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DETERMINANTS OF POSTFIRE RECOVERY AND SUCCESSION IN MEDITERRANEAN-CLIMATE SHRUBLANDS OF CALIFORNIA

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Abstract. Evergreen chaparral and semideciduous sage scrub shrublands were studied for five years after fires in order to evaluate hypothesized determinants of postfire recovery and succession. Residual species present in the immediate postfire environment dominated early succession. By the fifth year postfire, roughly half of the species were colonizers not present in the first year, but they comprised only 7–14% cover. Successional changes were evaluated in the context of four hypotheses: (1) event-dependent, (2) fire interval, (3) self-regulatory, and (4) environmental filter hypotheses. Characteristics specific to the fire event, for example, fire severity and annual fluctuations in precipitation, were important determinants of patterns of change in cover and density, supporting the ''event-dependent'' hypothesis. The ''fire interval'' hypothesis is also supported, primarily through the impact of short intervals on reproductive failure in obligate seeding shrubs and the impact of long intervals on fuel accumulation and resultant fire severity. Successional changes in woody cover were correlated with decreases in herb cover, indicating support for ''self-regulatory'' effects. Across this landscape there were strong ''environmental filter'' effects that resulted in complex patterns of postfire recovery and succession between coastal and interior associations of both vegetation types.

Of relevance to fire managers is the finding that postfire recovery patterns are substantially slower in the interior sage scrub formations, and thus require different management strategies than coastal formations. Also, in sage scrub (but not chaparral), prefire stand age is positively correlated with fire severity, and negatively correlated with postfire cover. Differential responses to fire severity suggest that landscapes with combinations of high and low severity may lead to enhanced biodiversity. Predicting postfire management needs is complicated by the fact that vegetation recovery is significantly controlled by patterns of precipitation.

Key words: annuals; chaparral; environmental filters; fire interval; fire severity; nitrogen; obligate seeders; precipitation; residual species; resprouters; sage scrub.

''Plant populations respond in remarkably diverse ways to fire.''

—Bond and van Wilgen (1996)

INTRODUCTION

Fire is a natural ecosystem process throughout boreal, temperate, and tropical regions of the world. In mediterranean-climate shrublands it nearly always results in crown fires that replace stands and initiate a postfire succession, which returns these communities to a close approximation of their prefire state in one to two decades (Rundel 1981, Kruger 1983, Christensen 1985, Keeley 1986, Trabaud and Prodon 1993, Lavorel 1999). Mechanisms driving secondary succession can be accounted for by processes of facilitation, inhibition, or tolerance (Connell and Slayter 1977, Pickett et al. 1987), but core to all successional models are predictable temporal changes in plant populations (Peet and Christensen 1980, Huston and Smith 1987, Pickett et al. 1987).

Recently Bond and van Wilgen (1996) offered three hypotheses for plant population changes in fire environments. The ''*event-dependent*'' hypothesis argues that population fluctuations are driven by the unique circumstances of a fire, e.g., fire intensity or postfire climate. The ''*fire-interval*'' hypothesis sees variation in the fire return interval as the main cause of population response to fire, e.g., state of the vegetation at the time of fire is determined by the length of the fire-free period and this is the primary determinant of population changes after fire. Their third is the ''*self-regulatory*'' hypothesis, which contends that changes in populations are regulated, not by extrinsic factors, but by internal density-dependent controls. To these we add a fourth, the ''*environmental-filter*'' hypothesis, which argues that postfire changes in plant populations are regulated by spatially variable extrinsic environmental

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PLATE 1. Chamise (*Adenostoma fasciculatum*) basal burl with postfire resprouts. Photo credit: J. Keeley.

factors. These vary across landscapes, and species responses sort along various gradients; for example, generalizations about how communities reassemble after fire may differ on mesic vs. xeric sites, sandy vs. clay substrates, or coastal vs. interior locations. These four factors provide a framework for understanding vegetation response to fire disturbance and subsequent changes, and need not be viewed as mutually exclusive hypotheses.

Mediterranean-climate regions of California support two distinct shrubland vegetation types, evergreen chaparral and smaller stature semideciduous sage scrub that are periodically burned by high-intensity fires. These crown fires kill all aboveground biomass over broad portions of the landscape and initiate a successional sequence leading to community recovery within a few decades (Sampson 1944, Horton and Kraebel 1955, Keeley et al. 1981, Westman and O'Leary 1986). One important characteristic of postfire recovery is that the prefire dominants are typically represented by seeds or rootstocks in the postfire environment, leading to what Hanes (1971) termed the ''auto-successional'' model of chaparral succession (see Plate 1). In addition, most successional sequences involve a postfire-endemic flora of diverse life forms that is rather ephemeral. Life forms most important in these shrublands (and the Raunkiaer equivalents) are: annuals (therophytes), herbaceous perennials (cyptophytes and hemicryptophytes), suffrutescents (diminutive chamaephytes that exhibit substantial annual dieback), subshrubs (larger chamaephytes that exhibit little dieback), and shrubs and occasional trees (phanerophytes). While the fire response in these ecosystems is thought to center around residual species present prior to disturbance, there has been no study of the importance of colonization processes or the mechanisms determining pathways and outcomes of postfire succession.

In this paper we investigate these four hypotheses as explanations for postfire response in different life forms and evaluate the role of residual vs. colonizing species in postfire recovery and succession. Throughout this study our focus is on contrasting the evergreen chaparral vegetation type with the semideciduous sage scrub type. In much of the analysis we detected differences between coastal and interior locations for both vegetation types and have reported the responses of these four plant associations.

This study took advantage of a rare coincidence of wildfires that burned ~100 000 ha during a two-week period in the autumn of 1993 across southern California, USA, and included both evergreen chaparral and semideciduous sage scrub. This event provided an opportunity to examine postfire recovery and succession, stratified by both vegetation type and coastal vs. interior plant associations, without the confounding influence of different fire seasons (Beyers and Wakeman 2000).

SITES AND METHODS

Study sites

Sites were distributed across 16 fires that burned in the last week of October and/or first week of November of 1993 (Fig. 1). The number of study sites in each burn was based on fire size, diversity of vegetation types, fire severity, and accessibility. Criteria for selection included absence of other disturbances, proximity to roads for easy access, roughly equal proportion of chaparral and sage scrub (Fig. 2), and low- and high-severity fires in the collective sample. Ninety sites were distributed across a 300-km range and included a wide range of vegetation types and environmental variation (Table 1). This landscape has a very complex geology and sites were located on granitic fault block uplift, volcanic extrusions, marine terraces, and alluvial deposits, although these factors were not included in our analysis.

Sampling of these 90 sites began in the first spring after fire and continued for a total of five growing seasons (two sites were lost to development after the second year). Coastal sites were designated as those from the Laguna Canyon, Old Topanga, and Green Meadows fires, and interior sites comprised all of the remaining

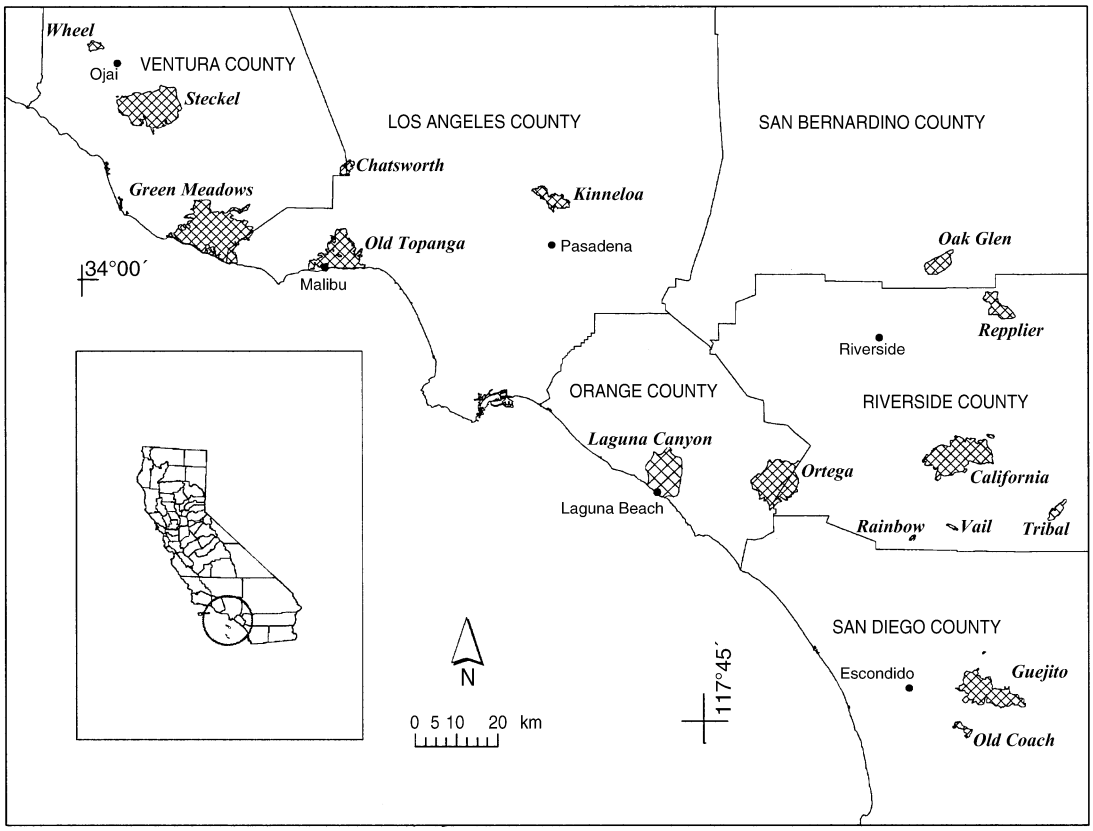

FIG. 1. Fires in southern California, USA, that burned in late October and early November of 1993 were studied in this investigation. Most fires included both chaparral and sage scrub vegetation types. Coastal associations were from the three fires adjacent to the coast in Ventura, Los Angeles, and Orange counties, the Green Meadow, Old Topanga, and Laguna Canyon fires. All other fires were considered interior associations.

