Chapter 6

Chaparral

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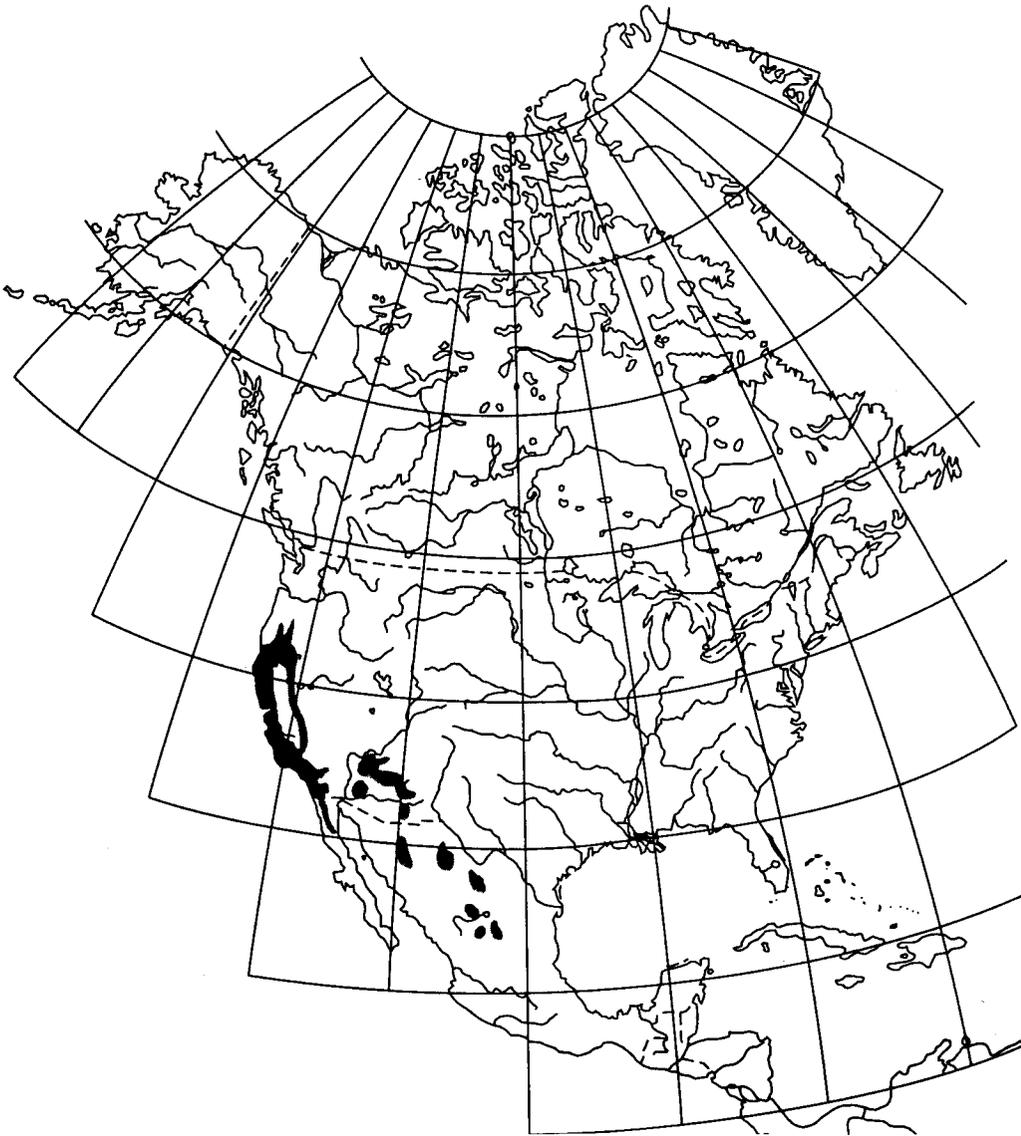
Figure 6.1. View of southern California mixed chaparral.

INTRODUCTION

"Chaparral" is the name applied to the sclero-phyllous shrub vegetation of southwestern North America. This chapter concentrates on the ever-green chaparral centered in California, although re-lated vegetation, including the interior chaparral of Arizona and northeastern Mexico, the winter-deciduous "petran" chaparral of the Rocky Moun-tains, and the West Coast summer-deciduous "soft chaparral," or coastal sage scrub, are also dis-cussed. For a complete bibliography of chaparral literature, see Keeley (1995a), and for reviews with a more historical perspective, see Mooney and Par-sons (1973) and Hanes (1977). Species lists are pre-sented in an earlier version of this chapter in Kee-ley and Keeley (1988a). For comparisons of chaparral with other mediterranean-climate scler-ophyllous shrub communities, see Mooney (1977b), Miller (1981), Shmida and Barbour (1982), Kruger and associates (1983), Barbour and Minnich (1990), and Keeley (1992a).

California chaparral dominates the foothills

from the Sierra Nevada to the Pacific Ocean (Wies-lander 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 Moun-tains of Baja California (30°N) (Shreve 1936), with isolated montane patches occurring as far south as 27°30'N (Axelrod 1973).

Throughout this region, chaparral characteristi-cally forms a nearly continuous cover of closely spaced shrubs 1.5–4 m tall, with intertwining branches (Fig. 6.1). Herbaceous vegetation is gen-erally lacking, except after fires, which are fre-quent throughout the range. Chaparral occurs from sea level to 2000 m on rocky, nutrient-deficient soils and is best developed on steep slopes. Because of complex patterns of topo-graphic, edaphic, and climatic variations, chapar-ral may form a mosaic pattern in which patches of oak woodland, grassland, or coniferous forest ap-pear in sharp juxtaposition. Fire frequency and substrate are important factors determining these patterns. Chaparral is replaced by grassland on frequently burned sites, especially along the more arid borders at low elevations where shrub recov-ery is more precarious because of drought, and on

deeper clay soils and alluvial plains, and by oak woodland on mesic slopes where fires are less frequent and often less intense.

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 from 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 precipitation is rare and arises from convectional 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, although coastal sites may occasionally experience subzero temperatures (Collett 1992). 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 it becomes progressively drier to the south.

Winter precipitation patterns are largely controlled by the orographic effect. On the windward side of mountains, air cools adiabatically with increasing elevation, so that temperature decreases and precipitation increases with elevation. On the leeward sides of mountains, air warms as it descends, creating a rainshadow that is hotter and drier than 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 that drives dry desert air toward the coast. These föehn types of winds may exceed 100 km hr^{-1} and bring high temperature and low humidity. Santa Anas are most common in spring and fall, and some of the most catastrophic wildfires occur under these conditions.

COMMUNITY COMPOSITION

Chaparral is a shrub-dominated vegetation, with other growth forms playing minor or temporal roles. More than 100 evergreen shrub species occur
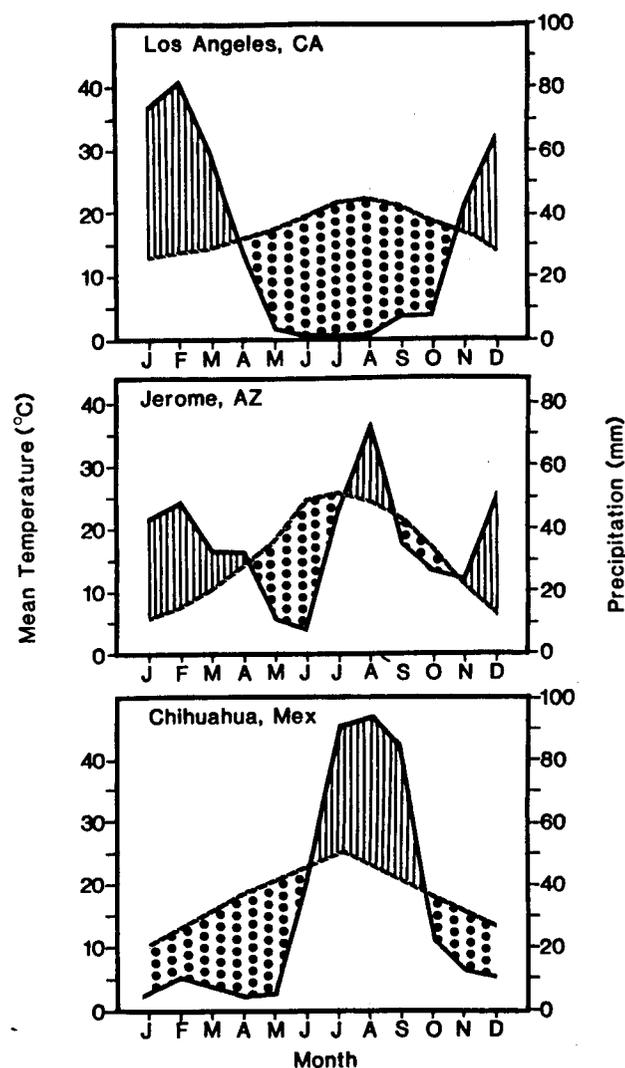

Figure 6.2. Climatic data for three chaparral sites (vertical line area = ppt>evap; dotted area = ppt<evap; solid line = precipitation, dashed line = mean temperature): Los Angeles, California (75 m, 34°05', 118°15'), Jerome, Arizona (1600 m, 34°45', 112°07'), and Chihuahua, Mexico (1350m, 28°42', 105°57').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

in chaparral (Keeley and Keeley 1988a). At any one site there may be as few as one or more than 20 species, depending on available moisture, slope aspect, slope inclination, distance from the coast, elevation, latitude, and fire history. Broad 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

Table 6.1. *Site characteristics and areal coverage (% ground surface cover) for 10 selected stands (A–J) of mature chaparral throughout the range (nomenclature according to Hickman 1993).*

Species	A	B	C	D	E	F	G	H	I	J
Elevation (m)	800	1000	1100	375	300	975	1100	1300	1000	400
Slope aspect	S	E	S	W	N	N	E	level	SE	S
Years since last fire	35	22	95	55	55	118	—	—	>45	—
Bare ground (%)	—	—	7	7	3	5	>47	>37	—	12
Woody species diversity (H')	0.07	1.53	0.79	1.83	1.96	2.96	—	—	1.91	—
Adenostoma fasciculatum	138	49	80	7		5			33	9
Arctostaphylos auriculata										64
A. glandulosa						2			58	
A. glauca			33				17	19		
Ceanothus cuneatus										10
C. greggii		22					9		7	
C. megacarpus				79						
C. spinosus					136					
Cercocarpus betuloides				26	3	11	5			
Heteromeles arbutifolia					5	10				
Quercus berberidifolia		8				93				
Other species	3		1	13	10	12	18	42	5	

Sources: (A) Parsons (1976) in the southern Sierra Nevada Range; (B) Keeley and Johnson (1977) in the interior Peninsular Range; (C) Keeley (1992b) in the southern Sierra Nevada Range; (D) Keeley (1992b) in the coastal Transverse Range; (E) Keeley (1992b) in the coastal Transverse Range; (F) Keeley (1992b) in the coastal Peninsular Range; (G) Vasek and Clovis (1976) in the interior Transverse Range; (H) Vasek and Clovis (1976) in the interior Transverse Range; (I) Schorr (1970) in the interior Peninsular Range; (J) C. Davis (1972) in the northern Central Coast Range.

generally produced weak correlations (Gauss 1964; Wilson and Yogi 1965; Zenan 1967; Hanes 1971; Steward and Webber 1981). On a local scale there is a regular turnover in species from one slope aspect to another and with elevation. For example, the diverse genus *Ceanothus* exhibits a regular turnover of species with elevation, and within an elevational band, species segregate by slope aspect or inclination (Nicholson 1993; Zedler 1995a).

The composition of chaparral stands varies along gradients of moisture, elevation, latitude, and the like, and attempts at classifying chaparral associations have named 28 communities (Holland 1986) and over 50 series (Sawyer and Keeler-Wolf 1995). Sites may be dominated by a single species, or several may co-dominate (Table 6.1). Due to overlapping branches, areal coverage can exceed 100% (ground-surface cover). Typically, bare ground is <10%, but it increases on drier desertic sites (Sites G & H, Table 6.1) and on stressful substrates such as serpentine or gabbro. Demography of mature chaparral has been described in Schlesinger, Gray, and Gilliam (1982a), Keeley (1992b, 1992c), Zammit and Zedler (1992); patterns for three stands are shown in Table 6.2. Sometimes a species that represents a minor part of the cover may be numerically important, as is *Cercocarpus betuloides* at Site 1 (Table 6.2) (nomenclature according to Hickman 1993). In dense chaparral, this spe-

cies spreads by rhizomes, an atypical characteristic for chaparral shrubs; however, it is arborescent on open sites. Sprouting shrubs such as *Adenostoma fasciculatum*, on the other hand, commonly produce only a few stems in dense chaparral but proliferate basal sprouts on more open sites. Nonsprouting species of *Arctostaphylos* and *Ceanothus* usually have a single stem per shrub, and arborescent individuals of the former taxon may dominate a site, even at low densities (Site 2 in Table 6.2).

The most widely distributed chaparral shrub is *Adenostoma fasciculatum* (Fig. 6.3), ranging from Baja to northern California in pure chamise chaparral or in mixed stands (Table 6.1). 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*. At higher elevations, *A. fasciculatum* often co-dominates with one or more species of *Arctostaphylos* or *Ceanothus* (Table 6.1).

Ceanothus and *Arctostaphylos* are large genera (>60 species) and often form pure stands commonly referred to as manzanita chaparral or ceanothus chaparral. Some species are highly restricted, whereas others are nearly as widespread as *Aden-*

Table 6.2. *Demographic structure of three older stands of chaparral in southern California*

Species	Postfire regeneration[a]	Live basal coverage m² basal area ha⁻¹	Shrub density Genets ha⁻¹	% Dead	Ramets /genet	Seedlings & saplings Genets ha⁻¹
Site 1. West-facing slope (19°) in Santa Monica Mountains (375 m), 55 yr old:						
Ceanothus megacarpus	(OS)	34.9	3360	25	1.2	0
Adenostoma fasciculatum	(FR)	4.8	1500	22	6.4	0
Salvia mellifera	(FR)	2.8	1920	45	3.8	0
Cercocarpus betuloides	(OR)	2.1	610	0	65.8	0
Rhamnus crocea	(OR)	0.5	260	23	2.3	80
Additional species (three lianas)	(OR)	0.1	360	31	9.0	0
Site 2. Southeast-facing slope (9°) in San Gabriel Mountains (1000 m), 88 yr old:						
Arctostaphylos glauca	(OS)	41.8	2440	19	4.4	0
Ceanothus crassifolius	(OS)	13.9	3810	82	2.1	0
Adenostoma fasciculatum	(FR)	20.3	6690	33	5.5	0
Quercus berberidifolia	(OR)	2.3	220	0	5.9	0
Additional species (two shrubs, one subshrub)	(OR)	0.1	240	38	1.7	0
Site 3. Northwest-facing slope (37°) in San Gabriel Mountains (975 m), 65 yr old:						
Quercus berberidifola	(OR)	8.9	860	0	7.6	80
Adenostoma fasciculatum	(FR)	7.3	1940	50	4.7	0
Garrya veatchii	(OR?)	6.5	420	7	8.5	0
Heteromeles arbutifolia	(OR)	4.9	330	0	30.5	0
Arctostaphylos glauca	(OS)	2.8	220	14	1.8	0
Ceanothus crassifolius	(OS)	2.3	750	77	1.7	0
Prunus ilicifolia	(OR)	2.3	310	10	29.6	4530
Additional species (four shrubs, two subshrubs, one liana)	(FR & OR)	9.1	480	17	19.1	0

[a] OS = obligate seeder (no resprouting capacity); FR = facultative resprouter (resprouts and establishes seedlings); OR = obligate resprouter (typically does not establish seedlings after fire).
Source: Keeley (1992b, and unpublished data).

ostoma. Most species are endemic to the California chaparral and have suites of characters reflecting a long association with fire. Both *Ceanothus* and *Arctostaphylos* have lignotuberous species that sprout after fire, as well as species lacking the capacity for vegetative regeneration. All species in these two genera produce deeply dormant seeds that require fire cues for germination. 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 1986; Nicholson 1993).

Adenostoma, Arctostaphylos, and *Ceanothus* species predominate in the drier areas of chaparral, but on more mesic sites other broader-leaved evergreen shrubs become important (Site 3, Table 6.2). This association, referred to by Cooper (1922) as broad-sclerophyll chaparral, is more diverse and includes *Quercus berberidifolia* (formerly *Q. dumosa*) (Fig. 6.4), *Q. wislizenii, Heteromeles arbutifolia, Pru-*

nus ilicifolia, Cercocarpus betuloides, Malosma laurina, and species of *Rhamnus, Rhus,* and *Garrya,* and occasionally small winter-deciduous trees such as *Sambucus* species and *Fraxinus dipetala.* Shrubs are generally taller in this chaparral, 3–6+ m. Beneath the canopy, light levels and soil temperatures are much lower than in chamise chaparral, and soil litter layers are much deeper (Keeley 1992c). Most species in this association are long-lived and can become arborescent if left undisturbed (e.g., *Heteromeles* and *Prunus* can reach 11 m or more; Keeley, personal observation), 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 woodland communities, where they persist as gap-phase shrubs (Keeley 1990a).

Montane chaparral at the upper elevational limits occupies sites that may be covered by snow for many months. It has a somewhat different physiognomy (see also Chapter 5); the evergreen shrubs

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

Figure 6.4. Quercus berberidifolia (formerly Q. 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.

have a more rounded, compact shape, with foliage to the ground surface. 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, Arctostaphylos patula*, and *Ceanothus integerrimus*), and winter-deciduous shrubs such as species of *Prunus, Ribes, Amelanchior*, and *Symphoricarpos*.

