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RECRUITMENT OF SEEDLINGS AND VEGETATIVE SPROUTS IN UNBURNED CHAPARRAL¹

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Abstract. Age structure of 12 stands of chaparral, unburned for 56–120 yr, was investigated. All shrubs produced discernible growth rings, and ring counts on stems from stands of known age, plus synchrony in annual growth ring width among species in the same stand, were taken as evidence that growth rings represented annual rings. Species that survive fire by vegetative regeneration from the root crown were capable, in the absence of fire, of continuously regenerating their canopy with basal sprouts. These multistemmed resprouting species had an uneven age structure, indicating continuous recruitment of new stems into the population. The predicted age distribution for resprouting shrub stem populations illustrated very different patterns for species within the same stand and for the same species in different stands. In most resprouting shrubs, <15% of the stems dated back to the first decade after fire, and in many species the majority of stems were <10 yr of age. This contrasts with obligate seeding shrubs that do not initiate new stems from the root crown, and for which, in undisturbed chaparral, 100% of the stems date back to the years immediately following the last fire.

Seedling recruitment was abundant in seven of these old chaparral communities. Species with abundant seedling populations, ranging from 1000 to 37 500 individuals/ha, were *Quercus dumosa*, *Q. wislizenii*, *Rhamnus crocea*, *Prunus ilicifolia*, *Heteromeles arbutifolia*, and *Cercocarpus betuloides*. These species share the characteristic of regenerating after fire solely by resprouting, and seldom recruit seedlings during the first few decades after fire. Thus, it is concluded that these postfire obligate resprouters require long fire-free periods for successful reproduction and potential population expansion. For all but the last species, seedlings were most abundant in stands with a closed canopy and deep litter layer. Safe sites for establishment were not in gaps, although gaps may be important for successful recruitment of saplings into the adult population. For all sprouting species the actual age distribution of seedlings and saplings indicated that recruitment did not occur every year; mortality was high but most populations had some saplings that survived beyond the first decade. For all postfire seeding taxa, viz., *Adenostoma*, *Arctostaphylos*, and *Ceanothus*, no significant tree species recruitment was observed in these ancient communities. Seedlings of woodland tree species had colonized several of these old chaparral communities; however, even in stands a century old, successional replacement of chaparral was not imminent.

Key words: age structure; California; chaparral; resprouting; seedling recruitment.

INTRODUCTION

California chaparral is widely considered to be a fire-type vegetation. Its resilience to fire is reflected in the repeated observation that communities are only briefly altered by this form of disturbance, and species composition is relatively stable from one fire cycle to the next. All dominant woody plants are able to persist in the face of recurrent fires, and certain species are even dependent upon fire for seedling establishment (Sampson 1944, Hanes 1977, Keeley and Keeley 1988).

Some have considered chaparral, in part or all of its range, to be a fire maintained disclimax or subclimax, which, if left unburned, would eventually be succeeded by grassland (Sampson 1944) or sclerophyllous wood-

land (Horton 1960, Wells 1962). Pejorative terms such as decadent, senescent, senile, trashy, and unnatural are often used to describe chaparral that remains unburned for >50 yr (Hanes 1971, Vogl 1977, Reid and Oechel 1984). This is based on the belief that chaparral shrubs require fire for seedling recruitment, and resprouting shrubs require fire for establishment of new shoots. In the absence of fire, seedling establishment has generally been reported to be nonexistent, and shrub stems are thought to be even age, dating back to the last fire (Hanes 1977).

These conclusions, however, are based on studies of chaparral during the first few decades after fire. There is relatively little information on demographic patterns in chaparral communities that escape fire for long periods of time. In this study I investigated the age structure of stands of chaparral unburned for at least half a century to test whether both vegetative and sexual re-

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recruitment are indeed restricted to the period immediately after fire.

STUDY SITES AND METHODS

Study sites

Human-ignited wildfires are frequent throughout the chaparral type on an interval of every 20–30 yr (Keeley 1982). Finding sites unburned for >50 yr required much searching and the sites selected reflect what was available throughout the range. Twelve stands of 0.5–1.0 ha, distributed from southern to northern California, were sampled in summer and fall between 1983 and 1985 (Table 1). Stand age was determined from ring counts of shrubs in the stand (see *Age structure*, below). Federal, state, or county agency “fire-maps” were not reliable because in most instances the stands predated record keeping and the level of resolution was often inadequate; e.g., United States Department of Agriculture Forest Service maps do not map fires, or islands of vegetation missed in a fire, <15 ha in size. Slope aspect was measured with a compass, and slope inclination with a clinometer. Elevation, latitude, and longitude were taken from United States Government Survey 7.5 minute quadrangle topographic maps. Precipitation data were not available for these sites, but were estimated as follows. The average annual precipitation for the nearest station (NOAA 1984) was adjusted for the difference in elevation using the regression model reported by Miller et al. (1981).

Other than fire, these sites appeared to have had little human-caused disturbance, with the single exception of the Sequoia Site (number 9). The openness of this site, relative to the surrounding vegetation, and the dense understory of non-native annual grasses, indicated the site had been severely disturbed, perhaps by clearing. For this reason the Sequoia Site was not included in the correlation analysis of stand characteristics.

Community composition

At each site 45 plots, 2 × 4 m, were selected randomly across the site from coordinates generated by a random number table. Within each plot the diameter within 10 cm of the ground was measured for all live and dead woody stems; stems (ramets) from the same root crown (genet) were recorded separately from those arising from other root crowns. Basal diameter at ground level and height were measured for seedlings and saplings of woody species. Seedlings and saplings are defined as genets that established in recent years, in contrast to shrubs with root crowns that dated back to the last fire or earlier. In all but one species the distinction was obvious due to the apparent lack of successful seedling establishment during the first 50 yr or more after fire. Seedlings and saplings were distinguished from vegetative sprouts by the combination of their

small stature, and by excavating all of them to determine whether they had a distinct taproot and lack of underground connection with a root crown or rhizome of a shrub. Only in *Rhamnus crocea* was the distinction between seedlings/saplings and adult shrubs sometimes difficult, suggesting that seedling recruitment had been relatively continuous since the last fire.

Basal area of live and dead stems was calculated by assuming each stem approximated a circle. Relative dominance of species was expressed as basal area divided by total basal area of all species in the stand.

Additionally, at each site, percentage bare ground was determined with the line intercept technique along 10 randomly placed 10-m transects (Cox 1985).

Soil and litter characteristics

Twelve of the 45 plots sampled for community composition at each site were randomly selected for sampling of the soil and litter. Within a circular plot of 314 cm², litter depth was measured, and all litter was collected. Soil was excavated to a depth of 15 cm or until bare rock was encountered. Litter, defined as organic matter not passing a 2-mm mesh sieve, was separated by flotation, oven-dried to constant mass, and weighed. Inorganic matter not passing a 2-mm mesh sieve was separated as rock and weighed. Soil organic matter was determined for three samples from each site by drying the soil to constant mass and determining the percentage mass loss after combustion for 1 h at 700°C (Cox 1985). For half of the sites the variance in organic matter was very high so a total of six samples were analyzed for these sites. Soil particle-size distribution was determined with a hydrometer as described by Cox (1985) for three soil samples from each site. Soil pH was measured on three samples incubated overnight in 1:1 (mass/volume) soil/distilled water.

Age structure

Ages were determined from ring counts made on all seedlings and saplings encountered in plots. Ages were determined on all stems for five shrubs of the dominant species. For subordinate species, or species with a large number of stems, fewer individuals were sampled. More individuals were sampled in cases where a large percentage of the population had stems with rotted cores. Coring was considered unfeasible because of small stem size, growth irregularities, and branching near the ground. Consequently, all stems were cut at 5–10 cm aboveground, and a several centimetre thick section was returned to the laboratory.

Stem sections were polished with high grade (200–300 grit) sandpaper on a belt sander. To make growth rings more readily distinguishable, various techniques were utilized that accentuated the distinction of the spring wood from the summer wood. These included applying one of the following: water, linseed oil, kerosene, or paraffin oil. Older *Adenostoma fasciculatum* stems were sometimes difficult to age due to dark col-

TABLE 1. Characteristics of the 12 chaparral study sites. Where an estimate of variation is given, data are means \pm 1 SD.