fires depicted in Fig. 1. For sage scrub, coastal associations are equivalent to the ''Venturan'' and ''Diegan'' association, and interior associations to the ''Riversidian'' association of Westman (1983*b*).

Precipitation (NOAA 1993–1998) totals for the growing season (September–August) during the five-year study were averaged from several climate stations distributed within the range of coastal sites and interior sites (Fig. 3). The second year was nearly double the long-term average, and the fifth year was an El Niño year of exceptionally high rainfall.

Sampling design and analysis

Vegetation was sampled in 20 × 50 m (0.1-ha) sites with nested subplots, and to this extent had much in common with the widely cited ''Whittaker plot'' method (Shmida 1984). However, the highly clumped distribution of subplots in the Whittaker design is appropriate only for sites where the vegetation is homogeneous at the 0.1-ha scale. Our sites were heterogeneous with species turnover along both the short and long axes (Keeley 2004), and in order to capture more of this pattern we used a design with greater dispersion of nested subplots across the 0.1-ha area (Fig. 4). Briefly, the 0.1-ha sites were subdivided into 10 nonoverlapping 100-m^2 square plots, each containing two 1-m^2 subplots in opposite corners (interior subplots were offset 1 m from the center to reduce contagion effects with the adjacent plot). Within each 1-m^2 subplot, density and cover were estimated for each species, and within the 100-m^2 plots a list was made of additional species. Site factors recorded were slope aspect and slope inclination. Sites were located on 15-minute USGS quadrangle topographic maps and used to determine elevation and distance from the coast. Annual solar insolation was estimated from slope aspect, inclination, and latitude (Frank and Lee 1966). Surface litter was collected within a 20 cm diameter hoop from three alternate plots at each site, dried, and weighed. Three soil samples from the top 6 cm of soils with poorly developed horizons were collected from alternate plots and combined and dried in paper bags. Texture analysis was done according to Cox (1995). The pH was determined with a pH meter on an equal mixture of soil and dH_2O incubated overnight at room temperature. Soil nutrients, total soil N, P, and C were determined on a subsample at the Soils Laboratory, USDA Forest Service, Forest Fire Laboratory, River-

FIG. 2. Example of first spring recovery in (a) interior chaparral, with shrub skeletons in the background and ephemeral fire-endemic annuals in the foreground, and (b) interior sage scrub, with resprouting subshrubs and annual grasses and forbs.

side, California. Soil analysis was done in the middle of the first growing season and used in regression analysis with vegetation responses of later years. Plant nomenclature follows Hickman (1993).

Prefire stand age was determined from basal stem sections on nonsprouting *Ceanothus* or *Arctostaphylos* when available; otherwise *Adenostoma fasciculatum* was sampled. Two measures of fire severity were based on skeletal remains of chaparral and sage scrub shrubs. Fire severity index no. 1 was based on the diameter of the smallest twig remaining on the shrub skeleton (Moreno and Oechel 1989) within or closest to the center of each 1-m^2 subplot. Stem diameters were classified into categories 1–10, with 10 being the largest diameter twigs and highest fire severity. A separate scale was used for evergreen chaparral shrubs and semideciduous sage scrub (Keeley 1998). Fire severity index no. 2 was based on the height above ground level of shrub skeletal remains within each of the 100-m^2 plots.

Data were analyzed initially by association (sites were classified as coastal chaparral, interior chaparral, coastal sage scrub, or interior sage scrub). Where significant differences were detected these were presented. Otherwise data were summarized by vegetation type (chaparral or sage scrub) or analyzed collectively for all sites. Data were analyzed and graphically displayed with SYSTAT 10.0 (SYSTAT, Chicago, Illinois, USA).

Relationships between variables were tested for significance by regression analysis and significant relationships were fitted with least squares regression lines. Where bivariate data did not fit an arithmetic relationship, semilog and log-log transformations were compared and the one giving the highest adjusted R^2 value was presented. Between-treatment comparisons used *t* tests, or one-way or two-way ANOVA with the Bonferroni post hoc test for differences between groups. Comparisons using calculated indices that were not normally distributed were made with the Kruskal-Wallis test.

Pre- and postfire changes in woody plant density were based on comparison of skeletal remains of shrubs and subshrubs (and occasional trees) with postfire plant resprouts and seedlings. In each 100-m^2 plot, all skeletons were recorded by species, identification aided by close examination of form, branching pattern, and bark. In a small percentage of cases (<1%) skeletal remains were unidentifiable. These data were compared with postfire density of shrubs and subshrubs using the following measure of similarity (Whittaker 1975):

$$\mathrm{PS} = 1 - 0.5 \sum_{i=1}^{s} |p_a - p_b|$$

where PS is percentage similarity, p_a is the proportional density of a species at a site before fire and p_b is the density after fire, and s is the total number of woody species.

Successional changes in the entire community were evaluated by calculating Jaccard's index (Barbour et al. 1999) for the first and fifth years postfire, weighted by either cover or density as

$$\mathrm{JI} = \left(\frac{\mathrm{MC}}{\mathrm{MA} + \mathrm{MB}}\right) \times 100$$

where MC is the cover or density of species present in both the first and fifth years, MA is cover or density for species present only in the first year and MB the same for the fifth year.

RESULTS

Prefire and postfire comparisons

Using woody skeletons as an indicator of prefire composition, all shrubs and subshrub species present before fire were represented in the first postfire growing season as resprouts and/or seedlings. Density-weighted percentage similarity values (Table 2) showed that all vegetation types exhibited a high proportion of structural similarity between pre- and postfire communities. After five years of recovery, coastal sage scrub communities had progressed significantly closer to their prefire woody plant density.

TABLE 1. Summary of site characteristics for the 90 sites in southern California, USA, established in spring 1994, following wildfires that burned between 26 October and 5 November 1993 (see Fig. 1).

Parameter	Range
Number of sites by plant association	coastal chaparral, n = 14 coastal sage scrub, n = 22 (21 after yr 2) interior chaparral, n = 26 interior sage scrub, n = 28 (27 after yr 2)
Latitude	33°30′–34°30′
Distance from coast (km)	1–74
Elevation (m)	60–1225
Aspect	all aspects represented
Inclination (°)	0°–42°
Insolation of calculated annual irradiance ($KJ \cdot m^{-2} \cdot yr^{-1}$)	611–1330
Prefire stand age fire (yr)	3–60
Fire severity†	
Index 1	1.2–9.2
Index 2	2.0–9.5
Rock cover (ground surface covered, %)	0–61
Soil	
Rock (%, by mass)	0–66
Organic matter (%, by mass)	0–1
pH	5.9–7.1
Sand (%)	25–79
Clay (%)	8–39
Total nitrogen (%)	0.06–0.49
Phosphorus (%)	0.01–1.20
Carbon (%)	0.81–8.10

† See *Sites and methods: Sampling design and analysis.*

Successional changes in life forms

Species richness ranged between 35 and 59 species/0.1 ha in the first postfire year (Table 3). Over the course of this five-year study a substantial number of species dispersed into these sites, and over this period richness averaged 72–95 species/0.1 ha, with one site having as many as 119 species. Species that colonized after the first postfire year comprised 37–50% of the flora in year 5, but comprised only 4–14% cover (Table 3). Thus colonization was an important component of biodiversity, but postfire succession was clearly dominated by residual species present in the first year from resprouts or dormant seed banks.