Broad generalizations about regional changes in shrub cover, height, spinescence, and leaf characteristics have been presented in Mooney and Harrison (1972), Parsons (1976), and Rundel and Vankat (1989).

Regional Patterns

The most extensive tracts of continuous, uninterrupted evergreen chaparral is 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 into northern Baja California (Marion 1943); it appears to replace *A. fasciculatum* on more mesic and fertile sites (Beatty 1987). Both species co-exist on some sites and niche partitioning occurs by differences in soil microhabitat (Beatty 1987), water relations (Redt-
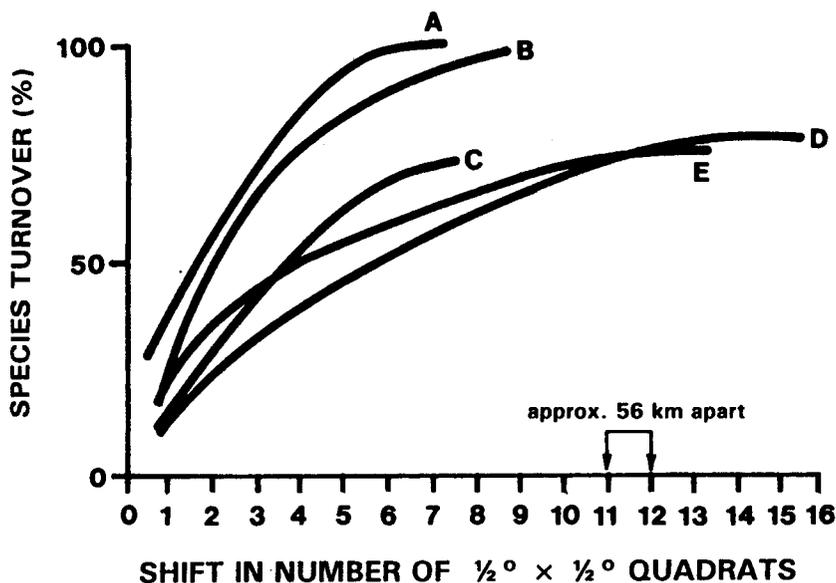
Figure 6.5. Species turnover rates in Ceanothus and Arctostaphylos in 0.5° × 0.5° latitude-longitude quadrats, expressed as a percentage of the species that the sites have in common. Santa Barbara/Santa Cruz to inland transects illustrate coast to interior changes (A, B, C), and coastal transects illustrate latitudinal changes (D, E) (redrawn from Cody 1986).

feldt and Davis 1996), and phenology (Hanes 1965). 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 that 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 Tertiary volcanics in coastal ranges, and granitic substrates of Precenozoic metamorphic and metavolcanic rock on interior ranges (Minnich and Howard 1984). Particularly common in the Peninsular Ranges are mafic (Mg and Fe rich) soils derived from coarse-grained plutonic rocks known as gabbro (Alexander 1993). Recognizable by their red coloration, these gabbro soils are less favorable for plant growth, resulting in more open chaparral associations. Many herbs, shrubs, and trees are restricted to gabbro throughout their range, or in some cases species disjunct from much farther north (where they are found on various substrates) are restricted to gabbro soils in the south (Oberbauer 1993).

Farther south in northern Baja California, coastal chaparral takes on a somewhat different flavor with an increasing number of drought-deciduous shrubs such as *Fraxinus trifoliata* and *Aesculus parryi* (Peinado, Alcaraz, Aguirre, Delgadillo, and Aguado 1995). Interior plateaus such as the western Sierra Juarez are noteworthy for their extensive stands of *Adenostoma sparsifolium*.

In the central coastal regions of California, chaparral forms a patchwork mosaic with grassland, coastal sage scrub, and broadleaf and coniferous forest (Shreve 1927; F. Davis, Stine, Stomss et al.

1994). 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). The region has numerous endemic *Arctostaphylos* and *Ceanothus* species, many of which are edaphic endemics (Wells 1962) or are restricted to coastal areas under marine influence (Griffin 1978). For example, the *Arctostaphylos andersonii* complex in the Santa Cruz Mountains comprises six species, each occupying a habitat characterized by a distinct combination of soil conditions, including water-holding capacity, texture, pH, depth, root penetrability, and fertility. (C. Davis 1972). In both *Arctostaphylos* and *Ceanothus* there is a rapid turnover of species along latitudinal and longitudinal gradients (Fig. 6.5). The steeper gradient is from the coast to the interior, reflecting greater heterogeneity in sediments and climate, suggesting that these taxa represent finely tuned morpho-physiological types adapted to fairly specific ecological conditions (Cody 1986). Both genera have endemics on the Channel Islands that are adapted to a more open, woodland-like chaparral (Bjorndalen 1978), arising from less frequent fires and more intensive grazing by feral animals (Minnich 1980a).

In the north coastal region, chaparral diminishes and is restricted to the driest sites (Clark 1937). *Adenostoma fasciculatum* is common in the drier interior valleys, whereas broad-sclerophyll species dominate the coastal chaparral, and some of them, such as *Prunus ilicifolia*, form small woodlands (Oberlander 1953). Throughout this region, localized outcrops of ultramafic serpentine substrate produce a more open vegetation referred to as serpentine chaparral or "serpentine barrens" (Kruck-

eberg 1984). Low levels of Ca and high levels of Mg, plus potentially toxic levels of Ni and Cr, in these soils (Koenigs, Williams, and Jones 1982) exclude many species (Whittaker 1960; Kruckeberg 1969, 1984). Serpentine endemics include shrubs such as *Q. durata* var. *durata, Garrya congdoni, Ceanothus jepsonii, C. ferrisae*, various subspecific taxa of *Arctostaphylos*, and herbaceous genera such as *Streptanthus*, where 16 species in one subgenus are restricted to serpentine. In addition, many widespread species have evolved serpentine ecotypes. Mechanisms for tolerating serpentine soils vary with the species; for example, White (1971) found that *Arctostaphylos nevadensis* was selectively able to take up Ca over Mg, whereas *Ceanothus pumilus* was not able to do so but 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). Montane chaparral is distributed above 1000 m, 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, montane chaparral forms a mosaic with coniferous forest, pinyon-juniper woodlands, or scrub vegetation with Great Basin affinities (Skau, Meeuwig, and Townsend 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, personal communication), montane chaparral is 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.

Patterns of Biodiversity

By Northern Hemisphere standards California is unusually diverse, and much of this diversity is in
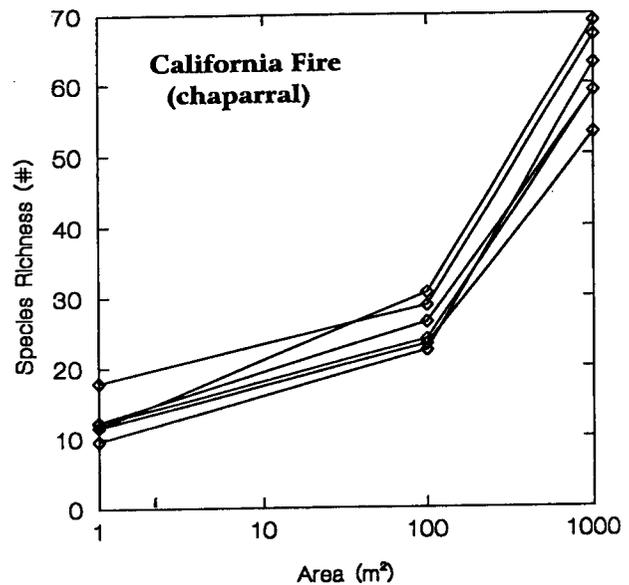

Figure 6.6. Plant species richness at different scales the first year after fire for six chaparral sites in southern California (from Keeley, unpublished data).

postfire chaparral (Jensen, Torn, and Hart 1990; Keeley and Swift 1995). Regionally, shrub diversity is highest in central coastal California, and annual diversity is greatest in the southern coastal ranges (Richerson and Lum 1980). Species richness is, of course, a function of scale. In the first postfire season, 10–20 species m^2 and 50–70 species per tenth ha are typical for southern California chaparral (Fig. 6.6). At these scales alpha-diversity patterns are comparable with the most diverse mediterranean-climate communities such as South African fynbos or Western Australian heath (Bond 1983). It is curious, however, that species richness in these other shrublands is significantly higher at the scale of 100 m^2, resulting in straight-line curves on semilog graphs such as in Fig. 6.6 (but cf. Schwilk, Keeler, and Bond 1997). As discussed later, species richness declines markedly after fire, and it appears that the species richness curves likewise change, for richness at 1 m^2 declines more rapidly than at 100 m^2 (Keeley, unpublished data).

Thus, at the scale of 100 m^2, postfire habitat is relatively homogeneous, but with succession this patch size becomes more heterogeneous. For sites <10 yr postfire, F. Davis, Hickson, and Odion (1988) reported an average of 36 species per 100 m^2 for sites in central California, and the slope of the regression line relating species richness to stand age was −0.93. In mature chaparral, however, site factors play a much greater role than age in determining species diversity; for example, the most diverse site in Table 6.1 was over 100 yrs of age. Topographic and climatic heterogeneity explains a

significant portion of diversity patterns in the state (Richerson and Lum 1980), and within chaparral there is considerable evidence for habitat specialization, thus high gamma diversity likely reflects high habitat heterogeneity (Zedler 1995a). Chaparral distributed in small patches (<3 ha) has lower alpha diversity but higher beta and gamma diversity than larger landscape patches, and patchiness enhances the differentiation in species composition among sites (Harrison 1997).

COMMUNITY RESPONSE TO WILDFIRE

The California mediterranean climate is conducive to massive wildfires. Mild, wet winters contribute to a prolonged growing season, which, coupled with moderately fertile soils, result in dense stands of contiguous fuels. Long summer droughts produce highly flammable fuels that are readily ignited by lightning from occasional convection storms. Fire frequency on average is about every two to three decades, but this may be more frequent than in the historical past (Byrne, Michaelson, and Soutar 1977 and unpublished data). Lightning strikes are the natural source of fire ignition, but today humans are responsible for most wildfires (Keeley 1982). Although lightning strikes are common, Minnich, Vizcaino, Sosa-Ramirez, and Chow (1993) reported for northern Baja California that only 2–5% resulted in fires. 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 common, particularly during Santa Ana wind conditions (Davis and Michaelsen 1995). Minnich (1983) suggested that fires of this size are an artifact of modern-day fire suppression, which results in unnaturally large accumulations of fuel. In support of this theory, he reported that large wildfires are relatively unknown from northern Baja California. One factor responsible for different fire regimes in these two regions is the fact that fires are three times more common in Baja California and are largely anthropogenic in origin. More frequent fires maintain a greater mosaic of fuel loads, and this, coupled with the fact that fires south of the U.S. border are generally not driven by Santa Ana winds (Minnich 1995), results in more localized burns. Although differences in fire regimes seem to have affected landscape patterns, on a smaller scale chaparral communities appear to be little affected (Minnich and Bahre 1995).

It is curious that despite large differences in fire size, Minnich (1995) reports that the average fire rotation period is approximately 70 yr in both Baja California and southern California. A similar estimate of fire recurrence interval was derived for the central Coast Ranges by Greenlee and Langenheim (1980). They did a careful survey of the distribution of lightning-caused fires in conjunction with known patterns of fire behavior and 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. Historical studies by Byrne (1977, unpublished ms.) support the notion that infrequent large catastrophic wildfires were part of the natural landscape prior to modern fire suppression. Simulations based on the Rothermal fire model concluded that for central coastal California, the modern landscape is subjected to much smaller fires and that the prehistoric landscape commonly experienced large-scale catastrophic wildfires (F. Davis and Burrows 1993).

These studies call into question the effectiveness of fire suppression and suggest that, within the chaparral zone, it has had minimal impact on the fire regime. In the largely chaparral-dominated Los Padres National Forest, comparison of early (1911–1950) and later (1951–1991) periods likewise showed fire suppression had no effect on the frequency of very large fires (Moritz 1997). Similar findings were reported for the chaparral belt in the San Bernardino National Forest (Conard and Weise 1998), although in the montane coniferous zone of this forest, fire suppression clearly has reduced fire frequency (Minnich, Barbour, Burk, and Fernau 1995). Undoubtedly, the natural fire regime in chaparral was a stochastic pattern of spatial and temporal heterogeneity in frequency, intensity, and size of fires (Zedler 1995b).

Chaparral fires are generally stand-replacing fires that kill all aboveground vegetation, although fire intensity, described by the total heat release, maximum temperatures, and duration of heating, varies markedly within and between fires. 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, Rice, and Conrad 1979; 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. Borchert and Odion (1995) illustrate the range of potential variation within a site, where one mi-

crosite had a maximum soil surface temperature over 900° C, but within minutes the temperature dropped to below 200° C, whereas another microsite maintained soil surface temperatures above 300° C for over 5 hr. Soil, however, is a good insulator, and at 2 cm depth maximum temperature was approximately 150° C and approximately half that value at 5 cm depth. Variation is due to patterns of fuel accumulation and wind, temperature, and relative humidity during the fire.

Temporary Postfire Flora

In the first year after fire, there is an abundant growth of herbaceous and suffrutescent vegetation (Fig. 6.7), the extent of which varies with site and year (Sampson 1944; Horton and Kraebel 1955; Sweeney 1956; Stocking 1966; Ammirati 1967; S. Keeley, J. E. Keeley, Hutchison, and Johnson 1981; F. Davis, Borchert, and Odion 1989; Rice 1993; Keeley 1997a). This "temporary" vegetation is relatively short-lived, and by the third or fourth year shrubs commonly dominate the site.

The postfire herbaceous flora is often 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 of which were annual species. However, Ammirati (1967) reported that herbaceous perennials were more important than annuals on mesic coastal slopes in the north coast ranges, comparable to the pattern discussed below for the southern part of the state. In southern California a study of 90 burned sites recorded 433 species in the first growing season, >60% being annuals. In this study average ground surface cover was 72%, although it ranged from as little as 5% on a few sites to fully one-third of the sites with more than 100% ground surface cover (due to overlapping branches) (Keeley, unpublished data). On average, annuals composed 50% of the cover, although some sites were dominated by herbaceous perennials and others by suffrutescents (Fig. 6.8). Canonical correspondence ordination (CANOCO) analysis of these sites (Fig. 6.9) showed that native annuals increased significantly with increasing distance from the coast and with percentage sand, whereas herbaceous perennials tended to follow an opposite pattern and were more strongly correlated with soil nutrients.

F. Davis et al. (1989) examined microscale vegetation recovery after fire and reported that postburn vegetation was very patchy, with some microsites devoid of seedlings and others with dense patches of seedlings. They also reported that, relative to canopy gaps, prefire soil seed bank density

Figure 6.7. Lush herbaceous growth the first spring after wildfire is in marked contrast to the depauperate herbaceous vegetation under the mature chaparral canopy.

varied with species, some being more concentrated in gaps and others not. However, postfire seedling recruitment was strongly correlated with prefire canopy gaps (Fig. 6.10). Their study also showed that gaps were microsites with reduced soil heating during fire, suggesting that temperatures lethal to seeds played an important role in driving postfire vegetation patterns, and it is noteworthy that these patterns were evident the second year after fire. On a similar scale of 0.1–10 m, Rice (1993) found that fire intensity (measured by the size of the skeletal remains of shrubs) was correlated with vegetation establishment; 38% of her areas of high fire intensity were not vegetated, whereas none of the areas of low fire intensity lacked vegetation. Tyler (1995) also reported an inverse relationship between soil heating during fire and seedling density.

