia californica*, *Encelia californica*, *Haplopappus squarrosus*, and *Eriogonum fasciculatum*) are nonrefractory and germinate readily (Keeley in press). Coastal sage scrub communities have a post-fire burst of fire annuals and other herbs composed of the same species as in chaparral (Keeley and Keeley 1984). There is some evidence that resprouting of the dominant coastal sage species is greatly reduced on inland sites, and thus recovery is much slower (Westman et al. 1981; Westman 1982). In the absence of fire, coastal sage species are capable of regenerating their canopy from basal sprouts, similar to the pattern observed for sprouting chaparral shrubs (Figs. 6.9 and 6.10).

### Interior Chaparral

Interior regions of western North America have vegetation showing various degrees of similarity to California chaparral. Of these, the Arizona chaparral is the most closely related, despite being separated by more than 200 km of desert. The majority of the shrub species are shared with California chaparral (Table 6.1), and others are closely related if not conspecific with California taxa (e.g. *Quercus turbinella*) (Tucker 1953). The nearly ubiquitous Californian *Adenostoma fasciculatum* is noticeably absent, and *Q. turbinella* is to Arizona chaparral what *A. fasciculatum* is to California chaparral: It occurs throughout the chaparral region and dominates most sites (Carmichael et al. 1978). Vast stretches of

chaparral, such as in southern California, are uncommon in Arizona; rather, chaparral is distributed in widely disjunct patches (1000–2000 m), and it intergrades with desert scrub or grassland at the lower margin and yellow pine forest or pinyon-juniper woodland at the higher elevation.

Across this range, precipitation is 400–650 mm yr<sup>-1</sup>; however, in contrast to the situation for the Californian mediterranean climate (Fig. 6.2) 35% of the annual rainfall comes as high-intensity summer thunderstorms (Carmichael et al. 1978). Because summer rains are of short duration and occur at a time of high evaporative loss which has been preceded by a several-month drought, this precipitation may not always recharge the soil volume occupied by the deep-rooted shrubs. Thus, the climate could effectively be mediterranean for these shrubs. If this were true, then the lower elevational limit would be about 260 mm yr<sup>-1</sup> "available" precipitation, comparable to that for California chaparral (Mooney and Miller 1985). This border occurs at a higher elevation in Arizona, and the colder winter temperatures at this level may account for the absence of the xerophyllous *Adenostoma fasciculatum*. Recent studies by J. Vankat (pers. commun.) show that water stress in Arizona chaparral shrubs is lessened by summer precipitation. However, the extent to which these plants remain photosynthetically active through the summer is unknown, although Swank (1958) noted that most growth is in the spring, and summer growth is unpredictable. Lessened availability of summer precipitation is suggested by the fact that for a specific level of average annual rainfall, Arizona chaparral sites consistently produce sparser and more open communities than California chaparral (Cable 1957). Areal coverage is typically from 35% to 80% ground surface in Arizona chaparral communities (Cable 1957; Carmichael et al. 1978) (cf. Table 6.2). The similarity of flowering behavior in *Arctostaphylos* and *Ceanothus* in Arizona and California—a pattern quite distinct from that recorded from northern Mexico, with only summer rain (Fig. 6.17)—further suggests that summer precipitation may not be reliable.

Because of the sparser cover, wildfires are apparently infrequent, occurring every 50–100 yr (Cable 1957), although the responses to fire of the dominant shrubs are similar to Californian plants. Obligate-seeding species such as *Ceanothus greggii*, *Arctostaphylos pringlei*, and *A. pungens* establish seedlings from soil-stored seeds only after fire (Pase 1965; Pase and Lindenmuth 1971). Other species sprout prolifically after fire. Perhaps the most striking difference is the lack of a distinct "fire-type" temporary flora. Herbs and suffrutescent

species are more abundant after fire, but they are different from those of California chaparral. Total herb growth may be two orders of magnitude lower, and the herb flora is composed of only a few herbaceous perennial species (Pase and Pond 1964). None of the subshrubs, suffrutescents, or annuals with seed germination cued to post-fire conditions are found in Arizona chaparral.

