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POST-FIRE REGENERATION OF SOUTHERN CALIFORNIA CHAPARRAL[1]

JON E. KEELEY AND STERLING C. KEELEY

Department of Biology, Occidental College, Los Angeles, California 90041;
and Department of Biology, Whittier College, Whittier, California 90608

ABSTRACT

Succession of chaparral shrubs was studied for the first 4 years after fire on the four major slope faces at three elevations in southern California. Although total cover fluctuated from year to year, shrub cover increased annually through the third year. There was little or no increase in shrub cover between the third and fourth years. Four years after fire the shrubs covered 55% ground suıface at the highest elevation site but only 28% at the lowest elevation site. Shrub cover was similar between slope faces with one exception; at the lowest elevation site shrub cover was twice as great on the north and east-facing slopes as on the south and west-facing slopes.

Post-fire recovery of shrubs was by seedlings and/or resprouts. *Yucca whipplei* was an exception in that it did not resprout once the aboveground parts were killed nor did seedlings establish after fire, however the aboveground parts of many *Y. whipplei* survived the fire. Species which reproduced entirely by seed did so in the first post-fire year from soil-stored seed with the exception of *Ceanothus greggii* at the highest elevation site. This species was entirely absent the first year after fire but abundant in the second year. Species producing both resprouts and seedlings varied from site to site in the proportion of resprouts:seedlings. Between 83–100% of the post-fire populations of *Cercocarpus betuloides, Arctostaphylos glandulosa,* and *Xylococcus bicolor* were resprouts whereas 12–13% of *Ceanothus tomentosus* were resprouts. For *Adenostoma fasciculatum,* resprouts constituted 27–54% of the population at the lowest elevation and 65–94% at the highest elevation; whereas, the *Quercus dumosa* population was 100% resprouts at the lowest elevation and 31–67% resprouts at the highest elevation. Data are presented on the height of resprouts and seedlings for all species at the end of the first post-fire year.

FIRE is an important disturbance factor in many ecosystems of the world (Mooney et al., 1980). Noteworthy among these is the shrub-dominated chaparral of California. Coincidence of summer drought, lightning and human ignitions, and dense community structure produce conditions in which fire is predictable (Keeley, 1980). It is generally believed that fire has been an important evolutionary factor in chaparral. The observations which suggest this are: 1) the even-aged (aboveground) shrub populations resulting from lack of recruitment in the absence of fire; 2) the long-lived refractory seeds which germinate readily in the first post-fire year; 3) the rapid regeneration by resprouting from specialized woody basal burls, and 4) the prolific post-fire herb flora with many "pyrophytic endemics" found only after fire.

The post-fire temporary cover of herbaceous and suffrutescent species is generally short lived and its persistence is closely tied to the recovery of the shrub populations. Previous studies indicate that for the first 5–10 yr after fire total cover (temporary plus shrubs) increases monotonically though shrubs account for a greater percent each yr (Sampson, 1944; Horton and Kraebel, 1955).

The rate of shrub recovery varies depending on several factors. A major one is the reproductive mode of the dominant shrubs (Sampson, 1944). Post-fire regeneration of most shrubs is through a combination of resprouts from underground parts and seedlings from soil-stored seed. Some species, though, lack the ability to resprout (Wells, 1969). Not only does the frequency of sprouting and non-sprouting species vary from site to site but the sprouting species vary in proportion of resprouts vs. seedling recruitment after fire (Keeley, 1977). Very little data are available on the factors which promote seedling establishment or regeneration from resprouts.

Other factors which affect shrub recovery include latitude, elevation, topography, slope aspect, and weather patterns (Hanes, 1977). In southern California a number of studies have

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TABLE 1. *Precipitation summary (July–June) from a station near the mid-elevation site (Boulder Creek) for the 1st 4 yr after fire. Measurable precipitation is generally between November and May. Annual patterns were similar at all sites though annual amount was positively related to elevation (Data from Dr. P. C. Miller, San Diego State University, pers. commun.)*

Precipitation (mm)				
1971	1972	1973	1974	21-yr mean[a]
340	310	700	330	551

[a] The 21-yr mode is ≈500 mm.

focused on post-fire shrub recovery, but few have been broad enough to consider many of these factors (Hanes and Jones, 1967; Vogl and Schorr, 1972; Keeley and Zedler, 1978). Hanes (1971) provided a broad overview of chaparral succession by comparing many different-aged stands on various slope aspects and at various elevations. The only intensive study of post-fire shrub recovery was that of Horton and Kraebel (1955). Their study provided information on the effect of elevation and weather patterns on shrub recovery but ignored the role of slope aspect. At present we are far from a complete understanding of how the factors listed above affect shrub regeneration.