Postfire Shrub Recovery

Rate of shrub recovery varies with elevation, slope aspect, inclination, degree of coastal influence, and patterns of precipitation (Hanes 1971; Keeley and
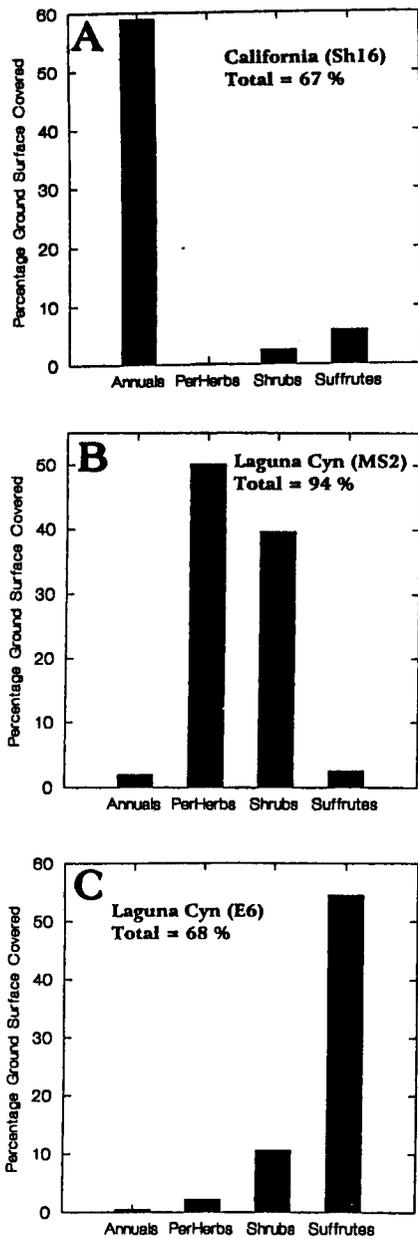
Figure 6.8. Cover of annuals, herbaceous perennials (per herbs), shrubs, and suffrutescents (suffrutes) in the first postfire year at three chaparral sites burned in the same week (from Keeley, unpublished data).
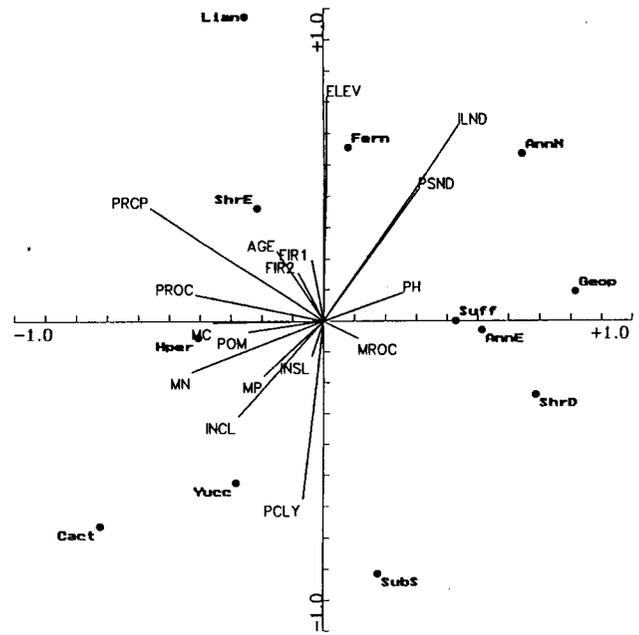

Figure 6.9. CANOCO plot of environmental factors and growth form distribution for the first year postfire flora from 90 sites burned in the same week in autumn 1993 (from Ne'eman and Keeley unpublished data). AnnE = exotic annuals, AnnN = native annuals, Cact = Opuntia spp., Fern = ferns, Geop = geophytes, Hper = herbaceous perennials, ShrE = evergreen shrubs, Lian = lianas; ShrD = deciduous shrubs, SubS = subshrubs, Suff = suffrutescents, and Yucc = Yucca spp.. Environmental parameters are: ELEV = elevation, ILND = distance inland, INCL = slope incline, INSL = calculated annual solar radiation, PRCP = precipitation, FIR1 = fire severity measure 1, FIR2 = fire severity measure 2, AGE = age prior to fire, MROC = rock cover; and soil parameters: MP = phosphorous, MN = nitrogen, MC = carbon, PH = pH, PSND = percentage sand, PCLY = percentage clay, POM = percentage organic matter, PROC = percentage rock.

Keeley 1981; F. Davis et al. 1989). Recovery of shrub biomass is from basal resprouts (Fig. 6.11) and seedling recruitment from a dormant soil-stored seed bank. After a spring or early summer burn, sprouts may arise within a few weeks, whereas after a fall burn, sprout production may be delayed until winter (Biswell 1974). Regardless of the timing of fire, seed germination is delayed until late winter or early spring and is uncommon after the first year.

Resilience of chaparral to fire disturbance is ex-

emplified by the marked tendency for communities to return rapidly to prefire composition (Keeley 1986). Of course, validity of this conclusion is a function of scale and mode of regeneration. Resprouting shrubs may pre-empt the same microsite through repeated fire cycles, whereas microsite variation in seedling recruitment may change fine-scale patterns of community composition. Although not well documented, the potential exists for fire-induced mortality of lignotubers and seeds to alter community composition.

Fire-caused mortality of potentially resprouting shrubs is variable, depending on species. For example, some, such as *Quercus berberidifolia*, *Heteromeles arbutifolia*, and *Malosma laurina*, are seldom killed, whereas others, such as *Adenostoma fasciculatum* and various *Ceanothus* (subgenus *Ceanothus*) species, sometimes suffer extensive mortality. Factors that may be involved include fire intensity, soil moisture, plant size, and physiological condition

DECORANA 1st Axis Plot Scores

Canopy
density indicates percentage of cover

pre-burn readily germinable seed, eigenvalue=.51

post-burn readily germinable seed, eigenvalue=.52

field, 3-87, eigenvalue=.42
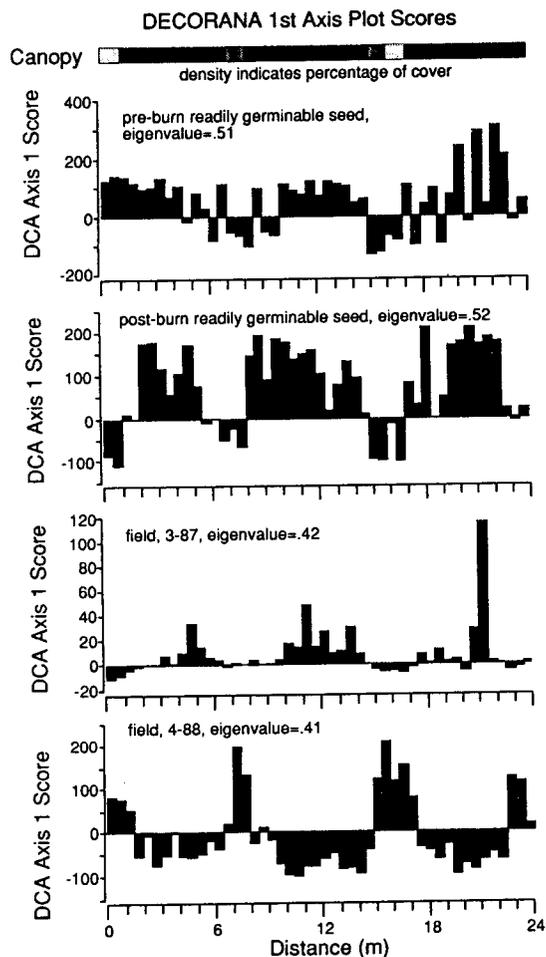
field, 4-88, eigenvalue=.41

Distance (m)

Figure 6.10. Detrended Correspondence Analysis scores for plots based on density of readily germinable seed before and after fire, and postfire seedling recruitment in March 1987 and April 1988, as a function of distance along the transect. Shading on the horizontal bar at the top of the figure indicates canopy coverage and gaps. Fire was in December 1986. (From Davis et al. 1989, Vegetatio 84: 53–67, Fig. 2, 1989 with kind permission of Kluwer Academic Publishers.)

Figure 6.11. Resprout from lignotuber of Adenostoma fasciculatum in the first spring after fire.

(Laude, Jones, and Moon 1961; Plumb 1961; Keeley and Zedler 1978; Tratz 1978; Radosevich and Conard 1980; Stohlgren, Parsons, and Rundel 1984; Rundel, Baker, Parsons, and Stohlgren 1987; Moreno and Oechel 1991b, 1993, 1994; Sparks and Oechel 1993). *Adenostoma faseiculatum* mortality varies from 0–100% but typically is <50% and increases with fire intensity. Accurate estimates of fire intensity are problematical, and thus numerous studies have relied on surrogate measures of fire severity, such as twig diameter on burned skeletons, which is correlated with measures of fire intensity (Moreno and Oechel 1989). Using this surrogate measure of fire intensity, Rundel et al. (1987) found that smaller plants suffered greater mortality and plants burned in late spring suffered

greater mortality than plants burned in late summer. Since they found a similar mortality pattern in unburned but clipped shrubs, they attributed the seasonal effect to a deficit of storage carbohydrates during late spring. Moreno and Oechel (1991b, 1993) likewise found that smaller plants suffered greater mortality; however, other studies have failed to find a relationship between plant size and survivorship (Anfuso 1982; Keeley 1997). Fire intensity not only affects survivorship but resprouting vigor as well (Malanson and O'Leary 1985; Rundel et al. 1987; Moreno and Oechel 1991b, 1993; Borchert and Odion 1995). Mortality of resprouting shrubs is also markedly influenced by fire frequency. For example, fires in adjacent stands burned once, twice, or three times in a 6 yr period generated 1300, 700, and 400 *A. fasciculatum* resprouts per ha, respectively (Haidinger and Keeley 1993), and a similar pattern was reported by Zedler (1995b).

Comparisons of prefire soil seed pools with postfire seedling densities suggest that vast numbers of seeds are killed (Keeley 1977; Bullock 1982; Davey 1982; F. Davis et al. 1989). Seedling density for prolific seeders such as *Adenostoma fasciculatum*

or *Ceanothus* spp. may exceed 100 m^{-2} (Sampson 1944; Sweeney 1956; F. Davis et al. 1989; Moreno and Oechel 1991a), although as discussed in the following section there is tremendous inter- and intraspecific variation. Fire intensity affects seed survivorship and consequently seedling recruitment. There is interspecific variation in seed survivorship, thus the potential exists for characteristics of a particular fire having long-term impacts on community composition. For example, by artificially enhancing fire intensity, Moreno and Oechel (1991a) demonstrated that seedling recruitment decreased for *A. fasciculatum* but increased for *C. greggii*. F. Davis and Odion (reported in Borchert and Odion 1995) found that microsites with higher fire intensities diminished *A. fasciculatum* seedling recruitment to a far greater extent than *Arctostaphylos purissima* seedling recruitment, and they attributed this to differences in depth of seed burial. Moreno and Oechel (1991a) suggest that higher temperatures generated by more intense fires play an important role in determining seed mortality during fires, and there is empirical evidence for this effect (Zammit and Zedler 1988). An additional factor is smoke, which has been found not only to induce germination in many chaparral species but also to be lethal at durations of 5–15 min exposure, and there is marked interspecific variation in tolerance of seeds to smoke (Keeley and Fotheringham 1998b).

Seedling mortality is generally high during the first year and is concentrated in the spring (Bullock 1982; Mills 1983; Rundel et al. 1987; Moreno and Oechel 1992). Seedlings are strikingly smaller than resprouts (Sampson 1944; Horton and Kraebel 1955; Keeley and Keeley 1981), however, Bond (1987) and Tyler and D'Antonio (1995) reported that proximity to resprouting shrubs had no negative effect on seedling growth or survivorship; indeed, the latter authors noted that proximity of seedlings to resprouts significantly reduced the incidence of herbivory. However, Tyler and D'Antonio (1995) did find that both postfire survivorship and growth of *Ceanothus impressus* seedlings were positively correlated with increasing distance to near neighbors of all species, and this appeared to be due to reduced competition for water. Moreno and Oechel (1988) likewise reported that high herb density significantly reduced the survivorship of both *Adenostoma fasciculatum* and *C. greggii* seedlings and that survivorship was strongly correlated with soil moisture (Moreno and Oechel 1992).

Herbivory of seedlings and resprouts is important after fire (J. Davis 1967; Howe 1982; Mills 1983, 1986; Mills and Kummerow 1989; Moreno and

Oechel 1991b, 1992) and potentially alters long-term demographic patterns. For example, Bullock (1991) showed that 6 yr after fire, *C. greggii* survivorship was an order of magnitude greater in plots fenced from small mammals. There is also evidence that predator preferences may alter the balance in shrub composition. Mills (1986) reported that the major mammalian herbivores (brush rabbits, *Sylvilagus bachmani*) preferred *C. greggii* over *A. fasciculatum*. This effect, however, was short-lived and 5 yr after fire, with or without predation, there was no significant difference in survivorship between these two species. Quinn (1994), reported an unusual and dramatic postfire shift in species composition from *Ceanothus crassifolius* domination before fire to *Salvia mellifera* domination 10 yr after fire, whereas a plot fenced from herbivores returned to *C. crassifolius*. For the most part, these studies have been done on small controlled burns surrounded by mature chaparral. Wildfires that are orders of magnitude larger may eliminate many potential herbivores, although Tyler (1996) found no difference between herbivory effects at the periphery versus middle of a 40 ha burn.

It has been hypothesized that in the absence of fire, chaparral would be succeeded by other vegetation types. Sampson (1944) suggested that in northern California, grassland would eventually replace chaparral; however, Hedrick (1951) found no evidence of this in a 90 yr stand. 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 accumulate deadwood, and many stems die, but these are replaced by additional crown sprouts (Keeley 1992c), indicating that resprouting shrubs rejuvenate themselves in the absence of fire. These observations are at odds with much published dogma on chaparral "senescence," a concept that has been widely criticized (Zedler and Zammit 1989; Keeley 1992b; Zedler 1995b). In addition to Hedrick's study, other investigations have shown no evidence of old chaparral being replaced (Keeley and Zedler 1978; Lloret and Zedler 1991; Keeley 1992b; Sites C & F, Table 6.1; Sites 2 & 3, Table 6.2), and the community appears to be resilient to fire-recurrence intervals of 100+ yr. For most but not all shrub species, mortality in old stands of chaparral is not accompanied by seedling establishment (Table 6.2). When there are unusually long intervals between fires, chaparral may be replaced by sclerophyllous woodland if sufficient seed sources are available (Cooper 1922; Wells 1962). For example, the woodland tree *Quercus agrifolia* readily recruits seedlings under adjacent chaparral shrubs (Calloway and D'Antonio 1991). However, in a study of 12 sites un-

burned for 55–118 yr, seedlings of several woodland species were reported but saplings were not found, indicating that recruitment was either recent or not successful and that successional replacement of chaparral was not imminent (Keeley 1992c). This conclusion is also supported by landscape level studies that compared vegetation change over 40 yr from aerial photographs (Scheidlinger and Zedler 1980; Callaway and Davis 1993). Although there are significant landscape changes between coastal sage scrub and grassland, as documented in other studies (Keeley 1990b), chaparral transition to other vegetation types is rare (Fig. 6.12).

Postfire Resource Management

Resource agencies often respond to wildfires with emergency revegetation programs designed to reestablish quickly a herbaceous cover sufficient to reduce soil erosion and eliminate the threat of mudslides and flooding. The rationale for this management is that burned soils are more hydrophobic than unburned soils, resulting in increased surface flow of rainwater and increasing soil erosion (DeBano et al. 1979). Emergency seeding is considered essential on sites following exceptionally intense fires because of anticipated negative effects of intensity on natural regeneration. Throughout the state the seed of choice has been the non-native annual ryegrass (*Lolium multiflorum*). There is abundant evidence that this practice fails to substantially reduce threats of mudslides and flooding (Gautier 1983; Conard, Beyers, and Wohlgemuth 1995; Spittler 1995; Booker, Dietrich, and Collins 1995; Keeley 1996) and competitively displaces the native flora (Schultz, Baunchbauch, and Biswell 1955; Corbett and Green 1965; S. Keeley et al. 1981; Griffin 1982; Barro and Conard 1987; Beyers, Conard, and Wakeman 1994; Keeley, Morton, Pedrosa, and Trotter 1995). In response to concern over seeding nonnative species in natural ecosystems, some agencies have discontinued the practice. Other agencies have continued the practice using native species; however, this approach is also fraught with problems (Keeley 1995b).

LIFE HISTORIES OF PLANTS

Although shrubs dominate chaparral, the community comprises a rich diversity of growth forms, many of which are conspicuous only after fire. In addition to evergreen shrubs and trees, there are semi-deciduous subshrubs, slightly ligneous suffrutescents, woody and herbaceous vines, and a rich variety of herbaceous perennials and annuals.
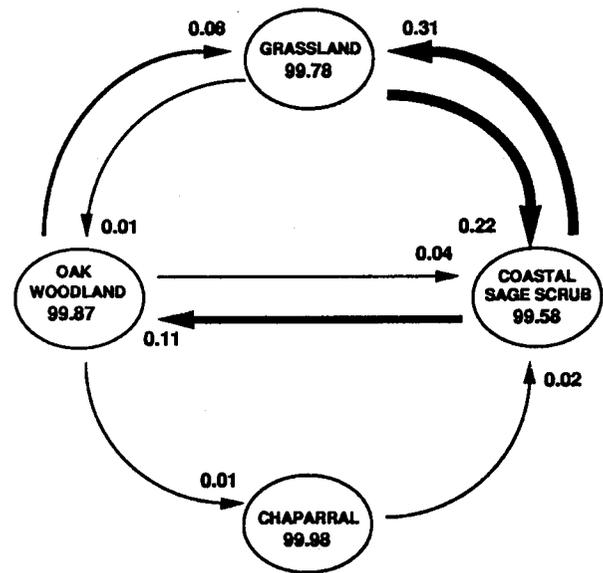

Figure 6.12. Annual transition rates among plant communities in Gaviota State Park, Santa Barbara County, California as determined from vegetation change observed on aerial photographs between 1947 and 1989 (reprinted from Callaway and Davis 1993).

Shrubs

Two modes of seedling recruitment are disturbance-dependent species that restrict recruitment to postfire conditions and disturbance-free species that successfully recruit only in the long-term absence of fire. The former exploit postfire environments for population expansion, and the latter require unusually long fire-free conditions for population expansion. Since fire is a recurrent catastrophic disturbance, species have been classified by their mode of postfire regeneration – that is, obligate seeders, facultative seeders, or obligate resprouters (see Table 6.2). Although these terms are useful, they describe life history response to only one facet of the environment and do not adequately describe reproductive modes for the entire shrub flora.

