Postfire Succession of the Herbaceous Flora in Southern California Chaparral

Sterling C. Keeley, Jon E. Keeley, Steve M. Hutchinson, Albert W. Johnson

Ecology, Volume 62, Issue 6 (Dec., 1981), 1608-1621.

Ecology, 62(6), 1981, pp. 1608–1621

POSTFIRE SUCCESSION OF THE HERBACEOUS FLORA IN SOUTHERN CALIFORNIA CHAPARRAL[1]

STERLING C. KEELEY,[2] JON E. KEELEY,[3] STEVE M. HUTCHINSON,[4] AND ALBERT W. JOHNSON
Department of Biology, San Diego State University, San Diego, California 92182 USA

Abstract. Postfire succession of the temporary herbaceous and suffrutescent cover was studied after chaparral fires in San Diego County, California, USA. Four categories of species make up the temporary cover. (1) "Generalized herbaceous perennials" are present before and after fire. Populations of these herbs are sparse under the shrub canopy. They resprout after fire from bulbs or other underground parts and postfire populations are sparse. (2) "Generalized annuals" are present in openings before fire but produce their peak population size in the first few years after fire. (3) Specialized "fire-annuals" are more or less restricted to the 1st postfire yr. (4) Specialized "fire-perennials" (subshrubs) are uncommon before fire, establish from seed in the 1st postfire yr and reach maximum cover in the 3rd and 4th yr.

Community-level changes in cover and diversity are interpreted in light of differences in population dynamics of the four groups. Species richness was highest in the 1st yr after fire because this was the only time all four groups were present together. Throughout succession herbaceous species richness was positively related to herb cover, negatively related to elevation and unrelated to slope aspect. The number of annual species fluctuated greatly through succession at all sites, but the number of herbaceous perennials did not. Herb cover fluctuated markedly from year to year and was positively related to amount of annual precipitation and negatively related to subshrub or "fire-perennial" cover.

Artificial seeding with annual rye grass *Lolium multiflorum* had no apparent effect on total herb cover since sites with poor *Lolium* establishment had as high or higher herb cover as sites with high *Lolium* establishment. *Lolium* success was at the expense of the native cover and this negative effect was greatest on the "fire annuals."

Key words: California; chaparral; fire; herbs; succession.

PROLOGUE

"Since only the kiss of the flame is needed to rouse dormant seeds from decades-long sleep, is it not strange that botanists do not turn arsonists on occasion that some floral phoenix might arise from the ashes?" (John Thomas Howell, Sierra Club Bulletin **31**(1946):18–23).

INTRODUCTION

In recent years fire has come to be recognized as an important component of ecosystem structure and function for a wide variety of natural systems (Mooney et al. 1980). In the California chaparral, fire has long been considered a dominant ecological and evolutionary influence (Hanes 1977). Several factors contribute to this. The Mediterranean climate results in a protracted summer drought during which vegetation flammability is high, and there is a ready source of ignition by man and lightning (Keeley 1977*b*). Equally important are the moderate winters with sufficient precipitation to produce a dense scrub capable of carrying fires over extensive distances.

In the absence of fire, particularly in southern California, chaparral is generally not replaced by other vegetation types, nor does it regenerate (Cooper 1922, Hanes 1971, Keeley 1977*a*). The mature canopy is even-aged and beneath the canopy there are few shrub seedlings and little herbaceous growth (Patric and Hanes 1964, McPherson and Muller 1969, Keeley and Johnson 1977). After fire, shrub seeds germinate and many shrub species resprout from basal burls (lignotubers) or other below-ground parts (Horton and Kraebel 1955, Hanes and Jones 1967, Vogl and Schorr 1972, Keeley 1977*b*, Keeley and Zedler 1978). Postfire recovery of shrub species has been widely studied and is reasonably well understood. Often by the end of the first decade after fire ground surface covered by shrubs approaches prefire levels (Hanes 1977). As the canopy closes in at 10–15 yr there may be extensive shrub thinning (Schlesinger and Gill 1978).

In the immediate postfire years there is also an abundant shortlived herbaceous and suffrutescent vegetation (Sampson 1944, Horton and Kraebel 1955, Sweeney 1956, Stocking 1966, Christensen and Muller 1975*a*). This component of chaparral succession is not as clearly understood as the shrub recovery. This can be attributed in part to the differing location and methods used in each study, as well as to the convention of grouping herbs and suffrutescent subshrubs under the heading "temporary cover" (Sampson 1944, Hor-

[1] Manuscript received 12 February 1980; revised and accepted 21 October 1980.
[2] Present address: Section of Botany, Museum of Natural History, 900 Exposition Boulevard, Los Angeles, California 90007, and Department of Biology, Whittier College, Whittier, California 90608 USA.
[3] Present address: Department of Biology, Occidental College, Los Angeles, California 90041 USA.
[4] Present address: San Diego Natural History Museum, San Diego, California 92112 USA.

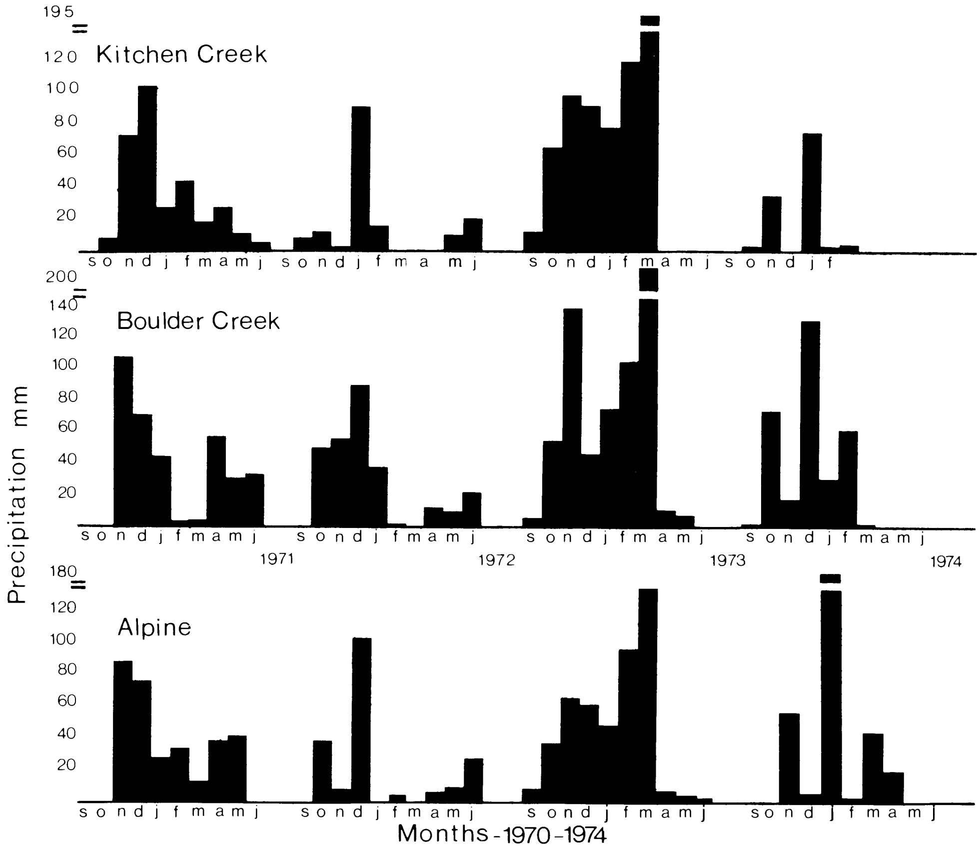

FIG. 1. Precipitation September through June 1971–1974 for weather stations near Intensive Study Sites. Data for Kitchen Creek and Boulder Creek from Dr. Philip Miller, San Diego State University at IBP research sites. Data for Alpine obtained from county records held at Lindbergh Field, San Diego and United States Weather Bureau Climatological Data by Sections.

ton and Kraebel 1955, Sweeney 1956) and making comparisons between "temporary" vs. "permanent" species. Successional events involving the herbaceous flora per se still remain relatively unexplored. For example, what is the effect of slope and elevation on herb cover and diversity? Does herb composition change with time after succession? What is the effect of precipitation on herb growth? Is there a predictable pattern of herbaceous succession and if so what determines the successional sequence? How are changes in shrub cover and subshrub cover related to herb cover?