This study was designed to provide information on the following questions: 1) What is the quantitative relationship between total cover and shrub cover in the first few post-fire years? 2) What effect does slope have on shrub recovery? 3) How does elevation affect rate of shrub recovery? 4) How does reproductive mode, resprouting vs. seedling recruitment, vary across slope and elevation and does it affect rate of shrub recovery? An opportunity for such a study was afforded by the extensive "Laguna" and "Boulder" fires which burned uncontrollably for over 70,000 ha in San Diego County during September and October 1970.

STUDY SITES AND METHODS—Three sites were chosen along an elevation gradient at Alpine (560 m), Boulder Creek (1,000 m) and Kitchen Creek (1,670 m). At each site, burned areas on the major slope exposures (N,S,E,W,) were sampled in late spring (April–June) of 1971, 1972, 1973, 1974. Seasonal precipitation totals for the mid-elevation site are shown in Table 1. These totals are for July–June, though measurable precipitation is normally restricted between November and May. The 1st, 2nd and 4th yr after fire were markedly subnormal whereas above average rainfall occured in the 3rd yr. Though the absolute amount of precipitation increases with elevation, the annual pattern is highly correlated across all sites (Miller et al., 1977).

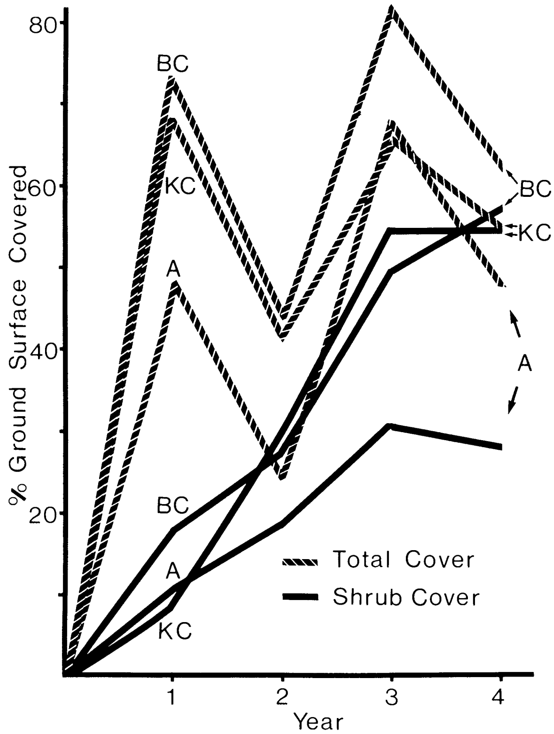

FIG. 1. Post-fire successional changes in total cover (temporary herbaceous and suffrutescent species plus shrubs) and shrub cover alone, at the low-elevation Alpine site (A), mid-elevation Boulder Creek site (BC) and high-elevation Kitchen Creek site (KC).

Each slope was sampled with 10–20 10-m transects using the line intercept method (Bauer, 1943). All plants intersecting the line were recorded as to the length of the transect covered and height. Multiple-stemmed plants such as shrub resprouts were recorded as a single individual. The exact number of transects was determined by species area curves (Rice and Kelting, 1955). Community indices of percent ground surface covered and relative density for each species were calculated as described by Cox (1967).