Disturbance-dependent recruitment. Disturbance-dependent species establish seedlings in the first year after fire, but seedling recruitment is almost nonexistent in subsequent years. Seedlings arise from a long-lived soil seed bank (Keeley 1977; Davey 1982; Parker and Kelly 1989) and germination is cued either by intense heat (Quick 1935; Hadley 1961; Quick and Quick 1961) or by chemical stimulus from smoke or charred wood (Fig. 6.13). The majority of species in the largest woody genera, *Arctostaphylos* and *Ceanothus*, lack the ability to regenerate vegetatively from basal burls or root crowns (Wells 1969).
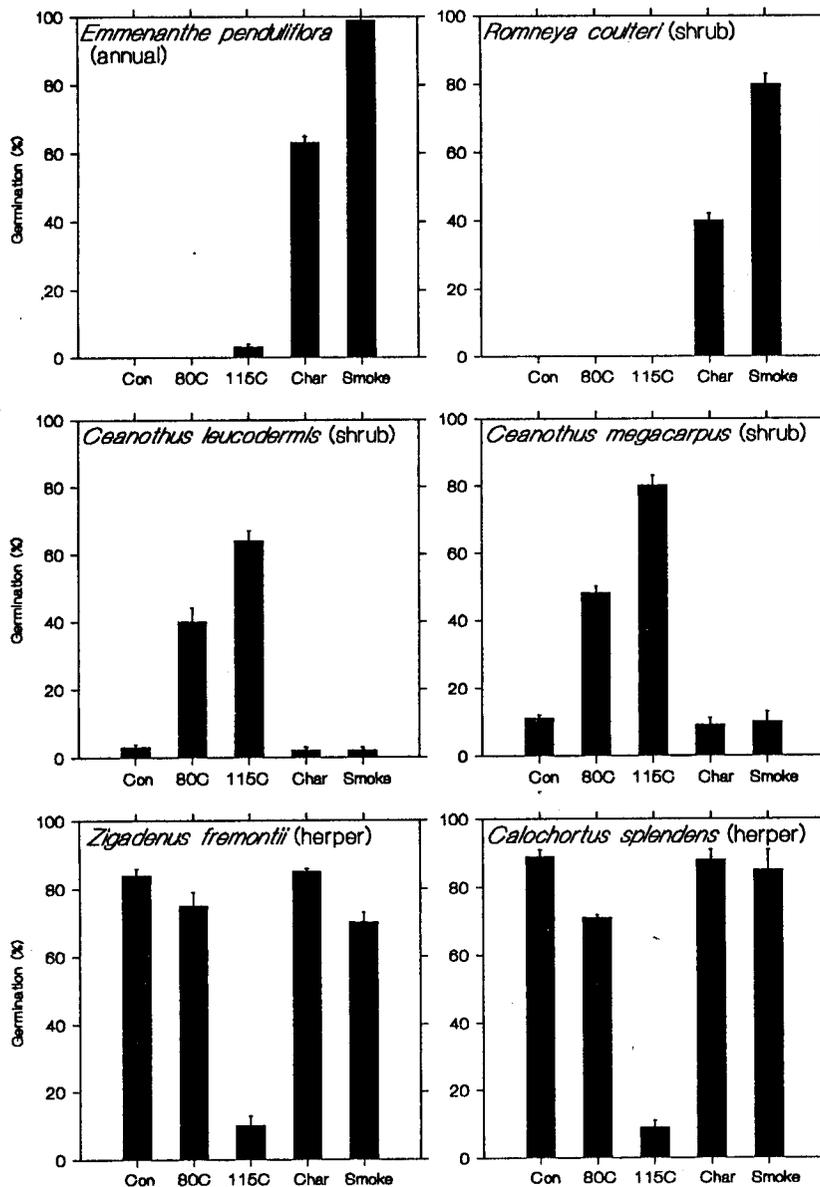
Figure 6.13. Germination of chaparral herbs and shrubs in response to control, 80°C heat for 1 hr, 115°C for 5 min, charred wood, or smoke for 5 min (from Keeley and Fotheringham, unpublished data.

These are often termed obligate-seeding shrubs, and their stems are even-aged, dating back to the last fire (Schlesinger and Gill 1978).

On recently burned sites, obligate-seeding species typically have very high seedling densities but low coverage relative to both facultative-seeding and obligate-resprouting species (Sampson 1944; Horton and Kraebel 1955; Vogl and Schorr 1972; Keeley and Zedler 1978; Keeley and Keeley 1981). Seedling density is typically two orders of magnitude greater than pre-fire shrub density (Fig. 6.14B; Moreno and Oechel 1992).

Reproductive maturity requires 5–15 yr before significant seed crops are produced, and thus fires at intervals more frequent than this can produce localized extinctions (Zedler, Gautier, and McMaster 1983; Zedler 1995a; Fig. 6.15). *Ceanothus* and

Arctostaphylos dispersal in space is very limited (Davey 1982; Evans, Biswell, and Palmquist 1987), but since seeds are dormant, they accumulate in a soil seed bank and thus are temporally dispersed. Despite relatively large seed crops, accumulation in the soil is slow because a large portion of the seed crop is rapidly removed from the soil by predators (Fig. 6.16), which often selectively take the largest viable seeds (Keeley and Hays 1976; Zammit and Zedler 1988; Mills and Kummerow 1989; Kelly and Parker 1990; Quinn 1994). In one study, two *Arctostaphylos* species were found to produce more seeds in a single year than were present in the soil seed bank (Keeley 1977), and 10 yr later there was no statistically significant change in the size of the soil seed banks (Keeley 1987b).

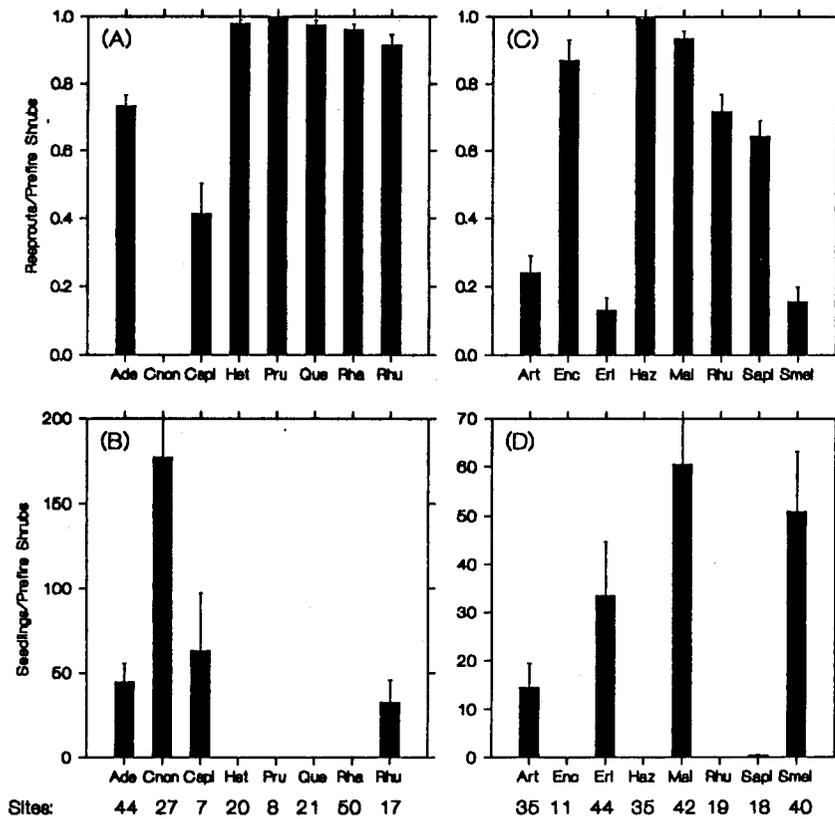Neither *Ceanothus* nor *Arctostaphylos* produces

Figure 6.14. Postfire resprouting success (A) and seedling recruitment (B) of chaparral and coastal sage scrub (C and D, resprouts and seedlings, respectively) expressed relative to prefire population size (from Keeley unpublished data). Data from 90 sites burned in southern California, autumn 1993, and number of sites each species was present at is given below; Chaparral shrubs (A&B): Ade = Adenostoma fasciculatum, Cnon = nonsprouting species of Ceanothus, Cspi = Ceanothus spinosus, Het = Heteromeles arbutifolia, Pru = Prunus ilicifolia, Que = Quercus berberidifolia, Rha = Rhamnus crocea, Rhu = Rhus ovata, and coastal sage subshrubs and shrubs (C&D): Art = Artemisia californica, Enc = Encelia californica, Eri = Eriogonum fasciculatum, Haz = Hazardia squarrosa, Mal = Malosma laurina, Rhu = Rhus integrifolia, Sapi = Salvia apiana, Smel = Salvia mellifera.
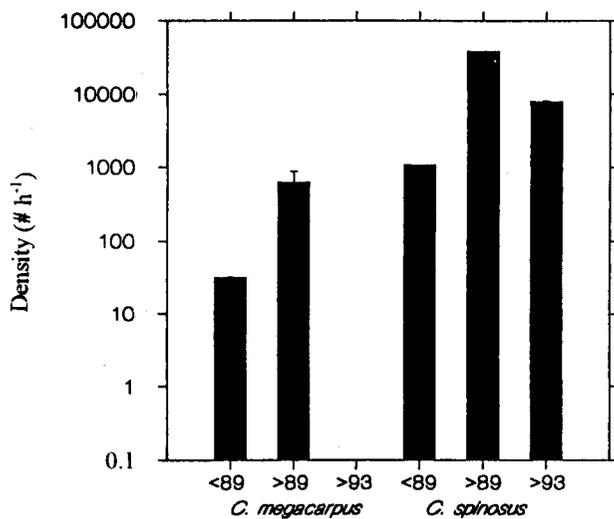

Figure 6.15. Impact of repeat fires (1989 and 1993) on density, prior to the 1989 fire, first year after the 1989 fire, and first year after the 1993 fire for non-sprouting Ceanothus megacarpus and resprouting C. spinosus, at the same site in the Santa Monica Mountains (from Keeley, unpublished data).

significant seed crops annually; rather, crops tend to be biennial (Keeley 1977, 1987c; Keeley and Keeley 1988b). Also, these studies and others (Keeley and Keeley 1977; Kelly and Parker 1990) have shown that congeneric pairs of obligate seeders

and resprouting facultative seeders do not differ significantly in seed output. In addition, Kelly and Parker (1991) reported that species of Arctostaphylos representing these two modes were not significantly different in their seed-to-ovule ratio; however, polyploid species were significantly lower than diploids. Zammit and Zedler (1992) did a detailed 5 yr study of seed production in C. greggii, comparing stands 6, 13, 32, 57, and 82 yr of age on north- and south-facing exposures. Seed production was maximized within two decades after fire and did not decline with shrub age, even on the oldest sites, and they concluded that there was no evidence of senescence in these very ancient shrubs. This pattern also holds for species of Arctostaphylos; in fact shrubs over 90 yr of age may greatly exceed seed production of much younger shrubs (Keeley and Keeley 1977).

As stands age and the canopy closes, there is intense competition and density-dependent thinning, resulting in high mortality (Schlesinger et al. 1982). In stands older than 50 yr, the fate of obligate-seeding species varies with the species and site. On mesic slopes, these shrubs are apparently out-competed by sprouting species (e.g., Site 3, Table 6.2; Fig. 6.17), but they can dominate arid sites 80 to 100 yr after fire (Keeley and Zedler 1978; Keeley 1992b; e.g., Site 2, Table 6.2). Obligate-seeding Ceanothus species may persist on a site for
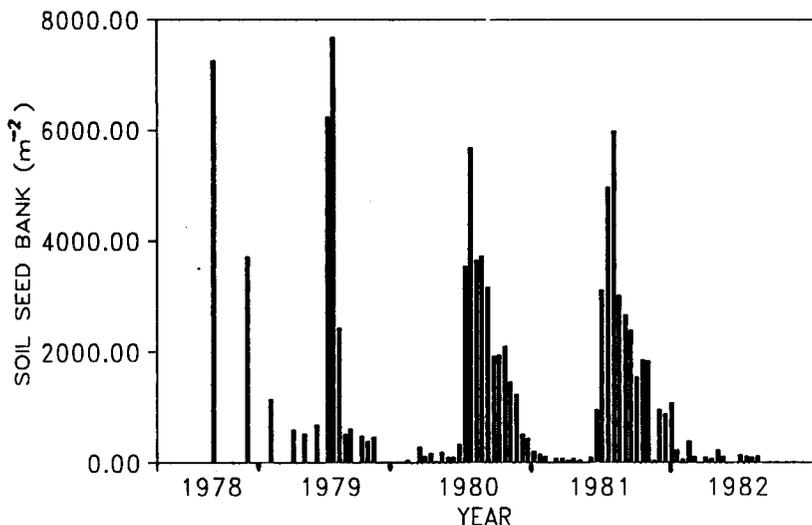
Figure 6.16. Annual fluctuations in the soil seed bank of Ceanothus crassifolius over a 4.5 yr period, n = 10 samples from beneath shrubs. Peak for each year is July (reprinted from Quinn 1994).
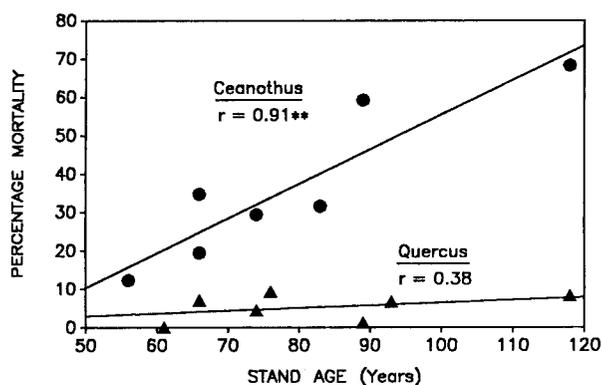

Figure 6.17. Mortality of non-sprouting Ceanothus species and sprouting Quercus species in stands of different ages (** = P <0.01) (from Keeley 1992b).

well over a century without fire, and a viable seed bank for much longer, suggesting selection by a fire regime with unpredictable frequency (Monty-gierd-Loyba and Keeley 1987; Zammit and Zedler 1992; Keeley and Swift 1995; Zedler 1995b).

Adenostoma fasciculatum and some *Ceanothus* and *Arctostaphylos* species establish seedlings after fire and resprout from a basal lignotuber (Fig. 6.14A, B), although the proportion of resprouting shrubs to seedlings is variable with the species, site, and fire. As with obligate-seeding species, seedling establishment by these facultative seeders is confined to the first postfire year, cued by heat or chemicals. *Adenostoma fasciculatum* is reported to produce two types of seeds: those that germinate readily at maturity and those that require intense heat shock (Stone and Juhren 1951, 1953; Zammit and Zedler 1988). 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 coloniza-

tion of other types of disturbance. Seedling recruitment by facultative seeders is often not as great as for obligate-seeding shrubs (Fig. 6.14B). These species, however, are far more resilient to recurrent fires; for example, two fires 4 yr apart are sufficient to cause the local extinction of an obligate seeder, whereas a facultative seeder persists (Fig. 6.15).

Disturbance-free recruitment. *Heteromeles arbutifolia, Quercus berberidifolia, Prunus ilicifolia, Cercocarpus betuloides, Rhamnus* species, and *Rhus integrifolia* seldom establish seedlings after fire (Fig. 6.14B). They persist on burned sites, however, because they are vigorous resprouters (Fig. 6.14A); thus the term "obligate resprouters" applies to these shrubs. In mature chaparral, they produce substantial seed crops that are widely dispersed (Bullock 1978; Horn 1984; Lloret and Zedler 1991; Keeley 1992d). Their seeds are short-lived (<1 yr) and germinate readily with adequate moisture (Keeley 1997b) and thus a dormant seed bank does not accumulate in the soil (Parker and Kelly 1989; Keeley 1991). This, coupled with the observation that these seeds are easily killed by intense heat, accounts for their failure to establish seedlings after fire.

Seedling recruitment is largely restricted to older, more mesic stands of chaparral, although seldom are seedlings of these species very abundant (Keeley 1992b, 1992c). Successful reproduction does occur under some conditions, as illustrated by the age distributions of *Rhamnus crocea* and *Prunus ilicifolia* seedlings and saplings in a 75-yr-old chaparral stand (Fig. 6.18). At this site, seedling recruitment was restricted to beneath the shrub canopy and was absent from gaps. Seedling recruitment is correlated with low light and high litter depth for these and other species (Williams
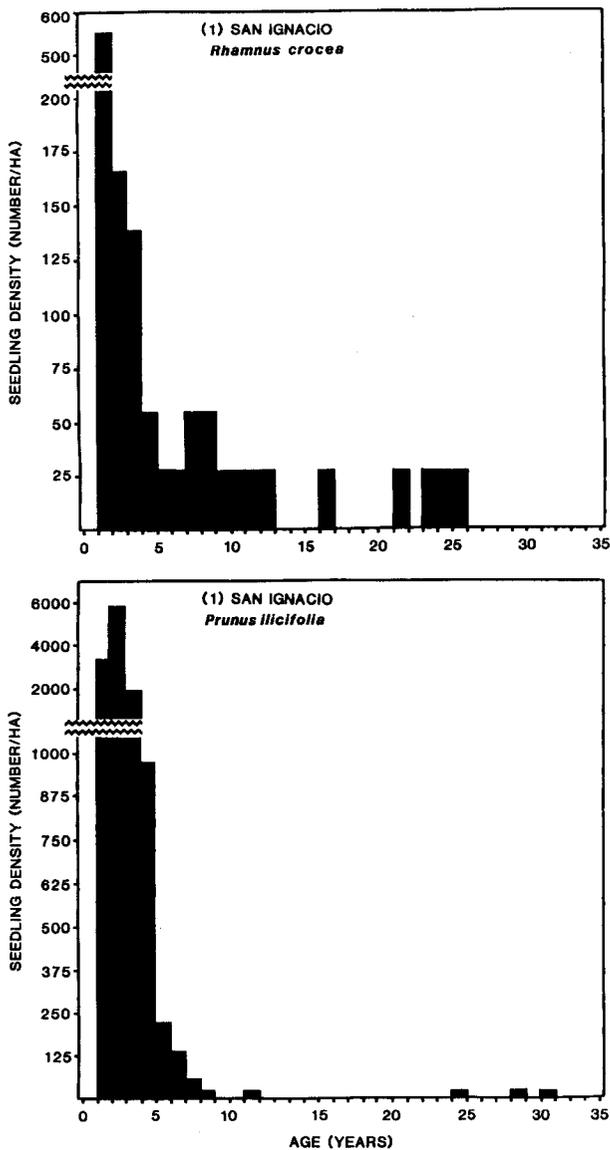
Figure 6.18. Age distribution of seedlings and saplings for two sprouting shrub species in a 75-yr-old stand of southern California chaparral (redrawn from Keeley 1992c).