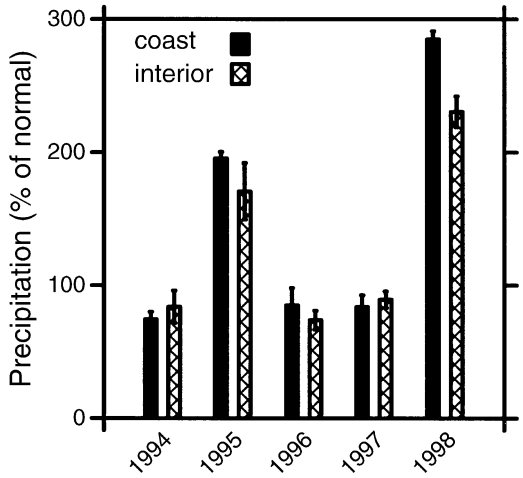

FIG. 3. Precipitation over the five years postfire averaged from stations near sites on the coast and in the interior, years 1994–1998. Error bars represent ±SE.

In the first postfire year total cover was ~68% ground surface cover on both coastal and interior chaparral sites, but ranged from 52% on coastal sage scrub sites to 83% on interior sage scrub. The prefire dominant shrubs and subshrubs regenerated in the first postfire spring from vegetative resprouts (see Plate 1) and germination of dormant seed banks. On average they comprised ~15% cover, except on interior sage scrub sites where they were only 5% (Fig. 5a, b). Semiwoody suffrutescent species were similarly represented in both vegetation types, but in interior sage scrub they comprised a greater proportion of cover than shrubs and subshrubs (Fig. 5c, d). The herbaceous cover was ~50% on both coastal and interior chaparral, but the former was dominated by herbaceous perennials and the latter by annuals (Fig. 5e, g). In coastal sage scrub, herbaceous species were mostly perennials, whereas in interior sage scrub the bulk of the herb flora was annuals (Fig. 5f, h).

During the first five postfire years there were significant differences in total cover and a highly significant interaction between year (i.e., time since disturbance) and plant association (Table 4). Both year and association showed significant differences and interactions for most life forms. Subshrubs, however, showed no significant interaction (Table 4), and this is

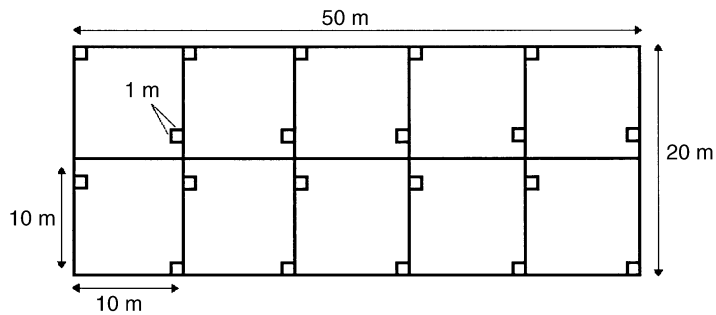

FIG. 4. Sample design (0.1 ha). Cover and density were recorded from each of the 20 1-m^2 subplots, and additional species were recorded from the surrounding 100-m^2 plots (see comparison with other sample designs in Keeley and Fotheringham [2005]).

reflected in the fact that the woody component followed similar trajectories for all four plant associations (Fig. 5a–d). In chaparral the herbaceous component declined, but remained high in sage scrub (Fig. 5h). On interior chaparral and sage scrub sites, annuals exhibited a peak in the second postfire year and on the latter sites a second peak in the fifth year (Fig. 5g, h).

During the first five years total cover was positively correlated with postfire year in all four plant associations (Table 5). With the exception of coastal chaparral, total cover was also strongly correlated with annual precipitation (Table 5). With few exceptions these patterns were true of shrubs and subshrub cover as well. Suffrutescent cover consistently exhibited a significant positive increase from year to year, but no relationship with precipitation. Herb cover was mostly not correlated with either year or precipitation, with a few exceptions. Herbaceous perennials increased with postfire year in coastal sage scrub, and annuals declined with year in interior chaparral and increased with precipitation in interior sage scrub.

Herbaceous species commonly dominate the early postfire years and many are ephemeral. In chaparral these life forms were not significantly correlated with woody cover until year 5, when both annuals and herbaceous perennials showed significant negative relationships with woody cover (Fig. 6a, c). In sage scrub there was a negative relationship between woody cover and annual cover in all but the first year (year 5 shown in Fig. 6b), and a positive relationship between woody cover and herbaceous perennials in all but the second and fifth years (Fig. 6d). For both chaparral and sage scrub, year 5 suffrutescent cover was unrelated to woody cover (Fig. 6e, f).

Jaccard's index was used to contrast communities in the first year with those on the same site in the fifth postfire year (Table 6). Similarity in species composition was approximately 40%, or in other words there was roughly a 60% turnover in species for all four plant associations. There were three main drivers of change: mass flow of other postfire species from surrounding burned areas, colonization by outside alien species, and loss of postfire-endemic species. When Jaccard's index was weighted by density or cover, the structural similarity of the first and fifth postfire years was substantially reduced over that based on species composition alone (Table 6). Successional changes in cover-weighted community composition were significantly less in interior chaparral than in coastal associations.

In sage scrub total cover was strongly correlated with Jaccard's index of change between the first and fifth years (Fig. 7). In other words, sage scrub communities with high postfire cover changed the least in the subsequent postfire years. In chaparral the structural changes evident after five years were unrelated to the initial cover. Cover of different life forms in the first year exhibited different changes during postfire succession (Fig. 8). In chaparral, presence of herbaceous perennial species was negatively correlated with the change in Jaccard's index between the first and fifth years. In other words, sites dominated by herbaceous perennials in the first year exhibited the greatest structural changes by year 5. Chaparral sites dominated by suffrutescent species in the first year exhibited the least structural changes, and annuals and subshrubs exhibited no significant correlation. In sage scrub the initial cover of herbaceous perennials and suffrutescents were unrelated to structural changes by year 5 but first-year

TABLE 2. Percentage similarity in woody species density between prefire and first year postfire and prefire vs. fifth year postfire for each of the four plant associations.

Association	Percentage similarity: Prefire vs. year 1 (mean + SE)	Percentage similarity: Prefire vs. year 5 (mean + SE)	P
Coastal chaparral	0.554 + 0.053	0.534 + 0.059	NS
Coastal sage scrub	0.438 + 0.070	0.616 + 0.038	<0.05
Interior chaparral	0.539 + 0.042	0.507 + 0.039	NS
Interior sage scrub	0.607 + 0.043	0.659 + 0.039	NS

Note: The similarity index was compared using a Kruskal-Wallis test, NS = $P > 0.05$.

TABLE 3. Species density in the first year and across all five postfire years, and percentage of species and their density and cover for species colonizing after the first postfire year.

Association	Species density (no. species/0.1 ha)				Year 5 species not present in year 1 (%)		
	Year 1		Years 1–5				
	Mean ± SE	Max.	Mean ± SE	Max.	Species	Weighted by density	Weighted by cover
Coastal chaparral	45.6 ± 3.3	65	78.5 ± 3.6	96	46	23	8
Coastal sage scrub	35.4 ± 2.1	58	72.3 ± 1.9	91	50	23	14
Interior chaparral	53.0 ± 2.6	74	85.5 ± 3.3	119	37	17	4
Interior sage scrub	58.5 ± 2.4	85	94.7 ± 2.4	119	39	11	7

dominance of annuals and subshrubs was correlated with greater structural similarity between years 1 and 5.

Environmental filters

Vegetation response to environmental factors is complicated by correlations between various site factors. For example, in both chaparral and sage scrub, distance inland was strongly correlated with elevation and negatively correlated with soil characteristics such as percentage clay, nitrogen, and carbon (Table 7). In sage scrub, distance inland was also negatively correlated with stand age and prefire shrub and subshrub density. Other correlations consistent in both vegetation types were the following. Calculated annual solar insolation was positively correlated with percentage sand. Fire severity measure no.1 was negatively correlated with prefire density, and fire severity measure no. 2 was negatively correlated with percentage phosphorus in the soil. Soil rockiness was positively correlated with prefire density and soil carbon. Sand was negatively correlated with clay, nitrogen, and prefire density, and clay was positively correlated with prefire density.

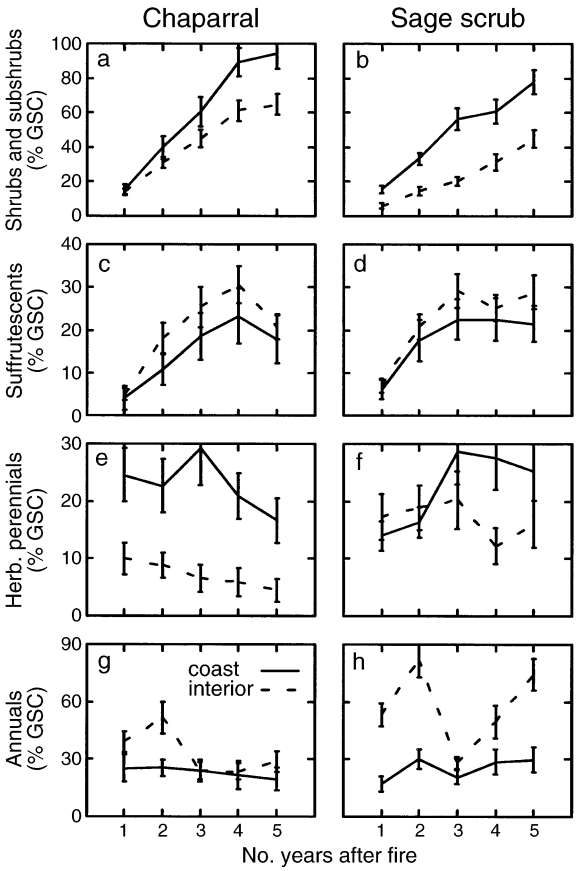

FIG. 5. Postfire changes in cover of life form types, stratified by vegetation type, and coastal vs. interior plant associations. Shrubs and subshrubs are lumped because they represent the dominant woody life form in chaparral and sage scrub, respectively. Data points show percentage of ground surface covered (% GSC). Error bars represent ±SE.

