Postfire Recovery of California Coastal Sage Scrub

Jon E. Keeley, Sterling C. Keeley

American Midland Naturalist, Volume 111, Issue 1 (Jan., 1984), 105-117.

Postfire Recovery of California Coastal Sage Scrub

JON E. KEELEY

Department of Biology, Occidental College, Los Angeles, California 90041

and

STERLING C. KEELEY

Department of Biology, Whittier College, Whittier, California 90608

ABSTRACT: Postfire regeneration of the shrub and herb vegetation on eight coastal slopes of California coastal sage scrub was studied in the first two growing seasons after fire. All shrub species resprouted with the exception of the suffrutescent *Lotus scoparius*, though it is not known if this species was alive prior to the fire. It was estimated that 70% of the prefire shrub populations resprouted and these sprouts covered one third of the ground surface by the end of the second season. In contrast to chaparral, seedling establishment from soil-stored seed was low ($\sim 10^2$-10^3/ha) in the 1st postfire year. Resprouts of most major species (*Artemisia californica, Encelia californica, Haplopappus squarrosus, Eriogonum cinereum*) flowered and set seed in the 1st year. Seedling densities were $\sim 10^4$-10^6/ha in the 2nd year. Herbs dominated the first postfire season vegetation in number of species, cover and biomass. The magnitude of the postfire herb flora was comparable to that in chaparral after fire and included many of the same species. On several slopes, "pyrophyte endemic" annuals (*Lupinus succulentus, Lotus salsuginosus, Phacelia parryi*) dominated the first season and were rare or absent in the 2nd year. One major distinction between these coastal sage sites and chaparral was that resprouting perennial herbs dominated some slopes in the first postfire season and most slopes in the second season in coastal sage. Seedling recruitment of perennial herbs was rare; 26 of the 28 species were present only as resprouts. Total herb cover was markedly lower in the 2nd year despite the fact that it was a wetter year. Between the 1st and 2nd years, shrub cover ~doubled, largely from resprouts, annual herb cover declined markedly and perennial herb cover remained relatively constant. The perennial bunchgrass *Stipa lepida* was an important component of the herb flora on all slopes and was the only species (herb or shrub) to exceed 1/m^2 on all eight slopes.

INTRODUCTION

Ecosystems in mediterranean climate regions of the world are commonly dominated by two vegetation types: an evergreen schlerophyll shrubland and a drought deciduous or semideciduous scrub (Westman, 1981a). In southern California the evergreen chaparral is dominant and the semideciduous coastal sage scrub is generally restricted to more xeric sites arising from the orographic effect on precipitation at lower elevation or shallow soils at higher elevation (Miller and Hajek, 1981). These two vegetations are distinct structurally and functionally (Mooney, 1977). Coastal sage scrub is smaller statured, more open than chaparral and is dominated by subligneous shrubs in the Asteraceae, Lamiaceae and Polygonaceae families which are not well-represented in mature chaparral. The more open nature of coastal sage results in a greater herb component than is commonly associated with chaparral (Westman, 1979).

Smaller stature, faster growth rate and lighter wind-dispersed seeds make coastal sage species more invasive than chaparral species (Wells, 1962), and under repeated or severe disturbance coastal sage species are capable of dominating chaparral sites. If disturbance is too frequent, coastal sage sites are often replaced by annual grassland species, though with decreased disturbance coastal sage species do return (Westman, 1976). Due to a long history of disturbance in southern California, coastal sage scrub often forms a complex and dynamic mosaic with grasslands (Wells, 1962; Haines,

1966; Oberbauer, 1978). The present distribution of coastal sage scrub has been considered anthropogenic by Vogl (1976), Axelrod (1978) and Heusser (1978), though extensive human disturbance has likely caused replacement of scrub by annual grassland in many areas (Keeley, 1981). Nonetheless, over large parts of its range coastal sage scrub is a stable self-reproducing vegetation (Westman, 1981a, 1981b; Bradbury, 1978; Kirkpatrick and Hutchinson, 1980).

Wildfires are a major influence on the structure and function of most mediterranean-type ecosystems, particularly in California (Mooney and Conrad, 1977). Throughout much of California, humans account for most of the burned acreage though the potential for lightning-caused fires is also high (Keeley, 1982). Postfire regeneration of chaparral has been well-studied and a number of observations suggest that fire has been an important evolutionary force. In contrast, much less is known about the postfire regeneration of coastal sage scrub. Coastal sage shrubs resprout after fire though the extent of such sprouting varies among sites (Westman *et al.*, 1981). Unlike chaparral, seedling recruitment occurs in the absence of fire (Zedler, 1982), resprouts arise continuously throughout the lifespan of a shrub (Malanson and O'Leary, 1982) and branches are capable of "layering" and initiating adventitious roots (Little, 1981). Thus, a stand of coastal sage scrub is typically not even aged. Herb diversity and cover are generally much higher in mature coastal sage scrub than in mature chaparral, but as in chaparral, herbs dominate the 1st postfire year flora in coastal sage scrub (Westman, 1981a).

