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## RELATIVE IMPORTANCE OF FACTORS CONTRIBUTING TO POSTFIRE SEEDLING ESTABLISHMENT IN MARITIME CHAPARRAL<sup>1</sup>

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**Abstract.** Several mechanisms have been proposed to explain the postburn flush of seedlings in the chaparral; these include direct effects of fire, such as heating of the soil and seed bank, and indirect effects of fire, such as a temporary reduction in competition by shrubs or herbivory by mammals. I conducted an experiment in burned and adjacent unburned chaparral to assess the relative importance of these mechanisms to seedling emergence and mortality of four functional plant groups: shrubs, subshrubs, perennial herbs, and annual herbs. I assessed direct effects of burning by comparing experimental plots in a burned area to plots in adjacent, unburned chaparral that were cleared of shrubs. In the unburned chaparral, competition with shrubs was manipulated by removing aboveground vegetation; herbivory by large mammals was manipulated using fence exclosures. The direct effects of burning enhanced emergence of shrub and subshrub seedlings, but reduced emergence of annual herbs. Shrub removal alone did not affect seedling emergence, but did improve survivorship of annuals. Exclusion of mammalian herbivores improved the survivorship of annual herbs and all seedlings combined. No single factor explained the high abundance of perennial herbs in the burn area; my results suggest that the combined removal of shrubs and herbivores following fire enhanced their growth and establishment. Thus, both the direct and indirect effects of fire contributed to the high postburn recruitment of seedlings in maritime chaparral, but different mechanisms were responsible for the increase in specific plant groups.

**Key words:** *burning; chaparral; competition; fire; herbivory; seedling emergence; shrub removal.*

### INTRODUCTION

Natural disturbances have been shown to be important in structuring many plant and animal communities, particularly by affecting patterns of recruitment (Pickett and White 1985). Where free space or associated resources are limited, disturbances that remove residents may create conditions favorable for recruitment. This could be accomplished by direct or indirect effects of the disturbance, including: (1) stimulation of seed germination or seed release; (2) alteration of the physical structure of the substrate; (3) replenishment of depleted nutrients; (4) elimination of toxic chemicals; (5) reduction of residents and, thus, competition; and (6) reduction of predator or parasite densities (Sousa 1984).

Fire is one agent of disturbance that affects a wide range of plant communities including grasslands, shrublands, savannas, woodlands, and closed forests (Kozlowski and Ahlgren 1974, Gill et al. 1981, Christensen 1985, Goldammer 1990). Following fire, there is often a "flush" of germination and growth not evident before the burn (Specht et al. 1958, Vogl and Schorr 1972, LeHouérou 1973, Whelan 1988). This postfire flush can include impressive displays of flowering plants, as well as species not seen in the community since the previous burn.

Chaparral, the shrubland found in the foothills of the southwestern United States, provides an excellent example of this phenomenon. Fire is a natural occurrence in this habitat, which is characterized by a Mediterranean climate with hot, dry summers and cool, wet winters. In the mature chaparral, few seedlings or herbs establish (Sampson 1944, Horton and Kraebel 1955, Christensen and Muller 1975a, Hanes 1977). After fires, however, great numbers of annual and perennial herbs and new shrub seedlings appear (Sampson 1944, Sweeney 1956, Keeley et al. 1981). The patterns of succession in chaparral have been observed for over a century (Brandeggee 1891), but the relative contribution of the mechanisms responsible for them remains poorly understood. Several mechanisms have been proposed and investigated to determine the means by which fire promotes the flush of new growth.

1) Fire may directly cause the burst of germination and growth in the chaparral by burning the soil and its contents, thereby stimulating seed germination, changing soil structure and nutrient levels, or volatilizing allelochemicals. There is considerable evidence that heating or burning significantly enhances emergence of some chaparral species (McPherson and Muller 1969, Christensen and Muller 1975a, Keeley et al. 1985, Keeley and Keeley 1987, Parker 1987).

2) Fire may indirectly affect seedling recruitment by removing competitors, particularly shrubs, allowing seedlings to gain access to resources. Therefore, the bloom observed after fire could be a result of either

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reduced competition for light and water, or reduced allelopathic influences. Previous workers have shown that removal of shrubs in unburned chaparral results in abundant emergence of seedlings (Went et al. 1952, Muller et al. 1968, McPherson and Muller 1969).

3) Finally, fire may reduce the abundance of natural enemies, both directly and indirectly. Insect and vertebrate herbivores, and pathogenic microorganisms and fungi may be directly killed by fire. In addition, shrubs serve as cover for some mammalian herbivores; when the shrubs are burned, herbivory may be reduced. Several investigators have shown that certain mammalian herbivores are associated with shrubs in mature chaparral, and that herbivory can limit seedling emergence and growth (Connell 1954, Bartholomew 1970, Halligan 1973, Christensen and Muller 1975b, Swank and Oechel 1990). It has also been shown that the density of some small mammalian grazers is reduced in a burned area (Lawrence 1966, Christensen and Muller 1975a). Thus, there is indirect evidence that a postfire reduction of herbivory, due to a temporary elimination in cover, may increase seedling recruitment.

The first hypothesis suggests that fire is directly responsible for the postburn phenomenon, whereas the last two suggest that fire indirectly produces the flush of seedlings by removing competitors (plants) or natural enemies (animals). Although each of the three factors described here has been shown to be significant independently, only one previous study, which was conducted in montane chaparral (Tyler 1995), has measured the relative importance of all three in producing the postburn burst of recruitment. In the present study, I manipulated several aspects of burning, competition by shrubs, and herbivory by mammals to assess the relative contribution of these direct and indirect effects of fire to seedling establishment in maritime chaparral.

## METHODS

### Site description

The study area was on the Burton Mesa within Vandenberg Air Force Base,  $\approx 100$  km northwest of Santa Barbara, California ( $34^{\circ}41'$  N,  $120^{\circ}36'$  W). The site was located on a plateau (elevation 199 m) in a  $\geq 50$ -yr-old stand of coastal maritime chaparral. The climate is Mediterranean, with hot, dry summers and cool, wet winters. Mean annual rainfall is 360 mm (Gibbs 1990; records from Lompoc Station, elevation 30.5 m, 6 km from the study site). Total precipitation for the rain year, September 1988 through August 1989, was 54.3 mm, well below average. Soils at the study site are derived from Orcutt sandstone, and are composed of sand deposits overlying shale or clay at a depth of 1–4 m. The soils are somewhat poorly drained because of the shallow hardpan, and have low fertility (Shipman 1972).

The topography at the study area is level and the vegetation is relatively short (maximum height  $\approx 1.5$

m). The dominant shrub is *Adenostoma fasciculatum* (chamise), intermingled with *Arctostaphylos purissima* and *Arctostaphylos rudis*. This maritime chaparral includes several endemic species, such as *Arctostaphylos rudis* and *Ceanothus impressus*, but most genera occurring at the site are also found in other chaparral environments (see Appendix). The vegetation and fire history of this area have been described in detail by Davis et al. (1988). Mammalian herbivores and seed predators that were present at the site included deer (*Odocoileus hemionus*), rabbits (*Lepus californicus*, *Sylvilagus bachmani*, and *S. auduboni*), and rodents (*Dipodomys agilis*, *Peromyscus* spp., *Neotoma fuscipes*, *Perognathus californicus*, *Reithrodontomys megalotis*).

A prescribed burn of 40 ha was carried out in October 1988 by the U.S. Air Force. Wildfires in chaparral generally occur in late summer and autumn, when the dry vegetation is further desiccated by hot, dry winds. Unlike wet-season management burns, the prescribed fire in the current study was conducted in the dry season, and thus simulated conditions of a "natural" wildfire.