TABLE 4. Two-way ANOVA for plant cover vs. postfire year and plant associations (coastal chaparral, coastal sage scrub, interior chaparral, and interior sage scrub) for each life history type.

Dependent variable	df	*F*	*P*
Total cover			
Year	4	49.273	<0.001
Plant association	3	5.072	<0.01
Year × association	12	4.441	<0.001
Error	424		
Shrub cover			
Year	4	39.846	<0.001
Plant association	3	86.013	<0.001
Year × association	12	5.381	<0.001
Error	424		
Subshrub cover			
Year	4	28.249	<0.001
Plant association	3	21.951	<0.001
Year × association	12	1.561	>0.05
Error	424		
Suffrutescent cover			
Year	4	16.106	<0.001
Plant association	3	2.715	<0.05
Year × association	12	4.441	<0.001
Error	424		
Herbaceous perennial cover			
Year	4	1.208	>0.05
Plant association	3	17.603	<0.001
Year × association	12	1.328	>0.05
Error	424		
Annual cover			
Year	4	6.937	<0.001
Plant association	3	29.997	<0.001
Year × association	12	2.691	<0.01
Error	424		

TABLE 5. Regression coefficients between cover and postfire year and precipitation (Ppt.) by life history type for the four plant associations.

Association and variable	Total cover			Shrub cover			Subshrub		
	R	R^2	P	R	R^2	P	R	R^2	P
Coastal chaparral (n = 70)									
Year	0.599	0.349	***	0.602	0.352	***	0.417	0.161	***
Ppt.	0.172	0.015	NS	0.252	0.050	*	0.178	0.017	NS
Coastal sage scrub (n = 107)									
Year	0.698	0.482	***	0.541	0.286	***	0.466	0.210	***
Ppt.	0.328	0.099	***	0.310	0.088	***	0.213	0.036	*
Interior chaparral (n = 130)									
Year	0.390	0.145	***	0.523	0.268	***	0.396	0.150	***
Ppt.	0.227	0.044	**	0.165	0.020	NS	0.221	0.041	*
Interior sage scrub (n = 137)									
Year	0.407	0.160	***	0.295	0.080	***	0.581	0.333	***
Ppt.	0.534	0.279	***	0.182	0.026	*	0.344	0.112	***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Phosphorus was positively correlated with nitrogen, which in turn was correlated with carbon.

Of particular interest is the observation that fire severity was strongly correlated with prefire stand age in both coastal and interior sage scrub, but unrelated to stand age in chaparral (Fig. 9). Fire severity index no. 2 (height of skeletons) in both vegetation types was negatively correlated with soil phosphorus levels, but severity was not correlated with either soil nitrogen or carbon (Table 7). Nitrogen and carbon were strongly correlated with each other, and the residuals were largely negative at the lowest nitrogen levels (Fig. 10a), indicating that the expected carbon:nitrogen ratios were higher at low nitrogen. Across all sites postfire soil nitrogen was correlated with prefire density of nitrogen-fixing *Ceanothus* species (Fig. 10b). Because of these marked colinearities, this section focuses strictly on bivariate relationships between plant responses and environmental parameters.

Total cover in the first postfire year in chaparral was correlated only with elevation ($R = 0.312$, $P < 0.05$, $n = 40$), whereas in sage scrub it was negatively correlated with prefire stand age and fire severity ($R = -0.618$ and $R = -0.578$, respectively, $P < 0.001$, $n = 50$). Patterns in other years are detailed in the Appendix. By the fifth postfire year, total cover in both chaparral and sage scrub was negatively correlated with solar insolation ($R = -0.467$, $P < 0.01$, $n = 40$ and $R = -0.357$, $P < 0.05$, $n = 48$, respectively) and fire severity index no. 2 ($R = -0.339$ and $R = -0.389$, respectively, $P < 0.01$).

Relationships between environmental parameters and cover of different life forms were complex and varied with postfire year (Table 8). In the first postfire year in chaparral, fire severity was negatively correlated with subshrub and herbaceous perennial cover, whereas in sage scrub, fire severity was positively correlated with shrub and suffrutescent cover and negatively correlated with subshrub, and herbaceous perennial and annual cover. These relationships were evident for many years after fire. For example, five years after fire, subshrub and herbaceous perennial cover were still negatively correlated with fire severity in both chaparral and sage scrub.

Soil texture and nutrient levels were correlated with various life forms (Table 8). In the first postfire year in chaparral, clay content was negatively correlated with shrub cover, whereas in coastal sage scrub it was positively correlated with subshrubs, herbaceous perennials, and annuals. Soil nitrogen in the first year was positively correlated with herbaceous perennials in chaparral and negatively correlated with annuals in sage scrub, and this first-year soil nitrogen level continued to show these relationships later in succession. First-year soil nitrogen level was also positively related to shrub cover in later years in chaparral and sage scrub, and in the latter vegetation with subshrub cover. Of interest is the observation that solar insolation was not correlated with cover of any life form in the first postfire year, but in subsequent years it was negatively correlated with shrub and subshrub cover and late in succession with herbaceous cover in sage scrub.

The relationships between environmental parameters and successional change are illustrated by correlations with Jaccard's index, based on species in common between the first and fifth years unweighted or weighted by log density or log cover (Table 9). In chaparral the greatest change in density was correlated with distance from the coast and negatively correlated with rock cover and soil nitrogen. Unweighted species composition changes were greatest on sites exposed to less severe burning, but the most severely burned sites exhibited the greatest change in cover-weighted comparisons. In sage scrub, weighted and unweighted measures of postfire change were negatively correlated with prefire stand age and fire severity (Table 9). Density-weighted changes were strongly correlated with distance inland, elevation, and various soil parameters.

TABLE 5. Extended.

Suffrutescent			Herbaceous perennials			Annuals		
R	R^2	*P*	*R*	R^2	*P*	*R*	R^2	*P*
0.296	0.074	*	−0.138	0.005	NS	−0.098	0.000	NS
0.030	0.000	NS	−0.170	0.014	NS	−0.053	0.000	NS
0.249	0.053	**	0.230	0.044	*	0.136	0.001	NS
0.092	0.000	NS	0.001	0.000	NS	0.149	0.013	NS
0.313	0.091	***	−0.164	0.019	NS	−0.217	0.040	*
0.006	0.000	NS	−0.068	0.000	NS	0.099	0.002	NS
0.370	0.131	***	−0.062	0.000	NS	0.028	0.000	NS
0.146	0.014	NS	−0.003	0.000	NS	0.371	0.131	***

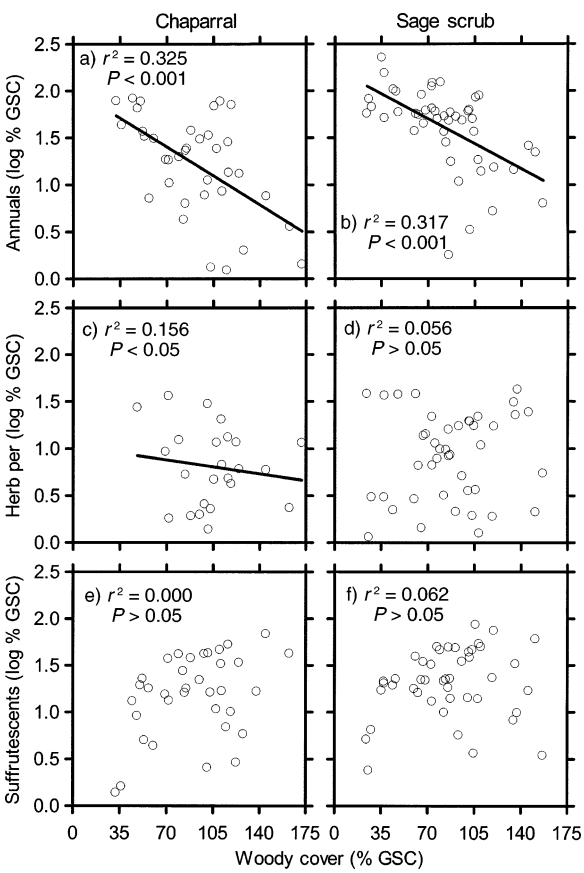

FIG. 6. Year 5 relationship of woody cover (shrubs and subshrubs) and annual, herbaceous perennial, and suffrutescent cover in chaparral (n = 40 sites) and sage scrub (n = 48 sites). Data points show the log percentage of ground surface covered (% GSC). The exponential model provided the highest r^2 value of the models tested (arithmetic and power).