The purpose of the present study was to examine in detail postfire regeneration of both the shrub and herb components of coastal sage scrub. Two sites were selected on different substrates to estimate site-to-site variability, and the four major slope faces at each site were sampled to estimate the effect of exposure. For both shrubs and herbs attention was given to the mode of regeneration, *i.e.*, resprout or seedling. This study was carried out for two seasons after fire.

METHODS

Study sites. — Two study sites were selected in the Santa Monica Mtns., Los Angeles Co., Calif. These mountains are part of the E-W transverse ranges of California and border the Pacific Ocean along much of their southern flank. Coastal sage vegetation dominates most slopes below 200 m on the coastal side and below 300 m on the interior side of the range. The climate is mediterranean with the 300-400 mm precipitation mainly falling between December and April; temperatures exceed 35C in the summer but seldon drop below 10 C in the winter.

Both sites were located on the coastal side of the mountains and the four major slope faces N, E, S, W ($\pm 10°$) were sampled at each site. One was near the mouth of Ramirez Canyon ~1.5 km N of Hwy. 1 and adjacent to Kanan-Dume Road (34°03′, 118°48′) at ~100 m elevation. This site is located on the Modelo Formation composed of sandstone and cherty shale (Guynes, 1959). Soil *p*H (in 1:1 H_2O:soil) of the N- and E-facing slopes was acidic (N = *p*H 6.1, E = *p*H 5.9), but the S- and W-facing slopes were closer to neutral (S = *p*H 7.4, W = *p*H 7.1). The other site was near the mouth of Encinal Canyon ~3 km N of Hwy. 1 and adjacent to Encinal Canyon Road (34°03′, 118°53′) at ~200 m and is underlain by the Lower Topanga Formation composed of black shales (Boss, 1960). Soil *p*H ranged from 6.5 on the N-facing slope to 7.0 on the E- and W-facing slopes. The inclination of all eight slope exposures was between 30-45°.

Both sites burned in the Agoura-Kanan fire on 23 October 1978. Prior to the fire the Encinal Canyon site had been free from fire for 22 years and the Kanan-Dume site for 11 years (Los Angeles Co. Fire Department, unpubl. fire maps). The Encinal Canyon site was seeded with annual ryegrass (*Lolium perenne* ssp. *multiflorum*, names according to Munz, 1974). It is not known if the Kanan-Dume site was seeded; however, *Lolium* was not found at that site.

Both seasons after the fire were wettir than normal. Precipitation totals for Oxnard (~15 km NW) and Canoga Park (~15 km NE) were 516 mm and 623 mm for July 1978-June 1979 and 623 mm and 715 mm for 1979-1980 (Climatological Data, National Oceanic and Atmospheric Administration); average rainfall for Canoga Park is 356 mm (Harrison *et al.*, 1971).

SAMPLING

Shrub and herb regrowth was sampled early in the first growing season (February 1979, 4 months after fire), and in May 1979 and 1980 (the end of the first and second growing seasons). Shrub resprouts were sampled on each slope exposure by recording height and approximate areal diameter for each shrub in 10 randomly placed 2 x 2 m quadrats. Plot number and size for shrub seedlings and herbs varied with the density. Shrub seedlings were sampled in 10 2 x 2 m plots in February 1979, 10 2 x 0.5 m plots in May 1979 and five 2 x 0.5 m plots in May 1980. Herbs were sampled in 2 x 0.5 m plots; 10 in February 1979 and five in May 1979 and 1980. Areal coverage was calculated on the assumption each plant approximated a circle.

Shrub individuals were classed as resprouts or seedlings by partially excavating shoots. Resprouts were recognized by roots (underground stems) that lacked branches, remained approximately the same diameter with depth, and were connected to woody underground parts. Some species initiated sprouts from shallow lateral roots as much as 0.5 m from the charred stems. Seedlings were easily distinguished by the presence of cotyledons (early in the season) and smaller diameter roots with secondary and tertiary branches all of which narrowed with depth. Perennial herbs were similarly examined; however, for the few herb species establishing both by resprouts and seedlings these two modes were not recorded separately in the sampling.

At the end of the first growing season total aboveground biomass was estimated on each slope in five 2 x 1 m plots for shrubs and in five 1 x 0.5 m plots for herbs. All aboveground material in these plots was clipped, separated by species, oven-dried to constant weight and weighed.