	San Ignacio	Chihuahua	Silverado
Latitude (degrees and minutes)	33°17'	33°22'	33°45'
Longitude (degrees and minutes)	116°37'	116°42'	117°33'
Elevation (m)	1000	1175	950
Inclination (degrees)	8	17	27
Aspect (degrees)	330	155	45
Time since last fire (yr)	76	66	118
Dominant species (relative dominance in parentheses)	<i>Quercus dumosa</i> (76) <i>Adenostoma fasciculatum</i> (8) <i>Ceanothus cuneatus</i> (4)	<i>Adenostoma fasciculatum</i> (42) <i>Ceanothus greggii</i> (38) <i>Adenostoma sparsifolium</i> (14)	<i>Quercus dumosa</i> (56) <i>Ceanothus crassifolius</i> (21) <i>Heteromeles arbutifolia</i> (9)
Total basal coverage (m ² /ha)	50.6	47.1	54.8
Percentage dead basal coverage	16.0	13.7	25.0
Seedling and sapling density (no./ha)	24 610	0	2320
Percentage bare ground	18	31	17
Litter depth (mm)	55 \pm 21	16 \pm 17	32 \pm 19
Litter oven-dry biomass (kg/m ²)	2.62 \pm 1.28	0.67 \pm 0.89	2.04 \pm 1.22
Percentage rock	17 \pm 6	30 \pm 12	50 \pm 27
Soil organic matter (% dry mass)	12 \pm 2	11 \pm 5	17 \pm 6
Percentage sand	72 \pm 10	68 \pm 3	32 \pm 3
Percentage clay	19 \pm 4	26 \pm 3	49 \pm 9
Soil pH	6.4 \pm 0.2	6.3 \pm 0.5	6.4 \pm 0.4

oration of the heartwood. Soaking overnight in 5.25% sodium hypochlorite solution bleached out this color.

The following shrubs produced recognizable growth rings: *Adenostoma* spp., *Arctostaphylos* spp., *Ceanothus* spp., *Cercocarpus betuloides*, *Garrya* spp., *Heteromeles arbutifolia*, *Prunus ilicifolia*, *Quercus dumosa*, *Q. wislizenii*, and *Rhamnus crocea* ssp. *ilicifolia*. Some species with diffuse porous wood had less distinct boundaries between rings, making counts difficult. The most difficult were *Rhus ovata* and *Malosma (Rhus) laurina*. *Quercus dumosa* was confusing at first because large spring wood vessels were produced in waves during the growing season. Summer wood was, however, characterized by the production of a dense layer of dark fiber cells and only by examination of stems of known age was this recognized. Taxa differed in the sharpness of the boundary between the spring and summer wood, and the most distinct growth rings were produced by obligate seeding taxa of *Ceanothus* and *Arctostaphylos*. Use of ring counts to determine the age of woody stems not only requires the presence of distinct growth rings, but also verification that they represent annual rings. Ring counts on stems from stands of known age, plus synchrony in annual growth ring width among species in the same stand, were taken as evidence that growth rings represented annual rings (Keeley, *in press*).

Growth rings were counted under a dissecting microscope at 7–10 \times power by two independent observers. For each species at each site, stem diameter was regressed against age with a stepwise regression, but in all cases higher order polynomial equations did not significantly improve the fit over a linear model. In addition to the correlation coefficient, an estimate of relative error was calculated for each equation. This is

calculated as the standard error divided by the mean value of y , and is analogous to the coefficient of variation, which gives a standardized measure of comparison between equations (Whittaker and Marks 1975). This regression equation was used to estimate the age structure of the population based on stem diameters recorded in the plot sampling.

Nonsprouting species of *Arctostaphylos* and *Ceanothus* establish from seed in the first growing season after fire. Theoretically their populations should be of even age and an accurate indicator of stand age. Since resprouting shrubs may establish new sprouts throughout their life-span, they are less reliable indicators of the year when the stand last burned. Thus, whenever possible, stand age was based on the counts taken from nonsprouting species. On sites lacking nonsprouting species, only an estimate of the minimum stand age was possible.

Seedling and sapling recruitment

Density of seedlings and saplings at a site was correlated with stand parameters using the Spearman's coefficient of rank correlation. At a single site the distribution of seedlings beneath the canopy vs. within canopy gaps was analyzed as follows. Fifty 2 \times 2 m plots were randomly located in gaps and 50 underneath the shrub canopy. Within each plot seedlings and saplings were recorded, litter depth measured, and 12 randomly located irradiance measurements (photosynthetic photon flux density) were taken. The hypothesis of no significant difference between gaps and beneath canopy was tested with a two-tailed t test for seedling density and litter depth and for arcsine-transformed data on percentage of full sunlight.

TABLE 1. Continued.

Pacific View	Serrano	Glendora	Monte Cristo
34°05'	34°06'	34°12'	34°20'
118°58'	118°58'	117°51'	118°46'
375	300	975	1000
19	22	37	9
270	15	315	90
56	56	66	89
<i>Ceanothus megacarpus</i> (61)	<i>Ceanothus spinosus</i> (92)	<i>Adenostoma fasciculatum</i> (25)	<i>Arctostaphylos glauca</i> (43)
<i>Adenostoma fasciculatum</i> (11)	<i>Rhamnus crocea</i> (5)	<i>Quercus dumosa</i> (20)	<i>Ceanothus crassifolius</i> (29)
<i>Cercocarpus betuloides</i> (5)		<i>Heteromeles arbutifolia</i> (12)	<i>Adenostoma fasciculatum</i> (27)
66.9	51.3	48.6	118.0
22.2	22.6	24.2	33.5
80	1170	4640	30
7	4	7	17
28 ± 20	53 ± 23	50 ± 45	46 ± 24
3.01 ± 2.30	2.75 ± 1.09	2.18 ± 1.92	3.63 ± 1.52
9 ± 4	28 ± 10	35 ± 16	25 ± 12
24 ± 1	25 ± 5	10 ± 5	15 ± 7
34 ± 2	26 ± 2	49 ± 2	51 ± 2
33 ± 6	34 ± 2	40 ± 3	35 ± 3
5.8 ± 0.3	5.8 ± 0.1	5.3 ± 0.1	6.2 ± 0.1

Life history comparisons

Seedling and sapling recruitment and vegetative recruitment on mature shrubs were contrasted for groups of species with different postfire response (viz., obligate resprouters, facultative resprouters, and obligate seeders) with one-way analysis of variance. All species encountered in the sampling were included in the analysis of seedling plus sapling recruitment. Only the dominant shrub species at a site were included in the analysis of vegetative recruitment.

RESULTS

Vegetative recruitment

All resprouting shrubs had an uneven stem age structure (Fig. 1) indicating recruitment of new sprouts was not restricted to the postfire environment, but rather occurred more or less continuously up until the present time. There was a significant regression of stem age on diameter for all species (Table 2).

Examples of the predicted age distributions for all stems estimated from the regressions are shown in Fig. 2. While this is not an exhaustive description of the shrub stem age structures encountered, the examples selected illustrate several patterns and conclusions that can be drawn about chaparral communities. The stem age structure for the same species may vary from site to site in some taxa. For example, *Adenostoma fasciculatum* had much new recruitment at two sites but no stem <15 yr at another site. On the other hand, the patterns observed for *Cercocarpus betuloides* and *Heteromeles arbutifolia* in Fig. 2 were similar across all sites where the species was present. Another pattern is

illustrated by *Adenostoma sparsifolium* from Chihuahua, which had many stems in the youngest age class but a distinct gap in stems between that age and 30 yr. An additional pattern is illustrated by *Prunus ilicifolia* at San Ignacio, which had no living stem older than 25 yr even though the last fire at the site was 76 yr before.

A summary of the percentage of live stems initiated in the first decade after fire and in the most recent decade is one way of describing the age structure of these species (Table 2). For sprouting species, relatively few stems dated back to the time of the last fire. For most sprouting species, a quarter or more of the live stems were recruited within the last 10 yr, and in several species recent recruits accounted for two-thirds or more of the stem population.

For nonsprouting *Arctostaphylos* and *Ceanothus* species, all stems dated back to the last fire, except at the disturbed Sequoia Site (Table 2).

Seedling and sapling recruitment

Substantial recruitment was present at over half of the sites (Table 1). Seedling and sapling populations ranging from 1000 to 37 500 individuals/ha were found for *Quercus dumosa*, *Q. wislizenii*, *Rhamnus crocea*, *Prunus ilicifolia*, *Heteromeles arbutifolia*, and *Cercocarpus betuloides*. Significant establishment of seedlings and saplings was observed at several sites for *Quercus dumosa* and *Rhamnus crocea*. *Heteromeles arbutifolia* and *Cercocarpus betuloides* shrubs were dominant at several sites, but seedlings and saplings were abundant at only a single site for each species. Seedlings of chaparral species were never observed at sites where adults of that species were not present.