An excellent opportunity to investigate these questions was provided by the Laguna and Boulder fires of 1970. During late September and early October over 70 000 ha of chaparral burned in San Diego County. This large even-aged burned area allowed us to compare sites as three elevations and over the four major slope aspects (N, S, E, W) at each elevation. Detailed sampling at these sites was continued over a period of several years to observe changes in species composition with time, and to assess the effects of slope and elevation. One of the limitations of this intensive sampling approach, however, was the inability to generalize over a wider area or to burns of greater age. Therefore, burned sites from 1 to 16 yr old were chosen in other areas of the county and sampled in a single year. It was believed that these combined data would provide better understanding of postfire herbaceous succession.

METHODS

Extensive Study Sites (ESS) were chosen at selected locations throughout San Diego County and just north of the boundary in Riverside County (Appendix I). The sites were in burns of different ages from 1 to 16 yr old and were sampled during the spring of 1974. Criteria for selection were (1) known age (fire dispatcher's records, United States Forest Service), (2) area >45 ha, and (3) availability of duplicate sample stands. Detailed information on site characteristics for all sites is given in Appendix I and in Hutchinson (1975).

Intensive Study Sites (ISS) were chosen within San Diego County in areas of sandy loam soils and average precipitation ≈40–60 cm/yr (Close et al. 1970). These sites were located at three elevations along a transect running roughly parallel to Interstate Highway 8; 560

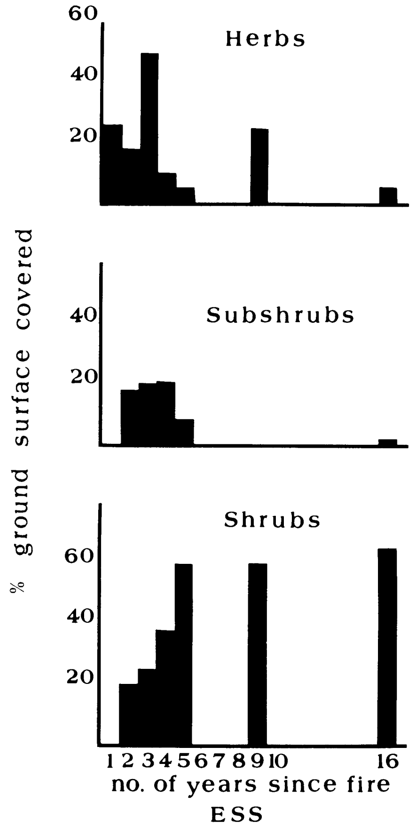

FIG. 2. Average percent ground surface covered by shrubs, subshrubs, and herbs at the Extensive Study Sites of various ages. Sampling was done in spring 1974. Cover was averaged across all sites of the same age. See Appendix I.

m near Alpine, 1000 m along Boulder Creek Road north of Descanso, and at 1670 m off Kitchen Creek Road south of Mount Laguna (see Appendix I). Each site had burned areas on the four major slope aspects, N, S, E, W. These sites were first sampled May–June 1971 and resampled each spring between April and June through 1974. All areas had been seeded in December 1970 with annual ryegrass *Lolium multiflorum* by the United States Forest Service as an erosion control measure. Precipitation patterns for the 1st 4 yr after fire (Fig. 1) indicate marked annual fluctuations. As is typical for southern California, the lowest elevation site (Alpine) had the lowest precipitation in most years.

All sites were sampled by line-intercept (Bauer 1943). The transects were 10 m in length; 10–20 transects of this length were used per slope face in the intensive sites, whereas 5 transects were generally used in the extensive sites. The number of transects was determined by species area curves (Rice and Kelting 1955) and by the physical dimensions of the area. Data were analyzed according to Cox (1967). Species names are according to Munz (1959).

Statistical comparisons of changes in cover and species richness during succession were done with a two-way ANOVA, grouping data either by slope or site. Relationships between variables were investigated using correlation analyses.

RESULTS

Extensive Study Sites

Cover of shrubs, subshrubs and herbs in different aged chaparral stands throughout San Diego County is shown in Fig. 2. Five years after fire, shrub cover approached prefire levels. There were two temporary components in the early postfire successional vegetation: the suffrutescent subshrubs and the herbs. Subshrub cover was lacking in the 1st-yr burn and reached its peak in the 3rd- and 4th-yr burns. Herbaceous cover was 25% of ground surface in the 1-yr-old burn and peak herb cover was observed in the 3-yr-old burn. Lowest herb cover levels were observed in 5- and 16-yr-old stands. High herb cover was observed in the single 9-yr-old stand. This area was heavily grazed by cattle. Floristically, the herb cover in this stand was quite different from that observed in the immediate postfire flora (see below).

Herbaceous species richness (Table 1) was greatest in the 1st postfire yr and lowest after the 4th yr. The

TABLE 1. Herb floristic composition of Extensive Study Sites, by year since last fire. All sites sampled in 1974.

		Life history type		Class*		Origin	
		Annual vs. perennial		Dicot vs. monocot		Native vs. introduced	
Years since fire	Total number of species	% species annual	% cover annual	% species dicot	% cover dicot	% species native	% cover native
1	37	70	95	80	96	95	98
2	34	76	86	81	36	89	94
3	21	81	99	74	52	78	29
4	31	58	69	71	36	83	83
5	21	64	33	61	63	87	92
9	20	76	88	67	32	81	64
16	16	65	38	71	36	88	83

* One species of fern is not represented in these figures.

majority of species present the 1st yr were native annual dicots. The bulk of herb cover in the 1st 3 yr was annual but by the 5th yr was largely perennial, except in the heavily grazed 9-yr-old stand.

A breakdown of the herb cover by time of appearance after fire is given in Table 2. Over half of the herb species (which constituted nearly half of the herb cover) in the 1st-yr burns were not present in older burns. Prominent species in this 1st-yr-only group were the annual dicots *Phacelia brachyloba*, *Calyptridium monandrum*, and *Cryptantha micrantha*.

As herb cover decreased in the 4th and 5th yr after fire, perennials comprised a greater proportion of the cover. Dominant herbs in the 5- and 16-yr-old stands included *Calochortus splendens*, *Convolvulus aridus*, *Galium nuttallii*, *Marah macrocarpa*, and *Stipa lepida*. The heavily grazed 9-yr-old stand was quite different from these stands. It had a high herb cover composed of the introduced annuals *Bromus rubens* and *Erodium cicutarium* and the native annual grass *Festuca octoflora* and perennial grass *Stipa lepida*.

TABLE 2. Percent ground surface covered by herbaceous species and number of species, grouped by time of appearance after fire for burns of various ages at the Extensive Study Sites, sampled in the spring of 1974.

Years since fire	Species present 1st yr only	Species present 1st and following yr	Species present 2nd yr or later
	Average percent ground surface covered*		
1	14.0† (22)	17.0 (15)	. . .
2	. . .	10.0 (14)	23.0 (20)
3	. . .	10.0 (6)	17.0 (15)
4	. . .	6.0 (9)	6.0 (22)
5	. . .	4.0 (13)	2.0 (8)
9	. . .	4.0 (8)	4.0 (12)
16	. . .	1.3 (4)	1.5 (12)

* All sites of each age averaged (see Appendix I for number of sites of each age); number of species is in parentheses.
† 6.3% ground surface covered by *Phacelia brachyloba*.

Intensive Study Sites

Shrubs.—Postfire successional changes in shrub cover are shown in Fig. 3. Recovery at the lowest elevation site (Alpine) was rapid on the north-facing slope and slow on south- and west-facing slopes. Slope aspect differences were less evident at the higher elevation sites. Total shrub cover varied significantly ($P < .05$) among sites during succession; Alpine had 50% lower cover than the other two sites after the 2nd yr. By the 3rd yr after fire all slopes at Boulder Creek and Kitchen Creek and the north-facing slope at Alpine had ≈50% ground surface covered by shrubs. Total shrub cover at a site did not increase between the 3rd and 4th yr.