On the west slopes of the Sierra Madre Oriental of northeastern Mexico are isolated patches of vegetation with strong similarities to California chaparral (Muller 1939, 1947; Shreve 1942). Muller (1939) suggested that the slightly lower precipitation and greater diurnal and annual temperature fluctuations in this region accounted for the replacement of thorn scrub by evergreen sclerophyllous vegetation. The strictly summer-rain climate of this region is markedly unlike that of other chaparral regions (Fig. 6.2). This Mexican chaparral is restricted to limestone or shallow rocky soils at 2000–3000 m, with desert scrub below and evergreen forest above. It is distinguished from the surrounding vegetation types by its predominance of shrubs, the importance of evergreen species, greater density of plant cover, and paucity of herbs. Important genera include *Quercus*, *Garrya*, *Cercocarpus*, *Rhus*, *Ceanothus*, and *Arctostaphylos*, including two California obligate-seeding species, *C. greggii* and *A. pungens*. Rzedowski (1978) considered this zone to have a high fire frequency, and he noted that the several scrub oak species were vigorous sprouters. A similar chaparral-type formation, often with greater numbers of deciduous elements, has been described from other isolated montane sites to the south of the Sierra Madre (Rzedowski 1978).

Petran "chaparral" is a largely winter-deciduous shrub vegetation at 2000–3000 m in the central Rocky Mountains (Vestal 1917; Daubenmire 1943). Despite its high elevation, annual precipitation is 380–535 mm yr<sup>-1</sup>, well within the range of values for other chaparral regions (Pase and Brown 1982). Winter temperatures are below freezing, and the summer growing season may be <100 d long. The vegetation has an overall physiognomy similar to evergreen chaparral in its height and thicket-like aspect (Hayward 1948). *Quercus gambelii* is the dominant throughout the range, and it, like the majority of species, is winter-deciduous. Evergreen species, including a few from California chaparral (Table 6.1), are minor components, although some, such as *Cercocarpus* species, are sometimes locally abundant (Brooks 1962; Davis 1976). A well-developed herb flora is characteristic of the mature vegetation (Christensen 1949; Allman 1952). Fires occur, and *Q. gambelii* responds like other scrub oaks by sprouting vigorously from the rootstock