Floristic affinities

In both density and cover the first postfire year flora was dominated by species endemic to California (Table 10). In sage scrub a substantially greater proportion of the flora was represented by species more widespread throughout the western United States. By year 5 aliens dominated in density but comprised proportionately less cover in both vegetation types, although substantially greater in sage scrub.

DISCUSSION

Life forms and early successional changes

Postfire succession in these mediterranean-climate shrublands is driven largely by residual species present at the time of fire. These residual species are predominantly California endemics that survive fire by underground or ground level vegetative structures (see Plate 1) and soil-stored seed banks. Postfire colonization is unimportant in determining the first-year flora. The vast majority of seedling species present in the first growing season were not present in the prefire stands, except as dormant seed banks (Keeley 2000). Most of these species could not have dispersed onto the site after fire because their normal phenological pattern is to disperse propagules in spring and summer, prior to these autumn fires, and in addition most have passive dispersal (Keeley 1991). The few species that disperse in late autumn, after the fires, were mostly minor weedy elements, and were not important until later postfire years. In terms of dominant shrub and subshrub density, pre- and postfire vegetation exhibited remarkable similarity, from 44 to 61% (Table 2).

The primary determinants of pre- and postfire similarity are related to whether the site is dominated by resprouters or seeders. In chaparral some of the dominant resprouting species suffer little mortality and do not recruit seedlings; thus sites dominated by these species exhibit high similarity between pre- and postfire conditions. In contrast, obligate and facultative

TABLE 6. Comparison of first- and fifth-year composition and structure in the four plant associations based on presence/absence or weighted by density or cover.

Association	*n*	Jaccard's index of similarity between years 1 and 5†		
		Species	Density	Cover
Coastal chaparral	14	40.8 + 8.3	13.1 + 10.8	11.4[a] + 8.2
Coastal sage scrub	21	39.9 + 8.7	6.9 + 7.3	16.0[a] + 9.2
Interior chaparral	26	39.4 + 7.6	8.1 + 7.6	25.0[b] + 15.8
Interior sage scrub	27	43.1 + 10.4	8.2 + 5.2	17.2[a,b] + 5.8
P		>0.05	>0.05	<0.001

Note: Comparisons of association means are with one-way ANOVA; means with the same superscript are not significantly different at $P > 0.05$.
† Mean + SD.

seeders usually exhibit massive increases in population density in the first postfire year. During the subsequent four years there is a slow attrition, and major thinning does not occur until canopy closure after a decade or more (Schlesinger et al. 1982); thus there is little change in woody plant density between the first and fifth postfire years (Table 2). In this study the only significant change in woody plant density was in coastal sage scrub, due to seedling recruitment patterns that were quite unlike those observed in the other three associations. This coastal sage scrub association is dominated by resprouting subshrubs, *Encelia californica* and *Hazardia squarrosa*, which lack a dormant seed bank, and thus they have no seedling recruitment in the first postfire year. However, the resprouts flower profusely, and massive seedling recruitment occurs in the second postfire year (Keeley and Keeley 1984; J. E. Keeley, C. J. Fotheringham, and M. B. Keeley, *unpublished manuscript*). Thus, coastal sage scrub exhibited the greatest change in woody plant density during the first five postfire years (Table 2). On interior sage scrub sites, these two species are absent and most of the prefire subshrubs resprout weakly and are present in the first season largely as seedlings. This lack of resprouting by interior sage scrub associations has been reported by others as well (Westman et al. 1981, Myers 1984, O'Leary and Westman 1988). In general, on all but the coastal sage scrub sites, the first five years postfire do not result in substantial changes in woody plant density. However, what does change during these early years is increased size, and thus cover of woody species (Fig. 5a, b, Table 5).

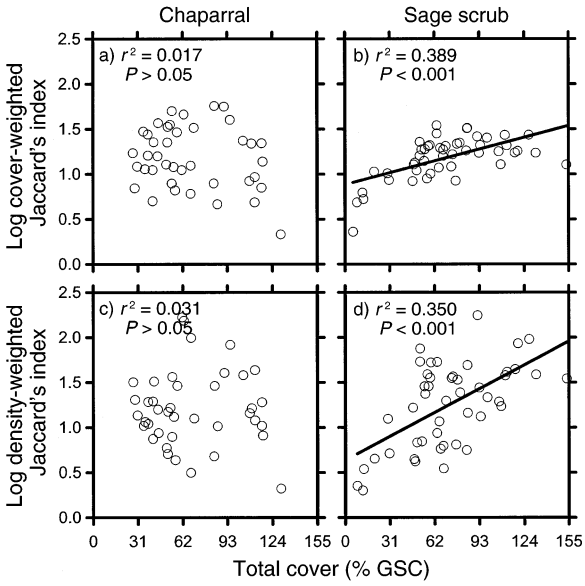

FIG. 7. Jaccard's index comparing community structure in year 1 with year 5 vs. total cover in the first postfire year, stratified by vegetation type.

Successional changes were largely driven by changes in cover of different life forms (Fig. 5). On all sites shrub and subshrub cover increased steadily during succession, but the patterns with other species varied with life form type, and there were significant interactions between yearly changes and vegetation type (Table 4). Coastal chaparral dominants recovered quickly and other life forms declined. Coastal sage scrub dominants recovered rapidly, but these subshrubs continued to share space with herbaceous perennials. Interior sage scrub was markedly unlike other vegetation types in that the woody dominants recovered slowly and sites were dominated by annuals in both early and late years, dependent on rainfall. Even in mature stands of both chaparral and sage scrub, annuals continue to fluctuate in response to patterns of annual precipitation (Westman 1983*a*).

In general, for the majority of species, the bulk of the density and the cover in year 5 was contributed by species that were present in the first postfire year (Table 3). While a substantial number of species colonized these sites during succession, by year 5, when dominants had recovered a substantial amount of their prefire size, colonizing species accounted for a relatively small amount of cover. Although residual species present in the first year accounted for most of the cover in year 5 (Table 3), cover-weighted analysis of the species indicate that there were major shifts in species dominance during these five years (Table 6). In sage scrub the level of residual species recovery in the first postfire year affected the rate of change in subsequent years, and sites with high cover in the first year ex-

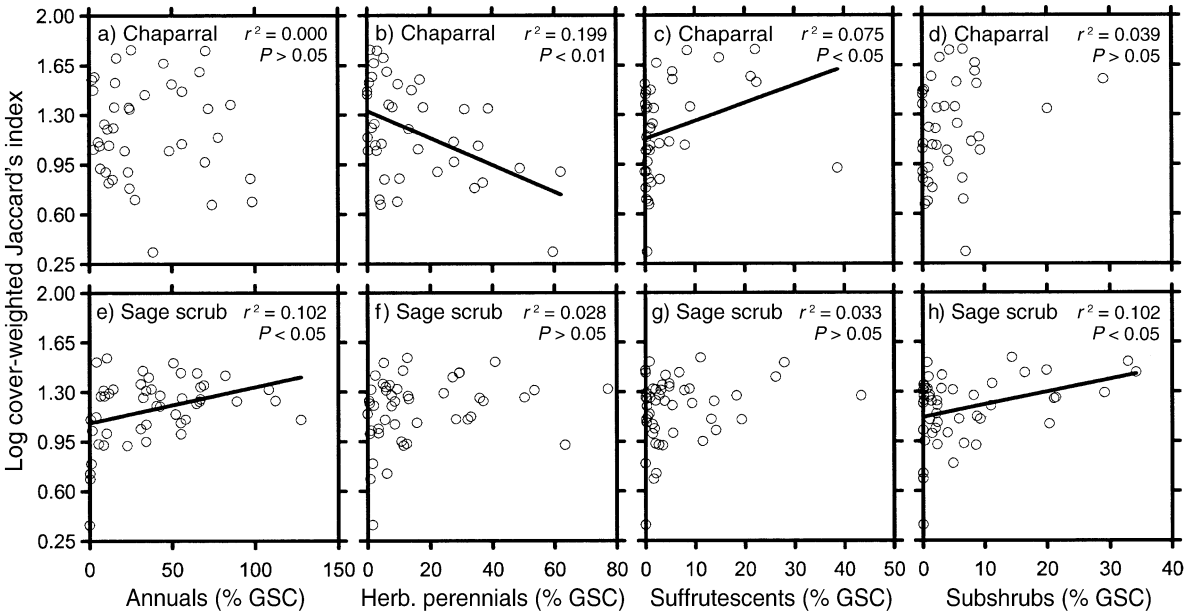

FIG. 8. Jaccard's index comparing community structure in year 1 with year 5 vs. first-year cover of (a, e) annuals, (b, f) herbaceous perennials, (c, g) suffrutescents, and (d, h) subshrubs in (a–d) chaparral, and (e–h) sage scrub vegetation types.

hibited the least change in later years (Fig. 7). Early successional changes were correlated with first-year dominance patterns of different forms, but chaparral and sage scrub were quite different (Fig. 8). Chaparral sites with low herbaceous perennial cover and those with high suffrutescent cover in the first year exhibited the greatest change during early succession. On sage scrub sites the greatest changes were associated with high initial cover of annuals and subshrubs.