### Estimates of vegetation and large mammal activity before the burn

Prior to the burn, in September 1988, after boundaries for the prescribed burn were established, vegetation was sampled and the percent of ground surface covered by mammalian scat was estimated along 20-m line transects. Thirty transects were established, 10 each in the following locations: (1) what would become the middle of the burn ( $>75$  m from the edge of the burn); (2) in the burn close to the edge ( $\approx 15$  m from the edge); and (3) in the adjacent unburned chaparral ( $\approx 15$  m from the edge). Vegetation was sampled using point-intercept methods; every 30 cm, all plant species from ground to canopy and canopy height were recorded. For a relative index of animal activity, I estimated the percent of ground surface covered by deer and rabbit scat within 1-m<sup>2</sup> quadrats every 2 m along the transects.

### Postburn experimental design

In December 1988, before noticeable seedling emergence or resprouting of shrubs in the burned area, I established experimental plots in three locations: the middle of the burn, the edge of the burn, and in the adjacent unburned chaparral. These plots were in the same general locations as the preburn transects, but were widely dispersed throughout the 40-ha burned area and the adjacent unburned chaparral.

Within the burn, fenced and unfenced plots were established in both the middle and at the edge sites (Fig. 1). In the adjacent unburned chaparral (along the south and east edges of the prescribed burn), treatments were (1) fenced cleared plots, (2) unfenced cleared plots, (3) fenced plots containing shrubs, and (4) unfenced control plots that contained shrubs (Fig. 1). In

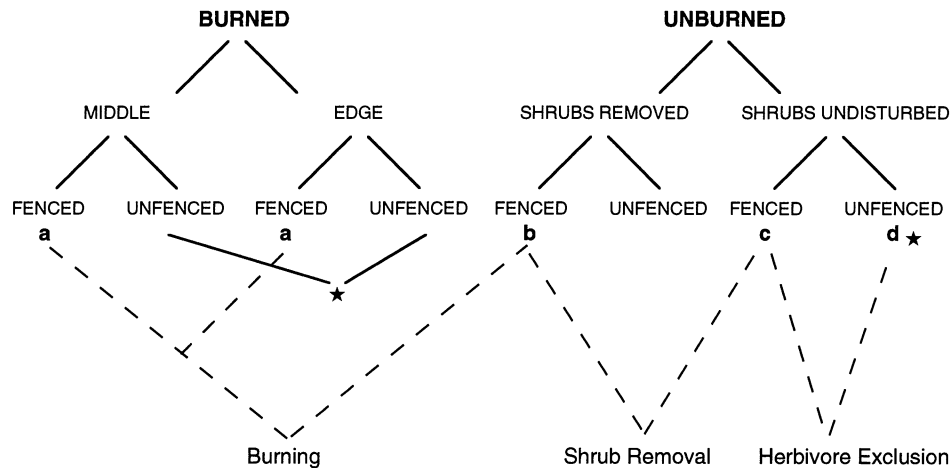


FIG. 1. Design of experiments and analyses. The top three rows indicate the eight experimental treatments. The lower dashed lines indicate the comparisons used to show the effect of each factor alone. Direct effects of burning: a vs. b; effects of shrub removal: b vs. c; effects of herbivore exclusion: c vs. d. Stars indicate the treatments used to document the postfire "flush."

"cleared" plots, all aboveground vegetation was manually removed, at the beginning of the study period, from a  $4 \times 5$  m area (larger than the plot size to facilitate installation of fences and to reduce shading and other influences from adjacent vegetation).

The fences for exclusion of mammalian herbivores (deer, rabbits, and large rodents) were constructed of 2 m high aviary wire (mesh size 2.5 cm), with steel stakes at the sides and corners. The area fenced was  $2 \times 3$  m to provide a 0.5-m border around the  $1 \times 2$  m area being sampled. To prevent mammals from burrowing into the plot, fences were buried  $\approx 10$  cm into the ground.

Experimental treatments were arrayed in a randomized block design with six replicates per treatment. Treatments were applied to subject plots ( $1 \times 2$  m), and were chosen to contain one to two *A. fasciculatum* shrubs or stumps and some bare area. Within each plot, seedlings were subsampled in 50 permanent, randomly chosen  $10 \times 10$  cm quadrats, making the total area sampled  $0.5 \text{ m}^2/\text{plot}$ . Seedlings were counted three times: in February, May, and November 1989.

#### Analysis of postburn experiments

For analysis, species were grouped into four plant types: shrubs, subshrubs (herbaceous perennials that become woody at the base), perennial herbs, and annual herbs (see Appendix). These functional groups have been used in previous studies of chaparral vegetation (Keeley et al. 1981, Davis et al. 1988). Only new seedlings, not sprouts, were included in analyses, with one exception: for some perennial herb species (geophytes), new seedlings and individuals that emerged from bulbs or corms could not be distinguished, so analyses include both for the perennial herb group.

To isolate the effects of single factors, I made planned comparisons to test specific hypotheses (Fig.

1). To test the hypothesis that direct effects of fire cause the postburn flush, I compared fenced plots in the burn to cleared fenced plots in the adjacent unburned chaparral. This comparison removes shrub competition and mammalian herbivory as factors (since neither is present); thus, the difference between the two treatments is due to the burning of the soil and seed bank. This treatment includes all direct effects of fire, including reduction of insect herbivores and pathogens, stimulation of seed germination, changes in soil structure, volatilization of allelochemicals, and changes in nutrient content.

To test the hypothesis that release from competition or interference by shrubs is the factor producing the postburn flush of growth, I compared unburned fenced plots with shrubs present to those with shrubs removed (fencing removes the confounding influence of herbivory). This treatment cannot distinguish between competition for resources and interference via toxic chemicals (allelopathy).

To test the hypothesis that release from mammalian herbivory produces the postburn flush of recruitment, I compared fenced plots to unfenced plots in the unburned chaparral with shrubs present. (I used plots with shrubs rather than those cleared for this comparison because shrub removal might indirectly affect herbivory.) This comparison determined whether or not simply excluding mammalian herbivores would result in significantly greater seedling abundances.

For each of the plant functional groups and each hypothesis, two variables were examined: emergence and mortality. Emergence was defined as the number of new seedlings present in February (the first sampling period). Since seedlings might have emerged and died before sampling took place, or emerged after the February sampling, emergence may have been underesti-

ated. All data were transformed as  $z = \log(x + 0.1)$  to improve normality, and to otherwise satisfy assumptions of parametric statistics (Mosteller and Tukey 1977). Differences in emergence were analyzed using  $t$  tests (Sokal and Rohlf 1981). Comparisons between burned and unburned areas (i.e., the effects of burning) were assessed with independent-samples  $t$  tests with separate variances. Comparisons within the unburned area (i.e., effects of shrub removal and herbivore exclusion) were assessed with paired-samples  $t$  tests.

Mortality was estimated by the rate of change in abundance between each time interval (i.e.,  $\log(N_t/N_{t-1})/\text{time elapsed}$ ) for each plot. This estimate assumes that no emergence occurred past February, so that changes in density were due solely to mortality. This may have been an underestimate of mortality, since it is possible that in the first time period (February–May), changes in density reflect not only mortality of seedlings counted in February, but also emergence and subsequent mortality of new seedlings since February. However, since germination of chaparral herbs usually occurs in the late fall to early spring following rainfall (Parker and Kelley 1989), it is unlikely that there was much germination in March or April, given the extremely low rainfall at the study site in those months. Also, 4 wk after the February census, I resampled six plots and found that, although a few species (the annual herbs *Filago* spp. and the perennial herb *Dichelostemma pulchella*) had newly emerged individuals (from 0 to 70), all other species had the same number or fewer individuals in this recount.