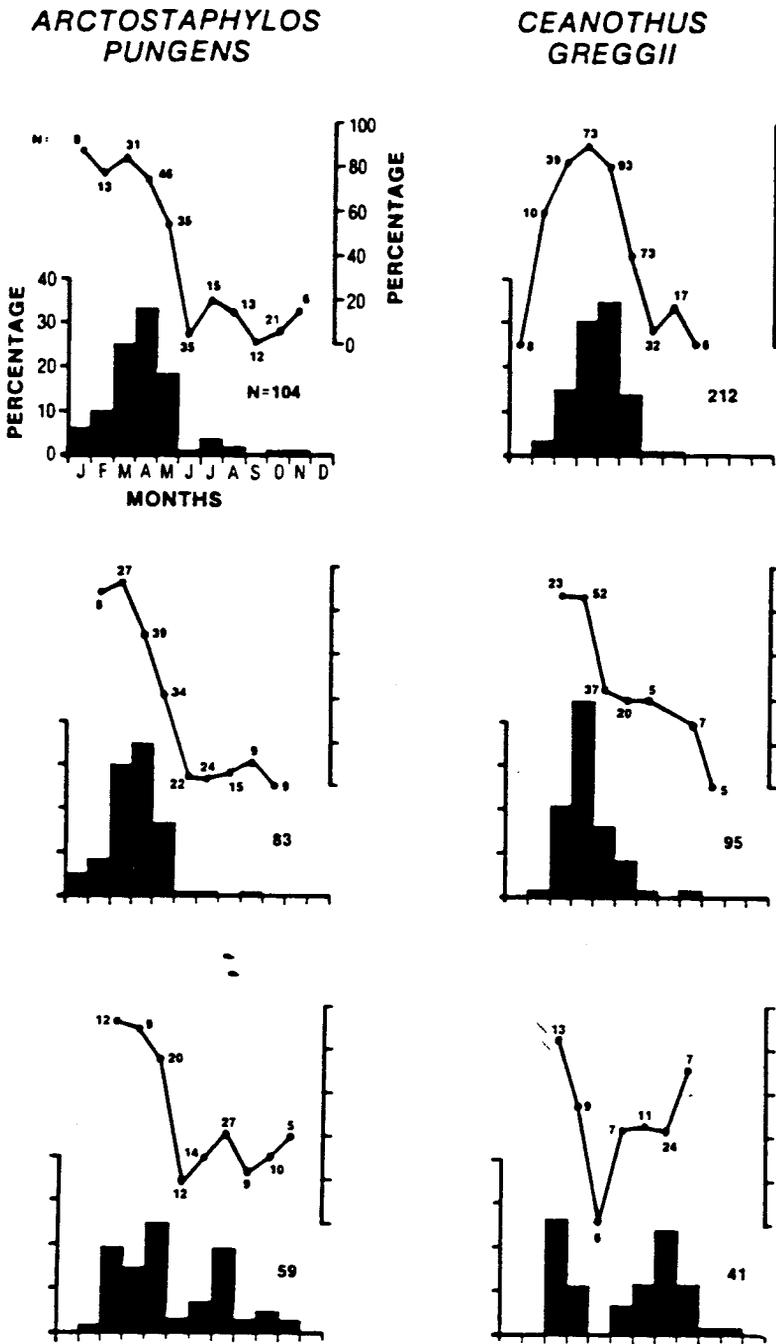


Figure 6.17. Season of flowering for *Arctostaphylos pungens* and *Ceanothus greggii* in California, Arizona, and northeastern Mexico. Bars indicate percentage of all herbarium sheets

in flower, by month, and lines show percentage of each month's sheets in flower; based on samples from 20 herbaria, at least five collections each (J. Vankat, unpublished data).

(Brown 1958; Kunzler and Harper 1980). All other common shrub species also sprout vigorously after fire, and obligate-seeding species are infrequent (McKell 1950). Most species maintain themselves in

the absence of fire through additional sprouts and seedling recruitment, although disturbance-free periods favor some species over others (Allman 1952; Eastmond 1968).

## EVOLUTION

Evergreen Cretaceous vegetation responded to the increasing aridity of the Tertiary period by the evolution of drought-deciduous and evergreen sclerophyllous taxa. California chaparral sclerophylls owe their origins to physiognomically similar taxa that appeared early in the Tertiary under conditions quite unlike the present mediterranean climate (Axelrod 1973). In light of the ample summer rains of that period, it is most reasonable that these species evolved in outcroppings of unusually stressful substrates. By analogy with modern vegetation, we can infer the critical factors to have been soil moisture and nutrient stress. Low-nutrient, coarse soils, with high infiltration rates, produce severe surface soil drought, but they also retain deeper water during droughts. Deep-rooted, woody evergreen sclerophylls can exploit these sites by their enhanced nutrient use efficiency and ability to remain metabolically active further into the drought. Very severe droughts, fine-textured soils, or high-nutrient conditions favor drought-deciduous types.

By the middle of the Miocene, evergreen sclerophylls were widespread across the Southwest, forming various broad-leaved sclerophyllous woodlands and shrublands associated with subtropical species no longer found in this region (Axelrod 1975). Closed-cone pine forests dominated the more mesic coastal regions (Raven and Axelrod 1978), suggesting that fires (and consequently droughts at some time of the year) must have been a predictable feature of the Miocene environment.

By the close of the Tertiary, the climate of California was taking on a mediterranean flavor, possibly a bimodal precipitation regime similar to that in Arizona today (Fig. 6.2), with a greater range of sites exposed to periodic droughts. This, coupled with increased tectonic activity and uplift of mountain ranges, increased the extent of well-drained shallow rocky soils and thus enhanced the spread of evergreen sclerophylls.

The Pleistocene marked the firm establishment of a mediterranean climate in California, accompanied by greater temperature extremes, elimination of summer-rain-dependent taxa, and widespread distribution of modern chaparral species within southern and central California.