The total number of shrub species was 13 at Alpine, 11 at Boulder Creek, and 12 at Kitchen Creek; only 5 species were present at all three sites. *Adenostoma fasciculatum* was the dominant prefire and postfire shrub at all sites; 4th postfire yr ground surface coverage was 13% at Alpine, 39% at Boulder Creek, and 31% at Kitchen Creek. Codominants were *Ceanothus tomentosus* var. *olivaceous* (Alpine), *C. leucodermis* (Boulder Creek), *C. greggii* var. *perplexans* (Kitchen Creek), and *Quercus dumosa* at all sites (see Keeley and Keeley 1980 for more detailed information).

Temporary cover of subshrubs.—Postfire successional changes in subshrub cover are shown in Fig. 4. These subshrubs are herbaceous perennials that become woody at the base, and most are drought deciduous species found in lower elevation coastal sage scrub vegetation. Thus, it is not surprising that this component was essentially absent from the high elevation burn; subshrub cover never exceeded 2% ground surface cover at Kitchen Creek. There were eight species at Alpine, nine at Boulder Creek, and six at Kitchen Creek. Typically there were 2–3 species per slope. The number of subshrub species did not vary significantly through succession ($P > .05$), regardless of whether they were grouped by slope aspect or site. *Helianthemum scoparium* and *Lotus scoparius* were clear dominants at Alpine and Boulder Creek, respectively. Other subshrub species encountered at two or more sites were *Eriophyllum confertiflorum*, *Eriodictyon crassifolium*, *Eriogonum fasciculatum*, *Gutierrezia californiaca*, *Salvia apiana*, and *Trichostema parishii*.

These suffrutescent species are generally not represented in mature chaparral, so establishment after fire must have been from soil-stored seed. These species were present in abundance the 1st yr after fire though relatively small; *H. scoparium* had an average height of 12 cm and *L. scoparius* 29 cm.

Subshrub cover increased substantially in the 3rd yr and decreased in the 4th yr a pattern similar to that observed at the ESS. Throughout succession subshrub cover varied significantly ($P < .01$) across slopes, being generally highest on south-facing slopes. In the 3rd yr after fire *H. scoparium* comprised 65% of the subshrub cover at Alpine and 20% at Boulder Creek, and *L. scoparius* accounted for 29% at Alpine and 74% at Boulder Creek. For both sites the 3rd-yr peak was partially a result of increased recruitment. The number of *H. scoparium* per transect at Alpine and the number of *L. scoparius* per transect at Boulder Creek increased 1.8-fold between the 1st and 3rd yr. Since coverage of *H. scoparium* (Alpine) increased 3.8-fold and *L. scoparius* (Boulder Creek) 5.6-fold during this time it is obvious the bulk of the 3rd-yr peak was due to increased subshrub size. In the 3rd yr *H. scoparium* (Alpine) had an average height of 51 cm and *L. scoparius* (Boulder Creek) 38 cm. During the 3rd-yr peak, shrub cover and subshrub cover showed no significant relationship across all 12 slope aspects ($r = .16$, $P > .05$, $N = 12$, for the three sites

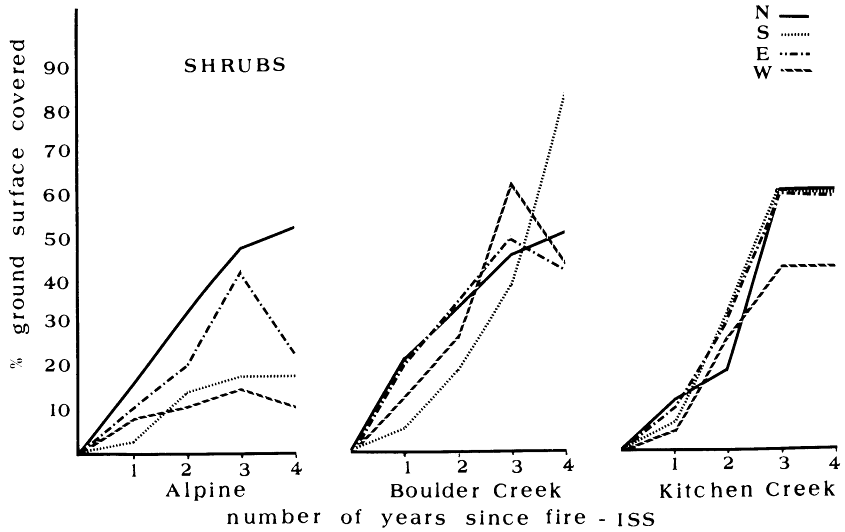

FIG. 3. Percent ground surface covered by shrubs on each slope aspect at the three Intensive Study Sites for the 1st 4 yr after fire. Sampling began in spring 1971.

combined). In the 4th yr average subshrub cover decreased owing to a 25% reduction in number of *H. scoparium* (Alpine) and 16% reduction in number of *L. scoparius* (Boulder Creek).

Temporary cover of herbs.—At all three sites herb cover showed highly significant differences across years ($P < .01$), being highest in the 1st yr after fire (Fig. 5). This 1st yr peak was significantly lower ($P < .01$) at the lowest elevation site (Alpine). The south-facing slope at all three sites had the highest herb cover, though it was not significantly higher than the other slopes ($P > .05$).

In the 2nd postfire yr all sites showed greatly reduced herb cover (Fig. 5). This was largely due to reduced density as seen in Table 3. The few individuals present the 2nd yr were greatly stunted relative to individuals in the previous year; at Boulder Creek the dominant herb species in the 2nd yr had an average height of 65–90% below that observed the 1st yr.

In the 3rd yr herb cover increased well above the 2nd-yr levels with the single exception of the south-facing slope at Boulder Creek. Recall (Fig. 4) that in the 3rd yr this was the aspect with the greatest subshrub cover. Subshrub and herb cover on all 12 aspects (the three sites combined) in the 3rd yr showed a highly significant negative relationship ($r = -.60$, $P < .02$). On all slope faces in the 3rd yr herb cover was lower than in the 1st yr. At Boulder Creek and Kitchen Creek herb cover was not significantly related to shrub cover, though at Alpine there was a significantly positive relationship ($r = .92$, $P < .05$, $N = 4$). In the 4th yr after fire herb cover dropped to the lowest levels observed throughout the study.

The pattern of herb cover at these sites is markedly unlike that observed at the ESS. The fluctuations in herb cover common to all three Intensive Study Sites may be causally related to weather differences (e.g., Fig. 1) and will be considered later.

Patterns of species richness are shown in Table 4. Within a site the number of herb species was positively correlated with the annual changes in herb cover ($r = .85$, Alpine; $r = .65$, Boulder Creek; $r = .63$, Kitchen Creek; $P < .01$ and $N = 16$, at all sites). Species richness also varied with elevation. In the 2 yr of high herb cover (1st and 3rd) the lowest elevation site had the greatest species richness and the highest elevation site had the least. Within a site in a given year, the

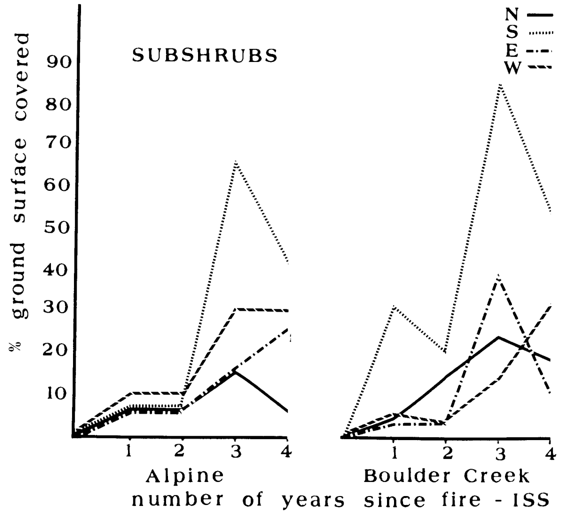

FIG. 4. Percent ground surface covered by subshrubs on each slope aspect at Alpine and Boulder Creek for the 1st 4 yr after fire. Sampling began in spring 1971. Subshrub cover at Kitchen Creek never exceeded 2% ground surface cover.