RESULTS AND DISCUSSION—*Community changes*—The first spring after fire there was a prolific herbaceous and suffrutescent growth at all sites. Total cover (temporary vegetation plus sparse shrub growth) was 48–72% ground surface, dependent upon site (Fig. 1). Total cover fluctuated markedly during the first 4 yr after fire. Averaged across all 12 slopes, there was a statistically significant ($P \leq 0.01$ with 2-tailed t-test) drop the second year after fire, a significant ($P \leq 0.01$) increase the 3rd yr followed by a significant ($P \leq 0.01$) drop in the 4th yr. These fluctuations in total cover were obviously due to changes in the temporary cover as the shrub cover (Fig. 1) showed significant increases each year through the third year ($P \leq 0.01$ with 2-tailed t-test averaged across all slopes). Thus in the early post-fire years temporary cover was not closely linked to shrub cover; e.g., in the second year shrubs constituted a much greater proportion of the total cover than in the 3rd yr even though absolute shrub cover increased.

These fluctuations in total cover are likely related to annual differences in weather conditions adversely affecting temporary cover in certain years. This is suggested by the strong similarity between sites in these annual fluctuations. The 2nd- and 4th-yr drops in total cover are perhaps due to subnormal precipitation in those yr, and the 3rd-yr peak may be related to the above normal precipitation that yr (Table 1 and Fig. 1). If precipitation accounts for these patterns it appears that 1st-yr cover values are not greatly reduced by rainfall deficits.

Rate of increase in shrub cover was positively related to elevation through the 3rd yr. There was little or no increase in shrub cover at any site during the fourth year. Total cover and shrub cover alone, were significantly different between sites in all but the 4th yr; generally the lowest elevation sites had the lowest cover (1-way ANOVA comparing sites across slopes). In the 4th-yr shrubs consitiuted ca. 100% of the total cover at Kitchen Creek but only 58% at Alpine.

Shrub cover showed no obvious relationship with precipitation patterns, with two possible exceptions. The lower shrub cover observed at Alpine in most years may be tied to the fact that precipitation typically is less at lower elevations. Related to this is the observation that shrub cover is also typically less at lower elevations (Horton and Kraebel, 1955; Horton, 1960). The 4th-yr hiatus in shrub growth (Fig. 1) is not commonly observed in chaparral (Sampson, 1944; Horton and Kraebel, 1955) and may result from the 4th-yr precipitation deficit. If so, the fact that total rainfall in the 1st and 2nd yr was also subnormal suggests that shrub sensitivity to soil moisture deficits increases as cover increases (eg., Schlesinger and Gill, 1978, 1980). Observations in later years indicated this plateau in shrub cover was temporary.

Throughout succession slope aspect had no significant effect on total cover. Shrub cover was significantly affected by slope only at the lowest elevation site: Alpine. At this site, cover on the north-facing slope was significantly greater through the first 4 yr than on the south- or west-facing slopes ($P \leq 0.05$ with 1-way ANOVA comparing slopes across years).

Twenty shrub species were found including five common to all three sites: *Adenostoma fasciculatum* H. & A., *Arctostaphylos glandulosa* Eastw., *Quercus dumosa* Nutt., *Rhamnus crocea* Nutt. in T. & G. (including *R. C.* ssp. *ilicifolia* (Kell.) C. B. Wolf), and *Yucca whipplei* Torr. Ground cover and relative density for the dominant shrubs is given in Tables 2 and 3.

Adenostoma fasciculatum was important in terms of numbers and cover on all slope aspects at all sites. At Alpine *Adenostoma* cover was approximately the same on all slopes (Table 2) but relative density varied greatly (Table 3). It was the sole dominant on the south- and west-facing slopes. On the more mesic north-facing slope, for the 1st 2 yr, *Adenostoma, Ceanothus tomentosus* var. *olivaceus* Jeps., and *Xylococcus bicolor* Nutt. had very similar cover values (Table 2). However, numerically over this time period *Ceanothus tomentosus* was ca. 3 × ≥ *Adenostoma* and *Adenostoma* was ca. 3 × ≥ *Xylococcus* (Table 3). This pattern is tied very closely to the ratio of resprouts:seedlings observed for these species (Table 4). In this instance the heavily seeding *Ceanothus* eventually dominated the north-facing slopes; by the third year it had 3 × > cover than either of the other dominants.

