# FIRE, SOIL HEATING, AND THE FORMATION OF VEGETATION PATTERNS IN CHAPARRAL

Dennis C. Odion[1] and Frank W. Davis

[1]*Department of Geography, University of California, Santa Barbara, California 93106 USA*

*Abstract.* We documented patterns of surface heating associated with chaparral fire to characterize fundamental scale variation in the intensity of this stand-replacing disturbance. To test how this variation may influence community structure, we studied its effect on the soil seed bank and the distribution of seedlings and resprouts that emerged after fire. To evaluate the long-term significance of initial patterns, we monitored vegetation development for 4–5 yr, thereby encompassing the dynamic portion of the chaparral fire cycle.

We studied two stands on level uniform terrain before, during, and after fall fires. Stands were dominated by chamise (*Adenostoma fasciculatum*), a postfire seeder/sprouter. Nonsprouting *Arctostaphylos* and *Ceanothus* spp. were also present. Preburn vegetation, seed populations, soil heating, and postburn plant growth were analyzed along transects of contiguous 1-m² plots, so that we could block them together incrementally to identify scale dependence of patterns. In addition, we directly compared heating effects under the fuel array with those just outside by establishing plots in canopy gaps, under the adjacent canopy, and in gaps created and eliminated by reciprocally translocating fuel. Pre- and postburn seed populations were estimated in soil samples collected from all plots. The proportion of seed that survived above and below 2.5 cm in the soil was determined in a subset of plots.

The amount and distribution of canopy fuel that collapsed during fire and smoldered on the ground caused pronounced spatial variation in total surface heating. The strength of relationships among patterns of soil heating, preburn canopy, surviving seeds, and seedlings and herbaceous resprouts was consistently most pronounced in blocks 3–5 m long. At this scale, postburn patterns were strongly negatively associated with the amount of preburn canopy and the pattern of soil heating this fuel created. Seedlings or herbaceous resprouts of numerous species were abundant where soil heating was relatively low, most notably in natural and created canopy gaps. Conversely, areas where dense canopy occurred before fire, especially gaps displaced by fuel addition, were barren except for occasional *Arctostaphylos* and *Ceanothus* seedlings. These obligate postfire seeders, along with the subshrub *Helianthemum scoparium*, had more deeply buried seeds, and some of them were able to survive where soil heating was prolonged. However, *Helianthemum* did not emerge from depth. Seedlings of *Arctostaphylos* and *Ceanothus* nearest *Adenostoma* burls survived significantly better when *Adenostoma* failed to resprout. This was common in one burn where heating was relatively high and burl size was small. Seed mortality prevented *Adenostoma* seedling emergence from occurring where its seeds were most abundant prior to fire, which was in proximity to its burls. *Adenostoma* seedlings did emerge in areas of lower soil heating, but their survival was inversely related to the density of *Helianthemum* seedlings. No shrub seedlings emerged after the first year following fire because their seed banks were exhausted by fire-induced mortality and/or germination. After 4–5 yr, few young *Adenostoma* remained. The combination of seedling and resprout regeneration allowed this shrub to maintain dominance, but to a lesser extent in the older stand.

Our results support a vegetation pattern–process model in which local species distributions after fire in *Adenostoma* chaparral are antecedently linked to the physical and chemical properties of the canopy. These control the nature of combustion, the soil heating that results, and the distribution of seeds and resprout tissues that survive. The vegetation develops entirely from these sources, so fire-induced patterns are manifest in the long-term structure of this vegetation.

*Key words:* Arctostaphylos; Adenostoma fasciculatum; Ceanothus; *chaparral; fire disturbance intensity;* Helianthemum scoparium; *obligate seeder; seed germination, distribution, and mortality; seedbank; shrub canopy; soil heating; vegetation patterns.*

## Introduction

*I met a great fire, and as fire is the master scourge and controller of the distribution of trees, I stopped to watch it . . . It came racing up the steep chaparral-covered slopes of the East Fork canyon with passionate enthusiasm in a broad cataract of flames, now bending down low to feed on the green bushes, devouring acres of them at a breath, now towering high in the air as if looking abroad to choose a way, then stooping to feed again.*

—*John Muir*

In the dramatic fashion captured by Muir, fire routinely ''devours'' chaparral. This dense shrubland is dominated by evergreen sclerophylls such as chamise