TABLE 1. Continued.

	Mineral King	Sequoia	Mt. Tamalpais
Latitude (degrees and minutes)	36°28'	36°28'	37°56'
Longitude (degrees and minutes)	118°46'	118°46'	122°34'
Elevation (m)	1100	1200	350
Inclination (degrees)	14	20	24
Aspect (degrees)	190	265	140
Time since last fire (yr)	102	83	>93
Dominant species (relative dominance in parentheses)	<i>Arctostaphylos</i> <i>viscida</i> (49) <i>Adenostoma</i> <i>fasciculatum</i> (50)	<i>Ceanothus</i> <i>cuneatus</i> (70) <i>Cercocarpus</i> <i>betuloides</i> (29)	<i>Quercus</i> <i>wislizenii</i> (45) <i>Arctostaphylos</i> <i>glandulosa</i> (47) <i>Heteromeles</i> <i>arbutifolia</i> (6)
Total basal coverage (m ² /ha)	105.4	48.7	44.8
Percentage dead basal coverage	22.7	29.0	15.6
Seedling and sapling density (no./ha)	0	37 580	28 530
Percentage bare ground	7	26	2
Litter depth (mm)	15 ± 10	5 ± 4	79 ± 22
Litter oven-dry biomass (kg/m ²)	1.47 ± 1.48	1.19 ± 0.47	5.66 ± 0.94
Percentage rock	10 ± 6	6 ± 3	56 ± 20
Soil organic matter (% dry mass)	13 ± 4	12 ± 1	42 ± 14
Percentage sand	50 ± 8	46 ± 5	32 ± 3
Percentage clay	33 ± 2	34 ± 4	43 ± 3
Soil pH	6.1 ± 0.3	7.0 ± 0.3	5.2 ± 0.1

Significant seedling populations were never observed for species of *Adenostoma*, *Arctostaphylos*, or *Ceanothus*, even though these taxa dominated some sites. *Adenostoma* was present at nine sites but seedlings were never encountered. *Arctostaphylos* species were present at seven sites and seedlings were absent from all but one site where 125 individuals/ha were present. *Ceanothus* species were present at nine sites, but seedlings were absent on all but one site where 30 individuals/ha were present.

In southern California recruitment of seedlings and saplings was observed only on north-facing slopes but in northern California recruitment was present on other slope aspects. Seedling and sapling density at a site was not correlated with latitude, longitude, elevation, precipitation, slope inclination, or stand age (Table 3). Density of seedlings and saplings was also not significantly correlated with coverage of live or dead trees or with percentage bare ground, but was positively correlated with litter biomass and litter depth (Table 3).

At all sites recruitment of seedlings and saplings was largely restricted to beneath the shrub canopy, and recruitment was not observed in gaps. This was quantified, along with irradiance and litter depth, at the San Ignacio Site (Table 4). Gaps were largely in full sunlight and had no seedlings or saplings, in contrast to beneath the shade of the canopy where all seedlings and saplings were concentrated. In most instances gaps were not the result of mortality of shrubs and thus the litter layer in gaps was very sparse.

The age distribution of the largest seedling and sapling populations at each site are shown in Fig. 3. Saplings included here were all plants which, based on size, clearly were the result of reproduction in recent decades. Most seedlings and saplings were quite dimin-

utive, and even in saplings as old as 20–30 yr the distinction between them and mature shrubs dating back to the last fire was relatively obvious. Gaps in some age classes were evident in many populations.

Although many species had successful recruitment of saplings, at most sites they remained relatively stunted. This pattern is illustrated for *Quercus dumosa* at the San Ignacio Site (Fig. 4). In this population of seedlings and saplings, none of those recruited during the last two decades exceeded 1.9 m, which was >1 m beneath the canopy of the mature shrubs. Of all the saplings encountered at the sites in this study, none exceeded 2 m height, and the oldest recruit observed was a *Quercus dumosa* sapling of 34 yr at the Silverado Site, and it was <1 m.

Colonization by nonchaparral taxa was observed at the San Ignacio Site where *Quercus agrifolia*, a tree typical of oak woodlands and present around the boundary of the site, had significant recruitment of seedlings and saplings (Fig. 3). Other than occasional seedlings, significant recruitment by woodland species was not observed at the other sites.

Life history comparisons

A comparison of vegetative and seedling recruitment for shrubs that differ in their mode of postfire regeneration showed significant differences in recruitment patterns in the absence of fire (Table 5). Shrub species that do not establish seedlings immediately after fire (obligate resprouters) had significantly greater seedling and sapling establishment in the absence of fire than did species that routinely establish seedlings immediately after fire (facultative resprouters and obligate seeders). Vegetative recruitment patterns also differed. Obligate seeding species had a significantly greater pro-

TABLE 1. Continued.

Northridge	Bartlett Springs
37°56'	39°09'
122°33'	122°45'
250	1075
24	25
170	225
>61	74
<i>Arctostaphylos glandulosa</i> (52)	<i>Arctostaphylos elegans</i> (24)
<i>Quercus wislizenii</i> (22)	<i>Ceanothus cuneatus</i> (20)
<i>Heteromeles arbutifolia</i> (18)	<i>Quercus dumosa</i> (15)
55.3	67.6
12.7	15.5
0	1520
1	7
45 ± 25	60 ± 34
1.68 ± 1.01	1.70 ± 1.37
49 ± 14	43 ± 10
25 ± 8	22 ± 1
36 ± 1	35 ± 2
47 ± 6	25 ± 5
4.9 ± 0.5	6.0 ± 0.2

portion of stems dating back to the last fire than did resprouters (Table 5). Of these resprouters, obligate resprouting species had a significantly greater proportion of stems initiated during the last decade than did facultative resprouters. Obligate seeders had no recently recruited stems.

DISCUSSION

Vegetative recruitment

One bit of dogma held by chaparral ecologists has been that the aboveground stems of chaparral shrubs are even age, dating back to the last fire. For postfire obligate seeding shrubs this is largely true (Table 2). It is not true for resprouting shrubs, which are, in nearly all cases, composed of an uneven age distribution of stems (Figs. 1 and 2). The ability to initiate new shoots from adventitious buds in the root crown or basal burl has historically been viewed as an adaptation selected for regeneration after destruction of the shrub canopy by fire or other disturbance (Wells 1969, Mooney 1977, James 1984). Indeed, in such species fire has been viewed as a factor necessary for the "rejuvenation" of the canopy. The results presented in this study show that for all resprouting chaparral shrubs, rejuvenation, through vegetative regeneration, is a process that occurs continuously in the absence of fire.

Despite the wide latitudinal and elevational range of sites, there is a remarkable degree of convergence in the presence of multiple-age stems on individual sprouting shrubs (Fig. 1). Patterns of variation in the actual age structure of individual shrubs of these taxa may be summarized as follows.

1) Shrubs with one or two stems dating back to the last fire and little or no stem recruitment since then.

This is uncommon but was observed in a few instances, e.g., *Rhamnus crocea* at the Silverado Site (Fig. 1).

2) Shrubs with stems dating back to the last fire and more or less continuous recruitment and mortality of stems since that time, e.g., *Adenostoma fasciculatum* at the Glendora Site (Fig. 1).

3) Shrubs with stems dating back to the last fire and more or less continuous recruitment since that time but very little mortality of stems, e.g., *Quercus dumosa* at the San Ignacio Site (Fig. 1). It is doubtful that stems have died and decomposed. I have observed charred stems dating back to the previous fire in stands over 100 yr, suggesting decomposition is relatively slow (see also Gray and Schlesinger 1981). This pattern suggests that, rather than a "turnover" of stems as in the previous example, there is a potential expansion of canopy size.

4) Shrubs lacking any stem dating back to the last fire and no dead stems that could have been initiated after the last fire, e.g., *Rhamnus crocea* number 2 or 3 at Silverado (Fig. 1). In light of abundant seedling recruitment by this species it is likely that such shrubs represent saplings that were successfully recruited into the adult population. As mentioned earlier, the distinction between saplings and adults was problematical for this species. Another example of a shrub with no stem dating back to the last fire is *Adenostoma fasciculatum* number 2 at Monte Cristo (Fig. 1). Since this species was never observed to recruit seedlings an alternative explanation is that growth of this shrub was suppressed to the extent that many growth rings were missing, as has been noted for other woody species (Fritts and Swetnam 1989).