Differences in mortality rates among treatments and seasons were assessed for shrubs, subshrubs, and perennial herbs by repeated-measures ANOVA (Winer 1971). In these analyses, time period or season (i.e., February to May, and May to November) is the repeated factor. These analyses allow for the examination of differences in mortality over the study period without assuming that samples are independent from one time period to the next. Annual herbs were all dead by November, so there was only one season (February to May) in which to examine changes in abundance; mean mortalities were compared using  $t$  tests (Sokal and Rohlf 1981). Mortality rates of all seedlings combined were similarly analyzed for the period February to May, using  $t$  tests for comparison to other studies that examined total mortality. Total seedling mortality from May to November was not examined, because changes in total seedling densities in this period include the complete mortality of all annual species; thus, variation in mortality of all seedlings in May to November would be highly influenced by abundance of annuals.

“Edge” plots were included in the experimental design to determine whether or not there were differences in herbivory in the middle vs. the edge of the burned area. If herbivore abundance is reduced following a fire, due to a temporary elimination of their cover, herbivory should be more intense near the edge of the

burn that is closer to shrub cover. To assess “edge effects” of herbivory in the burned area, I tested the hypothesis that grazing was more intense near the edge of the burn than the middle, by comparing the magnitude of the difference between fenced and open treatments at these two locations. Independent-samples  $t$  tests were used to compare the difference between fenced and open plots ( $\log N_{\text{fenced}} - \log N_{\text{unfenced}}$ ) in the middle of the burn vs. the difference at the edge of the burn.

In addition to assessing the effects of single factors, my experimental design allowed the analysis of two biological interactions of fire: (1) shrub removal and herbivore exclusion (in unburned chaparral); and (2) burning and herbivore exclusion. The interaction between burning and shrub removal was not examined, because one of the required experimental treatments for that analysis (i.e., burning with shrubs intact) could not be done. I defined a significant biological interaction or combined effect as one in which neither single factor alone produced a significant increase in seedling abundance, but the combination of factors did. To detect such an effect, I conducted ANOVAs, and then posthoc Dunnett’s tests comparing treatments to the control.

Since plots within a single burned area are compared to those in unburned chaparral, inferences about direct fire effects (Fig. 1, a vs. b) are unavoidably based upon pseudoreplication (Hurlbert 1984); the question raised is whether or not experimental results can be explained simply by differences that existed before the fire. In the present study, estimates of vegetation cover and mammal activity were made prior to the prescribed burn to address this question. If the preburn conditions were found to be relatively uniform, then differences between burned and unburned areas following the fire were likely due to the effects of fire rather than to preexisting differences in the vegetation or herbivore activity. Comparisons used to analyze the effects of shrub competition and herbivory in unburned chaparral (Fig. 1, b vs. c and c vs. d) did not use the burned area, so are not based on a pseudoreplicated design.

## RESULTS

### *Vegetation composition and large-mammal activity before the burn*

Before the burn, the composition of shrub vegetation was similar throughout the experimental area; ANOVAs indicate that the percent cover values of *Adenostoma fasciculatum*, *Arctostaphylos purissima*, and bare ground were not significantly different among locations (burn middle, burn edge, adjacent chaparral) (Table 1). The canopy was rather short, on average <50 cm. Vegetation at the edge of the proposed burn site was taller (10 cm, on average) than that in the middle (Table 1).

Estimates of the activity of large mammals suggest that rabbits and deer were present in the study area at

TABLE 1. Differences among locations in the percent cover of common shrubs and open space, mean canopy height, and percent cover of animal scat prior to the burn, in what would become the middle of the burn, the edge of the burn, and outside of the burned area ( $n = 10$  for each location).  $P$  values are based on ANOVA (df: location = 2, error = 27).

Location	Percent cover (mean $\pm$ 1 SE)			Canopy height (cm) (mean $\pm$ 1 SE)	Percent cover (mean $\pm$ 1 SE)	
	<i>Adenostoma fasciculatum</i>	<i>Arctostaphylos purissima</i>	Open space		Rabbit scat	Deer scat
Middle	57.2 $\pm$ 3.4	18.6 $\pm$ 3.0	10.8 $\pm$ 1.6	41.2 $\pm$ 2.3	5.8 $\pm$ 1.2	0.7 $\pm$ 0.2
Edge	63.5 $\pm$ 4.2	11.7 $\pm$ 3.4	9.7 $\pm$ 1.4	51.6 $\pm$ 3.3	6.4 $\pm$ 1.2	0.4 $\pm$ 0.1
Outside	53.7 $\pm$ 3.7	14.4 $\pm$ 2.9	12.0 $\pm$ 2.3	50.3 $\pm$ 3.0	4.2 $\pm$ 0.6	0.7 $\pm$ 0.2
$P$	0.20	0.29	0.69	0.03†	0.32	0.51

† Mean canopy height of edge of burn significantly greater than that of middle ( $P = 0.03$ ).

all locations sampled (Table 1). All rabbit scat appeared to be from brush rabbits, *Sylvilagus bachmani*, rather than jack rabbits, *Lepus californicus*, which have larger, less compact fecal pellets. There was no significant difference in percent cover of deer or rabbit scat among locations, indicating that the activity of large mammals during the preburn period was similar in what would become the middle and edge of the burn, and the adjacent unburned areas (Table 1).

#### "Flush" of seedlings after the fire

In the spring of 1989, the burned area was covered with new seedlings as well as *A. fasciculatum* shrub resprouts, whereas the adjacent unburned chaparral had little new growth. To document this striking pattern, I compared unmanipulated plots in burned and unburned chaparral (see Fig. 1). Densities of seedlings in May were significantly greater in the burn for all plant types except annual herbs (Fig. 2). The dominant species of seedlings present in the burned area were the shrubs *Arctostaphylos purissima* and *Ceanothus impressus*, the subshrubs *Helianthemum scoparium* and *Eriophyllum confertiflorum*, and the perennial herbs *Dichelo-*

*stemma pulchella* and *Blumeria crocea*. The dominant annual herbs *Filago californica*, *F. gallica*, and *Navarretia atractyloides* were equally abundant in the burned area and the adjacent unburned chaparral. The goal of this study was to determine the degree to which these patterns (Fig. 2) could be attributed to burning, shrub removal, and exclusion of mammalian herbivores.

#### Effects of burning on seedling emergence and mortality

Burning significantly enhanced the emergence of shrubs and subshrubs, reduced the emergence of annuals, and did not affect the emergence of perennial herbs (Fig. 3). Mortality rates were not significantly affected by burning for any individual plant group in any time period (Table 2), although the mortality rate of all seedlings combined was lower in the burned area (Table 2,  $P = 0.47$ , independent-samples  $t$  test). There were no significant seasonal differences in mortality or interactions between burning and season for any plant group.

#### Effects of shrub removal on seedling emergence and mortality

Manual removal of shrubs did not significantly affect the emergence of shrub seedlings, perennial herbs, or annual herbs (Fig. 4); however, emergence of subshrub seedlings was significantly higher when the shrub canopy was present. The mortality rates of annual herbs and all seedlings combined were significantly reduced by shrub removal in the period February–May (Table 2;  $P = 0.007$  for both plant groups, paired-samples  $t$  tests). Mortality of shrub, subshrub, and perennial herb seedlings was not significantly affected by this treatment over the whole study period (Table 2). The significant interaction between shrub removal and season for shrub seedlings (Table 2;  $P = 0.040$ , repeated-measures ANOVA) indicates that there was a difference between treatments in the period May–November, but not February–May. This difference is due to the fact that, in the treatment with shrubs present, all seedlings were dead by May and, thus, showed no mortality in the second time period.