1991; Keeley 1992c). Significant seedling recruitment in mature chaparral has also been noted for *Cercocarpus betuloides, Heteromeles arbutifolia, Prunus ilicifolia, Quercus wislizenii, Q. durata,* and *Rhus integrifolia* (Gibbens and Schultz 1963; Patric and Hanes 1964; Zedler 1982; Lloret and Zedler 1991; Williams et al. 1991; Keeley 1992c). Despite evidence of successful seedling and sapling recruitment in older stands, it appears that recruitment into the shrub canopy is rare. Most saplings remain stunted beneath the canopy; however, they are capable of resprouting after fire, and therefore fire may ultimately be required in order to make the transition from sapling to adult.

Sprouting shrubs are distinguished from obli-

gate-seeding species by the uneven-aged structure of stems (Keeley 1992c). All sprouting species continually produce new shoots from the root crown throughout their life spans (Fig. 6.19), so that most have one or more stems dating back to resprouts after the last fire, but continue to recruit new stems long after fire (Fig. 6.20). The pattern of stem recruitment varies with species and site; for example in stands >50 yr, the proportion of stems recruited in the previous decade ranged from 20–30% in *Adenostoma fasciculatum* to over 80% in *Cercocarpus betuloides* (Keeley 1992c). Some sprouting species are capable of vegetative spread by roots or rhizomes (e.g., *Fremontodendron decumbens,* Boyd and Serafini 1992; *Cercocarpus betuloides,* Keeley 1992c).

Trees

Evergreen coniferous trees, such as species of *Cupressus* and *Pinus,* often form dense even-aged stands within a matrix of chaparral (Vogl, Armstrong, White, and Cote 1977; Zedler 1977, 1981, 1995b), commonly on serpentine, gabbro, or other unusual substrates (McMillan 1956; Koenigs et al. 1982; Zedler 1995a). These species do not resprout after fire, and seedling establishment is in the first postfire year from a dormant seed bank held in serotinous cones. The serotinous pines produce cones sealed by resins that require high temperatures for opening; they may be sealed for decades and still retain viable seed. Serotinous cypress produce much greater quantities of smaller cones that open upon drying; as branches die or vascular connections are severed. Thus, cypress are more likely to disperse seeds in the absence of fire; however, recruitment within stands is apparently infrequent.

Pines exhibit remarkable variation in cone serotiny. *Pinus attenuata* is strongly serotinous and forms dense even-aged stands dating back to the last fire (Vogl et al. 1977). Flammability is high, and temperatures essentially sterilize the soil beneath the parent plant. Thus, when they are juxtaposed with chaparral, there is often a sharp contrast between the bare ash beds beneath the pines and the dense cover of postfire chaparral stands (Keeley and Zedler 1998). *Pinus coulteri* is strongly serotinous when associated with chaparral but not so in woodland habitats (Borchert 1985). In chaparral, this pine tends to form even-aged stands and exhibits characteristics such as lack of self-pruning that increase chances of stand-replacing fires. However, in forests and woodlands it has quite a different growth form and potentially continuous seedling recruitment. *Pinus torreyana* is not strongly serotinous, but some cones open gradually over many years (McMaster and Zedler 1981).

Figure 6.19. Multistemmed Adenostoma fasciculatum *shrub with shoots of various ages arising from a common root crown.*

Pinus radiata and *P. muricata* are coastal pines that often are juxtaposed with chaparral. They exhibit variable levels of cone serotiny, but because of the unusual delay in dispersal of current cone crops (late winter), some cones are almost certainly closed at the time of most wildfires (Keeley and Zedler 1998).

Pseudotsuga macrocarpa is a nonserotinous conifer but one of the few capable of resprouting after fire. Sprouts arise from epicormic buds along the trunk and main branches of mature trees, but saplings succumb to most fires. 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 are uneven-aged. Long fire-free periods are also apparently necessary for successful seedling establishment by *Pseudotsuga macrocarpa* (Minnich 1980b).

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). *Cupressus* species, for example, require 40 yr or more to accumulate sufficient aerial seed banks to ensure successful postfire seedling establishment, and

Zedler (1981, 1995b) has shown that postfire seedling establishment of *C. forbesii* 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.

Sclerophyllous hardwood trees such as *Quercus agrifolia, Q wizlizenii, Q. chrysolepis, Arbutus menziesii,* and *Umbellularia californica* form woodlands juxtaposed with chaparral, particularly in ravines and on mesic north-facing slopes. Higher fuel moisture makes such sites less susceptible to complete destruction by wildfires, and after low-intensity fires, all are able to 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 bank, due to production of short-lived, nondormant, heat-sensitive seeds (Keeley 1991, 1997b).

Subshrubs

Subshrubs, which are weakly ligneous small shrubs, are summer-deciduous (e.g., *Salvia mellifera*) or evergreen (e.g., *Eriogonum fasciculatum*) and are most important along the lower-elevation xeric borders (Hanes 1971). They are readily shaded out by the ev-
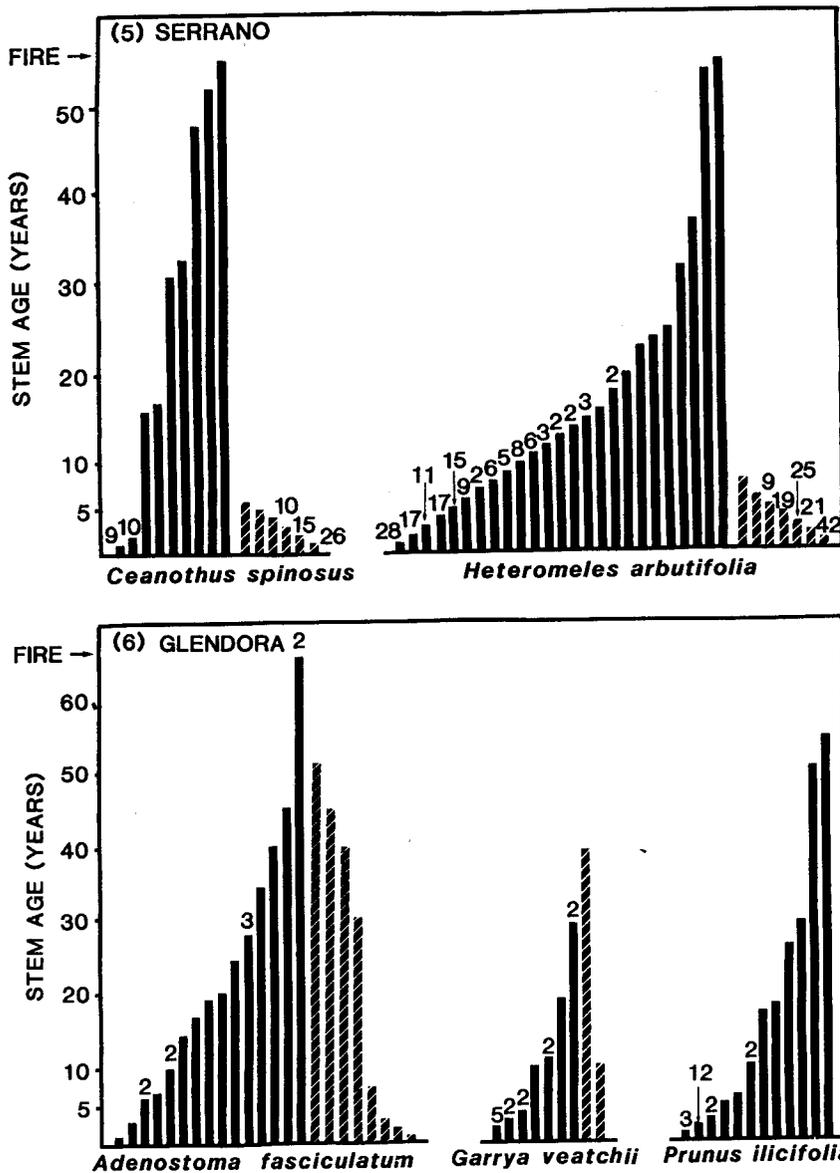
Figure 6.20. Age distribution for all stems on one individual each of five resprouting species in a 55-yr-old (Serrano) or a 66-yr-old (Glendora) stand of chaparral in the Transverse Range of southern California (from Keeley 1992c). Each filled bar represents one live stem, unless topped with a number indicating more than one stem at that age, and each hatched bar represents a dead stem.

ergreen 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 bank. Dendromecon rigida is a relatively short-lived subshrub (<5% survive 10 yr) (Bullock 1989) that is one of only a few myrmecochorous species in chaparral, with a prominent ant-attracting elaisome on each seed (other myrmechochores include the annual Claytonia perfoliata and Woody Fremontodendron spp. (Boyd 1996; Keeley, personal observations).

Suffrutescents

These dwarf, subligneous species (roughly equivalent to Raunkiaer's chamaephytes) are abundant

in the first year after fire from a soil seed bank. The seeds are dormant until heat shock or smoke or charred wood induces germination. One of these species, Lotus scoparius, Eriophyllum confertiflorum, or Helianthemum scoparium, typically, dominates a burn 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; S. 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 uneven aged. In southern California chaparral, this species is monocarpic; the rosette grows for a decade or more before flowering and dying. On desert slopes of the Transverse Ranges, however, plants produce up to 100 rosettes during the vegetative phase, and

flowering may be spread over many decades. In the central Coast Ranges, populations spread by rhizomes (Haines 1941; Keeley, Keeley, and Ikeda 1986). This species neither seeds nor resprouts after fire; however, the lower fuel volume on xeric sites, coupled with the tough, fibrous leaves that protect the apical meristem, result in significant survival during fire. Although many plants initiate flower stalks following fire, flowering is not dependent on such conditions.

Lianas and Vines

Both woody lianas and herbaceous perennial vines grow into the shrub canopy and are particularly abundant in older stands of broad-sclerophyll chaparral. Postfire regeneration modes include facultative seeders and obligate resprouters. *Calystegia macrostegia* germinates in profusion after fire from a soil seed bank. Germination is apparently induced by heat shock. It is noteworthy that this species typically germinates in profusion in early winter, months before most other postfire chaparral species. This liana often dominates sites in the second year, sprawling over regenerating shrub seedlings and resprouts, although it is unclear whether it competitively inhibits regeneration or plays a positive role as a nurse plant. *Marah macrocarpus* is an obligate resprouter after fire, with massive foliage cover generated in the first postfire season, although foliage of this herbaceous perennial dies back rapidly with the onset of summer drought. Seeds are very large and short-lived, and they germinate readily under the canopy, although recruitment is likely limited to years of high rainfall (Schlising 1969).

Perennial Herbs

The herbaceous perennial lifecycle of annual dieback preadapts this growthform to fire because they resprout vigorously from bulbs, corms, and rhizomes in the first postfire year. Seedling recruitment is rare immediately after fire due to the lack of a dormant seed bank (but c.f. Borchert 1989). Seeds are nonrefractory, that is, they do not require heat shock or smoke to induce germination (Fig. 6.13), although many require cold (Sweeney 1956; Keeley 1991). Seedling recruitment is possible anytime between fires but is apparently largely concentrated in the years subsequent to the first postfire season when resources are more generally available and flowering resprouts provide a rain of seeds (e.g., Martin 1995). As the canopy closes in, these herbaceous perennials are restricted to gaps in the canopy, and due to lower light levels, they

Table 6.3. *Growth form distribution of seed germination mode in California chaparral and coastal sage scrub ($\chi^2 = 71.2$, P < 0.001). Nonrefractory seeds germinate readily without fire-related cues, although some may be stimulated by brief cold stratification treatment.*

	Annuals	Herbaceous perennials	Woody plants
Nonrefractory	17	28	25
Heatshock	6	1	34
Smoke or charred wood	26	5	14

Source: Keeley and Bond (1997).

flower less frequently (Stone 1951; Stocking 1966; Christensen and Muller 1975a).

Annuals

Annuals make up the most diverse component of the chaparral flora, being abundant in disturbed areas and producing spectacular floral displays in the first spring after fire. Some, such as *Emmenanthe penduliflora* and species of *Phacelia, Lupinus, Lotus, Antirrhinum*, and *Allophyllum*, are "fire annuals" or "pyrophyte endemics," rarely found except on burned sites. Typically, these species have relatively specific site preferences (e.g., slope aspect, soil type, elevation, distance from coast, etc.) (Sweeney 1956; S. Keeley et al. 1981; O'Leary 1988). They have weakly developed dispersal ability (e.g., most Asteraceae) either lack pappus or have deciduous pappus); thus, the long-lived seeds are dispersed more in time (until fire) than in space.

Some native annuals such as *Camissonia micrantha, Crassula connata* (formerly *C. erecta*), *Cryptantha* spp., *Filago californica, Pterostegia drymarioides*, and others are opportunistic and most abundant on burned sites, but they persist in chaparral canopy gaps (Zammit and Zedler 1994) or in more open communities, arising from repeated disturbances or along xeric margins. In mature chaparral, closely related species may have quite different microsite requirements. For example, Shmida 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*.

Seed Germination and Allelopathy

Patterns of germination in chaparral species are summarized in Table 6.3 and Figure 6.13. Herba-

ceous perennials (e.g., *Zigadenus* and *Calochortus*) are capable of recruiting in the absence of fire, and their presence on burned sites is due to resprouts. Seeds germinate readily following cold stratification. Postfire recruiters use either heat shock or chemicals to cue germination. Germination induced by heat shock is the mode in shrubs such as *Ceanothus* (Rhamnaceae), suffrutescents such as *Helianthemum scoparium* (Cistaceae), and *Lotus scoparius* (Fabaceae), and in annual *Lupinus* and *Lotus* (Fabaceae). These species have water-impermeable cuticles, and dormant seeds fail to imbibe water. Heat disrupts this barrier, commonly by loosening cells around the strophiolar plug.

Induction of germination in many species has been shown to be due to chemicals leached from charred wood or from smoke (Fig. 6.13). Smoke-induced germination is known from annual and suffrutescent species in the Asteraceae, Boraginaceae, Brassicaceae, Caryophyllaceae, Hydrophyllaceae, Lamiaceae, Loasaceae, Onagraceae, Papaveraceae, Polemoniaceae, and Scrophulariaceae (Keeley and Fotheringham 1998b). Seeds of these plants differ from species that require heat-shock stimulation in that they lack a dense outer palisade cell layer plus exterior cuticle that block imbibition. Rather, smoke-stimulated seeds freely imbibe water in the dormant stage, and thus germination is not triggered by overcoming a barrier to imbibition, as is the case with heat-shock stimulated species. Nitrogen oxides in smoke have been shown to induce germination in some of these species, and potentially nitrogen oxides produced by postfire nitrification may also trigger germination (Keeley and Fotheringham 1997, 1998b). Nitrate was suggested as a potential germination stimulant in these postfire species (Thanos and Rundel 1995), but this ion alone is ineffective (Keeley and Fotheringham 1998a). Germination induced by charred wood (Wicklow 1977; Jones and Schlesinger 1980; Keeley et al. 1985) may represent the same mechanism as smoke-induced germination since the same species respond to both cues (Fig. 6.13). One mechanism tying these phenomena together is suggested by the fact that smoke will induce germination either directly or indirectly by first binding to soil particles and later evolving nitrogen oxides (Keeley and Fotheringham 1997). Some species, e.g. *Dicentra chrysantha, Dendromecon rigida,* and *Trichostemma lanatum,* have multiple barriers to germination and require long-term soil storage before they will germinate in response to smoke (Keeley and Fotheringham 1998b).

It has long been known that germination of some chaparral species requires a cold treatment

($<5°$ C) (Keeley 1991). In a great many cases duration of cold seems to be unimportant, and often one day of cold is sufficient to trigger germination (Santillenes and Keeley, unpublished data). Thus, unlike cold stratification, which measures duration of cold and signals the approaching end of winter, this "cold triggering" mechanism signals the beginning of winter. Under field conditions, germination of most native species is normally delayed until midwinter, even in years with substantial autumn rainfall.

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. This conclusion has been criticized by Keeley and Keeley (1989) because of the following:

1. The majority of McPherson and Muller's work focused on the effects of leached inhibitors on growth of non-native seedlings, not on germination of native species.
2. Leachate from *Adenostoma* foliage may inhibit the germination of some species, but apparently has no effect on many others (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 found in soil (Kaminsky 1981).
5. Christensen and Muller (1975a) found 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), germinated readily (Christensen and Muller 1975b).
7. Seeds of many chaparral herbs fail to germinate even if they are never exposed to so-called allelopathic toxins (Keeley 1991).

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 and Keeley (unpublished data), however, could not duplicate this effect with native seeds, and Christensen and Muller (1975a) reported that fungal and bacterial populations increased after fire.

Field studies show that most seedlings establishing under mature chaparral succumb to either small mammals or competition with the canopy shrubs (McPherson and Muller 1969; Christensen and Muller 1975a, 1975b; Swank and Oechel 1991; Quinn 1994). Studies in which animals have been excluded from plots beneath chaparral show highly significant increases in herb densities, although not comparable in species composition to the postfire flora.