Factors accounting for differences in age structure of individual shrubs are not apparent from the data presented here. Statistical comparisons are hindered by the fact that most species were distributed at only a few sites, and none occurred at more than half of the sites. Also, the range of variation observed between individuals at the same site was often as great as between sites (Fig. 1).

Also, the estimated age distribution of live and dead stems for populations of sprouting species reveals much variation between species and sites (Fig. 2, Table 2). These patterns are the result of differences in rates of stem recruitment and/or mortality. Since these parameters are unknown for the species studied here, a great deal of research will be required before the factors responsible for the different age structures are elucidated.

Seedling recruitment in the absence of fire

Seedling establishment in the absence of fire has seldom been observed in chaparral (see reviews by Sampson 1944, Hanes 1977, Keeley and Keeley 1988). The very significant seedling and sapling populations observed in this study (Table 1, Fig. 3) are undoubtedly due to the antiquity of the sites. There is, however, marked variation among species (Table 5). Considering

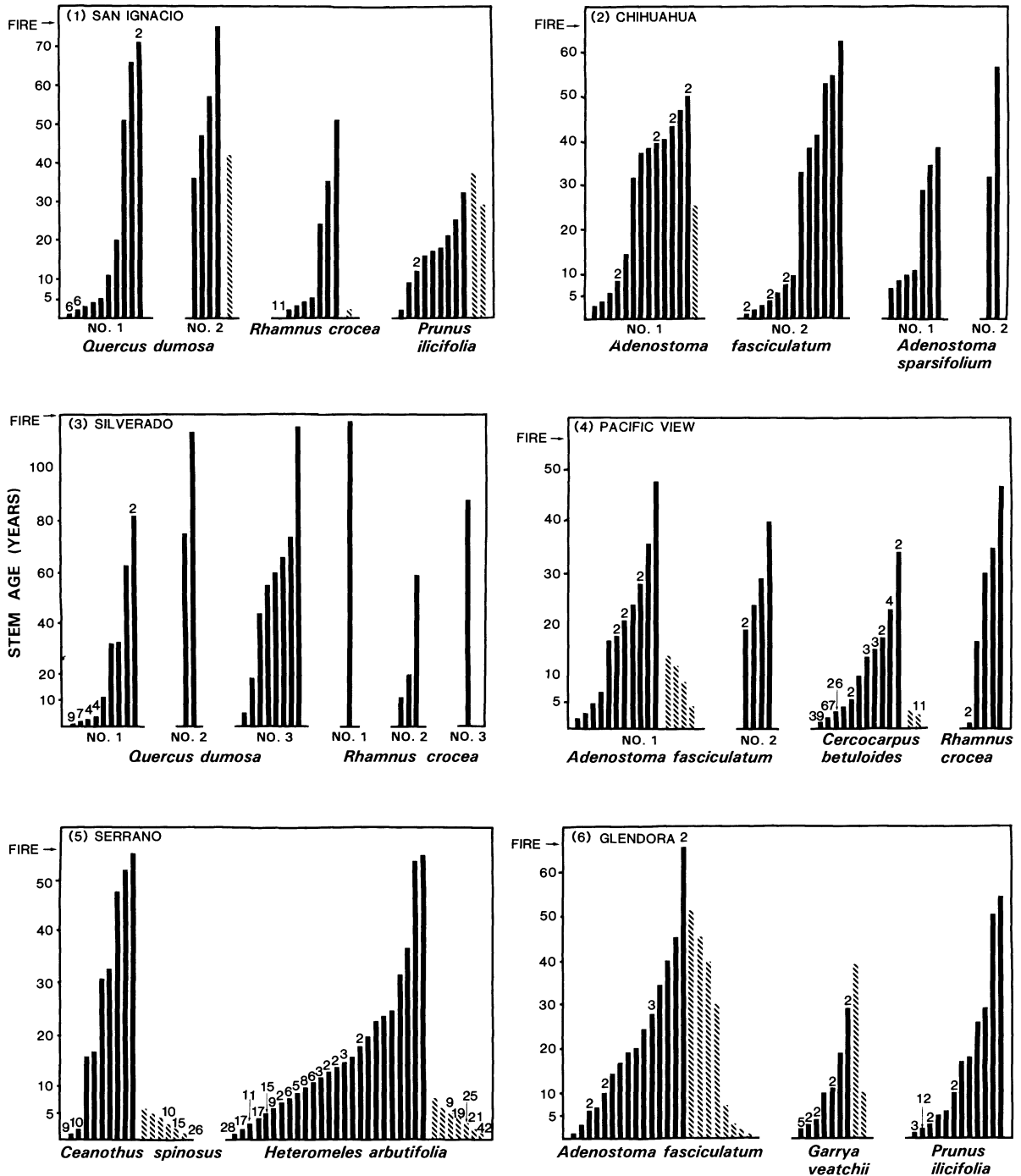


FIG. 1. Age distribution of all stems on a single shrub for selected sprouting species at the 12 sites. Each solid bar represents one live stem, unless topped with a number (the number of stems of that age); + atop bar indicates minimum age for stems with a rotten core. Hatched bars indicate dead stems. Multiple shrubs of the same species are indicated #1, #2, etc. above the species name.

the dominant species at these sites, two patterns are apparent.

1) *Adenostoma fasciculatum*, *Ceanothus* spp., and *Arctostaphylos* spp. did not have significant seedling and sapling recruitment in any of the stands studied

here. These taxa are also the only chaparral shrubs that routinely recruit seedlings after fire, a condition obviously necessary for seedling establishment. Some of these combine postfire seedling recruitment with resprouting (facultative resprouters), whereas others are

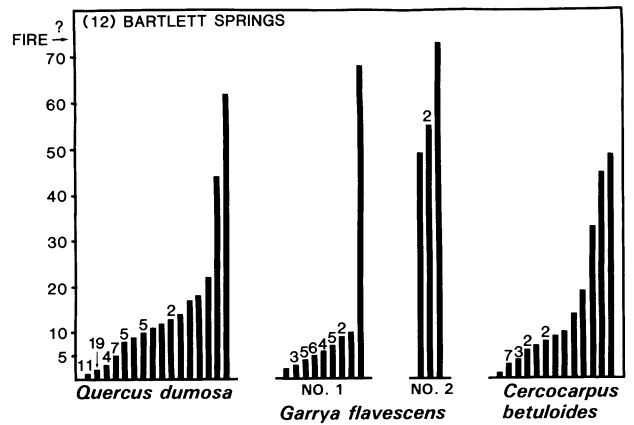
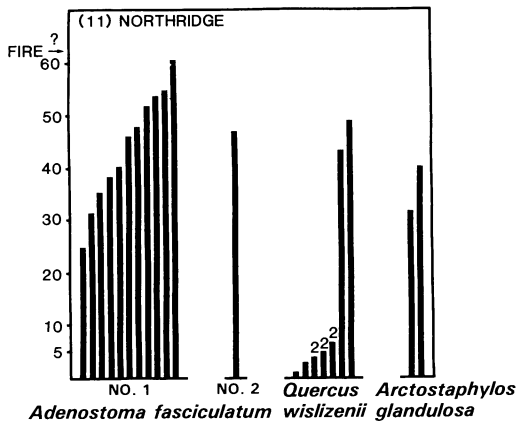
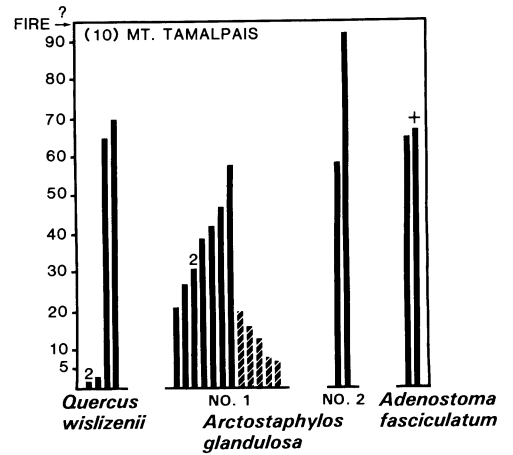
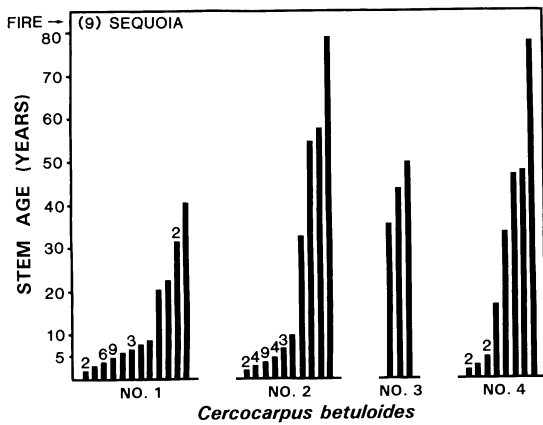
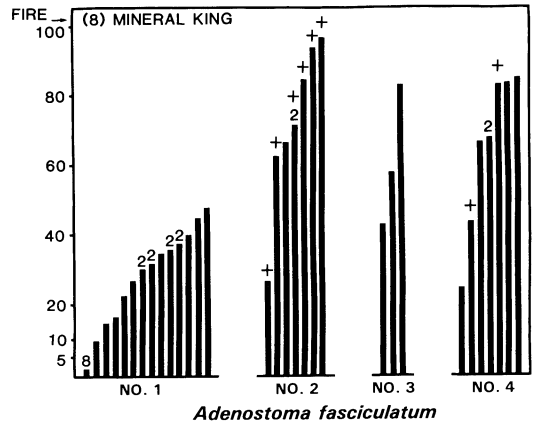
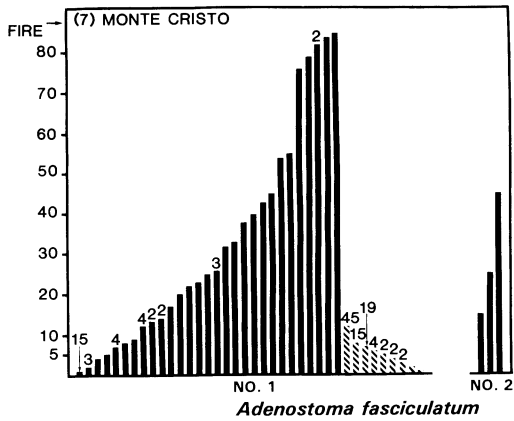