TABLE 1.—Density and cover of resprouts and seedlings of shrubs at the beginning of the first postfire growing season and at the end of the first and second growing seasons, and density of shrubs that failed to resprout on the major slope exposures at the Kanan-Dume site

		Resprouts		Nonsprouts[1]	Seedlings	
		Density (#/ha)	Cover (m^2/ha)	density (#/ha)	Density (#/ha)	Cover (m^2/ha)
North	Feb. 1979	11,750	20	9250	750[a]	<1
	May 1979	19,500[a2]	1770	--	7,000[a]	10
	May 1980	25,250[a]	2980	--	4.6×10^6	370
East	Feb. 1979	16,250[a]	175	7250	0	0
	May 1979	15,250[a]	1495[a]	--	0	0
	May 1980	10,500	2160[a]	--	66,000	50
South	Feb. 1979	19,750[a]	455	5000	0	0
	May 1979	22,250[a]	3565	--	0	0
	May 1980	16,500[a]	4920	--	2.8×10^6	1160
West	Feb. 1979	17,250[a]	445	8000	250[a]	<1
	May 1979	20,500[a]	2340	--	8,000[a]	20
	May 1980	21,000[a]	6535	--	0.9×10^6	600

[1] Shrub remains which failed to resprout. This density coupled with the resprout density approximates the prefire shrub density

[2] Dates (within a slope) with the same superscript are not significantly different ($P > 0.05$)

Statistical analysis was either with one-way ANOVA or the two-tailed t-test and correlations were performed with the Spearman's rank test.

RESULTS

Shrub regeneration by resprouts. — By February of the first growing season shrub species at both sites had resprouted. At the Kanan-Dume site (Table 1) resprout density increased significantly ($P<0.05$, $N = 10$) from February to May of the 1st year only on the N-facing slope. On the other slopes at this site and Encinal Canyon there was no significant ($P>0.05$) change in resprout density from February 1979 to May 1980 (Tables 1 and 2).

Resprout cover in February 1979 was significantly ($P<0.01$) less on N-facing exposures than on other slope faces. South-facing slopes had the highest cover at this time though it only amounted to 5% of the ground surface covered. Areal cover of resprouts increased significantly ($P<0.01$) between February 1979 to May 1979 on all slope exposures at both sites. Thus, at the end of the first growing season areal cover due to shrub resprouts ranged from 2% ground surface cover on one N-facing slope to 35% on one S-facing slope. Between the end of the first growing season (May 1979) and end of the second season (May 1980) resprout cover increased again. On the E-facing slope at Kanan-Dume this increase was not significant ($P>0.05$) but it was ($P<0.01$) on all other slopes. At the end of the second season shrub resprouts covered approximately one third of the ground surface on most slopes though the range was 15-65% ground surface covered.

In February the average shrub resprout on N-facing slopes at both sites was significantly ($P<0.05$) shorter and had significantly less cover than shrubs on E-facing slopes, which in turn were significantly lower than shrubs on S-facing and W-facing slopes (data not shown). Between February and May of the first growing season there was a highly significant ($P<0.01$) increase in height and average cover at both sites (Table 3). At the end of this first growing season (May 1979) there was no significant difference among slopes in either height or cover of individual shrubs. Between the end of the first and second growing seasons there was no significant change in height but there was a highly significant increase in average cover. Throughout the study, height tended to be more similar when averaged across species than areal cover. The relatively high variance for cover (Table 3) reflects in part the fact that resprout size varied wide-

TABLE 2. — Density and cover of resprouts and seedlings of shrubs at the beginning of the first postfire growing season and at the end of the first and second growing seasons, and density of shrubs that failed to resprout on the major slope exposures at the Encinal Canyon site

		Resprouts		Nonsprouts[1]	Seedlings	
		Density (#/ha)	Cover (m^2/ha)	density (#/ha)	Density (#/ha)	Cover (m^2/ha)
North	Feb. 1979	9000[a1]	10	5500	0	0
	May 1979	3500[a]	230	--	0	0
	May 1980	6000[a]	1540	--	10,000	45
East	Feb. 1979	19,250[a]	345	7250	1250[a]	<1
	May 1979	11,500[a]	1480	--	2000[a]	10
	May 1980	31,000	3500	--	$1.4x10^5$	1740
South	Feb. 1979	23,250[a]	520	3750	750[a]	<1
	May 1979	20,750[a]	1495	--	0[a]	0
	May 1980	27,250[a]	3965	--	33,000	1078
West	Feb. 1979	15,500[a]	185	3750	0	0
	May 1979	23,250[a]	2500	--	8000	40
	May 1980	18,500[a]	3380	--	$5.5x10^5$	226

[1] *See* footnotes in Table 1

ly with the species. However, even within the same species on the same slope, average cover typically had a coefficient of variation of 75-100%, reflecting a large variance in size of resprouts.

Thirteen shrub species were recorded on the two slopes and all but the suffrutescent *Lotus scoparius* were vigorous resprouters (Table 4). Resprouts typically arose from the root collar; however, *Encelia californica* and *Haplopappus squarrosus* commonly initiated root sprouts up to 0.5 m from the main shoot. Four to seven shrub species were found on each slope though typically a slope was dominated by 2-3 resprouting shrub species. At the Kanan-Dume site *Salvia leucophylla* comprised one-third of the resprouts (Table 4) and was more or less evenly distributed across all slope exposures. *Encelia californica* was the second most common resprouting shrub at this site but was restricted to just the S- and W-facing slopes. *Haplopappus squarrosus* and *Eriogonum cinereum* were distributed across all slopes whereas *Mimulus longiflorus* was restricted to the N-facing slope. At the Encinal Canyon site *Encelia* was a clear dominant (Table 4) though 97% of the resprouts were on the S- and W-facing slopes. The other dominant resprouts at this site were distributed across all slopes.