To summarize, in response to the poor conditions of low light, limited water, insufficient nutrients, high predation, and possibly allelopathic toxins under the shrub canopy, many species have evolved mechanisms that ensure seed dormancy until the canopy is removed. Germination cued by intense heat shock or chemicals from smoke or charred wood ensures establishment immediately following fire. Some species are strictly tied to fire, whereas other opportunistic species colonize gaps in the chaparral canopy by a polymorphic seed pool that comprises fire-dependent refractory seeds that remain dormant until fire and nonrefractory seeds capable of germinating in the absence of fire. For most opportunistic species, successful recruitment is restricted to canopy gaps. A hypothesis worth testing is whether or not nonrefractory seeds have evolved a sensitivity to allelopathic compounds leached from the overstory canopy as a means of inducing secondary dormancy until conditions become more suitable.

Nonnative annual grasses and forbs are found throughout chaparral regions. Under a regime of frequent fires, they readily displace the native herb flora if fires are frequent enough, converting chaparral to annual grassland (Cooper 1922; Sampson 1944; Arnold, Burcham, Fenner, and Grab 1951; Hedrick 1951; Wells 1962; Keeley 1990b; Haidinger and Keeley 1993). 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 more often due to colonization after fire. Most, such as species of *Bromus*, *Erodium*, and *Centaurea*, disperse prior to the summer fire season and consequently are less common in first-year burns but are present in subsequent years (Sampson 1944; Horton and Kraebel 1955; S. Keeley et al. 1981). Fall-fruiting species such as *Lactuca serriola* and *Conyza canadensis* are likely to be more common on first-year burns.

SHRUB MORPHOLOGY AND PHENOLOGY

Leaves

The dominant shrubs are evergreen, with small, sclerified, heavily cutinized leaves (Cooper 1922). Leaf longevity is typically 2 yr (Kummerow and Ellis 1989), although shade leaves are often much longer-lived (Mooney, unpublished data). The widespread *Adenostoma fasciculatum* has a linear-terete leaf less than 1 cm in length (0.06 cm^2) that is markedly smaller than leaves of other chaparral shrubs (Fishbeck and Kummerow 1977). The isofacial nature of these leaves, with stomata evenly distributed, has led to some confusion in calculations of the leaf area index (Kummerow and Ellis 1989). These leaves are produced individually on new growth and in short-shoot fascicles on old growth (Jow, Bullock, and Kummerow 1980). Juvenile 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 6.11); occasionally these occur on mature plants under abnormally mesic conditions. Similar leaf heterophylly is known from *Dendromecon rigida* (Stebbins 1959). Other shrub species have broad sclerophyll leaves remarkably convergent in size, shape, and anatomy. Most are simple (<5 cm length and 1–5 cm^2), with average thickness ~ 300 µm, plus 5–10 µm cuticle on upper and lower surfaces (Cooper 1922; Fishbeck and Kummerow 1977), and many are sharply serrated (Fig. 6.4). Most *Arctostaphylos* species and *Dendromecon rigida* have isofacial leaves with an upper and lower palisade and stomata on both surfaces (Fig. 6.21). 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*, *Rhamnus californica*, and *Yucca whipplei* (Keeley unpublished data), to the extreme case in certain *Ceanothus* species with stomatal crypts that are invaginated to over half the width of the leaf (Nobs 1963). These stomatal crypts are characteristic of the subgenus *Cerastes* (except in the seedling stage) and are absent in subgenus

Figure 6.21. Cross section of isofacial leaf of non-sprouting Arctostaphylos bakeri *from northern California chaparral showing distribution of stomata and palisade mesophyll on both the adaxial and abaxial sides; leaf width = 0.33 mm (from Boykin and Keeley, unpublished data).*

steeper angles than shade leaves (H. A. Mooney unpublished data), and other leaf characteristics are highly modifiable, depending on the microenvironment (Cooper 1922; Mortenson 1973; Krause and Kummerow 1977; Hochberg 1980; Ball, Keeley, Mooney, Seaman, and Winner 1983). Such changes in leaf angle can have a profound impact on total leaf absorptance and the heat budget (Ehleringer and Comstock 1989).

Stems and Growth Forms

Chaparral shrubs show a remarkable degree of convergence in growth form. Across landscapes of homogeneous topography, shrubs are of similar height and give the impression of a smooth blanket of vegetation. Detailed studies of plant structure have documented remarkable degrees of convergence in distribution of leaves and stems among unrelated taxa (Mooney et al. 1977; Kummerow et al. 1981). Aridity is a primary factor affecting growth form. Mesic environments result in denser stands of shrubs with arborescent proportions, whereas drier, more open sites result in lower, multistemmed broader shrubs (e.g., Vasek and Ciovis 1976; Keeley 1992b). 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. 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 *Arctostaphylos rudis* on mesas east of Lompoc (Keeley, unpublished data). Occasionally, seedlings of *Quercus* spp., *Heteromeles arbutifolia*, *Rhamnus* spp. and others will produce basal burls, apparently in response to intense herbivory under the shrub canopy. Mature shrubs of these species will 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, Table 6.2).

Lignotubers, or basal burls, are uncommon in

Ceanothus. Also, the *Cerastes* have markedly thicker leaves, higher leaf-specific weights, and thicker cuticles than species in the other half of the genus (Barnes 1979).

Leaf orientation is variable among shrub species and depends on environmental conditions. Nearly vertical leaves are prominent in isofacial-leaf species of *Arctostaphylos* and in *Dendromecon rigida*, and many other species have leaf angles greater than 50° (Kummerow, Montenegro, and Krause 1981). In *Arctostaphylos*, leaf angle increases along an aridity gradient (Shaver 1978). In *Ceanothus*, leaf orientation responds to water stress and is seasonally reversible (Comstock and Mahall 1985). If water stress is severe enough, *C. megacarpus* are capable of altering leaf angle by curling (Gill and Mahall 1986), and *Rhus ovata* alter leaf angle by folding (Ehleringer and Comstock 1987). In *Heteromeles arbutifolia* sun leaves have significantly

shrubs outside of mediterranean-climate ecosystems (Keeley 1986). In chaparral shrubs they are often large and commonly exceed the aboveground biomass (Kummerow and Mangan 1981). They are anatomically different 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. The number of epicormic buds is reflected in the fact that after fire, lignotubers typically produce hundreds of new shoots (Kummerow and Ellis 1989), which are 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, Krause, and Jow 1977). The fact that resprouting species tend to be very vulnerable to water stress led DeSouza and associates (1986) to suggest that a primary function of the burl is to provide nutrients that sustain the root system during the summer drought following fire. 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. 6.19 and 6.20).

Stems of most species are ring-porous, with well-developed annual rings, but in others such as *Prunus ilicifolia* and *Malosma laurina*, stems tend toward diffuse-porous, with poorly defined rings (Webber 1936; Watkins 1939; Young 1974; Carlquist 1980, 1989). These shrubs have deep root systems often providing year-round access to water, and this contributes to an unreliable record of annual growth rings (but cf. White 1997). On the other hand, nonsprouting species of *Ceanothus* and *Arctostaphylos* have shallow root systems, and they lay down distinct annual growth rings that have been shown to be a reliable indicator of stand age (Keeley 1993). 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, such as *Quercus* spp., are extremely resistant. Vascicentric tracheids, defined as tracheids present adjacent to vessels, are normally uncommon in dicots but present in stems from 26 families in chaparral (Carlquist 1985). These unusual conducting cells offer a subsidiary conducting system that can supply stems and leaves when the adjacent vessels fail as a result of air embolisms. Carlquist and Hoekman (1985) have developed an index of xeromorphy measured by the density and diameter of xylem vessels as well as the presence of vasicentric

tracheids, and this index appears to be greater for shallow-rooted, obligate-seeding shrubs than for deep-rooted resprouting species. The physiological significance of this index requires careful analysis because embolism induced by water stress is not a direct function of the xylem conduit size but, rather, of the cell wall pore size (Jarbeau, Ewers, and Davis 1995). However, as discussed later, xylem diameter is strongly correlated with freezing-induced embolism.

Stem development in species of *Arctostaphylos* and *Ceanothus (Cerastes)* follows a peculiar pattern. In *Arctostaphylos*, large stripes of bark die, leaving behind only a ribbon of living tissue (Adams 1934). In *Ceanothus*, 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 that self-prune (Mahall and Wilson 1986) or to roots in unfavorable microsites, and they are often produced during severe droughts (Parsons et at. 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 (C. Davis 1973; Keeley 1975).

Roots

Sprouting shrubs have more deeply penetrating roots than nonsprouting species (Cooper 1922; Hellmers et at. 1955b). Soil depth may limit root penetration, except in highly fractured substrates where roots penetrate bedrock to 9 m or more (Hellmers, Horton, Juhren, and O'Keefe 1955). Roots often penetrate rock fractures and proliferate mats of feeder roots in fine cracks, sometimes producing odd thallus-like structures hundreds of times wider than the thickness. Species differ in ability to penetrate rock fractures, and in one study *Arctostaphylos viscida* was shown to compete far better for water stored in bedrock than did similar aged conifererous trees (Zwieniecki and Newton 1996). During summer drought, this weathered rock mantle is often capable of holding more water within a matric potential range accessible to shrubs than the overlying soils can hold (Newton et al. 1988; Jones and Graham 1993).

Rooting depth may also vary with substrate. 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 berberidifolia* but not for the nonsprouting *Ceanothus greggii* (Kummerow and Mangan 1981). In northern California, Davis (1972) excavated nonsprouting *Arctostaphylos* species and noted 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 (<2.5 mm diameter) are concentrated below the canopy; however, they often overlap those of adjacent plants (Kummerow et al. 1977), suggesting the potential for direct competition for water and nutrients. These feeder roots lack secondary growth and have determinate growth with a life span of one growing season (Kummerow and Ellis 1989). Davis (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. For most shrubs, the radial spread of roots is several times greater than the canopy, although root: shoot biomass ratios are typically less than 1 (Kummerow 1981). Despite the fact that sprouting species maintain their major roots between fires, root: shoot ratios are reportedly similar between sprouting and nonsprouting species.

Root nodules with symbiotic nitrogen-fixing actinomycetes are known for species of *Cercocarpus*) (Vlamis et at. 1964) and *Ceanothus*, but their presence is dependent on various site factors (Vlamis, Schultz, and Biswell 1958; Furman 1959; Hellmers and Kelleher 1959; White 1967; Youngberg and Wollum 1976; Kummerow, Alexander, Neel, and Fishbeck 1978; Ellis and Kummerow 1989) Water stress in particular inhibits nodulation in *Ceanothus* spp. (Pratt, Konopka, Murry, Ewers, and Davis 1977). Ectomycorrhizal associations are common with *Quercus berberidifolia* and *Arctostaphylos glauca*, and vesicular-arbuscular mycorrhizae with *Adenostoma fasciculatum*, *Ceanothus greggii*, and *Rhus ovata* (Kummerow 1981). Ectomycorrhizae have been shown to be important in recovery from water stress in *Q. berberidifolia* (Borth 1986). Root grafting is apparently not common, although it has been observed in *Q. berberidifolia* (Hellmers et al. 1955) 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, initiation of growth depends on higher temperatures. In general, phenological events begin and end later on north- than on south-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).

Secondary stem growth begins earlier and extends later into the season than primary growth (Avila, Lajaro, Araya, Montenegro, and Kummerow 1975), and in *Rhus* species and *Malosma laurina* it may occur year-round. The width of growth rings is significantly lower in drought years (Gray 1982; Keeley 1993) 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 only a small proportion of flowers mature into fruits. Most species are self-incompatible (Raven 1973; Moldenke 1975), however, Fulton and Carpenter (1979) reported self-compatibility in *Arctostaphylos pringlei*, but Brum (1975) found this species to be entirely self-incompatible.

Most species are pollinated by insects, and this trait may have selected for the markedly asynchronous nature of flowering phenology in different species (Mooney 1977b; Steele 1985). *Arctostaphylos* and *Garrya* species flower earliest in the season, prior to the initiation of vegetative growth, followed by *Ceanothus*, *Quercus*, and *Rhus* species. Early flowering in these five genera may be related to the fact that they flower on old growth, from floral buds initiated during the previous year's growing season. *Adenostoma fasciculatum*, *Heteromeles arbutifolia*, and *Malosma laurina* flower later, on new growth after stem elongation is completed

(Bauer 1936; Kummerow et al. 1981; Baker, Rundel, and Parsons, 1982 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 (Keeley 1987a; Keeley and Keeley 1988b; Zammit and Zedler 1992). In these latter two genera, internal competition for photosynthetates during the period of fruit maturation affects the extent of floral bud differentiation for the following year and greatly complicates correlating fruit production with weather patterns.

SHRUB PHYSIOLOGY

Water Relations

Chaparral shrubs vary in their water relations characteristics largely in accordance with species-specific differences in rooting habit (Poole, Roberts, and 1981; S. Davis and Mooney 1986). Shallow-rooted species are able to respond to elevated levels of soil moisture early in the rainy season. During the summer, shallow-rooted nonsprouting species of *Arctostaphylos* and *Ceanothus* (subgenus *Cerastes*) are exposed to extremely negative soil water potentials (e.g., *Ceanothus m.* in Fig. 6.22). At this time they commonly have predawn stem xylem water potentials of −6.5 to −8 MPa versus −1 to −3 MPa during the summer drought for deeper-rooted shrubs such as *Rhus ovata, R. integrifolia, Malosma laurina* (labeled *Rhus l.* in Fig. 6.22), *Heteromeles arbutifolia*, sprouting species of *Arctostaphylos* and *Ceanothus* (subgenus *Ceanothus*, e.g., *Ceanothus s.*, Fig. 6.22), *Prunus ilicifolia*, and *Rhamnus californica* (Poole and Miller 1975, 1981; Dunn, Shrapskire, Song, and Mooney 1976; Burk 1978; Barnes 1979; Miller and Poole 1979; Schlesinger and Gill 1980; Parsons, Rundel, Hedlurd, and Baker 1981; Oechel 1988; S. Davis 1989; Mooney 1989; Rundel 1995).

The critical role rooting depth plays in determining water stress is illustrated by the similarity in water potentials for *Malosma laurina* and *Ceanothus* seedlings in contrast to the marked differences between adults (Fig. 6.22A, B) (Thomas and Davis 1989). Low survivorship of *Malosma* seedlings (Fig. 6.22C) is tied to much greater susceptibility to embolism induced by water stress. *Malosma laurina* exhibits a 50% loss in hydraulic conductivity when branches reach a xylem pressure potential of only

−1.6 MPa, whereas *Ceanothus megacarpus* does not exhibit 50% embolism until −11 MPa (Kolb and Davis 1994; Jarbeau et al 1995). These studies have been extended to include several other species and reveal the same pattern; namely, increasing susceptibility to embolism is correlated with decreased seedling survivorship after fire (Davis 1991; S. Davis, Kolb and Barton 1998). These patterns may be tied to differences in the size of pores in xylem pit membranes, with larger vessels and wider pores contributing to greater xylem efficiency but contributing to greater vulnerability to embolism (Jarbeau et al. 1995). Vulnerability to embolism appears to be typical of deep-rooted sprouting shrubs, and may account for why these species have seedling recruitment restricted to shaded understories of older chaparral.

Ceanothus megacarpus water potentials change markedly during stand development following fire. Comparing stands 6, 13, and 22 yr old, Schlesinger and Gill (1980) showed that throughout the year values were always more negative for plants in the youngest-aged stands and that smaller plants suffered more severe water stress during the summer drought than did larger plants – one small plant even reaching an amazing predawn water potential of −12 MPa (Schlesinger, Gray, Gill, and Mahall 1982a). They contended that water stress is a major factor in stand thinning and that it was reflected in nonrandom mortality that shifted the distribution of shrubs from clumped toward regular, a pattern seen in much older stands as well (Keeley 1992b).

In postfire resprouting shrubs, new sprouts have stem water potentials one-third to one-half as negative as mature shrubs, but these differences disappear by the second year after fire (Radosevich and Conard 1980; Oechel and Hastings 1983; Hastings, Oechel, and Sionit 1989; Stoddard and Davis 1990).