FIG. 1. Continued.

nonsprouting (obligate seeders). Since opportunities for population expansion occur only after fire these taxa may be described as “fire-recruiter” or “gap-dependent” species. Other disturbances may also facilitate establishment, as suggested by the presence of uneven-

aged *Ceanothus cuneatus* shrubs (Table 2) and some seedlings (data not shown) at the disturbed Sequoia Site.

2) Other taxa, *Quercus dumosa*, *Quercus wislizenii*, *Rhamnus crocea*, *Prunus ilicifolia*, *Heteromeles arbu-*

TABLE 2. Summary of age structure characteristics of live stems on the dominant shrub species at the 12 California sites; not all subdominant species at a site were included.†

	(Re- generation mode)‡	Percentage of stems initiated in the:			Regression equation statistics§					
		Most recent decade	First decade after fire	<i>N</i>	<i>b</i>	<i>m</i>	<i>SE</i>	<i>r</i>	<i>P</i>	<i>n</i>
1. San Ignacio										
<i>Quercus dumosa</i>	(OR)	38	4	505	0.65	1.4	0.18	0.99	**	32
<i>Ceanothus cuneatus</i>	(OS)	0	100	5	...					
<i>Rhamnus crocea</i>	(OR)	67	2	104	0.90	0.8	0.27	0.98	**	56
<i>Prunus ilicifolia</i>	(OR)	82	0	90	0.63	2.8	0.19	0.93	**	25
2. Chihuahua										
<i>Adenostoma fasciculatum</i>	(FR)	24	4	922	0.94	1.7	0.29	0.94	**	85
<i>Ceanothus greggii</i>	(OS)	0	100	7	...					
<i>Adenostoma sparsifolium</i>	(FR)	28	8	121	0.95	1.0	0.39	0.88	**	12
3. Silverado										
<i>Quercus dumosa</i>	(OR)	20	4	296	0.91	-0.3	0.51	0.90	**	241
<i>Ceanothus crassifolius</i>	(OS)	0	100	8	...					
<i>Heteromeles arbutifolia</i>	(OR)	34	0	172	1.09	0.6	0.33	0.94	**	14
<i>Adenostoma fasciculatum</i>	(FR)	32	0	79	0.95	3.2	0.26	0.95	**	12
<i>Cercocarpus betuloides</i>	(OR)	61	0	105	0.73	2.1	0.33	0.90	**	8
<i>Rhamnus crocea</i>	(OR)	35	1	23	0.90	-1.8	0.28	0.93	**	2
4. Pacific View										
<i>Ceanothus megacarpus</i>	(OS)	0	100	5	...					
<i>Adenostoma fasciculatum</i>	(FR)	17	3	151	0.48	6.8	0.34	0.82	**	43
<i>Cercocarpus betuloides</i>	(OR)	92	<1	1234	0.69	0.5	0.58	0.96	**	162
<i>Rhamnus crocea</i>	(OR)	17	33	12	0.84	0.2	0.28	0.94	**	31
5. Serrano										
<i>Ceanothus spinosus</i>	(FR)	64	10	771	0.51	0.9	0.41	0.98	**	167
<i>Heteromeles arbutifolia</i>	(OR)	70	7	169	0.73	1.2	0.52	0.93	**	263
6. Glendora										
<i>Adenostoma fasciculatum</i>	(FR)	24	13	140	0.74	2.0	0.45	0.89	**	91
<i>Garrya veatchii</i>	(OR)	29	13	69	0.53	1.2	0.29	0.97	**	17
<i>Arctostaphylos glauca</i>	(OS)	0	100	5	...					
<i>Ceanothus crassifolius</i>	(OS)	0	100	5	...					
<i>Prunus ilicifolia</i>	(OR)	65	2	221	0.83	-0.8	0.15	0.99	**	27
7. Monte Cristo										
<i>Arctostaphylos glauca</i>	(OS)	0	100	6	...					
<i>Ceanothus crassifolius</i>	(OS)	0	100	6	...					
<i>Adenostoma fasciculatum</i>	(FR)	21	6	589	0.73	1.00	0.46	0.90	**	241
8. Mineral King										
<i>Arctostaphylos viscida</i>	(OS)	0	100	14	...					
<i>Adenostoma fasciculatum</i>	(FR)	17	4	194	0.92	4.2	0.27	0.92	**	37
9. Sequoia										
<i>Ceanothus cuneatus</i>	(OS)	0	40	5	...					
<i>Cercocarpus betuloides</i>	(OR)	85	4	424	0.87	1.3	0.39	0.95	**	84
10. Mt. Tamalpais										
<i>Quercus wislizenii</i>	(OR)	52	1	155	0.52	4.7	0.43	0.93	**	11
<i>Arctostaphylos glandulosa</i>	(FR)	26	4	121	0.59	6.9	0.18	0.96	**	16
11. Northridge										
<i>Arctostaphylos glandulosa</i>	(FR)	20	14	101	0.60	4.9	0.38	0.86	**	24
<i>Adenostoma fasciculatum</i>	(FR)	1	6	131	1.02	5.8	0.32	0.93	**	18
12. Bartlett Springs										
<i>Arctostaphylos elegans</i>	(OS)	0	100	5	...					
<i>Ceanothus cuneatus</i>	(OS)	0	100	5	...					
<i>Garrya flavescens</i>	(OR)	41	10	174	1.00	1.4	0.35	0.97	**	103
<i>Quercus dumosa</i>	(OR)	73	<1	367	0.61	1.0	0.37	0.91	**	377
<i>Cercocarpus betuloides</i>	(OR)	67	0	172	0.61	1.5	0.37	0.96	**	138

TABLE 3. Correlation of seedling and sapling density with stand characteristics for all sites except the highly disturbed Sequoia Site no. 9 (Spearman's rank correlation, $N = 11$ sites; * = $P < .05$, ** = $P < .01$).

	Correlation coefficient
Latitude	0.10
Longitude	0.01
Elevation	-0.22
Precipitation	-0.08
Slope inclination	0.34
Stand age	0.26
Basal coverage	-0.51
Percentage dead basal coverage	0.17
Percentage bare ground	0.00
Litter depth	0.76**
Litter biomass	0.57*
Percentage rock	0.36
Soil organic matter percentage	0.09
Percentage sand	-0.27
Percentage clay	0.02
Soil pH	0.01

tifolia, and *Cercocarpus betuloides* had substantial seedling and sapling recruitment at one or more sites in this study. These shrubs seldom recruit seedlings immediately after fire (Keeley and Keeley 1988). All, however, are vigorous resprouters, and thus are resilient to fires. A coordinate term for these shrubs would be "fire-persister" species.