At Boulder Creek *Adenostoma* was almost the sole shrub on the south-facing slope and covered over 80% ground surface by the fourth year after fire (Table 2). This was over twice the *Adenostoma* cover found on any other slope. Only the north-facing slope was not dominated by *Adenostoma*; in the 1st post-fire yr it was numerically as abundant as *Q. dumosa* (Table 3) but *Adenostoma* had only one-third the cover of *Q. dumosa*.

All slopes at Kitchen Creek were dominated by a cover of *Adenostoma* (Table 2). Numerically though, *Ceanothus greggii* var. *perplexans* Jeps. far surpassed *Adenostoma* on all but the north-facing slope (Table 3). The nonsprouting *C. greggii* was a major exception to the general pattern of shrub recruitment in the 1st post-fire yr. It was entirely absent the 1st yr and subsequent checks showed *C. greggii* seedlings did not establish until spring of the 2nd yr.

Population dynamics—The above ground parts of most shrubs were destroyed by fire and regeneration was by resprouts from un-

TABLE 2. *Percent ground surface covered for dominant shrubs on all slopes for the 1st 4 yr after fire at the low- (Alpine), mid- (Boulder Creek), and high- (Kitchen Creek) elevation sites*

	Percent ground surface covered presented by yr after fire															
	North				South				East				West			
	Yr				Yr				Yr				Yr			
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Alpine:																
Adenostoma fasciculatum	4	10	12	10	3	10	15	16	5	7	15	14	5	8	12	10
Ceanothus tomentosus	5	9	28	31					2	<1	19	7				
Xylococcus bicolor	4	10	7	11	<1	1			4	7	10	<1	1	2		
Yucca whipplei	1	1		<1	<1	<1	1	<1	<1	<1	2	7	2	1	<1	
(nine other species)	3	4	1	<1	1	2			<1	1	<1	1	1	1		<1
Boulder Creek:																
Adenostoma fasciculatum	5	14	18	17	7	18	39	82	20	32	44	35	4	12	18	21
Quercus dumosa	15	20	15	28		<1			3		4	4	8	3	17	10
Ceanothus leucodermis	<1	4	3	3					<1	<1			1	3	27	12
Arctostaphylos glandulosa	2	2	5	3							<1	1		<1	<1	<1
(eight other species)	0	1	5	2	<1			<1	1	2	3	5	2	<1	<1	<1
Kitchen Creek:																
Adenostoma fasciculatum	5	13	31	41	4	28	37	34	7	20	29	26	5	14	15	22
Ceanothus greggii		3	10	9		5	20	24		7	23	23		1	9	9
Quercus dumosa	3	1	9	3	<1	1	<1		1		5	9	<1	9	6	5
(seven other species)	2	1	7	6	2	2	2	<1	<1	3	5	5	2	3	9	5

derground parts and/or by seedlings from soil-stored seed. *Yucca whipplei* was an exception in that no seedlings were encountered in the 1st post-fire yr and individuals with aboveground parts destroyed did not resprout, however, the aboveground parts of many individuals survived fire. One reason for this may be the fact that *Y. whipplei* generally occurs in openings within the chaparral matrix, where the fuel build-up is less.

Ceanothus greggii is also totally incapable of resprouting after fire. Typically, though, *C. greggii* and most other nonsprouting chaparral shrub species produce refractory seeds which require intense heat to break the seedcoat. Consequently, seedling establishment gener-

TABLE 3. *Relative density for dominant shrubs on all slopes for the 1st 4 yr after fire at the low- (Alpine), mid- (Boulder Creek) and high- (Kitchen Creek) elevation sites*