Determinants of early successional change

Postfire regeneration and successional changes in plant populations are determined by: (1) unique events due to the fire, the event-dependent hypothesis; (2) changes resulting from the length of the fire-free interval, the fire-interval hypothesis; (3) internal density-dependent controls, the self-regulatory hypothesis; and (4) external environmental factors, the environmental filter hypothesis. Distinguishing the important drivers of succession is of course complicated by the strong colinearity of many variables (Table 7).

Event-dependent effects

Two important determinants of postfire succession are the severity of the fire event and subsequent patterns of annual precipitation. In sage scrub both fire severity metrics were negatively related to first-year cover, and this effect was still evident in the fifth year. In contrast, fire severity was not correlated with total cover in chaparral, and we hypothesize that the difference in response of these two vegetation types is driven by the differences in woody dominants. Chaparral is dominated by large-stature shrubs, whereas sage scrub is dominated by smaller subshrubs that are less tolerant of high-severity fires. Supporting this conclusion is the fact that in chaparral, fire severity had a negative effect on subshrub cover in the first postfire year, and this effect persisted throughout early succession (Table 8). The effect of different fire severities on resprouting ability of subshrubs has been inferred in other studies

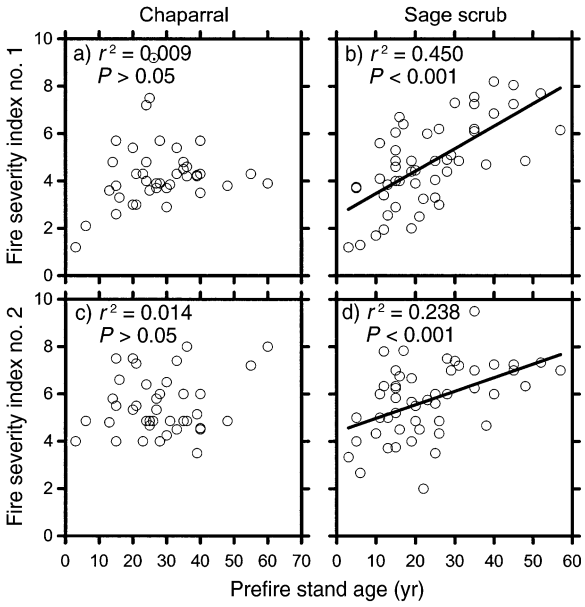

FIG. 9. Effect of prefire stand age on fire severity index in chaparral and sage scrub vegetation types.

TABLE 7. Matrix of correlation coefficients for environmental site factors; $n = 50$ for sage scrub, and $n = 40$ for chaparral.

Variable	Variable†							
	1	2	3	4	5	6	7	8
1) Distance inland								
Chaparral	—							
Sage scrub	—							
2) Elevation								
Chaparral	0.750***	—						
Sage scrub	0.851***	—						
3) Insolation								
Chaparral	0.337*	0.396*	—					
Sage scrub	···	···	—					
4) Fire severity no. 1								
Chaparral	···	···	···	—				
Sage scrub	···	···	···	—				
5) Fire severity no. 2								
Chaparral	···	···	···	···	—			
Sage scrub	···	···	···	0.644***	—			
6) Rock cover								
Chaparral	···	···	···	···	···	—		
Sage scrub	0.290*	···	0.385**	···	···	—		
7) Surface litter								
Chaparral	···	···	···	···	···	···	—	
Sage scrub	···	···	···	···	···	···	—	
8) Soil rock (%)								
Chaparral	−0.370*	···	···	···	···	···	···	—
Sage scrub	···	···	···	−0.382**	···	0.343*	···	—
9) Soil sand (%)								
Chaparral	···	···	0.344*	···	···	···	···	···
Sage scrub	0.475***	0.466***	0.355**	···	···	···	···	···
10) Soil clay (%)								
Chaparral	−0.448**	−0.412**	−0.364*	···	···	···	···	···
Sage scrub	−0.456***	−0.427**	−0.443***	−0.306*	−0.394**	−0.278*	···	···
11) Soil pH								
Chaparral	···	···	···	···	···	−0.406**	0.341*	···
Sage scrub	0.280*	···	···	···	···	···	···	···
12) Soil P (%)								
Chaparral	···	0.315*	···	···	−0.310*	···	···	···
Sage scrub	−0.288*	−0.360**	···	···	−0.322*	···	···	···
13) Soil N (%)								
Chaparral	−0.457**	···	···	···	···	···	···	0.586***
Sage scrub	−0.607***	−0.638***	···	···	···	···	···	···
14) Soil C (%)								
Chaparral	−0.569***	···	−0.380*	···	···	0.316*	···	0.581***
Sage scrub	−0.446***	−0.489***	···	···	···	···	···	0.432**
15) Prefire stand age								
Chaparral	···	···	···	···	···	···	···	···
Sage scrub	−0.327*	···	···	0.671***	0.488***	···	···	−0.411**
16) Prefire density‡								
Chaparral	···	−0.354*	···	−0.441**	···	···	···	0.317*
Sage scrub	−0.431**	−0.432**	···	−0.293*	···	···	···	0.364**
17) Resprout coverage‡								
Chaparral	0.425**	···	···	···	···	···	···	−0.467**
Sage scrub	···	···	−0.409**	···	−0.353*	···	···	···

Notes: Table entries are correlation coefficients (r), presented separately for chaparral and for sage scrub. No r values are shown for $P > 0.05$ (indicated by ellipses).

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

† Numbers in column heads correspond to numbered row variables.

‡ Shrub and subshrub.

TABLE 7. Extended.

Variable†							
9	10	11	12	13	14	15	16
—							
—							
−0.665***	—						
−0.847***	—						
···	0.342*	—					
···	···	—					
···	···	···	—				
−0.615***	0.427**	···	—				
−0.492***	···	···	0.363*	—			
−0.389**	0.327*	···	0.463***	—			
−0.494***	···	···	···	0.936***	—		
···	···	···	0.347*	0.900***	—		
···	···	···	···	···	···	—	
···	···	···	···	···	···	—	
−0.368*	0.422**	···	···	···	0.313*	−0.524***	—
−0.303*	0.447***	···	···	0.324*	···	···	—
···	···	···	···	−0.336*	−0.365*	···	···
−0.331*	0.367**	···	···	···	···	···	0.528***

TABLE 8. Regression coefficients for cover of life history types vs. environmental parameters for the first five postfire years.

Life form, association, and parameter	Year 1	Year 2	Year 3	Year 4	Year 5
Shrubs					
Chaparral					
Insolation		−0.402**	−0.407**	−0.379*	−0.395*
Soil clay (%)	−0.418**				
Soil pH	−0.354*				
Soil N (%)			0.325*	0.349*	0.382*
Soil C (%)			0.340*	0.386*	0.413**
Fire severity index no. 1†		0.323*	0.369*	0.471**	0.461**
Sage scrub					
Distance inland	−0.455***	−0.443***	−0.570***	−0.479***	−0.532***
Elevation	−0.342*	−0.276*	−0.433**	−0.373**	−0.429***
Soil N (%)		0.328*	0.343*	0.374**	0.372**
Soil C (%)	0.320*	0.335*		0.444**	0.394**
Prefire stand age	0.325*	0.524***	0.587***	0.436**	0.490**
Fire severity index no. 1	0.405**	0.572***	0.536***	0.434**	0.523***
Fire severity index no. 2	0.385**	0.447**	0.392**	0.354*	0.428**
Subshrubs					
Chaparral					
Elevation			−0.354*	−0.372*	
Soil clay (%)		0.435**	0.409**	0.494***	0.407**
Prefire stand age	−0.323*	−0.318*			
Prefire density‡	0.421**	0.413**			
Fire severity index no. 1	−0.475**	−0.492***	−0.360*	−0.375*	−0.356*
Fire severity index no. 2				−0.367*	−0.378*
Sage scrub					
Distance inland	−0.361**	−0.355**	−0.354*		
Elevation	−0.438***	−0.475***	−0.440**	−0.398*	−0.305*
Insolation		−0.285*	−0.298*	−0.367**	−0.363**
Soil rock (%)	0.394**	0.364**		0.335*	
Soil sand (%)	−0.283*	−0.430**	−0.418**	−0.353*	−0.413**
Soil clay (%)	0.385**	0.472**	0.421**	0.303*	0.406**
Soil P (%)		0.385**	0.331*	0.367**	0.354*
Soil N (%)		0.296*	0.312*		
Prefire stand age	−0.309*	−0.318*			
Prefire density‡	0.817***	0.810***	0.790***	0.649***	0.685***
Fire severity index no. 1	−0.320*	−0.331*			
Fire severity index no. 2		−0.305*			−0.314*
Postfire resprout cover‡	0.594***	0.518***	0.545***	0.505***	0.673***
Suffrutescents					
Chaparral					
Soil clay (%)				0.314*	
Soil pH				0.376*	0.405**
Postfire resprout cover‡	0.381*				
Sage scrub					
Soil sand (%)	0.359*	0.347*	0.412***	0.376*	0.326*
Soil clay (%)			−0.358*	−0.324*	
Prefire density‡		−0.314*	−0.320*	−0.305*	
Fire severity index no. 1	0.363**	0.449***	0.303*		
Fire severity index no. 2	0.325*	0.385**	0.396**	0.328*	
Postfire resprout cover‡		−0.365*	−0.420**	−0.348*	−0.290*
Herbaceous perennials					
Chaparral					
Distance inland	−0.324*	−0.496***	−0.441**	−0.455**	−0.481**
Soil rock (%)		0.657***	0.609***	0.565***	0.530***
Soil sand (%)		−0.314*	−0.402**	−0.353*	
Soil clay (%)				0.463**	0.418**
Soil pH				0.313*	
Soil P (%)			0.378*	0.469*	0.315*
Soil N (%)	0.481**	0.500***	0.686***	0.448**	0.322*
Soil C (%)	0.499***	0.566***	0.741***	0.433**	
Prefire density‡		0.584***	0.548***	0.310*	
Fire severity index no. 2	−0.357*		−0.366*	−0.426**	−0.326*
Postfire resprout cover‡		−0.367*			−0.364*