Several conditions are necessary for successful seedling establishment by these fire-persister shrubs. These species require a relatively long fire-free period for successful seedling reproduction. Without exception, previous reports of seedlings in unburned chaparral have been from old stands (>60 yr) such as those studied here (e.g., Patric and Hanes 1964, Zedler 1981, 1982, Parker and Kelly 1989, Lloret and Zedler 1991). Younger chaparral communities have been well studied, and seedling establishment by any woody species is rare. Discerning the factors responsible for lack of successful seedling establishment in chaparral <60 yr requires careful analysis.

One hypothesis is that younger shrubs are not reproductive, but this is clearly not the case since resprouting shrubs begin flowering in the second or third postfire year (Keeley and Keeley 1988). Another unlikely hypothesis is that these shrubs require long fire-free intervals in order to disperse to suitable sites. However, in this study seedling and sapling recruitment of

a particular species was largely restricted to communities dominated by that species. Species capable of seedling recruitment were not observed colonizing sites where adults of that taxon were absent.

A more likely hypothesis is that successful seedling establishment depends upon long-term changes in site characteristics. One parameter that could change with stand age is the extent of gap formation, and there is extensive literature that gaps are necessary for successful establishment in many forest ecosystems (Platt and Strong 1989). The reverse is apparently true in chaparral. In this study seedlings and saplings were nearly always restricted to beneath the canopy and, except at the disturbed Sequoia Site, were seldom in gaps (Table 4). In fact, a good description of shrubs that recruit seedlings in unburned chaparral would be "gap-avoiders." Recruitment by these species appears to require a "nurse plant" such as observed for other arid land species (Callaway and D'Antonio 1991). The fact that seedling recruitment increases in older stands of chaparral does not, however, appear to be related to a decrease in extent of gaps.

The significant correlation between seedling and sapling density and both litter depth and litter biomass (Tables 3 and 4) suggests that these features may determine establishment success. Due to slow decomposition, litter accumulates throughout the life of the stand, e.g., Black (1987) reported that on sites in southern California (near the Chihuahua Site of the present study), litter biomass increased up to fivefold between stands <20 yr and stands older than 80 yr. A deep litter layer may increase escape from seed predation or the high water-holding capacity of litter may prevent excessive drying of seeds; fire-persister species have relatively short-lived seeds that are sensitive to drying (Keeley 1991). Also, the decomposition of litter in-

TABLE 4. Seedling and sapling density, irradiance, and litter depth in canopy gaps and beneath the shrub canopy at the San Ignacio Site (means \pm 1 SD). $N = 50$ plots of 2×2 m.

	Canopy gaps	Beneath canopy	P
No. seedlings and saplings/plot	0.0 \pm 0.0	12.6 \pm 9.5	<.001
Irradiance (% of full sun)	95 \pm 7	22 \pm 11	<.001
Litter depth (mm)	1 \pm 5	69 \pm 32	<.001

† For resprouting species, percentage of stems initiated in different decades was estimated from diameter measurements obtained from field sampling ($N =$ number of stems) and regression equation.

‡ Mode of regeneration after fire: OR = obligate resprouter (seedlings are not established after fire); FR = facultative resprouter (resprouts and recruits seedlings); OS = obligate seeder (nonsprouting shrub regenerating after fire strictly from soil-stored seed).

§ Statistics for the equation (Age = [$b \cdot$ Diameter] + m) are: \widehat{SE} = estimate of standard error; r = correlation coefficient; P = significance (* <.05, ** <.01); n = number of stems aged and used to generate regression equation. For obligate seeding shrubs, ages were taken by direct counts of five or more shrubs (most were single stemmed); this was considered sufficient to verify that stems are even aged, dating back to establishment after the last fire; these nonsprouting species do not initiate vegetative sprouts from the root crown, and seedling establishment is nil except in the first season after fire.

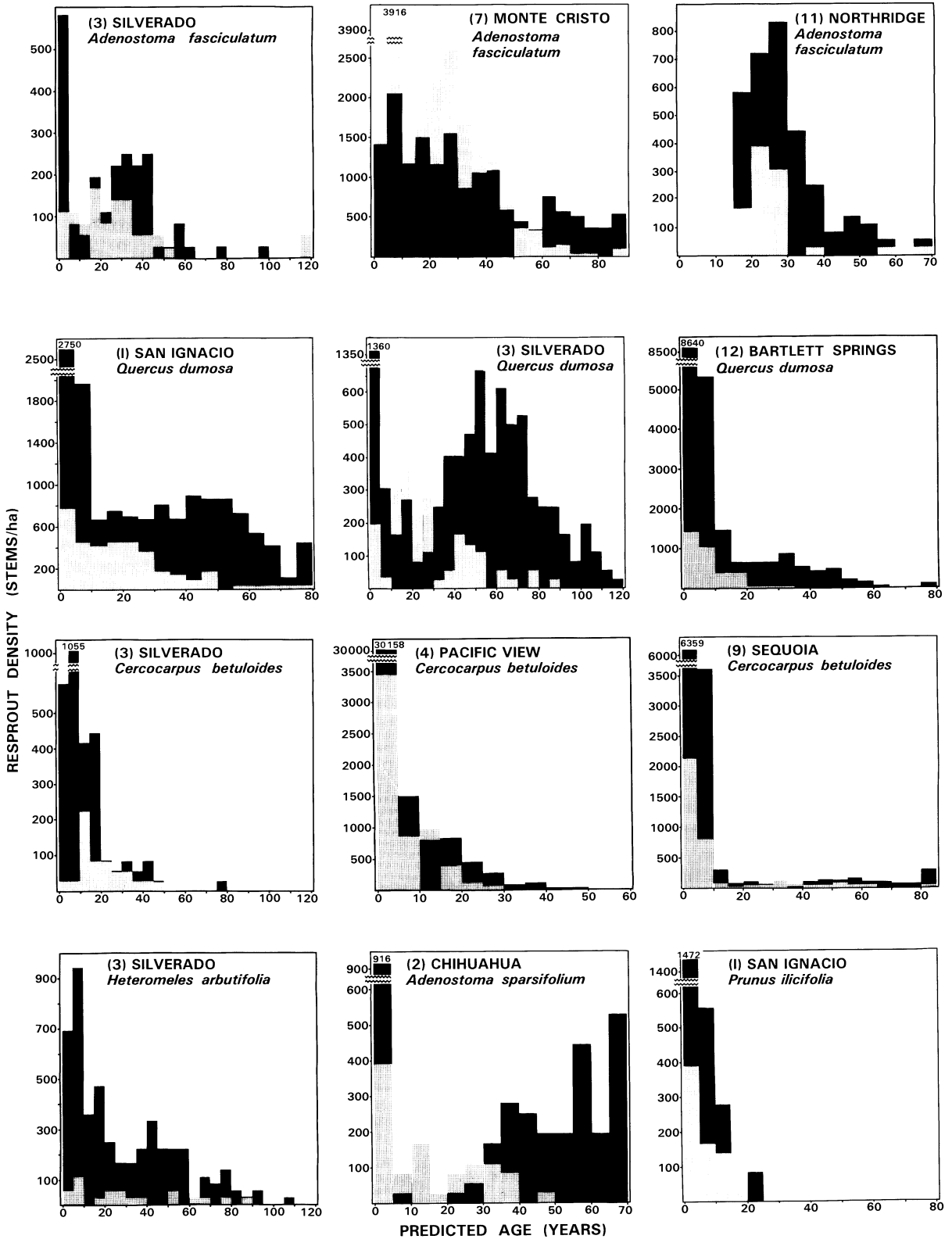
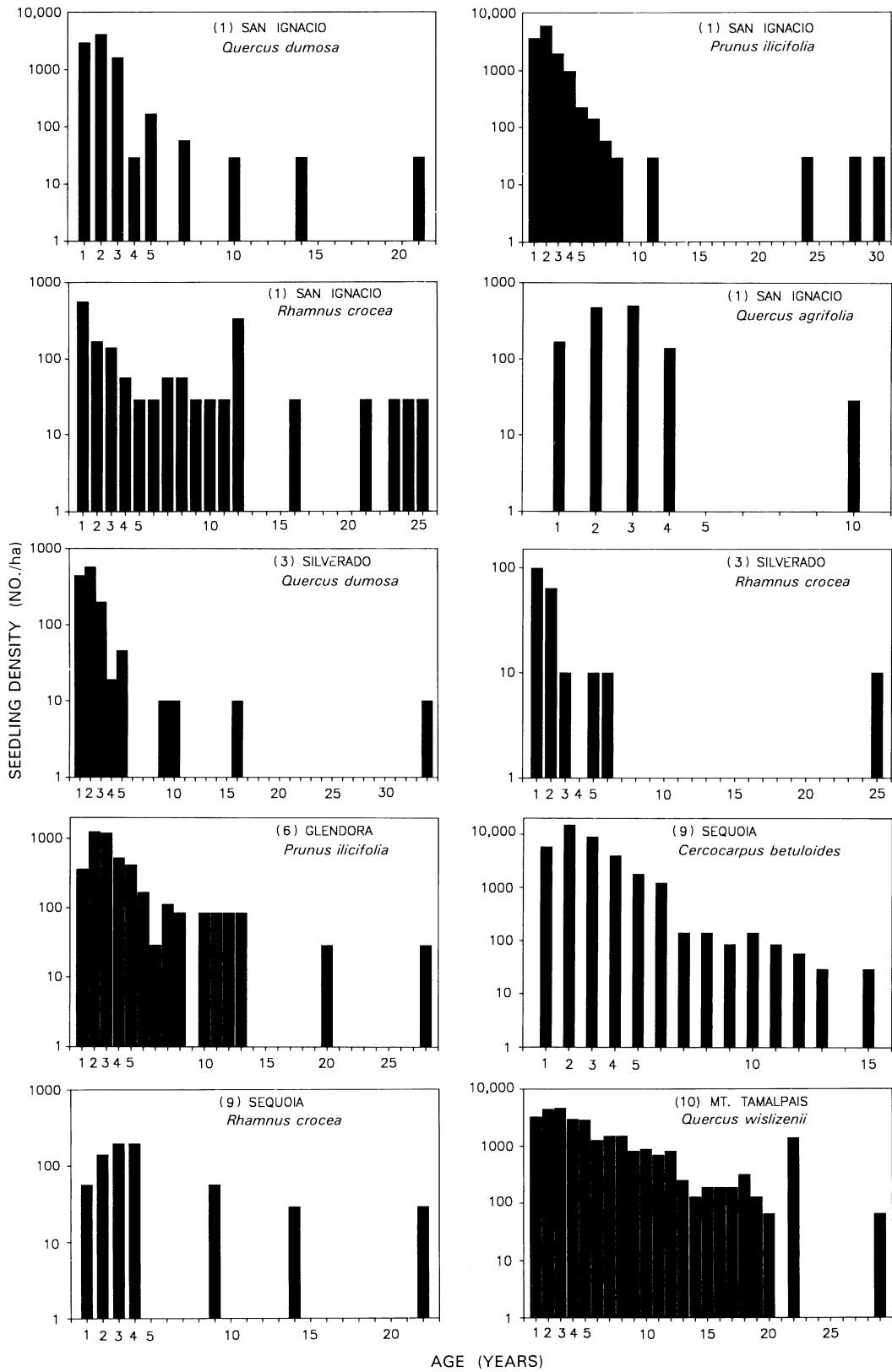