The density of shrubs which failed to resprout (Tables 1 and 2) gives an estimate of the fire-caused mortality. Possible errors in this estimate could arise from shrubs which were completely obliterated by the fire or shrubs which resprout later in succession. Observations suggest neither of these were serious sources of error. Shrubs burned to ground level were still evident whereas seedlings and suffrutescent species such as *Lotus scoparius* may have been entirely consumed by fire. This estimate, coupled with the resprout density, provides an estimate of the prefire shrub density. Thus, the proportion of shrubs resprouting was quite high, typically above 70% on most slopes.

Shrub seedling recruitment. — Seedling recruitment was low in the first postfire growing season (Tables 1 and 2). Resprouts were nearly an order of magnitude more common than seedlings and comprised over 99% of the shrub cover. However, many shrub resprouts flowered in the first postfire growing season and this seed fall resulted in abundant seedling establishment in the second growing season. Thus, in May 1980, seedlings accounted for 98% of the shrub density and over 15% of the shrub cover.

Shrub seedling establishment varied by as much as two orders of magnitude among slopes. However, there was no obvious association between seedling density and slope exposure. Overall, there was an order of magnitude greater seedling establishment at the Kanan-Dume site than at the Encinal Canyon site even though resprout density was comparable between the two sites.

Shrub species did not establish equally and there was no obvious relationship between resprout density and seedling recruitment in either the first or second season (Table 4). *Salvia leucophylla* was the dominant resprouting shrub at the Kanan-Dume site where it established a few seedlings in the first season (2.5×10^3/ha). Only an occasional resprout flowered in 1979 and seedling density increased only slightly in 1980. *Salvia mellifera* showed a similar pattern though seedling recruitment was greater in the second season. *Artemisia californica, Encelia californica, Eriogonum cinereum, Haplopappus squarrosus* and *Mimulus longiflorus* did not recruit any seedlings in the first season but

TABLE 3. — Mean height and cover of shrub resprouts at both sites

	Height (cm)				Cover (cm^2/shrub)	
	Kanen-Dume		Encinal Canyon		Kanen-Dume	Encinal Canyon
	N	$\bar{X} \pm$ SD	N	$\bar{X} \pm$ SD	$\bar{X} \pm$ SD	$\bar{X} \pm$ SD
Feb. 1979	263	9 ± 8	267	9 ± 10	160 ± 224	183 ± 602
May 1979	306	52 ± 23^{a1}	239	50 ± 19^{a}	971 ± 863	940 ± 1081
May 1980	288	50 ± 30^{a}	331	52 ± 21^{a}	1702 ± 1536	1253 ± 1280

[1] Dates (within a site) with the same superscript are not significantly different ($P > 0.05$)

their resprouts flowered abundantly and seedling establishment in the second season was high. For an estimate of timing of seedling establishment, seedling density was determined on one slope early and late in the second season. On the W-facing slope at Kanan-Dume, *Encelia californica* had 7.6 x 10^5 seedling/ha in March 1980 compared to 7.8 x 10^5 in May 1980, and *Haplopappus squarrosus* had 2.6 x 10^5 seedlings/ha in March and 1.2 x 10^5 in May. *Lotus scoparius* did not respond like any other species; none resprouted and no seedlings were found in the first season but many ($\sim$5 x 10^3/ha) were found in the second season. *Yucca whipplei* did not establish seedlings in either the first or second growing season.

At the end of the second season, seedlings of most species were still quite small. Seedlings establishing in the 2nd year were typically less than 10 cm tall and had an average areal cover less than 10 cm^2. Seedlings established in the 1st year were 40-50 cm tall with an average cover of 50-150 cm^2 by the end of the 2nd year, though none flowered. *Lotus scoparius* seedlings were substantially larger than other shrub seedlings with an average height of 47 cm and cover of 466 cm^2, suggesting they probably established in the 1st year but either were overlooked by being confused with *Lotus salsuginosus,* or established after the May sampling.

Herb re-establishment. —Herbs dominated the first postfire season flora at both sites (Tables 5 and 6) and comprised $\sim$80% of the total cover at Kanan-Dume and $\sim$90% at Encinal Canyon. There was a highly significant ($P<0.01$, $N=5$) increase in herb cover between February and May of the 1st year on all slopes. This was apparently due to an increase in herb size, as density showed no significant ($P>0.05$) increase on five slopes and only a weakly significant ($P<0.05$) increase on three slopes during this interval. At the end of the 1st year, herb cover was inversely related to shrub cover ($r_s = -0.67$, $P<0.05$, $N=8$, with Spearman's rank test). At this time, herb cover varied among slopes by an order of magnitude but there was no obvious relationship between herb cover and slope exposure.

In the second season, herb cover was substantially less on seven of the eight slopes ($P<0.01$). Herbs comprised 55% of the total cover at Kanan-Dume and 50% at Encinal Canyon.