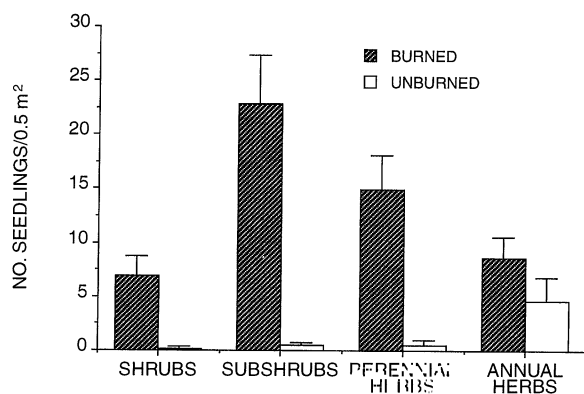


FIG. 2. Composition of the natural vegetation in the post-fire spring "flush," May 1989. "Burned" includes new seedlings in unfenced plots from the middle and edge of the burned area ( $n = 12$ ); "unburned" includes new seedlings from unfenced shrub plots in adjacent unburned chaparral ( $n = 6$ ). Data are means  $\pm$  1 SE. Independent-samples  $t$  tests with separate variances indicate a significant difference between treatments:  $P < 0.001$  for shrubs, subshrubs, and perennial herbs;  $P = 0.31$  for annual herbs.

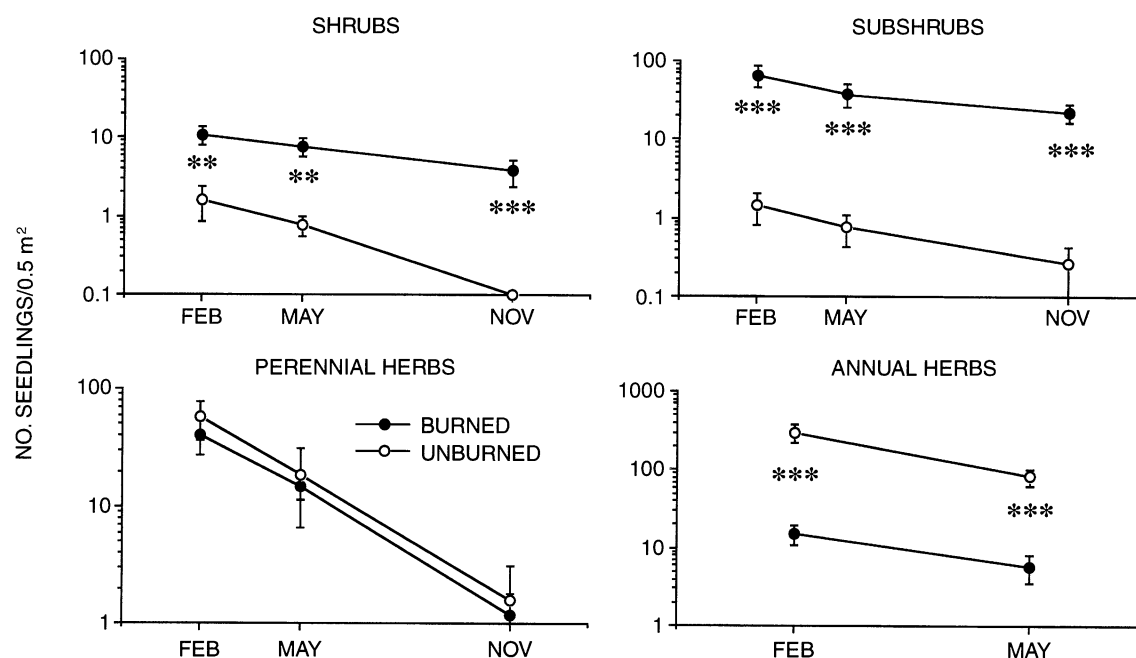


FIG. 3. Effects of burning on seedling densities (mean  $\pm$  1 SE) in the 1st yr after fire. The treatments used to make these comparisons are diagrammed in Fig. 1 (a vs. b). Asterisks indicate a significant difference between the means of the treatments at that time (\*\* $P \leq 0.01$ , \*\*\* $P \leq 0.001$ ) based on independent-samples  $t$  tests,  $n = 6$ . Note differences in scale on ordinates and abscissas among plots, and also note logarithmic scale on ordinates.

TABLE 2. Mean mortality rates in each treatment and season (with 1 SE reported in parentheses).

Plant type	Factors								
	Burning			Shrub removal			Herbivore exclusion		
	Burned [ $n = 12$ ]	Unburned [ $n = 6$ ]	$P$	Shrub removed [ $n = 6$ ]	Shrub present [ $n = 6$ ]	$P$	Herbivore absent [ $n = 6$ ]	Herbivores present [ $n = 6$ ]	$P$
A) February–May mortality rates									
Shrubs	0.05 (0.04)	0.05 (0.10)	NS	0.05 (0.10)	0.31 (0.11)	NS	0.31 (0.11)	0.13 (0.10)	NS
Subshrubs	0.08 (0.03)	0.05 (0.01)	NS	0.05 (0.10)	0.13 (0.07)	NS	0.13 (0.07)	0.28 (0.18)	NS
Perennial herbs	0.15 (0.03)	0.24 (0.09)	NS	0.24 (0.09)	0.51 (0.16)	NS	0.51 (0.16)	0.76 (0.09)	NS
Annual herbs	0.27 (0.07)	0.18 (0.03)	NS	0.18 (0.03)	0.44 (0.05)	**	0.44 (0.05)	0.71 (0.09)	*
Total seedlings	0.09 (0.01)	0.18 (0.03)	*	0.18 (0.03)	0.36 (0.06)	**	0.36 (0.06)	0.66 (0.07)	*
B) May–November mortality rates									
Shrubs	0.07 (0.03)	0.12 (0.04)	NS	0.12 (0.04)	0 (0)	†	0 (0)	0.03 (0.03)	NS
Subshrubs	0.02 (0.01)	0.07 (0.03)	NS	0.07 (0.04)	0.12 (0.05)	NS	0.12 (0.05)	0.06 (0.04)	NS
Perennial herbs	0.24 (0.04)	0.25 (0.04)	NS	0.25 (0.04)	0.14 (0.07)	NS	0.14 (0.07)	0.04 (0.04)	NS

Notes: Treatments used to make comparisons are shown in Fig. 1. Mortality was calculated as  $-\log(N_{\text{end}} + 0.1) - \log(N_{\text{initial}} + 0.1)/(\text{time elapsed})$ . Asterisks indicate a significant difference between treatments (\* $P < 0.05$ , \*\* $P < 0.01$ ) for annual herbs or total seedlings, based on  $t$  tests. † indicates a significant ( $P = 0.04$ ) treatment-by-season interaction based on repeated-measures ANOVA (i.e., significant difference in the second time period but not the first).