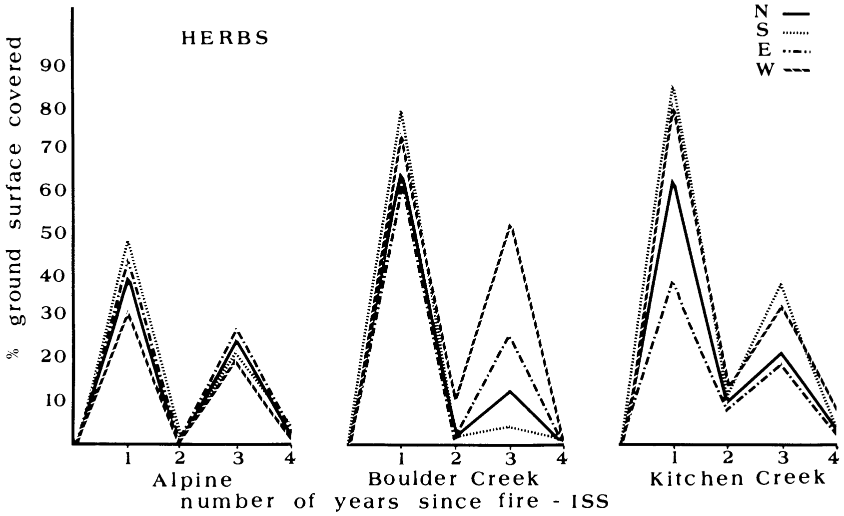

FIG. 5. Percent ground surface covered by herbs on each slope aspect at the three Intensive Study Sites for the 1st 4 yr after fire. Sampling began in spring 1971.

number of herb species varied by more than two-fold across slopes, though in these comparisons there was no consistent relationship between cover and species richness. In the 3rd yr at Boulder Creek the west-facing slope had the highest cover and highest species richness and the south-facing slope the lowest cover and lowest species richness. However, such a relationship was not evident at the other sites.

A summary of the floristic composition is given in Table 5. In general the herb flora consisted of native annual dicots. However, an important component of the herb flora the 1st yr at some sites was *Lolium multiflorum*, which had been seeded at all sites (see Methods). The 1st-yr success of the *Lolium* seeding varied with elevation; at Alpine it covered 28% ground surface and comprised 66% of the herb cover. At Boulder Creek *Lolium* covered 22% ground surface and comprised 32% of the herb cover, and at Kitchen Creek it covered only 6% and constituted only 8% of the herb cover. *Lolium* establishment accounts for site differences in herb composition; the 1st yr after fire Alpine had only ≈30% native dicot cover whereas Kitchen Creek had 92% native dicot cover (Table 5). Likewise the 1st yr burns in the ESS had low *Lolium* cover and ≈97% native dicot cover (Table 1).

From the native flora, *Antirrhinum coulterianum*, *Chaenactis artemisiaefolia*, *Chorizanthe* spp., *Cryptantha intermedia*, *Haplopappus squarrosus*, *Lotus salsuginosus*, *Oenothera micrantha* and *Phacelis* spp. were important at all three sites in the 1st 5 yr (Appendix II). Of these, all but one (*H. squarrosus*) are annuals. This postfire annual flora was heterogeneous in stature. The majority of the 1st yr herb species (Appendix II) were 25–50 cm in height. Two other height groups were important. *Lotus salsuginosus*, *Chorizanthe* spp., *Filago* spp., and *Linanthus* spp. had an average height of 5–15 cm and *Antirrhinum coulterianum*, *Chaenactis artemisiaefolia*, and *Gilia caruifolia* averaged between 70 and 100 cm.

It is significant that in the 1st yr perennials constituted 35–37% of the herb species but only 3–13% of the herb cover (Table 5). The herbaceous perennials occurred as widely scattered individuals, many of which apparently were present before the fire and persisted through the fire as bulbs (e.g., *Allium*, *Calochortus*, *Brodiaea*, *Chlorogalum*) or other underground parts (e.g., *Haplopappus*, *Lathyrus*, *Lomatium*, *Marah*, *Paeonia*). These perennials all flowered the 1st yr. When total herb cover dropped in the 2nd yr they comprised 30–80% of the herb coverage, but in the 3rd yr when herb cover peaked again (Fig. 5) annuals once again predominated (Table 5). In the 4th yr perennials comprised a large proportion of the herb cover at all sites. A similar pattern was observed for the ESS (Table 1).

Successional patterns in species richness differed between annuals and herbaceous perennials (Table 5). At all sites there were highly significant ($P < .01$) differences among years in number of annual species. Species richness of herbaceous perennials, however,

TABLE 3. Average number of herbs/10-m transect each year after fire at the Intensive Sites. All sites burned in the fall of 1970 and were sampled in the spring of each year.

Site	Years since fire: 1	2	3	4
	Number of herbs/10-m transect			
Alpine	17	<1	15	<1
Boulder Creek	31	4	20	1
Kitchen Creek	40	10	26	2

TABLE 4. Number of herb species, by slope and year, at the Intensive Study Sites. All sites were burned in the fall, 1970, and were sampled in the spring of each year.

		Years since fire			
		1	2	3	4
Site	Slope	Number of herb species			
Alpine	N	38	7	23	1
	S	26	7	24	5
	E	18	5	28	4
	W	19	4	21	4
Total number of species:		48	15	42	11
Boulder Creek	N	17	6	20	5
	S	21	2	12	1
	E	16	2	24	1
	W	38	18	29	9
Total number of species:		47	14	37	11
Kitchen Creek	N	12	8	11	7
	S	15	9	16	5
	E	19	9	14	9
	W	17	12	23	9
Total number of species:		26	19	33	20

showed no significant differences ($P > .05$) from year to year at Boulder Creek and Kitchen Creek. At these two sites number of herbaceous perennials did vary significantly across slopes ($P < .01$); south slopes were depauperate and west slopes most diverse. At Alpine, perennials showed significant differences in species richness from year to year but not across slopes.

A breakdown of the postfire herb flora by time of appearance after fire is given in Appendix II and summarized in Table 6. The placement of a species in a particular category represents its status in the present study. Undoubtedly the placement of some species reflects a fortuitous encounter. Other species are relatively constant; e.g., *Phacelia brachyloba* only occurred in the first postfire year whereas nonnative species such as *Erodium cicutarium* and various *Bromus* spp. typically were present only after the 1st yr. At the two lower elevation sites 50% of the species present the 1st yr after fire were not encountered in subsequent years.

DISCUSSION

The essential characteristics of postfire shrub succession in chaparral are well known (Hanes 1977, Keeley and Zedler 1978). The present study clarifies a number of details and provides a fuller picture of successional changes in the temporary herbaceous and subshrub cover.

Reproductive modes

It is suggested here that the temporary cover can be grouped into four categories which reflect differences in population dynamics and reproductive mode. These groups include two which are made up of species present both before and after fire, (1) generalized herbaceous perennials, and (2) generalized annuals, and two groups more or less restricted to postfire years, (3) specialized "fire annuals" and (4) specialized "fire perennials."

In mature chaparral herbaceous species are poorly represented, amounting to only a few percent ground surface cover (GSC) under the canopy, and these are mostly perennials (Hanes 1977, Keeley and Johnson 1977). However, in extremely old chaparral, herb cover may be more extensive; a 90+ yr stand of undis-

TABLE 5. Herb floristic composition of Intensive Study Sites, by year since fire, sites burned fall 1970 and sampled in subsequent springs.

	Life history type		Class		Origin	
	Annual vs. perennial		Dicot vs. monocot		Native vs. introduced	
Years since fire	% species annual	% cover annual	% species dicot	% cover dicot	% species native	% cover native
Alpine:						
1	63	87	83	30	92	32
2	53	20	73	71	80	87
3	67	55	83	60	91	66
4	64	26	91	98	100	100
Boulder Creek:						
1	64	91	87	67	96	67
2	71	70	71	82	71	82
3	54	85	81	80	89	81
4	55	20	91	97	91	97
Kitchen Creek:						
1	65	97	85	92	92	92
2	58	65	79	91	84	92
3	67	82	88	76	85	76
4	40	28	80	77	85	81

TABLE 6. Percent ground surface covered by herbaceous species and number of species, grouped by time of appearance after 1970 fire at Intensive Study Sites Alpine (A), Boulder Creek (B), and Kitchen Creek (K).