TABLE 8. Continued.

Life form, association, and parameter	Year 1	Year 2	Year 3	Year 4	Year 5
Sage scrub					
Distance inland	−0.291*	−0.403**	−0.492***	−0.433**	
Elevation		−0.346*	−0.508***	−0.494***	
Insolation			−0.354*	−0.435**	
Soil sand (%)		−0.285*	−0.484***	−0.453***	
Soil clay (%)	0.283*			0.402**	0.412**
Soil P (%)			0.390**		
Soil N (%)		0.382**	0.415**	0.434**	
Soil C (%)		0.399**	0.330*	0.322*	
Prefire stand age	−0.436**	−0.374**	−0.331*		−0.296*
Prefire density‡				0.545***	0.461***
Fire severity index no. 1	−0.389**	−0.290*			
Fire severity index no. 2	−0.430**	−0.312*		−0.319*	−0.328*
Postfire resprout cover‡				0.329*	0.503***
Annuals					
Chaparral					
Distance inland	0.375*	0.541***		0.356*	0.315*
Elevation		0.396**			
Rock cover		−0.352*			
Prefire stand age			0.334*		
Sage scrub					
Distance inland	0.556***	0.666***			0.407**
Elevation	0.458***	0.598***			0.382**
Soil sand (%)					0.289*
Soil clay (%)	0.351*				
Soil N (%)	−0.288*	−0.347*			−0.345*
Soil C (%)				−0.284*	−0.345*
Prefire stand age	−0.409**				
Prefire density‡		−0.365**	−0.342*		−0.391**
Fire severity index no. 1	−0.446**				
Postfire resprout cover‡			−0.316*		−0.348*

Notes: Number of study sites were $n = 40$ for chaparral and $n = 50$ (years 1 and 2) and $n = 48$ (years 3–5) for sage scrub. Regression coefficients are not shown for $P > 0.05$.

† See *Sites and methods: Sampling design and analysis.*

‡ Shrub and subshrub.

(Westman et al. 1981). These studies also showed that the impact of fire severity on postfire regeneration is markedly different in coastal vs. interior sites, primarily because of the weak resprouting ability of interior sage scrub.

Similarly, herbaceous perennial cover in both vegetation types is inhibited by high-severity fires, as is annual cover in sage scrub (Table 8). Suffrutescent species, on the other hand, are favored by high-severity fires in sage scrub. These include mainly suffrutescent life forms *Lotus scoparius* (Fabaceae) and *Helianthemum scoparium* (Cistaceae), both of which are nonsprouters with deeply dormant seed banks that are triggered by intense heat (Keeley 1991), which may account for the positive relationship between fire severity and suffrutescent cover (Table 8). Shrubs were also positively associated with fire severity in both chaparral and sage scrub, and we hypothesize that this too is due

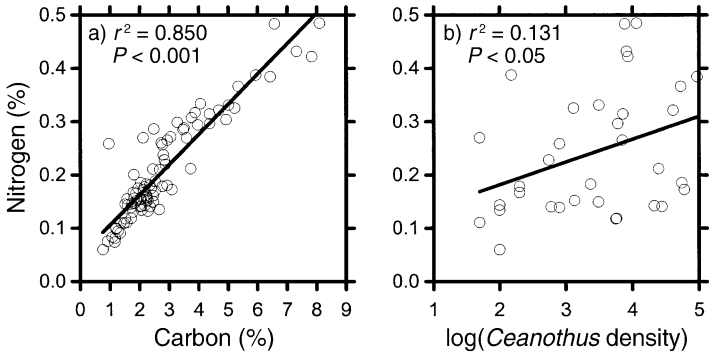

FIG. 10. First-year postfire relationship between (a) soil carbon and soil nitrogen and (b) between prefire *Ceanothus* density and soil nitrogen for all 90 sites combined.

TABLE 9. Regression coefficients for Jaccard's index between years 1 and 5 vs. environmental parameters.

Parameter and association	Jaccard's index		
	Species	Weighted by density (log)	Weighted by cover (log)
Distance inland			
Chaparral		0.327*	
Sage scrub	0.317*	0.632***	
Elevation			
Chaparral	−0.317*		
Sage scrub		0.499***	
Soil rock (%)			
Chaparral		−0.515***	−0.360*
Sage scrub			
Soil pH			
Chaparral			
Sage scrub	0.291*	0.339*	0.301*
Soil P (%)			
Chaparral			
Sage scrub		−0.306*	
Soil N (%)			
Chaparral		−0.339*	−0.319*
Sage scrub		−0.506**	−0.280*
Soil C (%)			
Chaparral			−0.338*
Sage scrub		−0.335*	
Prefire stand age			
Chaparral			
Sage scrub	−0.511	−0.570***	−0.544***
Fire severity index no. 1			
Chaparral	−0.340*		
Sage scrub	−0.403***	−0.523***	−0.439***
Fire severity index no. 2			
Chaparral			0.342*
Sage scrub			
Postfire resprout cover†			
Chaparral			
Sage scrub			0.305*

Notes: Sample sizes: $n = 40$ for chaparral and $n = 50$ (years 1 and 2) and $n = 48$ (years 3–5) for sage scrub. R values are not shown for $P > 0.05$.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.
† Shrub and subshrub.

to the effect of high temperatures on stimulating dormant seed banks, particularly of nonsprouting *Ceanothus* species as observed in other studies (Moreno and Oechel 1994). In the case of all of these taxa, high temperatures crack the seed coats of dormant seeds (Keeley 1991). Alternatively, it may be that higher *Ceanothus* seedling recruitment on sites with higher fire severity is not because seeds of these species are favored by high fire temperatures, but rather that the fuel characteristics of these species contribute to higher fire temperatures. Thus, as prefire *Ceanothus* density increases, both fuels contributing to higher fire intensities, and dormant seed banks, increase in parallel. Consistent with this is the hypothesis of Bond and Midgley (1995) that postfire recruiting species should be selected for maintaining fuel structure that increases fire intensity, and there is some empirical evidence for this (Schwilk 2003).

Precipitation exhibited weak effects on chaparral cover, but in sage scrub there were many more significant correlations between precipitation and cover of various life forms (Table 5). Precipitation was uniformly unrelated to changes in cover of either herbaceous perennials or suffrutescents, but annuals were markedly affected by precipitation in interior sage scrub associations (Table 5). In general there were peaks in annual cover in years 2 and 5 (Fig. 5h), years of exceptionally high rainfall (Fig. 3). Interior chaparral also exhibited a peak in annual cover in year 2 (Fig. 5g), but by year 5 the substantially greater shrub cover (Fig. 5a) apparently suppressed the response of annuals to the high El Niño rains. The strong control by precipitation is illustrated by the marked differences in annual responses from a chaparral study in which year 2 was a drought and the annual cover was greatly depressed that year, but peaked again in year 3, an El Niño year of high precipitation (Keeley et al. 1981). Similar controls on herb growth annual precipitation patterns have been reported for sage scrub as well (Myers 1984).

Thus, it is apparent that the fire event itself, both through differences in fire severity, and by the temporal

TABLE 10. Biogeographical comparison of first- and fifth-year floras based on relative cover and density.