The present spatial pattern of chaparral distribution, from the summer-rain region of northern Mexico, through Arizona with bimodal rainfall, to mediterranean California, may represent a useful model of the temporal development of California chaparral. It suggests a pattern of evolution of

chaparral taxa on islands of poor soils and seasonal drought, in an otherwise mesic landscape. As the climate changed, these drought-prone "islands" coalesced into larger patches, with consequent elimination of other vegetation. Despite the fact that chaparral taxa originated under a summer-rain climate, there is evidence that evolutionary changes have occurred in response to a mediterranean climate. For example, the flowering phenology of *Arctostaphylos pungens* and *Ceanothus greggii* is bimodally distributed in the summer-rain climate of Mexico (Fig. 6.17). Unimodal flowering in California is the result of flower-bud dormancy through the summer and fall and may have been selected for by the mediterranean climate. Lignotubers, as ontogenetic traits, such as in species of *Adenostoma*, *Arctostaphylos*, and *Ceanothus* (Keeley 1981), or fused endocarp segments in *Arctostaphylos* fruits (Wells 1972), are traits presently absent from Arizona chaparral species, and they possibly arose in response to a greater predictability of fire in a mediterranean environment.

The present distribution patterns of most species date to the xerothermic of recent times (8000–3000 BP) (Raven and Axelrod 1978), a time of most severe soil drought conditions in California that initiated a major expansion of chaparral vegetation. Evidence of this is seen in the elimination of more mesic forests throughout coastal southern and central California (Axelrod 1973; Warter 1976; Heusser 1978). It is quite likely that these climatic changes were exacerbated by humans in a scenario not unlike the "Pleistocene overkill" model (Martin 1973). Wells (1962) suggested that early Holocene humans in California played a major role in shaping present vegetation patterns through widespread use of fire. Lightning-ignited fires have played a role in chaparral evolution from the beginning, but humans have accelerated this process.

The evolutionary history is better known for some chaparral taxa than others. The ubiquitous *Adenostoma fasciculatum* is unknown from the fossil record (Axelrod 1973). It likely evolved on the most severe sites, and this in itself may account for it not being recorded in the fossil record. Most of the broad-sclerophyll species, in more or less present form, date back to middle Miocene times, although as components of various other vegetation types (Axelrod 1975). Many herbaceous genera and *Arctostaphylos* and *Ceanothus* underwent rapid speciation during the Pleistocene, in part because of the creation of new habitats during extensive mountain building (Raven and Axelrod 1978).

Hybridization has played a major role in the evolution of the latter two genera. All *Ceanothus* species are  $2n = 24$ , and although crosses between

*Cerastes* and *Euceanothus* are rare, hybrids within the subgenera are common (McMinn 1944; Nobs 1963; Phillips 1966). In *Arctostaphylos*, there are diploid ( $2n = 13$ ) and tetraploid taxa. In this genus, foliaceous floral bracts are considered ancestral, and these are restricted to tetraploid lignotuberous taxa (Wells 1969). These are taxonomically difficult species, because the resprouting mode allows for perpetuation of many forms; across their range, numerous subspecies or varieties are recognized, and even within a population there may be a number of very different forms. Obligate-seeding taxa all have the (apparently) derived characteristic of reduced bracts and are mostly diploid, although tetraploid populations are known for some (Wells 1968; Roof 1978). *Arctostaphylos rudis* and *A. patula* are diploids, with reduced bracts, and they are typically burl-forming resprouters; both species, however, are variable in this respect. Hybridization has been implicated in explanations of variation for over 30 taxa in the genus (Keeley 1976), most commonly between diploid species, although diploid  $\times$  tetraploid crosses are thought to account for the origin of many taxa (Wells 1968, 1972; Keeley 1974). The most thoroughly documented case for hybridization in *Arctostaphylos* involves the low-elevation obligate-seeding *A. viscida* ssp. *mariposa* and the montane-sprouting *A. patula*. At 1000 m, near Mather in the Sierra Nevada, sympatric populations occur, along with forms intermediate to these species and shrubs with unique combinations of traits (Dobzhansky 1953); isozymic evidence indicates hybridization and introgression (N. Elstrand, unpublished data). Ball and associates (1983) have documented the microhabitat distribution and physiological characteristics of the hybrids and parents.