Stem water potentials are more negative during summers following winters of low rainfall (Poole and Miller 1981). For example, during a severe drought in the Sierra Nevada foothills, the shallow-rooted *Arctostaphylos viscida* reached predawn stem xylem water potentials of −7 MPa and showed very little diel variation (indicating little photosynthetic activity), whereas the following summer, after a very wet winter, the lowest predawn potentials were −4 MPa, and there was a large diel change (Parsons et al. 1981). In addition, the monthly pattern of rainfall may be as influential as the seasonal total (Gill 1985). 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;
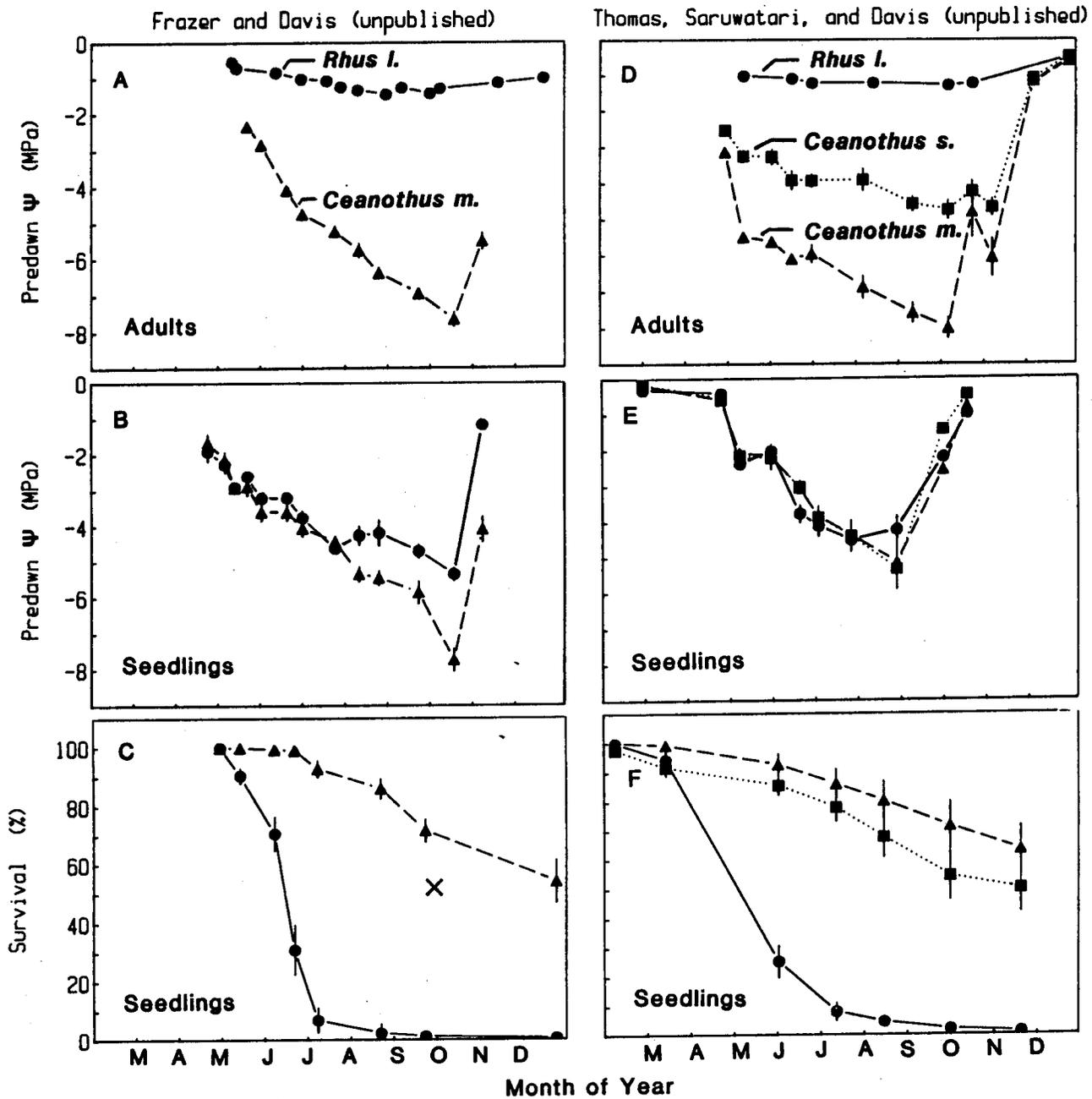
Figure 6.22. Change in predawn water potential in mixed chaparral stands for adult shrubs (A, D) and seedlings (B, E) and postfire seedling survivorship (C, F) for non-sprouting Ceanothus megacarpus *and sprouting* Malosma laurina *(formerly* Rhus laurina) *and sprouting* C. spinosus *(reprinted from Davis 1989).*

Mooney et al. 1977). Root competition may directly induce water stress, as evidenced by the observation that reduction in shrub cover by artificial stand thinning results in a significant reduction in water stress (Knipe 1985), and the ability of grasses to prevent shrub invasion into grasslands by depletion of soil moisture (S. Davis and Mooney 1985; Williams and Hobbs 1989).

For most species there is a midday depression in stomatal conductance that begins earlier in the day as the growing season progresses. Although deep-rooted shrub species may maintain access to water longer into the summer drought, they exhibit complete stomatal closure under far less water stress than do shallow-rooted species (Poole et al. 1981; Barnes 1979). As a consequence, shallow-rooted *Arctostaphylos* and *Ceanothus* species are likely to maintain more active photosynthesis longer into the drought than many deep-rooted species. Nonetheless, by late summer, these shallow-rooted species frequently exhibit complete stomatal closure for a month or more, whereas

deeper-rooted species commonly have a brief period of stomatal conductance each day. Undoubtedly these differences are tied to anatomical characteristics discussed earlier and to seasonal and diel osmotic adjustments (Roberts 1982; Calkin and Pearcy 1984; Bowman and Roberts 1985) and are cued by absccisic acid (Tenhunen, Hanano, Abril, Weiler, and Hartung 1994).

Chaparral communities comprise associations of taxa with 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 communities on different sites should converge at maturity in terms of transpiration per unit of leaf area, and they put that figure at 150–200 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.

Soil Nutrients

Enhanced vegetative and reproductive growth, after fertilizer application suggests that chaparral shrubs are nutrient-limited (Hellmers, Bonner, and Kelleher 1955; Vlamis et al. 1958; Christensen and Muller 1975a; McMaster, Jow, and Kummerow 1982; Gray and Schlesinger 1983). *Adenostoma fasciculatum* is clearly nitrogen-limited, whereas others (e.g., *Ceanothus megacarpus* and *C. greggii*) may not be, although the latter species does respond to phosphorus addition. *Ceanothus* species are nitrogen-fixers, and there is evidence they are capable of enhancing the nitrogen status of surrounding soils (Quick 1944; Hellmers and Kelleher 1959; Vlamis, Schultz, and Biswell 1964; Kummerow et al. 1978). Nitrogen-fixing nodules in *Ceanothus* are deeply buried, and thus some published rates are underestimates. Ellis and Kummerow (1989) reported that young plants derived 10% of their nitrogen from biological fixation by the actinomycete species of *Frankia*. On some chaparral sites, free-living asymbiotic nitrogen fixers may contribute significantly to the nitrogen budget (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 a result of atmospheric deposition, and this, plus foliar-leached ammo-

nium, could exceed the input by symbiotic nitrogen fixation. In many parts of California, deposition of anthropogenic sources of nutrients is becoming an increasingly important part of the nutrient budgets of these ecosystems (Schlesinger et al. 1982b; Bytnerowicz, Miller, and Olszyk 1987; Bytnerowicz and Fenn 1996). Under natural conditions, 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. Because fire recycles 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, 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 postfire proliferation of suffrutescent and annual legumes may add nitrogen through their symbioses with nitrogen-fixing *Rhizobium* bacteria (Poth 1982). Postfire herbaceous species may have different strategies for nitrogen use. Swift (1991) reported that "fire-endemic" species preferentially used the high ammonium levels present immediately after fire but used nitrogen less efficiently than did generalist species that were likely to persist for many years after fire.

Photosynthesis

Shrubs and other growth forms in chaparral are C_3 (Mooney, Troughton, and Berry 1974), reflecting the fact that summer drought restricts most photosynthetic activity to the cooler winter and spring months. Nonetheless, photosynthetic activity is possible year-round, although maximum rates are low (5–15 mg CO_2 dm^{-2} hr^{-1}, Mooney 1981) due to internal structural limitations of the sclerophyl-

lous leaf (Dunn 1975) and to efficient strategies for use of nitrogen (Field, Merrino, and Mooney 1983; Field and Davis 1989). For most species there is a broad optimum temperature range for photosynthesis between 10° C and 30° C and little capacity for temperature acclimation (Oechel Lawrence, Mustafa, and Martinez 1981). Growth analysis indicates aboveground processes are not highly sensitive to belowground temperature (Larigauderie, Ellis, Mills, and Kummerow 1991).

Peak photosynthetic rates are typically observed only during the spring growing season, and as the season progresses, declining soil moisture reduces stomatal conductance, thus limiting daily CO_2 uptake (Oechel 1982). Surprisingly, in some species the photosynthetic rate is controlled directly by changes in the photoperiod (Comstock and Ehleringer 1986).

Many of the broad-leaf species such as *Heteromeles arbutifolia*, *Prunus ilicifolia*, *Quercus berberidifolia*, and *Rhus* spp. are relatively tolerant of shade (e.g., photosynthesis of *Heteromeles arbutifolia* is saturated at less than one-third full sunlight) (Harrison 1971), whereas others, such as *Ceanothus* and *Arctostaphylos*, are not fully saturated at two-thirds full sunlight (Oechel 1982) and if shaded they have substantially reduced water use efficiency (Mahall and Schlesinger 1982). Efficiency in use of water is higher for species distributed in xeric habitats and lowest in species from mesic habitats, although the latter species have the highest efficiency of nitrogen use (Rundel 1982; Field et al. 1983).

The thermal insensitivity of photosynthesis suggests that low temperatures are likely to play a minor role in limiting wintertime carbon gain, and this suggestion is supported by simulations that Mooney and associates (1975) performed on seasonal patterns of photosynthesis in *Heteromeles arbutifolia*. Their simulation suggests that wintertime depression of photosynthesis is largely a result of limited irradiance.

Across large elevational and climatic gradients, relatively small differences are observed in carbon uptake rates (Oechel et al. 1981). Scaling up potential photosynthetic activity of chaparral patches by using remote sensing techniques is a promising means of examining landscape level patterns (Gamon et al. 1995).

Freezing Tolerance

Freezing damage is occasionally significant, as evidenced by the spectacular freeze of December 1990 (Collett 1992), when widespread dieback was reported throughout the state (Cowden and Waters 1992). One of the most sensitive chaparral shrubs

is *Malosma laurina*, and there is reason to believe its distribution is controlled in part by low temperatures (Misquez 1990). Differential vulnerability to freezing-induced embolism, which is a function of xylem vessel diameter, may explain microhabitat segregation by this and other shrub species (Langan, Ewers, and Davis 1997).

The Myth of Stand Senescence

The concept of chaparral senescence is reminiscent of the Clementsian view of community succession being analogous to development of an organism. Old stands of chaparral have been described as "senescent," "senile," "decadent," and "trashy" – terms that lack clear definition. Without citing any source, Hanes (1971) described older stands of chamise chaparral as unproductive, with little annual growth, and others have suggested that older stands lack diversity and are nutrient-limited, with an overaccumulation of allelopathic toxins. None of these statements has been substantiated.

Apparently the notion that older stands of chaparral are unproductive derives from measurements of browse production for wildlife (Biswell, Taber, Hedrick, and Schultz 1952; Hiehle 1961; Gibbens and Schultz 1963). These studies showed that older chaparral produces very little deer browse. However, these 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 above 2 m. Studies of living biomass accumulation have shown that it remains stable for 60 yr or more (Fig. 6.23). Studies of production that have compared stands a decade or two after fire with stands nearly a century old have repeatedly failed to find any evidence of declining productivity (Keeley and Keeley 1977 unpublished data; Hubbard 1986; Larigauderie, Ellis, Mills, and Kummerow 1991). The idea that older stands are nutrient-limited has been questioned (Schlesinger et al. 1982b) and shown to be erroneous (Rehlaender 1992; Fenn, Poth, Dunn, and Barro 1993). In terms of resilience, stands a century old have seed banks capable of adequate postfire regeneration (Keeley and Zedler 1978; Zammit and Zedler 1994), and some species even require ancient stands for seedling recruitment (Keeley 1992c). Physiological studies of *Adenostoma fasciculatum* and *Ceanothus greggii* show that photosynthetic capacity, on a per leaf basis, does not decrease and even increases in very old stands (Reid 1985).

The primary observations that have led to the suggestion of stand senescence is the inevitable accumulation of dead wood and the occasional mass
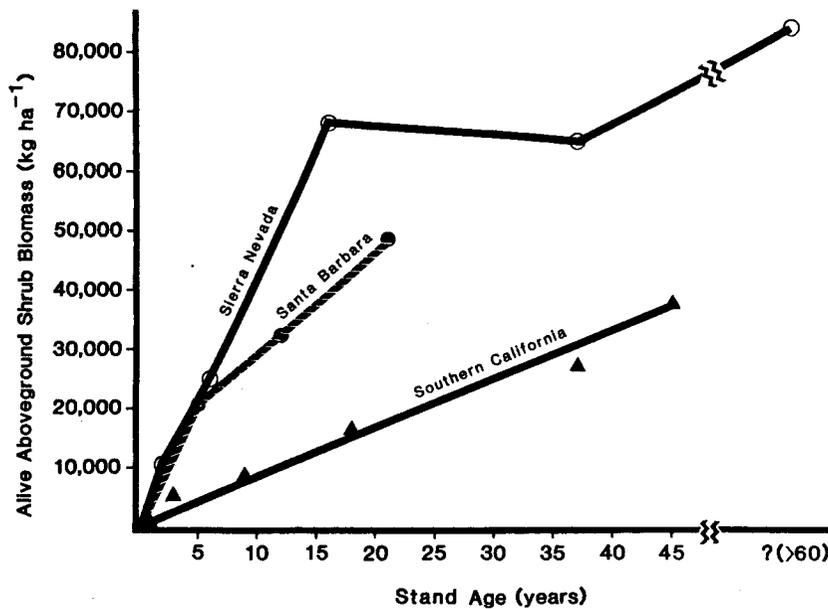
Figure 6.23. Standing living biomass in chaparral stands as a function of age since last fire: southern California mixed chaparral at San Dimas Forest from Specht (1969) (last datum point from Conrad and DeBano 1974); Santa Barbara Ceanothus megacarpus chaparral from Schlesinger and Gill (1980); Sierra Nevada foothills chamise chaparral from Rundel and Parsons (1979), Stohlgren et al. (1984), and Stohlgren (pers. commun. 1984).

dieback of the obligate seeder *Ceanothus*. It is abundantly clear that *Ceanothus* dieback is not due to senescence, for these species are capable of great longevity. Dieback is often associated with drought years (Riggan, Franklin, Brass, and Brooks 1994), which are likely to affect such shallow-rooted shrubs more than others. Sparks and associates (1993) have found differences in allocation of photosynthate between young and old shrubs, which they interpreted as indicators of senescence; however, there are other reasonable interpretations. Additionally, Sparks and Oechel (1993) contend that senescence is suggested by the fact that older stands of *Adenostoma fasciculatum*, with higher biomass of standing dead, sprout less vigorously after fire. However, they failed to rule out fire intensity as a causal factor.

An alternative to the model of stand senescence is one of a shifting balance in the competitive relationships as the community ages, sometimes resulting in successional replacement of disturbance-dependent recruitment species being displaced by disturbance-free species (Keeley 1986; Hilbert and Larigauderie 1988; Zedler and Zammit 1989; Keeley 1992b, 1992c; Zammit and Zedler 1992; Zedler 1995b). For example, on mesic slopes, *Ceanothus* and *Arctostaphylos* species are often displaced by more competitive taxa such as *Quercus, Heteromeles, Prunus,* and the like, which if left undisturbed long enough would form a self-replacing miniature sclerophyll woodland. However, on arid sites, *Ceanothus* and *Arctostaphylos* will persist for a 100 yr or more and continue to replenish the soil seed bank sufficiently to rejuvenate the stand after the inevitable fire.

RELATED PLANT COMMUNITIES

California Coastal Sage Scrub

Often called "soft chaparral," California coastal sage scrub, a largely summer-deciduous vegetation, tolerates more xeric conditions than evergreen chaparral (Mooney 1977a; Westman 1981a). Because of the orographic nature of rainfall, this community is well developed at low elevations near the coast as well as on arid interior slopes, usually below chaparral but occasionally at higher elevations on outcroppings of shallow soil (Bradbury 1978), on fine-textured soils that inhibit downward percolation of winter rains, or on frequently disturbed sites. The dominants include all the subshrubs and suffrutescent species (*Salvia, Eriogonum, Artemisia, Lotus,* and *Mimulus*) that often are associated with chaparral, either in gaps or after fire, plus more restricted species such as *Encelia californica, Hazardia squarrosus, Baccharis pilularis, Viguiera laciniata,* and *Malocothamnus fasciculatus*. 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; Malanson 1984; DeSimone and Burk 1992; Davis, Stine, and Stoms 1994) and show alliances with the northern coastal scrub (Heady et al. 1977). Succulents in the Crassulaceae and Cactaceae are important components toward the southern limits, particularly near the coast (Mooney and Harrison 1972). Oftentimes, ev-

ergreen sclerophyllous shrubs, such as *Malosma laurina* and *Rhus integrifolia*, are distributed at widely spaced intervals throughout coastal sage, apparently exploiting widely spaced favorable soil microsites.

Most dominants have nonsclerified malacophyllous leaves (3–6 cm²) that initiate growth in early winter and expand until soil moisture, temperature, and photoperiod induce leaf abscission (Nilsen and Muller 1981; Gray 1982). With the onset of drought, these winter leaves are replaced by a few smaller axillary leaves termed brachyblasts (Harrison, Small, and Mooney 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 (Gill and Mahall 1986). In many species, flowering is on new growth and thus is delayed until summer or fall (Mooney 1977a).

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). Mooney and Dunn (1970) suggested that the shallow-rooted subshrubs avoid summer drought by losing foliage, and these coastal sage subshrubs have often been termed "drought-avoiders," in contrast to the "drought-tolerators" in evergreen chaparral. Recent studies, however, reveal that the brachyblasts on *Salvia mellifera* can tolerate water potentials as low as −9.0 MPa (Gill and Mahall 1986) and maintain active photosynthesis at −5.0 MPa (Mooney 1982).

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. Exclosure experiments in both vegetation types, however, have shown that small mammals are an important factor in the formation of bare zones because of their propensity to forage on grassland species as close to the protective shrub canopy as possible (Bartholomew 1970; Halligan 1974; Bradford 1976; Quinn 1986). Experimental evidence in support of allelopathy has been criticized (Keeley and Keeley 1989); but, the phenom-

enon has not been ruled out. The facts that coastal sage aromatics represent a substantial carbon drain on the plant (Tyson, Dement, and Mooney 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 antiherbivore functions have not been fully explored.