Biogeographical province	Chaparral				Sage scrub			
	Relative density		Relative cover		Relative density		Relative cover	
	Year 1	Year 5	Year 1	Year 5	Year 1	Year 5	Year 1	Year 5
California endemics	1.00	0.72	1.00	1.00	1.00	0.45	1.00	1.00
Western United States	0.28	0.74	0.31	0.39	0.55	0.41	0.44	0.55
North America	0.05	0.20	0.02	0.01	0.07	0.11	0.03	0.03
Alien	0.19	1.00	0.17	0.14	0.58	1.00	0.24	0.30

Notes: All values are normalized to the group with the highest cover or density. California includes northern Baja California and southern Oregon; the Western United States includes mainland Mexico.

sequence of subsequent precipitation levels, can have significant effects on postfire recovery. Of particular interest is the fact that fire severity has species-specific effects, which are negative for some species and positive for others; thus it may be an important mechanism for maintaining biodiversity in these ecosystems (Davis et al. 1989, Odion and Davis 2000).

Fire-interval effects

Zedler (1995) categorized direct fire-interval effects on postfire shrubland regeneration as senescence effects due to deterioration of seed and bud banks resulting from very long fire-free periods, and immaturity effects due to short fire-free intervals insufficient for recovery of seed and bud banks. Senescence risk and immaturity risk, respectively, can be considered a form of the Intermediate Disturbance Hypothesis (e.g., Huston 1994). While there are no clear examples of regeneration failure due to senescence in California shrublands, there is evidence for such an effect in other shrubland ecosystems (Menges and Hawkes 1998). The major threat to California shrublands is immaturity risk, as there are numerous examples of reproductive failures due to immaturity (Zedler et al. 1983, Haidinger and Keeley 1993), and short fire intervals may cause extirpation of populations in other ecosystems as well. In the present study one example of immaturity risk was observed in one of the coastal chaparral sites that was four years of age at the time of the 1993 fire. The prefire population was codominated by the obligate-seeding *Ceanothus megacarpus* and the facultatively seeding (i.e., seeding and sprouting) *C. spinosus*. This fire-free interval was too short for the former species to develop a seed bank, and thus it was extirpated from the site (illustrated in Keeley 2000: Fig. 6.15).

In the present study long fire-free intervals were negatively correlated with postfire cover in sage scrub (Table 8), but it is unknown how much of this is due to direct age effects vs. the effect of stand age on subsequent fire severity (Fig. 9). The oldest stands were between 40 and 50 years, which would not seem to be long enough to cause the deterioration of seed banks or bulb and corm populations (Keeley 1977, Zammit and Zedler 1988, Odion 2000, Odion and Tyler 2002, Tyler and Borchert 2002); thus age-related changes in fire severity are a more likely explanation. On the other hand, we have observed for two dominant sage scrub species, *Artemisia californica* and *Eriogonum fasciculatum*, a negative age effect on resprouting (J. E. Keeley, C. J. Fotheringham, and M. B. Keeley, *unpublished manuscript*), similar to that reported for *Baccharis pilularis* (Hobbs and Mooney 1985).

Thus, above a certain threshold of a decade or more, fire interval appears to have little impact on recovery of chaparral. In sage scrub there may be both age effects on subshrub regeneration as well as fire severity impacts on recovery of other life forms.

Internal density-dependent effects

Sorting out the effect of self-regulatory processes would require experimental studies that were outside the scope of the present investigation. However, we can cite correlations that suggest some level of internal regulation. For example, in sage scrub, herbaceous perennials are positively correlated, and annuals negatively correlated, with soil nitrogen (Table 8). Because nitrogen levels are closely tied to the density of the nitrogen-fixing dominant *Ceanothus* (Fig. 10, see also Quideau et al. 1998), they may ultimately exert some control over these other life forms. This phenomenon has been shown with another Californian nitrogen-fixer, *Lupinus arboreus* (Maron and Jefferies 1999), in which elevated nitrogen levels in patches where the shrub has died favor invasion by alien grasses.

Huston and Smith (1987) suggest that one of the determinants of successional change involves life history trade-offs that result in competitive displacement of certain life forms with others by preempting resources. In the present study, shrub and subshrub recovery was negatively correlated with cover of annuals (Fig. 6), which supports this idea. The mechanism is likely the inhibitory effect of increasing cover on soil surface light levels (Tilman 1982), and such inverse relationships between overstory and understory cover have been widely noted (Specht and Morgan 1981, Westman 1983*a*, Davis et al. 1988). However, these competitive interactions are not asymmetrical, because abundant annual cover after fire may inhibit shrub seedling recruitment and growth (Kummerow et al. 1985, Bond 1987, Tyler 1996).

External environmental effects

In both chaparral and sage scrub, postfire recovery and successional changes vary markedly in response to a wide variety of environmental filters as described in other studies (e.g., Sweeney 1956, Keeley and Keeley 1984, Davis et al. 1988, O'Leary 1988). Based on the present study, chaparral cover is positively tied to elevation immediately after fire, but later in succession other factors such as solar insolation, and soil nitrogen, carbon, and clay content appear to be more important (Table 8). Similar changes in the importance of environmental factors during succession are also apparent for sage scrub as well. The rate of change in community composition during early succession also appears to vary with respect to fire severity and other environmental factors (Table 9). These, of course, are merely correlations suggestive of hypotheses that need testing. This is particularly important to keep in mind since there are many colinearities between environmental parameters (Table 7), and thus correlations with one variable may reflect a causal relationship with another variable that is linearly related.

Determinants of successional patterns are strongly tied to life form responses to different environmental

filters (Table 8). In chaparral, shrub recovery is slowest on south-facing slopes with high insolation and highest on sites with high soil nitrogen and carbon, but subshrub recovery is greatest on sites with high clay content. Herbaceous perennials decrease markedly with distance from the coast and on sandy substrates, but are promoted by the amount of rock cover and soil nutrients. In contrast, annuals increase with distance from the coast.

Sage scrub vegetation is dominated by subshrubs, and early in succession cover is negatively tied to distance from the coast (Table 8) (Kirkpatrick and Hutchinson 1980, O'Leary and Westman 1988), undoubtedly due to the predominance of resprouters near the coast and seeders in the interior (J. E. Keeley, C. J. Fotheringham, and M. B. Keeley, *unpublished manuscript*). Subshrub cover is less on sandy substrates, particularly on hot south-facing slopes, and herbaceous perennials follow the same pattern. Both also decline with elevation, probably because of the tendency for sage scrub to be replaced by chaparral at higher elevations, except on severe substrates. Some sage scrub associations have an evergreen shrub component, and this appears to be best developed on low-elevation coastal sites. In most years subshrub cover increased with increasing soil phosphorus, whereas shrub cover increased with soil nitrogen. On sandy substrates suffrutescents tend to replace subshrubs in sage scrub vegetation.

For both chaparral and sage scrub, life forms varied from year to year in their response to environmental filters (Table 8), which is likely tied to interactions between time since disturbance and precipitation. Annual cover is more closely tied to annual patterns of precipitation (Fig. 5g, h, Table 5), and in years of low rainfall showed limited association with other environmental factors, but exhibited numerous correlations with physical features of the landscape following the El Niño rains in year 5. Herbaceous perennials exhibited no relationship with precipitation (Fig. 5e, f, Table 5) and cover was markedly tied to numerous physical features of the environment during the very low rainfall years 3 and 4 (Table 8).

Conclusions

Determinants of postfire succession are complex and thus one should expect that tests of hypothesized effects will produce equivocal answers that apply to some life forms in the community but not others. Across the landscape, strong effects from environmental filters produce complex patterns that result in different responses between coastal and interior associations. In these mediterranean-climate shrublands all four of the hypothesized determinants play a role, with one of the important determinants being characteristics during and following the fire event, specifically the severity of the fire and the subsequent precipitation.

Of relevance to fire managers is the finding that postfire recovery patterns are substantially slower in the interior sage scrub formations, and thus require different management strategies than coastal formations. Also, in sage scrub (but not chaparral), prefire stand age is positively correlated with fire severity, and thus older stands are likely to have lower postfire cover. In addition, postfire resprouting of some sage scrub dominants is substantially weaker in older individuals. These findings would tend to support the use of fuel treatments such as prescription burning for resource benefit; however, there are other reasons why that may not be desirable. Higher cover produced by burning younger stands of sage scrub comes at the expense of native species, and favors the spread of alien invaders (Keeley et al. 2005). In addition, not all life forms are negatively affected by high-severity fires, and thus landscapes with combinations of high and low severity may lead to enhanced biodiversity. Predicting postfire management needs is complicated by the fact that vegetation recovery is significantly controlled by patterns of precipitation. High rainfall in the first postfire winter will contribute to more rapid vegetation recovery, and this contributes to greater slope stability and reduced sediment loss. Low rainfall slows vegetation recovery; however, during such dry winters postfire sediment loss is relatively minor and requires minimal management action (Loomis et al. 2003).

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APPENDIX

A table showing regression coefficients for total cover vs. environmental parameters for the first five postfire years is available in ESA's Electronic Data Archive: *Ecological Archives* A015-044-A1.