The herb flora included 22 perennial species and 25 annual species. The perennial species were largely cryptophytes though a few were hemicryptophytes. All but two perennial species were present in the first two seasons *only as resprouts* from underground parts, and all flowered in the 1st year.

At Kanan-Dume two thirds of the herb species were perennial and these species dominated the cover on the N- and E-facing slopes (Table 5). On the N-facing slope, native perennial grasses, *Elymus condensatus* and *Agrostis diegoensis,* dominated the herb cover during the first two growing seasons. The E-facing slope had 26 herb species, and no single species was dominant. The W-facing-slope herb cover was dominated by *Stipa lepida* in February 1979, but by May the nonnative annual *Brassica nigra* and *Bromus rubens* dominated. In the 2nd year, herb cover declined markedly with *Stipa lepida* dominating $\sim$60% of the total. The S-facing slope had the fewest herb species and the highest herb cover (Table 5) in the first season, with *Brassica nigra* dominating 75% of the herb cover. In the 2nd year, herb cover was substantially lower and *Bromus rubens* comprised >90% of the total herb cover.

At the Encinal Canyon site, two thirds of the species were annuals and these mostly native species dominated the extensive herb cover the 1st year (Table 6). In the 2nd year, these native annuals largely disappeared, total herb cover declined and native perennial herbs became dominant. The N-facing slope was dominated in the first season by the native annual, *Lupinus succulentus,* which comprised 90% of the total cover; densely packed and overlapping individuals resulted in >300% ground surface covered. In the 2nd year this species comprised <0.01% of the herb cover and the perennial *Calystegia macrostegia* dominated 87% of the greatly reduced total herb cover. The S-facing slope showed a similar pattern though with different species. The native

TABLE 4.—Dominant shrub species as a percent of total density at each site at the end of the first and second growing seasons

	Resprouts (%)				Seedlings (%)			
	Kanan-Dume		Encinal Canyon		Kanan-Dume		Encinal Canyon	
	May 79	May 80	May 79	May 80	May 79	May 80	May 79	May 80
Artemisia californica	13	19	1	5	0	1	0	30
Encelia californica	24	19	55	34	0	10	0	12
Eriogonum cinereum	8	7	8	7	0	<1	0	37
Haplopappus squarrosus	14	8	10	27	0	34	0	2
Mimulus longiflorus	9	12	-[1]	-	0	54	-	-
Salvia leucophylla	31	35	2	6	67	<< 1	0	0
S. mellifera	-	-	4	11	-	-	100	13
Yucca whipplei[2]	-	-	10	8	-	-	0	0
Misc.[3]	1	<1	10	2	33	0	0	6
Total density (#/ha)	1.9×10^4	1.8×10^4	1.5×10^4	2.1×10^4	3800	2.1×10^6	2500	1.8×10^5

[1] Dash indicates species not present at site

[2] Strictly speaking, *Y. whipplei* did not resprout; the proportion described as resprouts were individuals in which the aboveground portions survived fire

[3] Includes: *Lotus scoparius, Malacothamnus fasciculatus, Rhus laurina, R. integrifolia* and *Ribes malvaceum*

annual *Lotus salsuginosus* dominated >65% of the substantial herb cover the 1st year along with *Lolium perenne* which comprised ~25% of the cover. In the 2nd year *Lotus* was absent, *Lolium* was uncommon, total covered declined an order of magnitude, and the perennial *Stipa lepida* dominated 56% of the herb cover. The E-facing slope, as at the Kanan-Dume site, had one third more species than the other slopes. In the first growing season the native annuals, *Lotus salsuginosus, Phacelia parryi, Lupinus succulentus* and *Eucrypta chrysanthemifolia,* comprised 70% of the substantial herb cover. In the second growing season these species were completely absent and herb cover dropped an order of magnitude. The nonnative annual (biennial?) *Lolium perenne* had a fivefold drop in cover but comprised >60% of the herb cover. At this time *Stipa lepida* comprised >20% of the cover and *Calystegia macrostegia* comprised 10% of the cover. On the W-facing slope native annuals were rare in the first season and herb cover was an order of magnitude lower than on other slopes. *Lolium perenne* dominated the 1st year and *Calystegia macrostegia* dominated in the 2nd year.

First-year biomass.—Herb and shrub biomass produced in the first postfire growing season varied from 200-1000 g oven-dry weight/m^2 (Table 7). Herb biomass greatly exceeded shrub biomass on all but one slope. For many of the shrub resprouts reproductive parts accounted for a sizable proportion of the biomass. This was assessed for *Encelia californica* on one slope exposure and it was found that reproductive parts accounted for 25% (SD = 7%, N = 10) of the total aboveground biomass.