Wells (1969) suggested that speciation in *Arctostaphylos* and *Ceanothus* is a result of the obligate-seeding reproductive mode that increased the number of sexual generations, relative to resprouting species. In *Ceanothus*, all species in the subgenus *Cerastes* have the obligate-seeding mode. In *Euceanothus*, some species are easily killed by fire, but "true" obligate seeders—taxa lacking adventitious buds in the root crown—are uncommon. The obligate-seeding mode in *Arctostaphylos* has clearly been polyphyletic, because many species have both obligate-seeding and burl-forming sprouting subspecies. In both genera, the obligate-seeding mode is undoubtedly a derived condition, because sprouting from adventitious buds in the root crown is a nearly ubiquitous trait in woody dicots and has undoubtedly been selectively maintained because of its value in recovering from many types of disturbances. Raven (1973) suggested that

loss of the crown-sprouting trait allowed for a more rapid fine-tuning of adaptation to the relatively recent mediterranean climate. Others have suggested that evolution of the obligate-seeding mode was tied to conditions that created large gaps for seedling establishment after fire, and thus it was favored along arid borders or in places of infrequent, intense fires (Keeley and Zedler 1978). Under such conditions, allocation of energy to seeds, as opposed to lignotubers, would be adaptive (Keeley and Keeley 1977). However, the energetic cost of lignotubers may not be high, and elimination of that structure does not preclude maintaining the ability to lay down adventitious buds in root and stem material.

A comparison of the structural and functional characteristics of obligate-seeders and sprouters in both genera suggests that they represent quite different syndromes (Keeley 1986). Sprouting shrubs are typically deep-rooted and require access to deep reserves of soil moisture during the summer drought. Once established, they preempt space for considerable periods of time, but as aridity increases, the number of safe sites for establishment goes down. Safe sites for shallow-rooted obligate-seeders are essentially open sites between resprouting shrubs. As the number of resprouting shrubs that can be maintained on a site decreases, the number of safe sites for seeders goes up. This strategy, however, depends on an ability to withstand severe water stress. Physiological data suggest a marked divergence between sprouters and obligate-seeders in this regard, and evolution of this divergence may have been enhanced by the greater number of sexual generations resulting from loss of the resprouting ability.

## AREAS FOR FUTURE RESEARCH

Long-term ecosystem studies are needed in order to evaluate management practices. Possible problems include the following:

1. The negative effect of artificial seeding after wild-fires on reestablishment of the native flora.
2. The present fire frequency of every two to three decades may be producing significant alterations in nutrient pools, as well as eliminating certain obligate-seeding species.
3. The detrimental ecological and esthetic effects of type-conversion projects, biomass programs, and the present fuel-break system.

Much of the early research in chaparral focused on the community response to wildfire. There has been much speculation about community-level changes in the absence of fire, and although much

dogma has been published, basically no studies have investigated the long-term changes in productivity and species diversity.

Demographic studies have the potential for explaining a great deal about the patterns observed in chaparral. Considering the wealth of species, relatively little is known of the life-history characteristics for species of all growth forms. Specific areas in need of study include the following:

1. Resilience of species to short as well as long fire-free intervals.
2. The timing and extent of seedling establishment for many sprouting shrubs and all herbaceous perennial species.
3. Seed-germination biology of most species, particularly the mechanism of charred-wood-stimulated germination, the distribution and control of germination polymorphisms, the degree of allelopathic control of germination, and longevity of seeds in the soil.

Physiological studies of chaparral shrubs have produced very detailed pictures of how a few species function. Broader comparisons with many more species and different growth forms are needed. Recent studies show that much is yet to be learned about the trade-offs involved in maximizing water use and nutrient use efficiency.

Detailed biosystematic studies in large woody genera such as *Arctostaphylos* and large herbaceous genera such as *Phacelia* are needed for a clearer picture of the evolutionary changes involved in adapting to the mediterranean climate.

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