	Percent relative density by year after fire															
	North				South				East				West			
	Yr				Yr				Yr				Yr			
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Alpine:																
Adenostoma fasciculatum	23	20	16	12	88	90	92	98	53	31	27	52	86	89	95	95
Ceanothus tomentosus	61	67	77	80					38	50	61	39				
Xylococcus bicolor	8	9	6	7	1	2	2		7	5	11	2	2	2		
Yucca whipplei	3	1		<1	7	3	6	2	1	2	<1	6	7	2	2	
(nine other species)	3	3	1	1	3	5	0	0	1	11	1	1	5	6	3	5
Boulder Creek:																
Adenostoma fasciculatum	39	50	37	41	98	97	100	99	87	87	85	75	51	65	34	56
Quercus dumosa	41	26	13	22		1			7		3	3	35	10	10	9
Ceanothus leucodermis	4	12	16	17					4	<1			6	22	54	33
Arctostaphylos glandulosa	15	7	6	8								3		3	2	1
(eight other species)	1	5	28	12	2	1	0	1	2	12	12	19	8	0	0	1
Kitchen Creek:																
Adenostoma fasciculatum	51	47	49	55	64	46	37	39	67	36	32	33	59	44	28	41
Ceanothus greggii		40	40	37		51	59	60		59	63	60		35	52	50
Quercus dumosa	33	2	3	1	20	<1	<1		23		2	4	17	10	5	4
(seven other species)	16	11	8	7	16	3	4	1	10	5	3	3	24	11	15	5

TABLE 4. *Percent of 1st-yr population from resprouts for dominant sprouting species for each slope face at the three sites*

	Percent (resprouts/resprouts and seedlings)											
	Alpine				Boulder Creek				Kitchen Creek			
	N	S	E	W	N	S	E	W	N	S	E	W
Adenostoma fasciculatum	54	45	27	33	76	68	83	57	65	94	89	86
Quercus dumosa	100			100	100		53	100	31	67	47	62
Cercocarpus betuloides	83							100		100	100	100
Arctostaphylos glandulosa					89				100	100	100	
Xylococcus bicolor	100	100	100	100								
Ceanothus tomentosus	12		13									

ally occurs in the 1st post-fire yr (Hanes, 1977). The pattern of 2nd-yr seedling establishment observed for *C. greggii* at Kitchen Creek (Tables 2, 3) suggests a unique set of circumstances at that site. Since such a phenomenon may be of practical use as a manipulative tool by land managers it might be useful to suggest reasons for this anomaly.

Because of the lack of any proximate seed source after fire the most likely hypothesis is that fire failed to scarify the *C. greggii* seeds properly. If the *C. greggii* seeds were not scarified by the fire they very likely would have been scarified by the soil temperatures in the 1st post-fire yr; Christensen and Muller (1975) found soil temperatures in areas devoid of shrubs could reach 78 C, which is sufficient to scarify *Ceanothus* seeds (Quick, 1935; Quick and Quick, 1961; Hadley, 1961). Since these seeds require stratification after scarification, seedling establishment would be postponed to the following spring. Since scarification of *Ceanothus* seeds requires only ca. 5 min at 70 C, it would be an exceptional fire which failed to stimulate germination. Several factors may have contributed to such conditions. In August 1970, just prior to the fire, the Kitchen Creek area received an unusual 52 mm of precipitation (P. C. Miller, San Diego State Univ., unpubl. data). The greater litter layer at this high-elevation site (Wilson and Vogl, 1965) may have been important in providing insulation, since litter is capable of holding its own weight in moisture and will not burn when it contains more than 8% moisture (Show, 1919).

For the resprouting shrubs there were marked differences between species and within species, in proportion of post-fire individuals from resprouts vs. seedlings (Table 4). *Adenostoma* had a greater proportion of seedlings at the lowest elevation site but a very high proportion of resprouts at the highest elevation site. The reverse pattern was observed for *Quercus dumosa*. Large differences in proportion of resprouts were evident at Alpine. *Xylococcus* and *Q. dumosa* failed to establish any seedlings, whereas seedlings made up the bulk of the *Ceanothus tomentosus* population.

There are great differences in growth rate of resprouts and seedlings, as evidenced by differences in height at the end of the 1st growing season, (Table 5). Resprouts were significantly taller than seedlings in all species ($P \leq 0.01$ with 1-tailed t-test). Within a site, there was no significant difference between species in seedling height ($P > 0.05$ with 1 way ANOVA). Resprout height on the other hand showed some significant differences between species ($P \leq 0.05$). *Adenostoma* typically had the shortest resprouts and *Quercus dumosa* and *Cercocarpus betuloides* Nutt. ex T. & G. had the tallest. Only *Adenostoma* heights are presented by slope because of small sample sizes obtained for other species. For this species there were large differences between slopes at Alpine and Boulder Creek, but no consistent pattern is obvious. At Kitchen Creek there was essentially no difference in resprout height between slopes for *Adenostoma*, and very little difference between species.