DISCUSSION

Postfire regeneration of coastal scrub differs from that of the closely associated chaparral. As noted previously (Westman *et al.,* 1981), sage scrub seedling establishment is uncommon in the 1st postfire year. Dependent upon the species composition, the magnitude of shrub seedling establishment in the second postfire season may be quite high relative to the first season (Tables 1 and 2). Second-year seedling density varied from 10^4 to 10^6/ha at the two sites in this study (Tables 1 and 2). Malanson and O'Leary (1982) also noted site-to-site variation in seedling density in 2nd-year coastal sage sites, though the highest density they recorded was 10^5/ha. Second-year seedling recruitment in coastal sage scrub was one to two orders of magnitude higher than the 20,000-40,000 seedlings/ha typically observed in southern California postfire chaparral (Horton and Kraebel, 1955; Vogl and Schorr, 1972; Keeley and Zedler, 1978). The second season seedling establishment was derived from vigorous seed production by shrub resprouts in the 1st postfire year, with some species (*e.g., Encelia californica*) allocating as much as a quarter of their aboveground biomass to flower and seed production. This commitment to reproduction is quite significant in light of the fact that the aboveground shrub biomass was only 10% of that observed in mature coastal sage (*e.g.,* Gray and Schlesinger, 1981). *Encelia californica* seeds collected from these sites germinated readily with moisture and moderate temperatures and it is likely that such is the case for other coastal sage shrub species which establish in the 2nd year. Not all shrubs followed this pattern (Table 4). A few, *e.g., Salvia leucophylla* and *S. mellifera,* established some seedlings in the first season. These probably arose from soil-stored seed that survived the fire, as the seedlings established prior to the current year seed dispersal and the nearest unburned site was 5 km away. Flowering by resprouts of these species was erratic in the first season and their seedlings comprised a small portion of the 2nd-year shrub seedling pool.

The rapid regeneration by resprouts in these coastal sage sites is similar to the immediate postfire recovery of chaparral. In this study it was estimated that over three quarters of the shrubs resprouted. However, Westman *et al.* (1981) found that such was not the case for two interior "coastal" sage scrub sites.

Herbs dominated both coastal sage sites in the first season after fire in this study. On most slopes herbs comprised more than three fourths of the total number of species, density, areal cover and biomass. This proportion is similar for the postfire chaparral

TABLE 5.—Density and cover of herbs at the beginning and end of the first postfire growing season and the end of the second season for the major slope faces at the Kanan-Dume site

		Density	Cover				
		#/ha	m^2/ha	% Perennials	% due to species only resprouting[1]	% due to species only establishing from seedlings[1]	% Natives
North	Feb. 1979	$4.7x10^5$	421	100	100	0	100
	May 1979	$8.1x10^5$	9613[a2]	83	83	16	84
	May 1980	$3.7x10^5$	9940[a]	100	97	1	50
East	Feb. 1979	$2.1x10^5$	495	96	95	4	100
	May 1979	$3.8x10^{5a}$	7854	81	54	19	99
	May 1980	$5.5x10^{5a}$	4694	85	65	15	88
South	Feb. 1979	$4.5x10^{5a}$	3532[a]	19	19	81	20
	May 1979	$3.5x10^{5a}$	15,000	7	7	93	11
	May 1980	$12.2x10^5$	2442[a]	1	1	99	2
West	Feb. 1979	$0.8x10^{5a}$	310	96	96	4	96
	May 1979	$0.9x10^{5a}$	7827	16	16	84	26
	May 1980	$8.4x10^5$	2807	62	62	38	72

[1] The difference between 100% and the combination of these two columns indicates the % due to species re-establishing by both resprouts and seedlings

[2] Dates (within a slope) with the same superscript are not significantly different ($P > 0.05$)

TABLE 6.—Density and cover of herbs at the beginning and end of the first postfire growing season and the end of the second season for the major slope faces at the Encinal Canyon site[1]

		Density	Cover				
		#/ha	m^2/ha	% Perennials	% due to species only resprouting[1]	% due to species only establishing from seedlings[1]	% Natives
North	Feb. 1979	$4.8x10^{5a1}$	4469[a]	12	12	88	99
	May 1979	$1.8x10^{5a}$	33,662	0	0	100	100
	May 1980	$1.6x10^{5a}$	7531[a]	91	91	9	96
East	Feb. 1979	$5.2x10^{5a}$	1248[a]	24	24	76	100
	May 1979	$4.4x10^{5a}$	21,542	3	3	97	74
	May 1980	$1.4x10^{5}$	1526[a]	38	38	62	39
South	Feb. 1979	$4.1x10^{5}$	1043	21	21	79	97
	May 1979	$6.4x10^{5}$	26,766	4	4	96	76
	May 1980	$1.6x10^{5}$	2550	82	82	18	82
West	Feb. 1979	$0.4x10^{5a}$	52	92	87	9	100
	May 1979	$0.6x10^{5ab}$	1963	13	13	87	13
	May 1980	$1.7x10^{5b}$	712	78	78	22	82

[1] *See* footnotes in Table 5

vegetation (Keeley *et al.*, 1981). Additionally, most of the species making up this postfire herb flora are also found in the postfire chaparral flora. Westman (1979) has noted that across their entire range coastal sage scrub and chaparral have similar herb floras.