FIG. 2. A sample of the estimated age distribution of the stem population for the dominant shrub species at each of the 12 sites; solid bars indicate live, fine hatching indicates dead. A summary of the age distributions for dominant and subdominant shrubs at each site are presented in Table 5.



AGE (YEARS)

FIG. 3. Age distribution of seedlings and saplings for species with the highest seedling populations at each of the 12 sites. Ages were determined from ring counts on all seedlings and saplings encountered in the sample quadrats and density is plotted as log (no. + 1) per hectare.

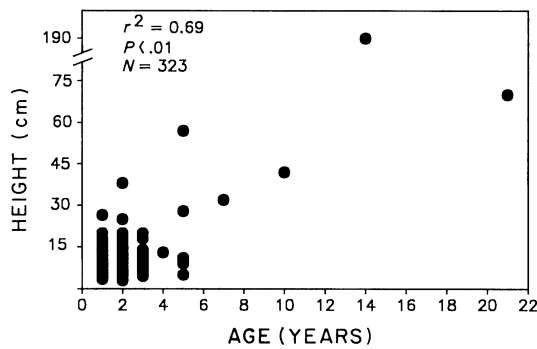


FIG. 4. Height distribution of *Quercus dumosa* seedlings and saplings of different ages at the San Ignacio Site.

increases the organic matter and water-holding capacity of the soil. These are factors that could be critical for successful seedling establishment, particularly in these fire-persister taxa, which are incapable of withstanding xylem water potentials as low as those observed for fire-recruiter species (Poole et al. 1981, Thomas and Davis 1989). Also reducing drought stress on seedlings would be the greatly reduced solar radiation load under the shrub canopy (Table 4). Williams et al. (*in press*) have found that chaparral oak seedlings of *Quercus durata* die within 3 yr on grassland sites, unless artificially shaded.

The only exception to these conclusions may be *Cercocarpus betuloides*, which had substantial seedling and sapling recruitment at the very open, disturbed Sequoia Site. It appears that the conditions for seedling recruitment may be different for this species than for taxa such as *Quercus*, *Prunus*, and *Rhamnus*.

The potential for seedling survival and eventual recruitment into the mature population is suggested by the age structures observed for seedlings and saplings (Fig. 3). Interpretation of these age structures requires consideration of rates of establishment and age-specific mortality. A population with constant rates of recruitment and mortality will, in the absence of disturbance, have a "stable age distribution" in which the youngest cohort is the largest and, since there is attrition with

age, older cohorts will be progressively smaller. Deviations from this distribution pattern are attributable to factors such as disturbance, herbivory, etc.

None of the seedling and sapling age structures presented here have such a distribution, and most have gaps in certain age classes (Fig. 3). Annual variations in recruitment and mortality undoubtedly are, at least partly, responsible. *Quercus* spp. are notorious for having mast years of acorn production followed by years of little or no fruiting, and this pattern is true for other chaparral taxa, such as *Rhamnus* spp. and *Prunus* spp., but not for *Heteromeles arbutifolia* (Keeley and Keeley 1988). Mast fruiting commonly occurs in years of above normal rainfall (J. E. Keeley, *personal observation*), and this may be required since fruit maturation in these taxa occurs during the summer and fall drought. Mortality rates of 1st-yr seedlings may also vary from year to year. Zedler (1981) reports that seedling survival for most of these species is dependent upon years of high rainfall. Herbivory is another factor known to have a marked impact on oak seedlings in chaparral (Williams et al., *in press*), although it is unknown if there is much annual variation in its intensity.

In summary, irregularities in annual seed production and mortality are insufficient to account for gaps in the seedling and sapling age structures (Fig. 3). Although there is much attrition with age, most populations have some saplings that survive beyond the first decade and potentially will be recruited into the canopy-level shrub population. The few, rather tall spindly saplings that did approach the height of the canopy often were associated with small gaps in the canopy. Thus, while seedling and sapling recruitment may avoid gaps, the eventual recruitment into the shrub population may require later development of a gap. It appears as though these shrubs maintain substantial "seedling banks" (P. H. Zedler, *personal communication*, 1986), which on occasion may be recruited into the shrub canopy. Many of these seedlings, particularly *Quercus wislizenii* and *Prunus ilicifolia* had well-developed basal burls, suggesting the potential for surviving wildfires. If this seedling bank survived fire, the ecological release they would experience in the postfire environment would allow for

TABLE 5. Comparison of recruitment patterns in old stands of chaparral for species of different postfire regeneration modes; obligate resprouters do not establish seedlings after fire whereas facultative resprouters and obligate seeders do establish seedlings immediately after fire. Means within a row with the same superscript letter are not significantly different at $P > .05$ (one-way ANOVA followed by Duncan's multiple-comparison test).

	Obligate resprouters		Facultative resprouters		Obligate seeders	
	$\bar{X} \pm 1$ SD	N	$\bar{X} \pm 1$ SD	N	$\bar{X} \pm 1$ SD	N
Seedling and sapling density (no./ha)	4247 ^b \pm 9352	23	7 ^a \pm 29	19	2 ^a \pm 8	12
Percentage of stems recruited in the first decade after fire	4 ^a \pm 8	15	9 ^a \pm 4	7	95 ^b \pm 17	12
Percentage of stems recruited in the most recent decade	57 ^a \pm 24	15	33 ^b \pm 15	7	0 ^c \pm 0	12

rapid regrowth and successful establishment as mature shrubs. Thus, while long fire-free periods may be necessary for seedling establishment, fire may ultimately play an important role in successful recruitment into the population.

Not surprisingly, fire-recruiter and fire-persister species have marked differences in their reproductive biology (Keeley 1991), which play a prominent role in the demographic patterns observed here.