Two modes of postfire recovery in coastal sage scrub include facultative seeders (Fig. 6.14 C,D) and obligate resprouters that flower the first year and recruit seedlings heavily in the second year (Westman, O'Leary, and Malanson 1981; Malanson and O'Leary 1982; Keeley and Keeley 1984). Coastal sage scrub communities have a postfire burst of fire annuals and other herbs comprising the same species as in chaparral (Keeley and Keeley 1984; O'Leary 1988; O'Leary and Westman 1988). Postfire resprouting of coastal sage subshrubs is greatly reduced on inland sites, where recovery is much slower (Westman et al. 1981; Westman 1982). Resprouting is most successful in young stands and least successful in older stands, and this is not driven solely by greater fire intensity, as some coastal sage subshrubs – for example, *Baccharis pilularis* (Hobbs and Mooney 1985) and *Eriogonum fasciculatum*, *Artemisia californica* (Keeley 1997a) – outgrow the capacity for resprouting. In the absence of fire, coastal sage species are capable of regenerating their canopy from basal sprouts (Malanson and Westman 1985), similar to the pattern observed for sprouting chaparral shrubs (Figs. 6.19 and 6.20), making these subshrubs reasonably resilient to long fire-free periods.

Coastal sage scrub is intermediate between grassland and chaparral in its resilience following frequent fires (Wells 1962; Kirkpatrick and Hutchinson 1980). Fire-recurrence intervals of 5–10 yr may result in chaparral being replaced with coastal sage scrub. More frequent fires, however, will result in transition of sage scrub to grassland (Fig. 6.12) that is dominated by nonnative grasses (Keeley 1990b; Haidinger and Keeley 1993).

Interior Chaparral

Interior regions of western North America have vegetation showing various degrees of similarity to California chaparral. Of these, the Arizona chaparral (Fig. 6.24) is the most similar, even though it is separated by more than 200 km of desert. It is distributed in widely disjunct patches at 1000–2000 m in northern and central portions of the state and intergrades with desert scrub or grassland at the lower margin and with yellow pine forest or pinyon-juniper woodland at the higher elevations

Figure 6.24. Chaparral from northern Arizona dominated by Quercus turbinella.

Table 6.4. Demographic structure of a northern Arizona chaparral stand unburned for 40 years (1450 m, east-facing, 15° incline, Yavapai County)

Species	Postfire regeneration[a]	Live basal coverage m² basal area ha⁻¹	Shrub density Genets ha⁻¹	% Dead	Ramets /genet	Seedlings & saplings Genets ha⁻¹
Quercus turbinella	(OR)	16.5	1,375	0	88.0	0
Ceanothus greggii	(OS)	2.7	500	0	84.6	0
Quercus pungens	(OR)	1.9	125	0	188.0	0
Rhus trilobata	(OR)	1.3	375	0	36.3	0
Rhamnus crocea	(OR)	0.3	190	0	8.7	0
Gutierrezia sarothrae	(OS)	0.3	12,625	0	7.9	0
Acacia greggii	(OR)	0.1	125	0	14.0	0
Eriogonum fasciculatum	(FS)	0.1	750	0	10.0	0
Three other subshrubs	(OR)	0.7	190	0	39.1	0

[a] Table 6.2 legend.
Source: Welsh and Keeley (unpublished data).

(Carmichael et al. 1978; Brown 1978). The Arizona chaparral shrub flora comprises a subset of the California chaparral, plus shrubs that are closely related if not conspecific with California taxa (e.g. Quercus turbinella) (Tucker 1953). Areal coverage is typically from 35–80% ground surface in Arizona chaparral communities (Cable 1957; Carmichael et al. 1978). A typical Arizona site is described in Table 6.4 and, relative to California chaparral (Tables 6.1 and 6.2), it has less basal area and greater bare ground than most California sites. The nearly ubiquitous Californian Adenostoma fasciculatum is no-

ticeably absent from Arizona chaparral, and *Q. tur-binella* 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). Absence of *A. fasciculatum* is likely tied to its optimum growth occurring where coldest monthly temperature ranges from 9–12°C, whereas those California shrub species present in Arizona chaparral have an optimum range from −3 to 3°C (Malanson, Westman, and Yan 1992).

Arizona chaparral sites average 400–650 mm precipitation yr^{-1} (Mooney and Miller 1985), but in contrast to mediterranean-climate California (Fig. 6.2), the summer drought is cut short and 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, precipitation may not be as effectively used as is winter precipitation. Nonetheless, Arizona chaparral shrubs readily use summer rains. Vankat (1989) has documented stem xylem water potential changes from −7 to −1 MPa following summer thunderstorms, although the extent to which these shrubs remain photosynthetically active through the summer is unknown. Swank (1958) noted that most growth is in the spring and that summer growth is unpredictable. Reduced 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 does California chaparral (Cable 1957).

Because of the sparser cover, wildfires are less frequent, occurring every 50–100 yr (Cable 1957), although responses to fire by the dominant shrubs are similar to those of California plants. Obligate-seeding species such as *Ceanothus greggii*, *Arctostaphylos pringlei*, and *A. pungens* establish seedlings from soil-stored seeds only after fire (Pase and Pond 1964; Pase 1965; Pase and Lindenmuth 1971). Others, such as *Quercus turbinella* and *Rhamnus crocea*, are obligate resprouters after fire. Despite much overlap in woody floras, there is relatively little similarity in the temporary postfire flora, with the notable exception of *Emmenanthe penduliflora*, which may dominate some postfire sites in Arizona. Although species richness is notably lower than in California, there is a temporary flora that flourishes following fire, but, unlike in California, herbaceous perennials are more important than annuals, likely reflecting the role of summer rain in this interior chaparral (J. Keeley, M. Keeley, Fotheringham, and Zipusch, unpublished data).

A detailed study of stem age structure in Arizona chaparral (Welsh and Keeley, unpublished data) has shown that, as in California chaparral, postfire resprouting species continue to rejuvenate their canopy with sprouts in the absence of fire. Also, as in California, obligate-seeding *Arctostaphylos* were more or less even-aged, dating back to the last fire. Surprisingly, however, the postfire obligate seeder *Ceanothus greggii* proliferated many different-aged stems from the root collar or lower stem, and all four *C. greggii* shrubs that were aged showed continuous recruitment of new stems. Observations suggest that this growth pattern is widespread wherever *Ceanothus* are distributed in open habitats.

On the more western slopes of the Sierra Madre Oriental Range of northeastern Mexico are isolated patches of chaparral-like vegetation (Muller 1939, 1947; Shreve 1942). Muller (1939) suggested that the slightly lower precipitation and greater diel 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 fewer herbs. Important genera include *Quercus*, *Garrya*, *Cercocarpus*, *Rhus*, *Rhamnus*, *Arbutus*, *Ceanothus*, and *Arctostaphylos*, including two California obligate-seeding shrubs, *C. greggii* and *A. pungens*. One striking difference is that this Mexican chaparral has an understory of herbaceous species, including C_4 bunchgrasses (Keeley, personal observations), not commonly observed in California chaparral. Rzedowski (1978) considered this zone to have a high fire frequency, and he noted that the scrub oak species were vigorous sprouters. Also, postfire seedling recruitment has been noted for obligate-seeding *Ceanothus greggii* and *Arctostaphylos pungens* (Valiente, personal communication). Beyond this, little is known of the postfire community, but based on distribution data it is apparent that very few of the hundreds of postfire species in California chaparral extend to northeastern Mexico. Considering the 433 native species found after fire in one southern California study, only 11% are distributed into mainland Mexico, and they include none of the species that contributed significantly to the postfire flora in California (Keeley, unpublished data). Thus, although the

shrub overstory is remarkably similar between Mexico and California, the communities are quite different.

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^{-1}, 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, are minor components, although some, such as *Cercocarpus* species, are sometimes locally abundant (Brooks 1962; J. Davis 1976). A well-developed herb flora is characteristic of the mature vegetation (E. Christensen 1949; Allman 1952). Fires occur, and *Q. gambelii* responds like other scrub oaks by sprouting vigorously from the rootstock (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). Although little has been reported in the way of a temporary postfire flora, one annual species from this region has smoke-stimulated germination (Baldwin, Staszak-Kozinski, and Davidson 1994).

EVOLUTION

Community History

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 on 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, rocky 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 efficiency in nutrient use and ability to remain metabolically active longer into the drought. Drought-deciduous types are favored by more severe droughts, fine-textured soils, or high-nutrient conditions.

By the middle of the Miocene (20 M yr BP), California was an ecotone between the more mesic adapted Arcto-Tertiary geoflora from the north and the xeric adapted Madro-Tertiary from the south. Evergreen sclerophylls were widespread across the Southwest, forming various broadleaf 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.

At 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 elimination of summer rains and greater annual temperature extremes. Some Arcto-Tertiary elements persisted on cooler, more mesic sites, and the Madro-Tertiary geoflora lost taxa depending on summer rain and those requiring more equable climates. Pleistocene glacial/interglacial shifts in climate resulted in latitudinal and elevational shifts in elements of both geofloras (Axelrod 1981, 1986), and thus, contemporary chaparral associations are the result of mixing and remixing of these plant assemblages.

The present spatial pattern of chaparral distribution, from the summer-rain region of northern Mexico, through Arizona with bimodal rainfall, to mediterranean-climate California, may be viewed as a model of the temporal development of California chaparral. This model suggests a pattern of evolution of chaparral taxa on islands of poor soils and seasonal drought embedded in a more mesic landscape. As the climate changed, these drought-prone "islands" coalesced into larger patches, with consequent elimination of other vegetation. De-

spite the fact that some chaparral dominants originated under a summer-rain climate, there is evidence that evolutionary changes have occurred in response to the mediterranean climate. For example, Vankat (in Keeley and Keeley 1988a) has shown that the flowering phenology of *Arctostaphylos pungens* and *Ceanothus greggii* is different in the summer-rain climate of Mexico. In California these genera exhibit flower-bud dormancy through the summer and fall, which may have been selected for by the mediterranean climate. Lignotubers as ontogenetic traits, such as in species of *Adenostoma*, *Arctostaphylos*, and *Ceanothus* and the coalescence of seed endocarp segments in *Arctostaphylos*, are traits presently absent from Arizona chaparral species, but they are widespread in southern California taxa, and possibly arose in response to a greater predictability of fire in a mediterranean-climate environment. The rapid radiation of annual taxa endemic to postfire environments, an element largely lacking in Arizona and Mexican chaparral, may also reflect the more predictable role of fire in California.

Pleistocene climates were significantly moister than contemporary conditions, with coastal paleoclimates in southern California comparable to modern climates 500 km to the north (Axelrod and Govean 1996). Evidence of this is seen in the elimination of more mesic forests throughout coastal southern and central California during the Holocene (Axelrod 1973; Warter 1976; Heusser 1978). These were largely closed-cone forests, which demonstrates that wildfires have long been important in this region. With the arrival of humans at the close of the Pleistocene, wildfire frequency likely accelerated due to increased ignitions (Wells 1962) and to habitat modification resulting from the elimination of two-thirds of the mammalian genera (Keeley and Swift 1995), as accounted for by the "Pleistocene overkill" model (Martin 1973). The present distribution patterns of most chaparral species date to the xerothermic of recent times (8000–3000 BP) (Raven and Axelrod 1978), a period when severe drought promoted the expansion of chaparral. More recently, between 1100 and 1350 A.D., severe droughts in California, lasting one to two centuries at a time (Stine 1994), further contributed to modern landscape patterns.

Evolution of Chaparral Taxa

The evolutionary history is better known for some chaparral taxa than others. Surprisingly, the ubiquitous *Adenostoma fasciculatum* is largely unknown from the fossil record (Axelrod 1973). It likely evolved on the most xeric 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, although as constituents of now extinct plant associations (Axelrod 1975). Many herbaceous genera and *Arctostaphylos* and *Ceanothus* underwent rapid speciation during the Pleistocene, in part because new habitats were created by extensive mountain building and exposure of diverse substrates (Raven and Axelrod 1978) and by an increase in the incidence of wildfires. The three shrubby genera, *Adenostoma*, *Arctostaphylos*, and *Ceanothus*, are among the most widespread in chaparral and are the taxa that have adapted most closely to fire in their production of lignotubers as a normal ontogenetic character and their timing of seedling recruitment to postfire environments. However, *Adenostoma* has done this without speciating and without extraordinarily high genetic variation (Lardner 1985), whereas the latter two genera have radiated extensively, largely by habitat specialization (Fig. 6.5; Cody 1986; Ball et al. 1983; Zedler 1995a).

Hybridization has played a role in the evolution of both of these large shrub genera. All *Ceanothus* species are diploid ($n = 12$), and hybrids within the subgenera are common (McMinn 1944; Nobs 1963; Phillips 1966; Frazier 1993), but the infrequency of crosses between subgenera *Cerastes* and *Ceanothus* (Hannan 1974) suggest two major clades in the genus *Ceanothus*. Hybridization has been implicated in the evolution of both diploid ($2n = 13$) and tetraploid *Arctostaphylos* taxa, and apparently there are no internal subgeneric barriers (Gottlieb 1968; Schmid, Mallory, and Tucker 1968; Keeley 1976; Ball et al. 1983; Kruckeberg 1977; Ellstrand, Lee, J. Keeley, and S. Keeley 1987; Schierenbeck, Stebbins, and Patterson 1992; Keeley, Massihi, Delgadille, and Hirales 1997). Much evidence points to widespread introgression that has led to a highly reticulate pattern of evolution, and thus the lack of distinct clades presents a challenge to understanding evolutionary radiation within this group. Speciation has led to a proliferation of obligate-seeding species, and the forced genetic mixing in each generation has undoubtedly contributed to the observation that these species tend to form morphologically homogenous populations relative to burl-forming taxa. Populations of the latter often comprise distinctly different clones, treated by Wells (1987) as "forms." An apparently widespread taxonomic problem in this group is the challenge of how to treat subspecific taxa, which appear to be of polyphletic origin; a phenomenon well documented for *A. mewukka* (Schierenbeck et al. 1992) and likely to be true for *A. glandulosa* (Keeley et al. 1997; unpublished data).

In *Arctostaphylos*, tetraploid lignotuberous taxa with foliaceous floral bracts were considered by Wells (1987) to be ancestral, whereas diploid obligate-seeding species with reduced floral bracts were considered to be recently derived (Wells 1969). Determination of derived conditions (apomorphies) is, however, problematical, and recent DNA data (Parker and Vasey, unpublished data) do not fully support the subgeneric alignments suggested by Wells (1992). However, the presence of lignotubers in closely related genera suggest that this is indeed a pleisomorphic (ancestral) character and supports the notion that evolution within the group has proceeded toward loss of the burl. Some patterns within the genus are evident. For example, the Baja California manzanita, *A. peninsularis* is a burl-forming shrub in one part of its range and, apparently due to diminished fire frequency, non-burl-forming shrub in another part of its range (Keeley et al. 1992), and a similar pattern is known for *A. patula*. Two other burl-forming species are known to produce non-burl-forming populations along their arid borders (Keeley, unpublished observations). Wells (1969) 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 this mode 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.

Coupling of Demography, Physiology, and Evolution in Chaparral Shrubs

Adenostoma, Arctostaphylos, and *Ceanothus* have adapted their reproductive biology to exploit wildfires for seedling recruitment and population expansion (disturbance-dependent recruitment). In contrast, *Quercus, Rhamnus, Prunus,* and others have not, and these taxa require long fire-free intervals for seedling recruitment (disturbance-free recruitment). These demographic modes are correlated with character syndromes that reflect physiological and morphological divergence (Keeley, in press; F. Davis et al. 1998)

Disturbance-dependent recruitment derives from the ready availability of resources in postfire environments that have placed high selective value on delaying germination to postfire conditions. Summer droughts in these hot, high light environments, however, have imposed strong selection for physiological tolerance of water stress. As a consequence, these disturbance-dependent species have evolved vascular cells more resistant to embolism and greater osmotic tolerance to extremely low water potentials. Selection for rapid growth rates may have selected against developmental patterns that generate adventitious buds and lignotubers, leading to the obligate-seeding mode, and this mode, with the increased frequency of sexual reproduction, may in turn have allowed for a greater fine-tuning of adaptation to drought. Additionally, with enhanced drought tolerance, there is less selective value to resprouting, an adaptation that can be interpreted as a means of maintaining an established root system with access to year-round moisture. Safe sites for recruitment are rare in time, but when they occur they are spatially extensive, putting little premium on mechanisms that enhance spatial dispersal but a high premium on maintenance of deep dormancy, with germination cues to fire.

Disturbance-free recruitment restricts seedling establishment to cooler, lower-light, moister conditions under the shrub canopy. These shrubs are highly susceptible to drought-induced embolism, and thus they avoid summer drought by maintaining year-round access to water by means of deep, massive root systems. This drought-avoidance strategy works well for adults but makes seedling recruitment in a drought-prone environment precarious. Thus, there has been no effective selection for delaying seed germination to postfire conditions, with the result that seeds are neither dormant nor long-lived (Keeley, 1997b). Additionally, safe sites for seedling recruitment are rare, and thus these taxa all have highly attractive animal-dispersed propagules.

Convergent and parallel evolution is evident in the very similar pattern of disturbance-dependent and disturbance-free recruitment in the Mediterranean macchia of Europe. Here, *Cistus, Cytissus,* and others are disturbance-dependent, whereas many taxa such as *Quercus, Prunus, Rhamnus,* and others require firefree conditions for recruitment. Particularly remarkable is the marked degree of similarity between California and Europe in the character syndromes tied to these demographic modes.

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