Years since fire	Species present 1st yr only			Species present 1st and following years			Species present 2nd yr or later		
	A	B	K	A	B	K	A	B	K
	Average percent ground surface covered*								
1	3 (25)	8 (26)	47†(6)	39‡(23)	61§(21)	25 ‖ (20)	...	...	...
2	...	...	...	2 (10)	3 (8)	10 (12)	1 (5)	1 (6)	2 (7)
3	...	...	...	18 (20)	22 (17)	22 (16)	5 (22)	3 (20)	3 (17)
4	...	...	...	3 (5)	2 (17)	3 (11)	1 (6)	1 (4)	3 (9)

* Average cover of the four slopes sampled in each site; number of species in parentheses.
† Due entirely to *Phacelia brachyloba*.
‡ 28% ground surface covered by *Lolium multiflorum*.
§ 22% ground surface covered by *Lolium multiflorum*.
‖ 6% ground surface covered by *Lolium multiflorum*.

turbed chaparral with 85% GSC by shrubs had 34% GSC by herbs, largely perennials (Keeley 1974).

Herbaceous perennials which occur as scattered individuals in mature chaparral constitute the group 1 "generalized herbaceous perennials." Monocots such as species of *Allium*, *Calochortus*, *Brodiaea*, *Chlorogalum*, and *Zygadenus* constitute a large component of this group. Due largely to the low light environment, these herbs exist vegetatively for years beneath the canopy, flowering only sporadically (Stone 1951, Horton and Kraebel 1955, Stockings 1966, Ammirati 1967, Muller et al. 1968, Christensen and Muller 1975*a*). When these species flower beneath the chaparral the inflorescences suffer extensive animal predation (Tinnin and Muller 1971). These species have bulbs buried at depths sufficient to survive fire. In the 1st yr after fire the bulbs initiate vigorous sprouts and nearly all flower (Stone 1951, Muller et al. 1968). Herbaceous perennial dicots such as *Paeonia californica*, *Lomatium* spp., and *Sanicula* spp. are similar in many respects to the monocots (Sampson 1944, Horton and Kraebel 1955, Sweeney 1956) except they do not possess deeply buried bulbs and surviving fire may be more tenuous.

Marah macrocarpus and *Convolvulus* spp. are herbaceous perennial vines, frequently reaching the canopy of mature chaparral. Perhaps because of the higher light levels in the canopy these species flower much more frequently than other herbs. These vines also have woody underground parts that survive fire.

An important question concerning these herbaceous perennials is the extent to which there is seedling recruitment in the 1st postfire yr. One observation suggests it may be negligible for many of these species. In a recent successional study in "soft chaparral" (which has a postfire herb flora indistinguishable from "hard chaparral") it was noted that 26 of 28 herbaceous perennials present in the 1st postfire yr were represented entirely by resprouts (J. Keeley, *personal observation*). Parallel to this is the observation that the seeds of most of these herbaceous perennials are nonrefractory, i.e., they germinate readily without heat treatment or scarification, e.g., *Brodiaea pulchella*, *Chlorogalum pomeridianum*, *Zygadenus fremontii* (Mirov 1940, but cf. Sweeney 1956) and *Marah macrocarpus* (J. Keeley, *personal observation*). *Convolvulus cyclostegius* will germinate without treatment though germination is significantly enhanced under heat treatment simulating soil temperature in an opening (Christensen and Muller 1975*a*, *b*). This last species typically establishes seedlings under *Adenostoma* chaparral (Christensen and Muller 1975*a*) as does *Marah macrocarpus* (J. Keeley, *personal observation*). It may be that the seeds of many of these herbaceous perennials are destroyed by fires since nonrefractory seeds typically are less tolerant of high temperatures (Wright 1931, Went et al. 1952, Sweeney 1956, J. Keeley, *personal observation*).

Perhaps due to their scattered occurrence under chaparral, coupled with dependence upon postfire establishment from resprouts, these herbaceous perennials generally do not comprise a large part of the immediate postfire herb cover. In this study these herbaceous perennials comprised 35–57% of the 1st postfire yr herb species, but only 3–13% of the herb cover. Unlike the annual flora, species richness of herbaceous perennials is relatively constant throughout succession. Likewise, there is much less fluctuation in herbaceous perennial cover. Stone (1951) noted that the density of one of these species, *Brodiaea ixioides*, did not vary between burned and unburned stands. Sweeney (1956) has reported a similar finding for *Chlorogalum pomeridianum* and *Zygadenus micranthus*. By the 4th or 5th yr after fire, as the total herb cover dwindles, herbaceous perennials comprise a larger percentage of that total (Tables 1 and 5).

A second group represented in the temporary cover are "generalized" annuals which occur in rock outcrops and openings in and around chaparral as well as in the postfire flora. Southern California examples of this group are *Cryptantha intermedia*, *Chaenactis artemisiaefolia*, *Gilia* spp., and *Oenothera micrantha* (Appendix II; Horton and Kraebel 1955, Vogl and Schorr 1972, Christensen and Muller 1975*a*). Seeds of many of these species are nonrefractory, e.g., seed germination is known to occur readily without any treatment in *Cryptantha intermedia* (Christensen and Muller 1975*a*), *Gilia capitata* (Grant 1949), and *Oenothera micrantha* (Sweeney 1956). It is likely that in some of these species seed germination is enhanced by high soil temperatures in exposed areas such as rock outcrops, etc. (Christensen and Muller 1975*a*).

In unburned chaparral these species are restricted to openings. The size of the population varies spatially with the size of openings, and also temporally with the amount of annual precipitation (J. Keeley, *personal communication*). In 1st-yr burns the population sizes of many of these species reach their highest levels. Keeley and Johnson (1977) found over a 20-fold increase in cover of *Cryptantha intermedia* from preburn to postburn environments. In the present study *C. intermedia* was the second dominant at all three intensive sites in the 1st postfire yr. This enhanced postfire recruitment may be due to increased survival over prefire years, but more likely it is from increased seed germination.

As succession proceeds and the shrub cover increases, these generalized annual species are restricted to smaller and smaller openings. Many of these species have a moderately developed dispersal ability (e.g., *Cryptantha* spp., *Filago* spp.) and thus are capable of invading scattered openings within the chaparral matrix. It is unknown to what extent individuals in openings contribute to the soil seed pool under the canopy. It has been suggested that the seed rain from some of these herbs in coastal sage scrub vegetation contributes to the chaparral soil seed pool (Westman 1979). This may be important where the two vegetation types are juxtaposed, but few postfire herbs have well-developed long-distance dispersal mechanisms. There are vast stretches of chaparral 50–100 km from coastal sage scrub, and for these areas it is highly unlikely that even herbs with high dispersability would contribute much to the dense postfire herb flora.

A third group represented in the postfire temporary cover are the specialized "fire-annuals" (group 3). These species occur in abundance the 1st postfire yr and are usually absent or greatly reduced in number in later years. Of all the temporary cover species they would be the only "pyrophyte endemics" (sensu Hanes 1977). Examples include *Emmenanthe penduliflora* and *Phacelia* species of which *P. brachyloba* is the best example (Tables 2 and 6; Horton and Kraebel 1955, Sweeney 1956, Christensen and Muller 1975*a*). These species have refractory seeds that are thought to require extremely intense heat to break the seed coat, though few studies have been very successful in demonstrating this (Sweeney 1956, Christensen and Muller 1975*a*). *Emmenanthe penduliflora* seeds have a highly specialized mechanism for cuing germination to the immediate postfire environment; they require contact with charred *Adenostoma* stems (Wicklow 1977, Jones and Schlesinger 1980). It is unknown if such a germination mechanism works with other "fire-annuals."