Fire-recruiter species disperse dormant seeds that accumulate in the soil until germination is triggered by intense heat shock or chemicals leached from charred wood. In most of these species some seeds will germinate without fire-related cues, however this transient portion of the seed bank (Parker and Kelly 1989) rarely results in successful seedling establishment under the canopy of mature chaparral, even in stands unburned for more than a century, and for nonsprouting fire-recruiter taxa, the population remains even age.

Fire-persister species, which establish seedlings in ancient stands of chaparral, are linked by the characteristic that their seeds germinate in the absence of cues related to wildfires. In many cases no form of seed dormancy is present at dispersal and the seeds germinate following winter rain; consequently these species do not accumulate a persistent seed bank. In contrast to fire-recruiter species, these shrubs have propagules specialized for wide dispersal (acorns, berries, plumose achenes), and most mature in fall and winter, just prior to the rainy season. These shrubs have seeds with a significantly greater mass (Keeley 1991), and this may have been selected to provide an advantage to seedlings establishing under the closed canopy.

CONCLUSIONS

Chaparral unburned for as much as a century or more shows little evidence of dying out or of successional replacement by other vegetation types. Resprouting shrubs rejuvenate their canopies by frequent initiation of new sprouts. Seedling populations may be abundant on many long-unburned sites, but they do not reflect colonization by new species. Seedlings of oak woodland trees were present at several sites, but the age structure suggests centuries would pass before the chaparral would be replaced. In the long absence of fire, mesic closed communities of chaparral are dominated by fire-persister shrubs (*Quercus*, *Rhamnus*, *Prunus*, *Heteromeles*) at the expense of fire-recruiter shrubs (*Adenostoma*, *Arctostaphylos*, *Ceanothus*), although on arid open sites fire-persisters fare poorly and fire-recruiters persist. Opportunities for population expansion increase immediately after fire for fire-recruiter species, but for fire-persister species, opportunities for population expansion arise only in the long absence of fire. These conclusions suggest that equilibrium in species composition of California chaparral may be enhanced by variable burning regimes.

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LITERATURE CITED

- Black, C. H. 1987. Biomass, nitrogen and phosphorus accumulation over a southern California fire cycle chronosequence. Pages 445–458 in J. D. Tenhunen, F. M. Catarino, O. L. Lange, and W. C. Oechel, editors. Plant response to stress. Functional analysis in mediterranean ecosystems. Springer-Verlag, New York, New York, USA.
- Callaway, R. M., and C. M. D'Antonio. 1991. Shrub facilitation of coast live oak establishment in central California. *Madroño* 38:158–169.
- Cox, G. W. 1985. Laboratory manual of general ecology. Fifth edition. William C. Brown, Dubuque, Iowa, USA.
- Fritts, H. C., and T. W. Swetnam. 1989. Dendroecology: a tool for evaluating variations in past and present forest environments. *Advances in Ecological Research* 19:111–187.
- Gray, J. T., and W. H. Schlesinger. 1981. Nutrient cycling in mediterranean type ecosystems. Pages 259–285 in P. C. Miller, editor. Resource use by chaparral and matorral. Springer-Verlag, New York, New York, USA.
- Hanes, T. L. 1971. Succession after fire in the chaparral of southern California. *Ecological Monographs* 41:27–52.
- . 1977. California chaparral. Pages 417–469 in M. G. Barbour and J. Major, editors. Terrestrial vegetation of California. John Wiley, New York, New York, USA.
- Horton, J. S. 1960. Vegetation types of the San Bernardino Mountains. United States Department of Agriculture Forest Service, Pacific Southwest Forest and Range Experiment Station, Technical Paper Number 44.
- James, S. 1984. Lignotubers and burls—their structure, function and ecological significance in mediterranean ecosystems. *Botanical Review* 50:225–266.
- Keeley, J. E. 1982. Distribution of lightning and man-caused wildfires in California. Pages 431–437 in C. E. Conrad and W. C. Oechel, editors. Proceedings of the symposium on dynamics and management of mediterranean-type ecosystems. United States Department of Agriculture Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California, General Technical Report PSW-58.
- . 1991. Seed germination and life history syndromes in the California chaparral. *Botanical Review* 57:81–116.
- . *In press*. Utility of growth rings in the age determination of chaparral shrubs. *Madroño*.
- Keeley, J. E., and S. C. Keeley. 1988. Chaparral. Pages 165–207 in M. G. Barbour and W. D. Billings, editors. North American terrestrial vegetation. Cambridge University Press, New York, New York, USA.
- Lloret, F., and P. H. Zedler. 1991. Recruitment pattern of *Rhus integrifolia* populations in periods between fire in chaparral. *Journal of Vegetation Science* 2:217–230.
- Miller, P. C., E. Hajek, D. K. Poole, and S. W. Roberts. 1981. Microclimate and energy exchange. Pages 97–121 in P. C. Miller, editor. Resource use by chaparral and matorral. Springer-Verlag, New York, New York, USA.
- Mooney, H. A. 1977. Frost sensitivity and resprouting behavior of analogous shrubs of California and Chile. *Madroño* 24:74–78.
- NOAA. 1968–1984. Climatological data annual summary—California. Volumes 72–88 (Number 13). National Oceanic and Atmospheric Administration, Environmental Data and Information Service, National Climatic Center, Asheville, North Carolina, USA.
- Parker, V. T., and V. R. Kelly. 1989. Seed banks in Cali-

- fornia chaparral and other mediterranean climate shrublands. Pages 231–255 in M. A. Leck, V. T. Parker, and R. L. Simpson, editors. *Ecology of soil seed banks*. Academic Press, New York, New York, USA.
- Patric, J. H., and T. L. Hanes. 1964. Chaparral succession in a San Gabriel Mountain area of California. *Ecology* **45**: 353–360.
- Platt, W. J., and D. R. Strong. 1989. Gaps in forest ecology. *Ecology* **70**:535.
- Poole, D. K., S. W. Roberts, and P. C. Miller. 1981. Water utilization. Pages 123–149 in P. C. Miller, editor. *Resource use by chaparral and matorral*. Springer-Verlag, New York, New York, USA.
- Reid, D., and W. Oechel. 1984. Effect of shrubland management on vegetation. Pages 25–41 in *Shrublands in California: literature review and research needed for management*. Water Resources Center, Contribution Number 191, University of California, Davis, California, USA.
- Sampson, A. W. 1944. Plant succession and burned chaparral lands in northern California. University of California Agricultural Experiment Station Bulletin **685**.
- Thomas, D. M., and S. D. Davis. 1989. Recovery patterns of three chaparral shrub species after wildfire. *Oecologia* (Berlin) **80**:309–320.
- Vogl, R. J. 1977. Fire frequency and site degradation. Pages 151–162 in H. A. Mooney and C. E. Conrad, editors. *Proceedings of the symposium on the environmental consequences of fire and fuel management in mediterranean ecosystems*. United States Department of Agriculture Forest Service, Pacific Southwest Forest and Range Experiment Station, General Technical Report **WO-3**.
- Wells, P. V. 1962. Vegetation in relation to geological substratum and fire in the San Luis Obispo quadrangle, California. *Ecological Monographs* **32**:79–103.
- . 1969. The relation between mode of reproduction and extent of speciation in woody genera of the California chaparral. *Evolution* **23**:264–267.
- Whittaker, R. H., and P. L. Marks. 1975. Methods of assessing terrestrial productivity. Pages 55–118 in H. Lieth and R. H. Whittaker, editors. *Primary productivity of the biosphere*. Springer-Verlag, New York, New York, USA.
- Williams, K., S. D. Davis, B. L. Gartner, and S. Karlsson. *In press*. Factors limiting the establishment of a chaparral oak, *Quercus durata* Jeps., in grassland. In R. B. Standiford, editor. *Proceedings of the symposium on oak woodlands and hardwood rangeland management*. United States Department of Agriculture Forest Service, Pacific Southwest Forest and Range Experiment Station, General Technical Report **PSW-126**.
- Zedler, P. H. 1981. Vegetation change in chaparral and desert communities in San Diego county, California. Pages 406–430 in D. C. West, H. H. Shugart, and D. Botkin, editors. *Forest succession, concepts and applications*. Springer-Verlag, New York, New York, USA.
- . 1982. Demography and chaparral management in southern California. Pages 123–127 in C. E. Conrad and W. C. Oechel, editors. *Proceedings of the symposium on dynamics and management of mediterranean-type ecosystems*. United States Department of Agriculture Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California, General Technical Report **PSW-58**.