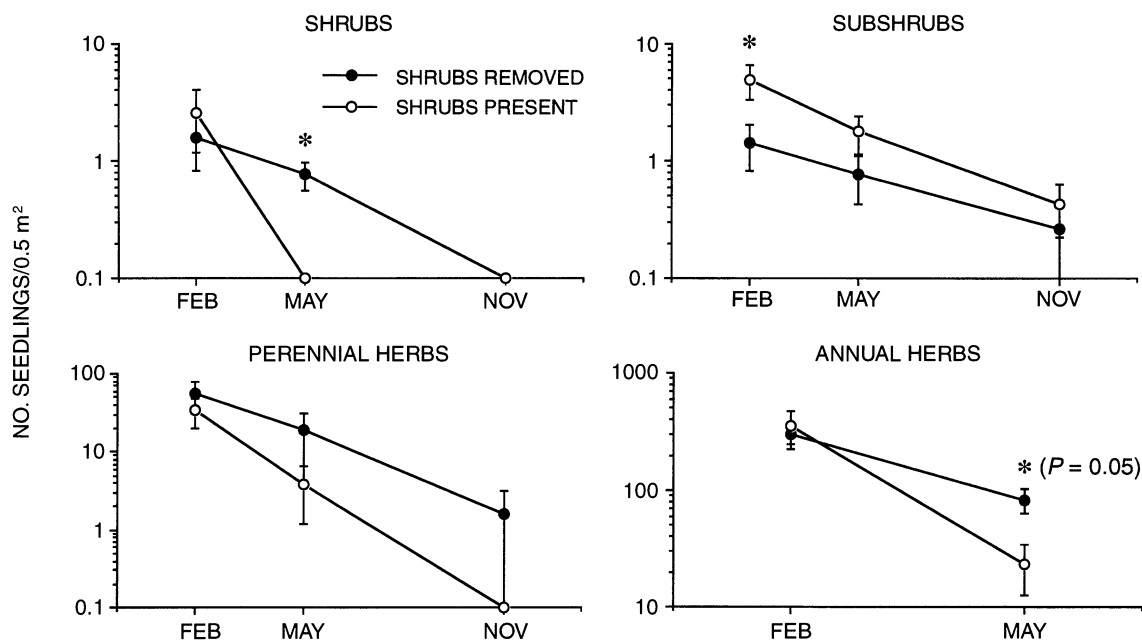


FIG. 4. Effects of shrub removal on seedling densities (mean  $\pm$  1 SE) in unburned chaparral. The treatments used to make this comparison are shown in Fig. 1 (b vs. c). Asterisks indicate a significant difference between the treatment means at that time (\* $P < 0.05$ , except as noted for annual herbs) based on paired-samples  $t$  tests,  $n = 6$ . Note differences in scale on ordinates and abscissas among plots.

#### Effects of herbivore exclusion on seedling emergence and mortality

The number of seedlings emerging in mature chaparral was unaffected by the exclusion of mammalian herbivores (Fig. 5). Mortality rates of shrubs, subshrubs, and perennial herbs were not affected significantly by herbivore exclusion (Table 2), but the mortality rates of annual herbs and all seedlings combined were significantly reduced when herbivores were excluded ( $P = 0.010$  and  $P = 0.030$ , respectively, paired-samples  $t$  tests). There was a significant seasonal effect on mortality for shrub seedlings and perennial herbs ( $P = 0.020$  and  $P = 0.002$ , respectively, repeated-measures ANOVA); both plant types had higher average mortality from February to May.

#### Reduction of herbivory in the burned area

The premise of the third hypothesis tested in this study (that the postfire "bloom" is a result of reduced herbivory) was that herbivory is reduced following a fire. To examine this premise, I compared fenced to unfenced plots in both burned and unburned areas in May (Table 3). Total seedling densities were significantly higher in fenced than in unfenced plots in unburned chaparral for both the "shrubs removed" and "shrubs intact" treatments. However, in the burned area there was no significant difference between fenced and unfenced plots, suggesting that, at this site, the impact of herbivory was reduced in the burned area, compared to adjacent unburned chaparral.

#### Edge effects of herbivory in the burned area

There was no evidence for stronger effects of herbivores at the edge of the burned area (Table 4). Perennial herbs were the only plant group showing differences in the intensity of herbivory between the middle and edge of the burn, but, counter to the prediction of greater herbivory at the edge, the difference between fenced and unfenced plots was greater in the middle than at the edge (Table 4).

#### Combined effects of experimental treatments

I detected several "interactions" or combined effects of shrub removal and herbivore exclusion in unburned chaparral. Seedling emergence (i.e., February density) was unaffected by either single or combined effects of shrub removal and herbivore exclusion in all of the plant groups (Fig. 6). In May, however, shrub seedlings, perennial herbs, and annual herbs were significantly more abundant in the combined treatment than in the control. Of particular interest is the finding that, whereas no single treatment affected shrubs and perennial herbs in May, there were significantly higher abundances of these two groups in the combined shrub removal and herbivore exclusion treatment than in the control (Fig. 6). For annuals, the difference between the combined treatment and the control was primarily due to the effect of shrub removal. Removing shrubs alone also led to higher densities of annuals than in the control (posthoc Dunnett's test:  $P = 0.030$ ); there was no significant difference between shrub removal



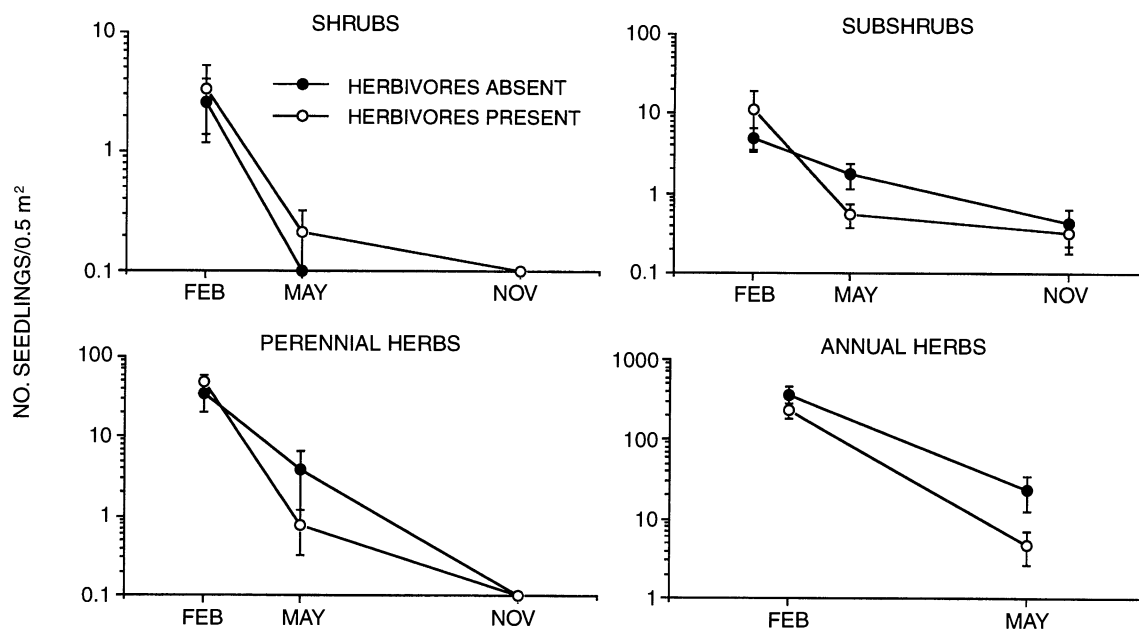


FIG. 5. Effects of herbivore exclusion on seedling densities (mean  $\pm$  1 SE) in unburned chaparral. The treatments used to make this comparison are shown in Fig. 1 (c vs. d). Note differences in scale on ordinates and abscissas among plots.

and the combined treatment (posthoc contrast:  $P = 0.770$ ).

I found no evidence of a "biological interaction" between burning and herbivore exclusion (Fig. 7). Effects of the combined burning and herbivore exclusion treatment did not differ statistically from effects of the single treatment, burning.

#### DISCUSSION

The results of this study indicate that several mechanisms, singly or in combination, are responsible for the postfire "flush" of seedlings at this maritime chaparral site. Furthermore, the effects of different factors, alone and in combination, vary among functional plant groups (Table 5). The experimental approach of this study permits comparison of the direct effects of fire with two indirect effects of fire, and demonstrates that, in maritime chaparral, a part of the response to fire may be ascribed to removal of shrubs and reduction in herbivory.

TABLE 3. Effects of herbivore exclusion on total seedling abundance in burned and unburned chaparral. Data are means ( $\pm$  1 SE) of total seedling densities in May.  $P$  values are based on paired-samples  $t$  tests ( $n = 6$ ).