After flowering and fruiting the seeds of these "fire-annuals" are probably deposited in a relatively small seed-shadow around the plant. The lack of any well-developed dispersal mechanism perhaps results from the fact that, unlike many colonizing species which must "find" disturbances, fires are predictable in time and space and thus will eventually come to them (Keeley 1980). Seed longevity is presumed to be great although few data are available. Went (1969) reported no germination after 20 yr for a few "fire-annuals," but in most cases he was unable to germinate them at any age. The occurrence of these strict "fire-annuals" after fire in old chaparral suggests a great longevity for their seeds.

A fourth component of the temporary cover is a group here termed "fire-perennials." These are herbaceous perennials which often become woody at the base and are equivalent to the subshrubs in this study, particularly *Helianthemum scoparium*, *Lotus scoparius*, and *Eriophyllum confertiflorum*. These species differ in several important respects from the group 1 "generalized herbaceous perennials" previously discussed. Although occasionally found on rock outcrops and in openings, these "fire-perennials" are normally absent beneath chaparral. Therefore, their occurrence in the postfire environment is a result of seedling recruitment rather than resprouts.

Unlike the "generalized herbaceous perennials" these "fire-perennials" have refractory seeds, though fire per se is not required for germination. The increased soil temperature in openings or burns (Christensen and Muller, 1975*a*, found a 20+°C difference between bare soil and soil beneath the chaparral canopy) is sufficient to stimulate seed germination. McPherson and Muller (1969) artificially cleared an area of *Adenostoma* and found 60 *Helianthemum scoparium* seedlings/m^2, but only 4 seedlings/m^2 in an adjacent shaded portion of the same clearing. Seed germination of *Lotus scoparius* and *Eriophyllum confertiflorum* is stimulated by treatment with temperature simulating either exposed soil or fire (Christensen and Muller 1975*a*, *b*).

As shown in this study the bulk of seed germination of *H. scoparium* and *L. scoparius* occurs in the 1st yr after fire. These flower and set seed, some of which germinate in succeeding postfire years. These species reach their maximum population size in the 3rd or 4th yr after fire. Dependent upon site differences, the particular species of "fire-perennial" will vary. In this study *Helianthemum scoparium* was the clear dominant at Alpine, and *Lotus scoparius* was dominant at Boulder Creek, whereas *Eriophyllum confertiflorum* was the dominant in Horton and Kraebel's (1955) study. In later years, as shrub cover closes in, seed germination drops and these "fire-perennials" are crowded out.

Community changes

The only time during community development when all four temporary-cover groups are present together is the 1st postfire yr, so species richness is greatest at this time. This pattern is true for nearly all chaparral succession studies despite geographical, topographical, climatic and floristic dissimilarities and differences in year of peak herb cover (Sampson 1944, Horton and Kraebel 1955, Sweeney 1956, present study Tables 1 and 4, but cf. Vogl and Schorr 1972). Although many of the dominant herb species are common to all investigations, the present study (Appendix II) lists over 60 species not previously reported from chaparral burns (cf. Hanes 1977). The number of herb species per slope varied from 20–40 in this study (Table 4), which is typical of most studies (Sampson 1944, Sweeney 1956), but about 10-fold greater than several of Horton and Kraebel's (1955) sites. The present study indicated that through succession species richness is positively correlated with cover, inversely correlated with elevation and unrelated to slope aspect (Table 1); lack of data prevents comparison with other studies.

Successional changes in herb cover vary spatially and temporally. The only broad generalization possible is that herb cover will be highest some time in the 1st 4 yr. Peak herb cover has been reported in the 1st yr after fire (all intensive sites in this study, also Vogl and Schorr 1972), the 2nd yr (Sampson 1944, Sweeney 1956), or the 3rd and 4th yr (extensive sites in this study, also Sampson 1944, Horton and Kraebel 1955). These differences may reflect geographical or topographical dissimilarities though there is no obvious pattern.

One factor which may account for these different years of peak herb cover may be floristic differences. Horton and Kraebel (1955) stated that at their sites the time of peak herb cover depended upon the dominant species in the temporary cover. However, they did not suggest any generalizations. Evidence from this study indicates that high subshrub ("fire-perennial") cover may inhibit herb growth ($r = -.60$, $P < .02$, for herb vs. subshrub cover in the 3rd yr). Therefore, the 1st-yr peak herb cover in this study may be related to low subshrub cover at this time, whereas the 3rd-yr subshrub peak may have kept herb growth below 1st-yr levels. The 2nd-, 3rd- and 4th-yr herb peaks in northern California studies may be related to a relative lack of subshrubs in these burns (Sampson 1944, Sweeney 1956). Although Horton and Kraebel (1955) reported 3rd- and 4th-yr herb cover peaks at sites with subshrubs, these subshrubs did not form an important part of the vegetation in most burns.

In those studies reporting few subshrubs (i.e., group 4 "fire-perennials") it was group 2 "generalized annual" species which accounted for the peak herb cover after the 1st yr. In these studies group 1 "generalized perennials" were at low levels throughout succession and group 3 "fire-annuals" showed a 1st-yr peak and rapid decline or absence afterwards, similar to the pattern observed in the present study.

Weather patterns, particularly precipitation levels, are known to affect herb growth (Slade et al. 1975), but little importance has been attached to the effect of weather patterns on succession. Its importance is suggested by the marked similarity in herb cover patterns through succession at the intensive sites (Fig. 4). All 12 slopes, distributed across a 1000-m elevation, but sampled during the same years, showed almost identical herb cover patterns; 1st-yr peak, 2nd-yr drop, 3rd-yr high, 4th-yr low. Precipitation patterns (Fig. 1) may account for the herb cover pattern during succession at the intensive sites. The 1st-yr wet season had below normal amount of precipitation and the 2nd yr at all sites was markedly subnormal.

This 2nd-yr low precipitation reduced germination, survival and vigor (and thus seed set) of the "generalized annuals" (group 2) and this bottleneck apparently reduced their potential population sizes for the 3rd yr, even though this year was above normal in precipitation. "Fire-perennials," on the other hand, established in the 1st yr and fared better in the 2nd yr, perhaps because of already being established. Since 3rd-yr populations were not dependent upon seed pool buildup during the second year, these individuals took advantage of the increased precipitation and tripled their size over the 1st-yr plants. This 2nd-yr precipitation deficit had little effect on the group 1 "generalized perennials." Some of them remained dormant as underground bulbs or corms, and it had no effect on the group 3 "fire-annuals" which are normally absent after the 1st yr.

Throughout succession at the intensive sites, an inverse relationship between herb cover and elevation was observed (Fig. 5). Since annual precipitation is also inversely related to elevation in San Diego County (Close et al. 1970) it may play a role in elevation differences in herb cover.

The observed decline in herb growth the 4th yr after fire in the ISS was very likely a result of subnormal precipitation. Typically, a 4th-yr low herb cover is attributed to closing-in of the shrub canopy. Such was not the case in the present study, as shrub cover did not increase between the 3rd and 4th yr (a phenomenon which also may be related to subnormal precipitation). It seems likely that precipitation deficits would have a greater inhibitive effect on herb growth later in succession when competition for soil moisture is greater (Schlesinger and Gill 1980). A model relating these factors has been presented previously (S. Keeley 1977).

Exotics

Seeding with annual ryegrass *Lolium multiflorum* had no apparent effect on total herb cover in the present study. Sites with poor *Lolium* establishment had as high or higher herb cover in the 1st postfire yr as sites with high *Lolium* establishment. *Lolium* success was generally at the expense of the native cover and this negative effect apparently was greatest on the group 3 "fire annuals"; in the 1st postfire yr these species covered 47% of the ground surface at Kitchen Creek (where *Lolium* constituted one-tenth of the herb cover) whereas these group 3 "fire-annuals" comprised only 3% GSC at Alpine (where *Lolium* constituted two-thirds of the herb cover) (Table 6). These field observations agree well with Rice and Green's (1964) experimental results, which indicated seeding with *Lolium* affected species composition but not total herb cover, and Corbett and Green's (1965) results which showed seeding had no significant effect on total vegetative cover but did prevent establishment of native species (herbs and shrubs). In the present study there was (overall) a 75% reduction in relative dominance of *Lolium* the 2nd yr after fire. By the 4th postfire yr *Lolium* was absent from the two lowest elevation sites.