One major distinction between the coastal sage sites studied here and chaparral was the occurrence of resprouting perennial herbs (as opposed to annual herbs) dominating some slopes in the first postfire season (Table 5) and most slopes in the second season in coastal sage. Westman *et al.* (1981) studied a single coastal site the 2nd year after fire and likewise found that perennials dominated the native herb cover and many of these remained the dominant herbs in mature coastal sage scrub (Westman, 1981a). Seedling recruitment by these perennial herbs does not occur to any important degree immediately after fire. Seeds of some of these species, *e.g., Marah, Stipa, Calystegia,* are nonrefractory and are easily killed by high temperature. Since the seeds do not require any special cue, germination may occur at any time, though seedling establishment may in general be an uncommon event.

On some coastal sage slopes (Table 6) the postfire herb flora was composed of typical chaparral annual pyrophyte endemics. At Encinal Canyon *Lupinus succulentus, Lotus salsuginosus* and *Phacelia parryi* dominated some slopes in the first postfire season but were rare or absent in the 2nd year. Seeds of the latter two species are known to require a stimulus such as heat or charred wood for optimum germination (Keeley and Keeley, 1982).

In the 2nd year, herb cover was markedly lower even though this was a wetter year (*cf.*, Keeley *et al.*, 1981). This reduction in herb cover during the second season was likely related to the fact that the shrub resprouts (averaged over all eight slopes) doubled their cover between the first and second seasons. Perennials dominated the herb flora in the second season and *Stipa lepida* was consistently an important species; it was the only species exceeding 1/m^2 on all eight slopes.

Clearly, California coastal sage scrub and chaparral have a number of marked differences in response to fire, seedling recruitment being foremost. In this regard many coastal sage shrubs resemble the dominant bunch grass species of perennial grasslands (Keeley, 1981). These latter species resprout vigorously after fire but apparently recruit very few seedlings in the first season. However, the resprouts flower and an abundant seed pool is present the second season. The herbaceous and subligneous habits may be more compatible with early flowering by resprouts than the woody habit typical of chaparral shrubs. The possibility that fires historically may have been less common along the coast (Keeley, 1977, 1982) could have selected against long-term soil storage and this would likely be reinforced by the relatively open, mature vegetation structure which would promote seedling establishment in the absence of fire.

Acknowledgments.—We thank W. Westman, P. Zedler, N. Christensen for a thorough and critical review of the manuscript.

TABLE 7.—Aboveground herb and shrub biomass at the end of the first growing season (May 1979) on the major slope exposures at both sites

	Kanan-Dume			Encinal Canyon		
	g oven-dry weight/m^2					
	Herbs		Shrubs	Herbs		Shrubs
North	192 ± 57[1]	**	82 ± 19	885 ± 357	**	16 ± 23
East	247 ± 98	ns	218 ± 83	516 ± 187	*	155 ± 185
South	666 ± 322	*	292 ± 143	490 ± 252	**	63 ± 87
West	671 ± 230	**	34 ± 29	220 ± 76	**	35 ± 50

[1] $\bar{X} \pm$ SD, N = 5, ns $P > 0.05$, *$P < 0.05$, **$P < 0.01$

LITERATURE CITED

AXELROD, D. 1978. The origin of coastal sage vegetation, Alta and Baja California. *Am. J. Bot.*, **65**:1117-1131.

BASS, R. O. 1960. Geology of the western part of the Point Dume Quadrangle, Los Angeles County, California. M.A. Thesis, Univ. Calif., Los Angeles. 52 p.

BRADBURY, D. E. 1978. The evolution and persistence of a local sage/chamise community pattern in southern California, *Yearb. Assoc. Pac. Coast Geogr.*, **40**:39-56.

GRAY, J. T. AND W. H. SCHLESINGER. 1981. Biomass, production, and litterfall in the coastal sage scrub of southern California. *Am. J. Bot.*, **68**:24-33.

GUYNES, G. E. 1959. Geology of the Triunfo Pass Area, Los Angeles and Ventura Counties, California. M. A. Thesis, Univ. Calif., Los Angeles. 91 p.

HAINES, B. L. 1966. Invasion of grasslands and their inhibition by *Artemisia californica* Less. M. A. Thesis, Univ. Calif., Santa Barbara. 72 p.

HANES, T. L. 1977. California chaparral, p. 417-470. *In:* M. G. Barbour and J. Major (eds.). Terrestrial vegetation of California. John Wiley and Sons, New York, New York.

HARRISON, A. T., E. SMALL AND H. A. MOONEY. 1971. Drought relationships and distribution of two mediterranean climate California plant communities. *Ecology,* **52**:869-875.

HEUSSER, L. 1978. Pollen in Santa Barbara Basin California; A 12,000-yr record. *Geol. Soc. Am. Bull.,* **89**:673-678.

HORTON, J. S. AND C. J. KRAEBEL. 1955. Development of vegetation after fire in the chamise chaparral of southern California. *Ecology,* **36**:244-262.