Location/ treatment	No. seedlings (mean $\pm$ 1 SE)		$P$
	Fenced	Unfenced	
Burn middle	68.5 $\pm$ 20.1	43.5 $\pm$ 11.1	0.142
Burn edge	63.5 $\pm$ 21.5	63.2 $\pm$ 6.8	0.395
Unburned, shrubs removed	103.3 $\pm$ 16.4	65.8 $\pm$ 14.9	0.049
Unburned, shrubs intact	28.7 $\pm$ 10.0	5.8 $\pm$ 2.5	0.025

The overall pattern of higher seedling densities in burned relative to unburned chaparral (Fig. 2) is similar to that reported in other surveys (Horton and Kraebel 1955, Sweeney 1956, Keeley et al. 1981), except in one regard: annual herbs at the present site were not more abundant in the burn. The relative contributions of the direct and indirect effects of fire in producing these patterns will be discussed.

#### Direct effects of burning

By significantly enhancing emergence, burning was the most important effect of fire in producing a post-burn "flush" of seedlings for two plant groups, shrubs and subshrubs. Previous work conducted in the laboratory or with heat-treated soils placed in the field (Sweeney 1956, Christensen and Muller 1975a, b, Keeley and Keeley 1987) has demonstrated that heating increases seed germination in several chaparral species, including most of the shrub and subshrub species of the present study. Results of this study suggest that this factor alone was primarily responsible for the high density of shrub and subshrub seedlings in the burned area relative to unburned chaparral.

In contrast, the emergence of annual herbs was strongly reduced by burning alone, probably as a result of high seed mortality during the fire. Extremely high temperatures can significantly reduce germination of annuals (Zammit and Zedler 1988, Davis et al. 1989, Moreno and Oechel 1991). However, the strong negative effects of burning on annual herbs found in the present study conflict with results of other chaparral studies in which annuals, particularly "pyrophyte endemics" (Hanes 1977), form a large percentage of the

TABLE 4. Variation between middle and edge of the burn in the intensity of herbivory. Data are the means of the differences in numbers of seedlings ( $\pm 1$  SE) between fenced and unfenced plots in the middle and edge of the burned area.  $P$  values are based on independent-samples  $t$  tests,  $n = 6$ .

Date	Plant group	Mean ( $\pm 1$ SE) difference in no. seedlings between treatments (fenced – unfenced)		$P$
		Middle	Edge	
February	Shrubs	6.2 $\pm$ 5.7	-4.3 $\pm$ 4.2	0.57
	Subshrubs	35.0 $\pm$ 25.9	28.3 $\pm$ 23.8	0.41
	Perennial herbs	35.7 $\pm$ 15.1	-47.0 $\pm$ 24.3	0.03
	Annual herbs	-2.0 $\pm$ 13.8	-7.0 $\pm$ 7.5	0.45
May	Shrubs	1.2 $\pm$ 5.2	0 $\pm$ 2.2	0.80
	Subshrubs	17.5 $\pm$ 15.8	13.0 $\pm$ 14.3	0.36
	Perennial herbs	10.8 $\pm$ 3.6	-11.2 $\pm$ 4.9	0.04
	Annual herbs	-4.5 $\pm$ 4.7	-1.5 $\pm$ 3.7	0.85
November	Shrubs	1.7 $\pm$ 3.4	0 $\pm$ 0.9	0.87
	Subshrubs	12.7 $\pm$ 8.7	4.5 $\pm$ 7.5	0.16
	Perennial herbs	1.2 $\pm$ 1.3	0.7 $\pm$ 0.5	0.84

postburn cover (Brandeggee 1891, Sampson 1944, Horton and Kraebel 1955, Sweeney 1956, Keeley et al. 1981). Although a few species of “pyrophyte endemics,” e.g., *Papaver californicum* and *Antirrhinum kellogii*, were present in my burned study area, they were extremely rare and were absent from experimental plots. Because soil surface temperatures during the burn were high (400°–700°C; D. Odion, unpublished

manuscript), it is unlikely that seeds of “fire annuals” were present in the seed bank but failed to germinate. This paucity of fire annuals in the local flora may explain the low abundance of annual herbs seen in the burn and the strong negative effect of burning on seedling emergence.

Emergence of perennial herbs was unaffected by burning alone. The seeds of all chaparral geophyte spe-

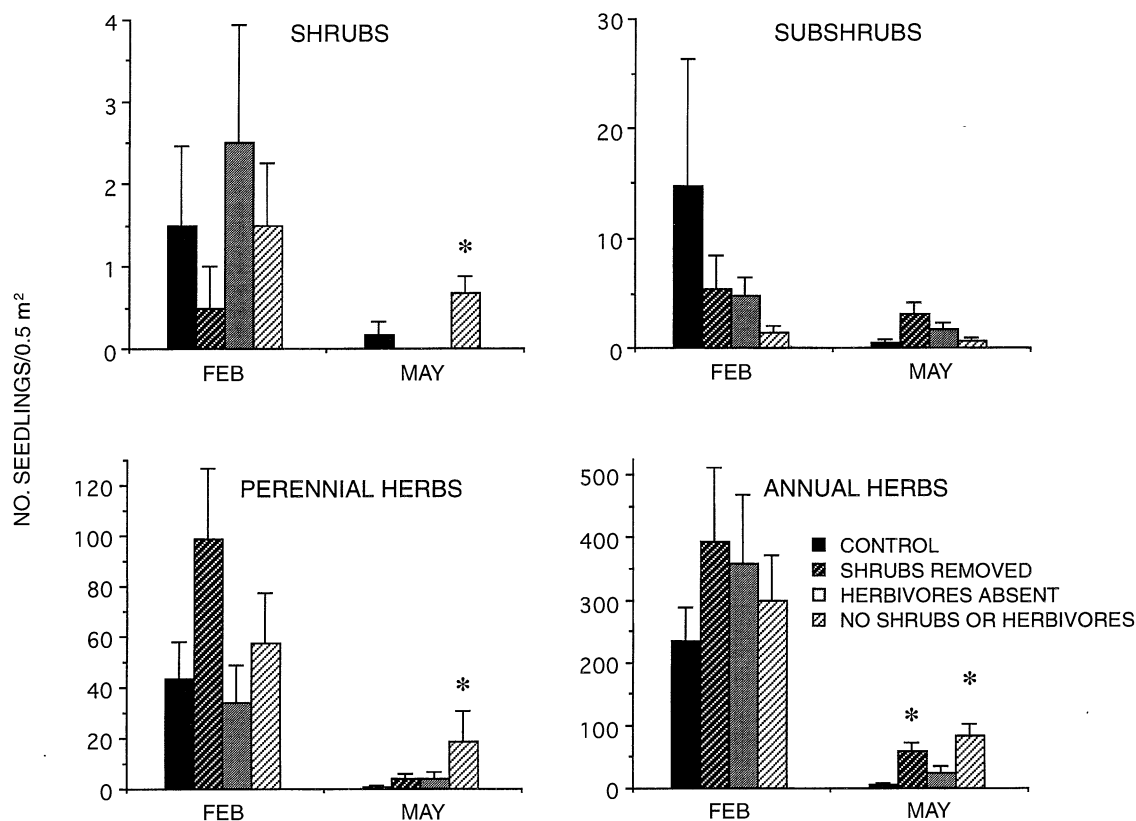


FIG. 6. Combined effects of the removal of shrubs and herbivores in unburned chaparral. Densities (mean + 1 SE) of seedlings of the different plant types are shown in the 1st yr after fire. Asterisks indicate a significant difference between treatment and control ( $P < 0.05$ ). Note differences in y-axis scale among plots.