There are numerous nonnative species not artificially seeded into burns but frequent after fire. Dominants in this group include the annual grasses *Bromus mollis*, *B. rubens*, *B. tectorum* and the annual herb *Erodium cicutarium*. In the present study these species were generally present after the 1st postfire yr. From northern California studies this pattern was evident in Sweeney's (1956) sites but not Sampson's (1944). Horton and Kraebel (1955) found that at all of their southern California sites *Bromus rubens* and *B. tectorum* increased from almost none in the 1st yr to several hundred per milacre (≈ 4 m^2) plot at some sites by the 4th yr. This pattern of establishment indicates either low soil-seed pools at the time of fire or poor survival of seeds during fire. In general these species exist in grasslands and openings in chaparral. After fire, peak populations require several years either for seed dispersal into burns and/or build-up in situ from a few 1st-yr plants.

With continued disturbance, such as the grazing observed at the 9-yr-old extensive site in this study, these species proliferate. Repeated fires, which are light fires because of less fuel load, also favor these nonnative herbs over native ones (Bauer 1930, Sampson 1944, Keeley 1980). In particular the group 3 "fire-annuals" are very sensitive to repeat fires and are quickly eliminated from a site under such conditions (Keeley 1980). These "fire-annuals" apparently are unable to compete with the dense stand of exotics produced by frequent fires; thus the "fire-annuals" are dependent upon return of the shrub cover before another fire.

Acknowledgments

We thank Ruth Botten, Marily Cordemas, Janet Lee and Gerald Wesley for hours of data collecting in the broiling sun, Nancy Coile for volunteering her lunch hours and breaks to help proofread the endless reams of data printout and punch cards, Bruce Haines for critical review and discussion, and Susan Penn for typing. Data on ESS were obtained by S. M. Hutchinson as part of his master's research. This project was supported in part by National Science Foundation Grant GB 27161-331754 to Albert W. Johnson.

Literature Cited

Ammirati, J. F. 1967. The occurrence of annual and perennial plants on chaparral burns. Thesis. San Francisco State College, San Francisco, California, USA.

Bauer, H. L. 1930. Vegetation of the Tehachapi Mountains, California. Ecology **11**:263–280.

———. 1943. Statistical analysis of chaparral and other plant communities by means of transect samples. Ecology **24**:45–60.

Christensen, N. L., and C. H. Muller. 1975*a*. Effects of fire on factors controlling plant growth in *Adenostoma* chaparral. Ecological Monographs **45**:29–55.

———. 1975*b*. Relative importance of factors controlling germination and seedling survival in *Adenostoma* chaparral. American Midland Naturalist **93**:71–78.

Close, D. H., D. E. Gilbert, and G. D. Peterson, editors. 1979. Climates of San Diego County: agricultural relationships. University of California Agricultural Extension Service, Davis, California, USA.

Cooper, W. C. 1922. The broad-sclerophyll vegetation of California. Publication Number 319, Carnegie Institute of Washington, Washington, D.C., USA.

Corbett, E. S., and L. R. Green. 1965. Emergency revegetation to rehabilitate burned watersheds in Southern California. Forest Service Research Paper PSW-22, Pacific Southwest Forest and Range Experiment Station, Berkeley, California, USA.

Cox, G. 1967. Laboratory manual of general ecology. William C. Brown, Dubuque, Iowa, USA.

Grant, V. 1949. Seed germination in *Gilia capitata* and its relatives. Madroño **10**:87–93.

Hanes, T. L. 1971. Succession after fire in the chaparral of southern California. Ecological Monographs **41**:27–52.

———. 1977. California chaparral. Pages 417–470 *in* M. G. Barbour and J. Major, editors. Terrestrial vegetation of California. John Wiley and Sons, New York, New York, USA.

Hanes, T. L., and H. Jones. 1967. Post-fire chaparral succession in southern California. Ecology **48**:257–264.

Horton, J. S., and C. J. Kraebel. 1955. Development of vegetation after fire in the chamise chaparral of southern California. Ecology **36**:244–262.

Hutchinson, S. M. 1975. Herbaceous succession in San Diego County chaparral. Thesis. San Diego State University, San Diego, California, USA.

Jones, C. S., and W. H. Schlesinger. 1980. *Emmenanthe penduliflora*: further consideration on germination response. Madroño **27**:122–125.

Keeley, J. E. 1974. *Senecio ganderi*: a uniquely adapted herb from southern California. Madroño **22**:401.

———. 1977*a*. Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and nonsprouting chaparral shrubs. Ecology **58**:820–829.

———. 1977*b*. Fire dependent reproductive strategies in *Arctostaphylos* and *Ceanothus*. Pages 371–376 *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. Forest Service General Technical Report WO-3, United States Department of Agriculture, Washington, D.C., USA.

———. 1980. Reproductive cycles and fire regimes. *In* H. A. Mooney, J. M. Bonnicksen, N. L. Christensen, J. E. Lotan, and W. A. Reiners, editors. Fire regimes and ecosystem properties. Forest Service General Technical Report, United States Department of Agriculture, Washington, D.C., USA.

Keeley, J. E., and S. C. Keeley. 1980, *in press*. Postfire regeneration of California chaparral. American Journal of Botany.

Keeley, J. E., and P. H. Zedler. 1978. Reproduction of chaparral shrubs after fire: a comparison of sprouting and seeding strategies. American Midland Naturalist **99**:142–161.

Keeley, S. C. 1977. The relationship of precipitation to postfire succession in the southern California chaparral. Pages 387–390 *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. Forest Service General Technical Report WO-3, United States Department of Agriculture, Washington, D.C., USA.

Keeley, S. C., and A. W. Johnson. 1977. A comparison of the pattern of herb and shrub growth in comparable sites in Chile and California. American Midland Naturalist **97**:120–132.

McPherson, J. K., and C. H. Muller. 1969. Allelopathic effects of *Adenostoma fasciculatum* "chamise" in the California chaparral. Ecological Monographs **39**:177–198.

Mirov, N. T. 1940. Additional data on collecting and propagating the seeds of California wild plants. Forest Research Note Number 21, California Forest and Range Experiment Station, Berkeley, California, USA.

Mooney, H. A., J. M. Bonnicksen, N. L. Christensen, J. E. Lotan, and W. A. Reiners, editors. 1980. Fire regimes and ecosystem properties. Forest Service General Technical Report, United States Department of Agriculture, Washington, D.C., USA.

Muller, C. H., R. B. Hanawalt, and J. K. McPherson. 1968. Allelopathic control of herb growth in the fire cycle of California chaparral. Bulletin of the Torrey Botanical Club **95**:225–231.

Munz, P. A. 1959. A California flora. University of California Press, Berkeley, California, USA.

Osborn, J., J. Letey, L. F. DeBano, and E. Terry. 1967. Seed germination and establishment as affected by nonwettable soils and wetting agents. Ecology **48**:494–497.

Patric, J. H., and T. L. Hanes. 1964. Chaparral succession in a San Gabriel Mountain area of California. Ecology **45**:353–360.

Rice, E. L., and R. W. Kelting. 1955. The species-area curve. Ecology **36**:7–11.

Rice, R. M., and L. R. Green. 1964. The effect of former plant cover on herbaceous vegetation after fire. Journal of Forestry **62**:820–821.

Sampson, A. W. 1944. Plant succession on burned chaparral lands in northern California. California Agricultural Experiment Station Bulletin Number 635, Berkeley, California, USA.

Schlesinger, W. H., and D. S. Gill. 1978. Demographic studies of the chaparral shrub, *Ceanothus megacarpus*, in the Santa Ynez Mountains, California. Ecology **59**:1256–1263.

Schlesinger, W. H., and D. S. Gill. 1980. Demographic studies of the chaparral shrub, *Ceanothus megacarpus*: biomass, production and changes in the availability of light, water, and nutrients during the development of pure stands after fire. Ecology **61**:781–789.

Stockings, S. 1966. Influences of fire and sodium calcium borate on chaparral vegetation. Madroño **18**:193–224.

Stone, E. C. 1951. The stimulative effect of fire on the flowering of the golden brodiaea (*Brodiaea ixioides* Wats. var. *lugens* Jepson). Ecology **32**:534–537.