KEELEY, J. E. 1977. Fire-dependent reproductive strategies in *Arctostaphylos* and *Ceanothus,* p. 391-396. *In:* H. A. Mooney and C. E. Conrad (eds.). Proceedings of the symposium on the environmental consequences of fire and fuel management in Mediterranean ecosystems. *U.S. For. Serv. Gen. Tech. Rep. WO-3.*

_____. 1981. Reproductive cycles and fire regimes, P. 231-277. *In:* H. A. Mooney, J. M. Bonnicksen, N. L. Christensen, J. E. Lotan and W. A. Reiners (eds.). Proceedings of the conference on fire regimes and ecosystems properties. *U.S. For. Serv. Gen. Tech. Rep. WO-26.*

_____. 1982. Distribution of lightning and man-caused wildfires in California, p. 431-437. *In:* C. E. Conrad and W. C. Oechel (eds.). Proceedings of the symposium on dynamics and management of Mediterranean type ecosystems. *U.S. For. Serv. Gen. Tech. Rep. PSW-58.*

_____. AND P. H. ZEDLER. 1978. Reproduction of chaparral shrubs after fire: a comparison of sprouting and seeding strategies. *Am. Midl. Nat.,* **99**:142-161.

KEELEY, S. C. AND J. E. KEELEY. 1982. The role of allelopathy, heat, and charred wood in the germination of chaparral herbs, p. 128-134. *In:* C. E. Conrad and W. C. Oechel (eds.). Proceedings of the symposium on dynamics and management of Mediterranean type ecosystems. *U.S. For. Serv. Gen. Tech. Rep. PSW-58.*

_____, _____, S. M. HUTCHINSON AND W. A. JOHNSON. 1981. Postfire succession of the herbaceous flora in southern California chaparral. *Ecology,* **62**:1608-1621.

KIRKPATRICK, J. B. AND C. F. HUTCHINSON. 1980. The environmental relationships of California coastal sage scrub and its component communities and species. *J. Biogeogr.,* **7**:23-28.

LITTLE, R. J. 1981. Adventitious rooting in coastal sage scrub dominants. *Madroño,* **28**:96-97.

MALANSON, G. P. AND J. F. O'LEARY. 1982. Post-fire regeneration strategies of California coastal sage shrubs. *Oecologia,* **53**:355-358.

MILLER, P. C. AND E. HAJEK. 1981. Resource availability and environmental characteristics of Mediterranean-type ecosystems, p. 17-41. *In:* P. C. Miller (ed.). Resource use by chaparral and matorral. Springer-Verlag, New York.

MOONEY, H. A. 1977. Southern coastal scrub, p. 471-489. *In:* M. G. Barbour and J. Major (eds.). Terrestrial vegetation of California. John Wiley and Sons, New York.

_____ AND C. E. CONRAD (EDS.). 1977. Proceedings of the symposium on the environmental consequences of fire and fuel management in Mediterranean ecosystems. *U.S. For. Serv. Gen. Tech. Rep. WO-3.* 498 p.

MUNZ, P. A. 1974. A flora of southern California. Univ. California Press, Berkeley. 1086 p.

OBERBAUER, T. A. 1978. Distribution dynamics of San Diego County grasslands. M. S. Thesis, San Diego State Univ., San Diego, Calif. 116 p.

VOGL, R. J. 1976. An introduction to the plant communities of the Santa Ana and San Jacinto Mountains, p. 77-98. *In:* J. Latting (ed.). Plant communities of southern California. *Calif. Native Plant Spec. Publ. 2.*

_____ AND P. K. SCHORR. 1972. Fire and manzanita chaparral in the San Jacinto Mountains, California. *Ecology,* **53**:1179-1188.

WELLS, P. V. 1962. Vegetation in relation to geological substratum and fire in the San Luis Obispo quadrangle, California. *Ecol. Monogr.,* **23**:264-267.

WESTMAN, W. E. 1976. Vegetation conversion for fire control in Los Angeles. *Urb. Ecol.,* **2**:19-137.

_____. 1979. The potential role of coastal sage scrub understories in the recovery of chaparral after fire. *Madroño,* **26**:64-68.

_____. 1981a. Diversity relations and succession in California coastal sage scrub. *Ecology,* **62**:170-184.

_____. 1981b. Factors influencing the distribution of species of Californian coastal sage scrub. *Ibid.,* **62**:439-455.

_____, J. F. O'LEARY AND G. P. MALANSON. 1981. The effects of fire intensity, aspect and substrate on post-fire growth of Californian coastal sage scrub, p. 151-179. *In:* N. S. Margaris and H. A. Mooney (eds.). Components of productivity of Mediterranean regions—basic and applied aspects. W. Junk, The Hague, Netherlands.

ZEDLER, P. H. 1982. Plant demography and chaparral management in southern California, p. 123-127. *In:* C. E. Conrad and W. C. Oechel (eds.). Proceedings of the symposium on dynamics and management of Mediterranean type ecosystems. *U.S. For. Serv. Gen. Tech. Rep. PSW-58.*

SUBMITTED 30 AUGUST 1982 ACCEPTED 3 JANUARY 1983