CONCLUSIONS—Post-fire succession in chaparral is unique in that in the 1st yr, two vegetation components are present: the temporary herbaceous and suffrutescent species, and the species which will comprise the permanent shrub cover. In general, as total cover increases through succession, shrubs comprise a greater proportion of it. Although shrubs eventually eliminate the temporary species, it is apparent from this study that early changes in temporary cover are unrelated to shrub cover but are rather closely tied to precipitation patterns.

Shrub cover typically increases each year after fire until it reaches a level characteristic of mature stands (Rundel and Parsons, 1979). The plateau in shrub cover observed between

TABLE 5. *Height of resprouts and seedlings at the end of spring, 1st yr after fire, for dominant species at each site*

		Height (cm)					
		Alpine		Boulder Creek		Kitchen Creek	
		Resprouts	Seedlings	Resprouts	Seedlings	Resprouts	Seedlings
Adenostoma fasciculatum							
Slope	N	34	11	30	9	29	7
	S	25	9	47	16	27	13
	E	40	6	31	12	27	8
	W	32	6	27	11	26	5
$\bar{X}$		33	8	33[a]	12	27[ab]	8
SD & (*N*)		13 (90)	4 (148)	11 (221)	6 (68)	9 (140)	7 (31)
Quercus dumosa							
$\bar{X}$		55[a]		47	12	30[ab]	7
SD & (*N*)		33 (4)		16 (58)	7 (8)	14 (31)	3 (43)
Cercocarpus betuloides							
$\bar{X}$		69[a]		45		31[ab]	
SD & (*N*)		16 (5)		(1)		9 (22)	
Arctostaphylos glandulosa							
$\bar{X}$)				29[a]	5	23[a]	
SD & (*N*)				11 (8)	(1)	14 (21)	
Xylococcus bicolor							
$\bar{X}$)		59[a]					
SD & (*N*)		18 (25)					
Ceanothus tomentosus							
$\bar{X}$		16	10				
SD & (*N*)		8 (21)	6 (150)				

[a] Species within a site with the same superscript are not significantly different ($P > 0.05$ with 1 way ANOVA). For all species seedling height is significantly less than resprout height ($P \leq 0.01$ with 1-tailed *t*-test).

the 3rd and 4th yr in this study was temporary as indicated by later observations. Perhaps this plateau was related to a rainfal deficit.

Elevation and slope aspect differences in soil moisture may affect rate of shrub recovery. In the present study, shrub cover was positively related to elevation as is annual precipitation (Miller et. al., 1977). Although total cover was similar across sites in the 4th yr, shrubs constituted 58% at the lowest elevation site and 100% at the highest. Slope aspect affected rate of shrub recovery only at the lowest elevation. At this site shrub cover on the more mesic north-facing slope was significantly greater, through the first 4 yr, than on the south- or west-facing slopes.

Mode of recovery by chaparral shrubs varies with species and site; some shrubs reestablish entirely by resprouts, others entirely by seedlings and many by a combination. In this study slope had no apparent effect on proportion of resprouts:seedlings. Elevation appeared to have an effect which varied with the species. The ratio of resprouts to seedlings increased with elevation for *Adenostoma*. High *Adenostoma* seedling establishment at low elevation has been observed in other localities (Howe and Carothers, 1980). The *Adenostoma* pattern however is not characteristic of all species. The present study found that the proportion of resprouts to seedlings was negatively related to elevation for *Q. dumosa*. Other studies report little or no seedling establishment for *Q. dumosa* and it has been suggested that the acorn is poorly adapted to fire (Keeley and Zedler, 1978). As a matter of speculation it may be that the high *Q. dumosa* seedling establishment observed at Kitchen Creek is tied to the unusual precipitation prior to fire, as discussed in the previous section. Although resprouts have an apparent size advantage over seedlings in the 1st post-fire yr, successful reestablishment occurs by either resprouts, seedlings, or their combination.

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