Sweeney, J. R. 1956. Responses of vegetation to fire. University of California Publications in Botany **28**:143–250.

Tinnin, R. O., and C. H. Muller. 1971. The allelopathic potential of *Avena fatua*: influence on herb distribution. Bulletin of the Torrey Botanical Club **98**:243–250.

Vogl, R. J., and P. K. Schorr. 1972. Fire and manzanita chaparral in the San Jacinto Mountains, California. Ecology **53**:1179–1188.

Went, F. W. 1969. A long term test of seed longevity. II. Aliso **7**:1–12.

Went, F. W., G. Juhren, and M. C. Juhren. 1952. Fire and biotic factors affecting germination. Ecology **33**:351–364.

Westman, W. E. 1979. A potential role of coastal sage scrub understories in the recovery of chaparral after fire. Madroño **26**:64–68.

Wicklow, D. T. 1977. Germination response in *Emmenanthe penduliflora* (Hydrophyllaceae). Ecology **58**:201–205.

Wright, E. 1931. The effect of high temperature on seed germination. Journal of Forestry **29**:679–687.

APPENDIX I

Location and physical characteristics of study sites. Intensive Study Sites were studied 1971, 1972, 1973, and 1974; Extensive Study Sites all studied in 1974.

Location/name	Year last burned	Dominant shrub*	Slope face	Percent slope	Elevation (m)
Intensive Study Sites:					
Alpine	1970	*Ceanothus*	N	25	500
	1970	*Adenostoma*	S	15	500
	1970	*Adenostoma*	E	25	500
	1970	*Adenostoma*	W	25	500
Boulder Creek	1970	*Quercus*	N	30	1000
	1970	*Adenostoma*	S	20	1000
	1970	*Adenostoma*	E	25	1000
	1970	*Adenostoma*	WSW	25	1000
Kitchen Creek	1970	*Adenostoma*	N	20	1670
	1970	*Adenostoma/Ceanothus*	S	20	1670
	1970	*Adenostoma/Ceanothus*	E	20	1670
	1970	*Adenostoma*	W	20	1670
Extensive Study Sites					
Morena Valley	1973	*Adenostoma*	W	6	982
	1973	*Arctostaphylos*	E	5	982
	1973	*Ceanothus*	SE	8	982
Tecate	1973	*Adenostoma*	W	55	673
Barona Mesa	1972	*Adenostoma*	SW	5	570
	1972	*Arctostaphylos*	NE	5	570
Stagecoach	1972	*Adenostoma*	SW	7	340
Buggy	1971	*Adenostoma*	W	16	818
McAlmond Canyon	1971	*Adenostoma*	SW	22	655
Laguna (Mt.)	1970	*Adenostoma*	E	10	624
	1970	*Adenostoma*	SW	9	879
	1970	*Arctostaphylos*	NE	62	800
	1970	*Ceanothus*	NW	15	442
Deluz	1969	*Arctostaphylos*	SW	31	364
	1969	*Adenostoma*	SW	19	388
	1969	*Ceanothus*	SW	29	400
Pamo Valley	1965	*Adenostoma*	S	17	309
Peutz Valley	1958	*Adenostoma*	SW	30	400
Viejas Mtn.	1958	*Adenostoma*	E	50	788

* Dominants chosen on basis of highest cover in 1974.

APPENDIX II

Herbaceous species present at Intensive Study Sites, categorized by time of appearance after fire and site; A, a = Alpine, B, b = Boulder Creek, K, k = Kitchen Creek (lower case indicates <0.1% ground surface cover). In parentheses after species name: an = annual, p = perennial, i = introduced.

Species	Present 1st yr only	Present 1st and following	Present 2nd yr or later	Species	Present 1st yr only	Present 1st and following	Present 2nd yr or later
Agoseris retrorsa (p)	a		b	*Galium angustifolium* (p)		k	b
Allium peninsulare (p)	a	b		*G. nuttallii* (p)		A, B	k
Amsinckia intermedia (an)			a	*Gilia capitata* (an)			a
Antirrhinum coulterianum (an)	A	B, k		*G. caruifolia* (an)		B, K	a
A. nuttallianum (an or p)		a, b		*G. ochroleuca* (an)		K	a, b
A. kelloggii (an)			a	*Gnaphalium purpureum* (an or p)			b
Apiastrum angustifolium (an)	a			*Haplopappus squarrosus* (p)		A, B, K	
Arabis sp. (p)			k	*Helianthus gracilentus* (p)			a, B, K
Asclepias californica (p)			a, b, k	*Heterotheca grandiflora* (an or p)	a, k		b
Astragalus douglasii (p)		k		*Hulsea californica* (p)	b		a, K
Athysanus pusillus (an)		A	b	*Hypochoeris glabra* (an-i)			a, k
Avena barbata (an-i)	b		a	*Lathyrus laetiflorus* (p)	a, b	k	
Brodiaea pulchella (p)	A, b	k		*Lepidium nitidum* (an)	a		k
Bromus mollis (an-i)			A, b, k	*Linanthus androsaceus* (an)			a
B. rupens (an-i)		A	b, k	*L. dianthiflorus* (an)	a, b		
B. tectorum (an-i)		a	b, k	*Lolium multiflorum* (an or p-i)		A, B, K	
Calochortus albus (p)	b			*Lomatium lucidum* (p)		B, K	
C. splendens (p)		A, b		*Lotus salsuginosus* (an)	A	B, K	
C. weedii (p)		b, k	a	*Lupinus hirsutissimus* (an)	B		
Castilleja foliolosa (p)	a			*Marah macrocarpus* (p)		a, B	
Caulanthus stenocarpus (an)			a	*Microseris* sp. (an)			a
Centaurea cyanus (an-i)	A			*Mimulus brevipes* (an)	a	B	
C. melitensis (an-i)	b		a	*M. fremontii* (an)		B	
Centaurium venustum (an)	a, b		a	*Navarretia atractyloides* (an)		a	
Chaenactis artemisiaefolia (an)		A, B, K		*Nemacladus pinnatifidus* (an)	b, k		a
Chorizanthe californica (an)	a, B	K		*Oenothera bistorta* (an or p)	a		k
C. fimbriata (an)	B	A		*O. californica* (an)		B	a, k
C. procumbens (an)	b	a		*O. micrantha* var. *jonesii* (an)		A, B, K	
C. staticoides (an)			b	*Paeonia californica* (p)	a, b		
Chlorogalum parviflorum (p)			b, k	*Penstemon spectabilis* (p)		k	a, B
Cirsium sp. (an)			A	*Phacelia brachyloba* (an)	a, b, K		
Clarkia purpurea (an)	a			*P. cicutaria* (an)	B		
Convolvulus aridus (p)		A	b, k	*P. parryi* (an)		B	a
Cordylanthus filifolius (an)			b, k	*Pterostegia drymarioides* (an)	b	a	
Cryptantha intermedia (an)		A, B, K		*Rafinesquia californica* (an)	a		
Cuscuta californica (p)			a, b, k	*Salvia columbariae* (an)	b		k
Daucus pusillus (an)	k	a	b	*Sanicula arguta* (p)	a		
Delphinium cardinale (p)			k	*Scrophularia californica* (p)			B
D. parryi (p)	a, b		k	*Silene gallica* (an-i)	b, k		a
Descurainia pinnata (an)		k		*S. laciniata* (p)	b	A	
Dicentra chrysantha (p)	b		A	*S. multinervia* (an)	b, k	A	
Ehrharta erecta (p-i)			k	*Solanum xantii* (p)			a
Emmenanthe penduliflora (an)	B	A	k	*Stipa pulchra* (p)	a		B
Erigeron foliosus (p)		B, k	A	*Streptanthus campestris* (an)		k	
Erodium cicutarium (an-i)			a, b, k	*S. heterophyllus* (an)		k	
Eschscholzia californica (p)			b	*Stylocline gnaphalioides* (an)			A, B, k
Euphorbia polycarpa (p)		a		*Trifolium repens* (p-i)	a	b	
Filago arizonica (an)	a, b			*Triodanis perfoliata* (an)	b		
F. californica (an)			a, b	*Vicia* sp. (an)			k
F. gallica (an)	A						