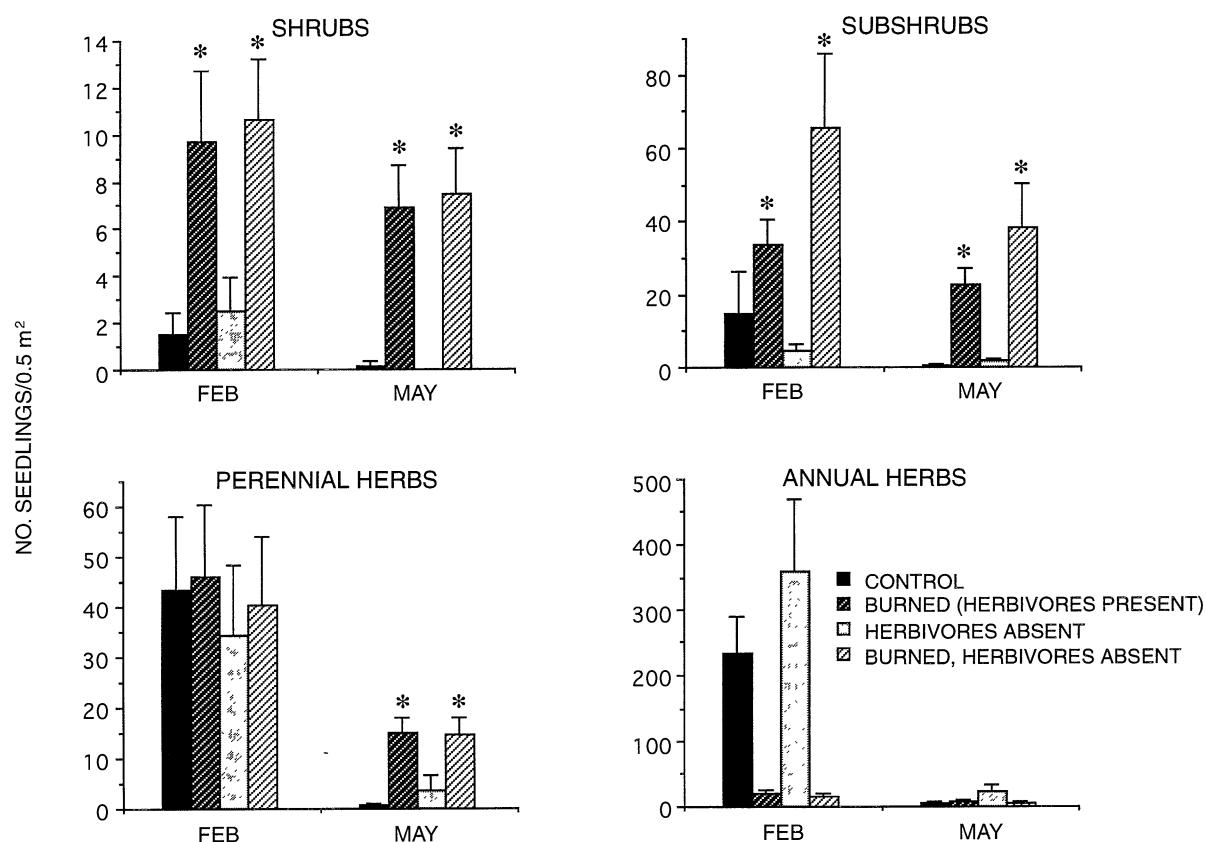


FIG. 7. Combined effects of burning and removal of herbivores. Densities (mean + 1 SE) of seedlings of the different plant types are shown in the 1st yr after fire. Asterisks indicate a significant difference between treatment and control ( $P < 0.05$ ). Note differences in y-axis scale among plots.

cies are nonrefractory (Keeley 1991) and, thus, would not be stimulated by fire to germinate; they probably survived the high temperatures in burns because their bulbs, corms, or rhizomes are deeply buried (Keeley 1991). Since perennials were not directly affected by burning, their higher density in the burn than in the unburned area (Fig. 2) was clearly due to other factors or combinations of factors.

Surprisingly, burning did not affect postemergence

mortality for any individual plant group. It was expected that the high concentrations of soil nutrients in the burn (see Tyler and D'Antonio 1995) would improve seedling survivorship, since growth should increase and larger plants should survive better than smaller ones. Addition of nutrients to unburned chaparral has been shown to increase growth of seedlings in some cases (Christensen and Muller 1975a, b), although Swank and Oechel (1990) found that addition

TABLE 5. Summary of the effects of fire on seedling emergence and survivorship. A + indicates a positive effect of that factor; - indicates a negative effect; and 0 indicates that the factor had no statistically significant effect.

Plant type	Variables	Experimental treatment			
		Burning	Shrub removal	Herbivore exclusion	Shrub removal and herbivore exclusion
Shrubs	Emergence	+	0	0	0
	Survivorship	0	+	0	+
Subshrubs	Emergence	+	-	0	0
	Survivorship	0	0	0	0
Perennial herbs	Emergence	0	0	0	0
	Survivorship	0	0	0	+
Annual	Emergence	-	0	0	0
	Survivorship	0	+	+	0

of nutrients alone did not affect survival of herbs in unburned chaparral.

In summary, the contribution of burning (isolated from the indirect effects of fire) to the postfire "flush" appears to be the stimulation of seed germination in shrubs and subshrubs. In contrast, burning may significantly reduce the abundance of annual herbs if the flora contains few "pyrophyte endemics."

#### *Effects of shrub removal*

Results of this study suggest that, in maritime chaparral, shrub removal is an important indirect effect of fire, primarily by improving the survivorship of annual herbs. Since the direct effect of fire (burning) on the emergence of annuals was strongly negative, the presence and persistence of moderate numbers of annual herbs in the burned area in May (Fig. 2) must be explained by indirect effects of fire (primarily shrub removal) that increased survivorship.

Previous studies in unburned chaparral support the finding that the removal of adult shrubs, or reduction in competition, is particularly important to survivorship of herbs. Herbaceous species have been observed to germinate under mature chaparral canopies, but rarely to survive, even when herbivores are excluded (Christensen and Muller 1975a, b; J. H. Connell and C. Tyler, *unpublished data*). Trenching to reduce root competition from shrubs was shown to significantly enhance survival of herbaceous seedlings in open spaces in chaparral (Swank and Oechel 1990).

Although shrub removal reduced the emergence of subshrubs, this indirect effect of fire is unlikely to play an important role in their postfire establishment; by the spring, there was no difference in subshrub densities between plots with shrubs present and those with shrubs removed. The density of subshrub seedlings was very low in both treatments.

#### *Effects of herbivore exclusion*

In the present study, the survivorship of annual herbs increased significantly when mammalian herbivores were excluded, suggesting that a reduction in herbivory may play a role in increasing the density of annual herbs in a burned area.

Although herbivory strongly limits seedling establishment in mature chaparral (McPherson and Muller 1969, Christensen and Muller 1975a, b, Swank and Oechel 1990; J. H. Connell and C. Tyler, *unpublished data*), the question remains as to whether or not fire causes a reduction of herbivory by large mammals. Results from the present study suggest that the effects of herbivores were, in fact, less in the burned area than in the unburned chaparral. Mammalian herbivores significantly reduced total seedling densities in unburned plots but not in the burned area. In addition, resprouting *A. fasciculatum* were grazed much more intensely in the unburned area (cleared plots) than in the burn (C. Tyler, *unpublished data*). However, there was no evi-

dence of an "edge effect" in the burned area to suggest that herbivores were concentrated near the intact shrub border. Contrary to predictions, the only significant effect of herbivory (reduced abundance of perennial herbs) was detected in the middle of the burn, suggesting that herbivores within the burn area may have been concentrated away from the edges.

Changes in the abundance, distribution, and behavior of mammalian herbivores following fire are species-specific. Following fire, the densities of some species of mammalian herbivores decrease whereas others increase (Biswell et al. 1952, Lawrence 1966, Christensen and Muller 1975a, Wirtz 1977, Longhurst 1978). At the present study site, I found by live-trapping that wood rats, *Neotoma fuscipes*, were present only in the unburned chaparral, whereas kangaroo rats, *D. agilis*, and deer mice, *Peromyscus* sp., were more abundant in the burn area than in the adjacent unburned chaparral for at least the first postfire year (C. Tyler, *unpublished data*).

In addition, detection of herbivore effects is probably a function both of the size of the area burned and of the scale at which experiments are conducted. Mills (1986) showed that herbivory significantly reduced the abundance of shrub seedlings (*Ceanothus greggii*), in a small, 2.5-ha burned area, whereas the present study, conducted in a larger 40-ha burn, found no herbivore effects on shrub seedling abundance within the burned area. Herbivores are likely to be drawn to and concentrated in a smaller burned area, and thus may have stronger effects on seedling abundance and survivorship.

#### *Combined effects of treatments*

No single factor was responsible for the high abundance of perennial herbs in the burn (Fig. 2). Results indicate that their increased densities in the burn may be explained by the combined effects of shrub removal and herbivore exclusion, two indirect effects of fire.

The importance of a "biological interaction" between competition and herbivory in chaparral has been suggested by previous studies, in which only the simultaneous reduction in both factors produces successful recruitment of seedlings. In the understory of mature chaparral, there is generally no effect of fencing alone (Christensen and Muller 1975a; J. H. Connell and C. Tyler, *unpublished data*). However, because there is often intense herbivory in small clearings or gaps in mature chaparral (Christensen and Muller 1975a, Swank and Oechel 1990; J. H. Connell and C. Tyler, *unpublished data*), removal of shrubs alone may not produce significant numbers of seedlings. Christensen and Muller (1975a) found that removing mature shrubs did produce higher seedling abundances, but only in fenced clearings (there was no unfenced cleared treatment). Significant interactions between herbivory and competition were reported by Swank and Oechel (1990), who noted that herbivores removed all vege-

tation from uncaged plots, so that effects of other treatments were evident only in caged plots.

Although I detected no "interaction" between burning and herbivore exclusion, it is difficult to assess the generality of this result. It is possible that, in the present study (conducted in a 40-ha burn), one of the experimental treatments (burning with herbivores present) was not actually achieved because herbivore effects were reduced in the burn area. However, the interaction between burning and herbivory could be a significant factor affecting seedling survivorship and growth in small burn areas, where grazers might be abundant. Mills (1986) found strong herbivore effects in experiments conducted in a small, controlled burn in chaparral. Also, in small, low-intensity burns (15 m<sup>2</sup>), Leigh and Holgate (1979) found strong interactions between burning and grazing in the Tablelands of southeastern Australia; seedlings and resprouts in plots exposed to both burning and herbivory (primarily by wombats, kangaroos, and wallabies) had greater mortality than those in plots subjected to only one treatment or the control.

#### Overview

The direct effect of burning was found to be the main factor responsible for the abundance of shrub and subshrub seedlings following a fire, by significantly increasing their emergence. The removal of shrubs and the exclusion of mammalian herbivores were found to be important primarily in improving the survivorship of annuals. The strong negative effect of burning on the emergence of annual herbs at this site may have been offset by the reduction in competition and herbivory following the fire. High perennial herb densities in the burn could not be explained by any single factor examined; results suggest that the increase in perennial herbs after a fire was due to the combined removal of both shrubs and herbivores. Thus, both direct and indirect effects of fire contributed to the postburn recruitment of seedlings in this maritime chaparral, but different mechanisms were responsible for the increases in specific plant groups.

It is interesting that, in this chaparral community, the shrub and subshrub flora appear to be dependent on fire for germination and establishment, whereas the annual herbs are not. Similar results have been reported by Zammit and Zedler (1994), who found two distinct classes of species in soil seed bank samples from mixed chaparral: a fire-dependent group whose germinable densities increased with fire, and a fire-independent group. Because the fire-dependent group made up only a small portion of the total seed density, they concluded that the soil seed assemblage was not tightly coupled to fire for recruitment. In the present study, several observations, such as the lack of fire-dependent annuals, suggest that the flora reflects a history of low fire frequency at the site. This chaparral stand last burned >50 yr ago and, historically, fires have probably

been infrequent in this coastal vegetation. Although further studies are needed, it is likely that fire frequency plays an important role in determining the relative importance of factors that contribute to the postfire response of chaparral plant communities.

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## APPENDIX

Plant species present in all experimental plots in maritime chaparral, Burton Mesa, California.

Species	Family	Maximum no./0.5 m <sup>2</sup>	
		Burned plots	Unburned plots
Shrubs			
<i>Adenostoma fasciculatum</i>	Rosaceae	10	1
<i>Arctostaphylos purissima</i>	Ericaceae	18	18
<i>Baccharis pilularis</i>	Asteraceae	11	1
<i>Ceanothus impressus</i>	Rhamnaceae	20	
<i>Ceanothus ramulosus</i>	Rhamnaceae	15	1
<i>Salvia mellifera</i>	Lamiaceae	2	1
Sub-shrubs			
<i>Carpobrotus edulis</i>	Aizoaceae		2
<i>Eriophyllum confertiflorum</i>	Asteraceae	4	20
<i>Helianthemum scoparium</i>	Cistaceae	215	72
<i>Lotus scoparius</i>	Fabaceae	2	1
Perennial herbs			
<i>Bloomeria crocea</i>	Amoryllidaceae	26 (145)†	8 (159)†
<i>Calochortus albus</i>	Liliaceae	23	17
<i>Chlorogalum pomeridianum</i>	Liliaceae	1	
<i>Dichelostemma pulchella</i>	Amoryllidaceae	6 (145)†	4 (159)†
<i>Dichondra donelliana</i>	Convolvulaceae	13	
<i>Dodecatheon clevelandii</i>	Primulaceae	58	31
<i>Erigeron sanctarum</i>	Asteraceae	7	31
<i>Galium californicum</i>	Rubiaceae	45	59
<i>Sanicula</i> sp.	Apiaceae	10	16
<i>Scutellaria tuberosa</i>	Lamiaceae		32
<i>Zigadenus fremontii</i>	Liliaceae	1	2
Annual herbs			
<i>Apiastrum angustifolium</i>	Apiaceae	10	100
<i>Calandrinia breweri</i>	Portulacaceae	7	1
<i>Centaurium davyi</i>	Gentianaceae		1
<i>Crassula erecta</i>	Crassulaceae	18	332
<i>Cryptantha</i> sp./ <i>Plagiobothrys</i> sp.	Boraginaceae	3	130
<i>Daucus pusillis</i>	Apiaceae		10
<i>Filago californica</i>	Asteraceae	7	262
<i>Filago gallica</i>	Asteraceae	1	287
<i>Gnaphalium purpureum</i>	Asteraceae	1	9
<i>Hypochoeris</i> sp.	Asteraceae	3	125
<i>Linaria canadensis</i>	Scrophulariaceae	4	31
<i>Lotus strigosus</i>	Fabaceae	30	14
<i>Madia exigua</i>	Asteraceae		6
<i>Microseris linearifolia</i>	Asteraceae		4
<i>Navarretia atractyloides</i>	Polemoniaceae	25	293
<i>Plantago hookeriana</i>	Plantaginaceae		8
<i>Sonchus</i> sp.	Asteraceae	1	
<i>Stylocline gnaphaloides</i>	Asteraceae		72
<i>Vulpia octoflora</i>	Poaceae		3

† The vegetative sprouts alone of *B. crocea* and *D. pulchella* were undistinguishable. In parentheses is the number of unidentified sprouts belonging to one of these two species.