(*Adenostoma fasciculatum,* hereafter *Adenostoma*) and species of *Arctostaphylos* and *Ceanothus.* Chaparral is the regional vegetation of the Mediterranean climate zone in southwestern North America (reviews by Hanes [1977] and Keeley and Keeley [1988]). Fire intervals in chaparral may average ~40 yr (Byrne et al. 1977, Minnich 1988) depending on ignition sources, climatic variation, and landscape patterns (Keeley 1981, Riggan et al. 1988, Moritz 1997). Though the interval may vary, fires are universally stand replacing, with profound effects ensured by physical and chemical properties of shrubs that favor combustion. Recovery of chaparral after fire is from endogenous sources, and is so pronounced and predictable that it has been termed ''autosuccession'' (Hanes 1971). The vegetation is maintained by fire-induced seed germination (Sweeney 1956, Keeley 1991, Keeley and Fotheringham 1997, 1998), obligate postfire shrub seedling regeneration (Keeley and Zedler 1978), and resprouting from geophytes and fire resistant lignotubers (Jepson 1916, Anfuso 1982; review by James [1984]).

Although fire is the dominant process affecting chaparral community patterns (Christensen and Muller 1975), little is known about how its effects and intensity vary spatially (Borchert and Odion 1995). Despite fire-dependent regeneration, seeds and resprout tissues occur near the soil surface, where they would appear vulnerable to heating. The intensity of heat impinging on these will be determined by the nature of combustion in the vegetation, a process that may contain inherent pattern as a result of the patchy fuel array provided by individual brush crowns and their nonrandom dispersion (Mutch 1970). Thus, like the autosuccession that follows, the pattern and intensity of the disturbance that chaparral has evolved with for $2 \times 10^6$ yr (Axelrod 1958) may be endogenous to the vegetation. Here we investigate the spatial variation in surface heating that occurs with chaparral fire and the resulting ecological consequences.

Although fire is needed for seeds of most chaparral species to be released from dormancy, excessive heating apparently kills much seed (Keeley 1977, Bullock 1982, Zammit and Zedler 1988, Davis et al. 1989, D'Antonio et al. 1993). In addition, Moreno and Oechel (1991a) found that seedlings of several species were less abundant in areas of greater soil heating, especially in fuel addition treatments. What, then, are the seedling patterns that develop after fire in relation to natural variation in soil heating? This is a difficult question to answer, because it is necessary to know the horizontal and vertical distributions of seeds prior to fire, in order to isolate the direct effects of heating (Borchert and Odion 1995). For example, evidence suggests that seeds are more abundant in the locations where soil heating during fire is lower (Davis et al. 1989). Thus, preburn seed distribution could explain the postburn patterns of seedling abundance, which have otherwise been correlated with canopy gaps (Davis et al. 1989),

less fuel (Moreno and Oechel 1991a), lower amounts of postfire ash on the ground (Rice 1993), and the clearing of chaparral patches prior to fire (Tyler 1995). Is the greater density of emerging seedlings found at such locations primarily the result of lower soil heating, or is it determined by the prior spatial distributions of seeds? Conversely, where emergents are lacking, is all seed killed, or are some too deeply buried to receive sufficient heat to break dormancy (e.g., Auld 1986), or to emerge if they do germinate (e.g., Bond and van Wilgen 1995: Fig. 5.12)?

Survival of dormant buds on lignotubers, bulbs, and tubers in the soil will also be determined by soil heating and how insulated these tissues are from it, as has been described for *Adenostoma* (Keeley and Zedler 1978, Anfuso 1982, Rundel et al. 1987, Moreno and Oechel 1991b). Heating effects on other postfire sprouters in chaparral, particularly herbaceous species, have been little studied. While the sensitivity of vascular plant tissue to high temperatures is known (Levitt 1972, Precht et al. 1973), the soil depth where most resprout propagules occur, the heat flux they are exposed to in chaparral fires, and the effects of long-duration heating are not known (Borchert and Odion 1995). Thus, it is uncertain how variable heating associated with chaparral fire affects subsequent resprout patterns.

Understanding of heating effects on seeds and resprout tissues in chaparral is further limited, because most data are from safe-season prescribed burns (e.g., Davis et al. 1989, Moreno and Oechel 1989, 1991a, b), which occur when soils and fuels contain relatively high moisture. Combustion and soil heating will be much different in the high-intensity fires that naturally occur in chaparral (Rothermel and Philpot 1973). In addition, during the wildfire season, seeds are dehydrated as well as metabolically inactive, allowing much greater heat tolerance. Conversely, seeds of a number of chaparral herbs and shrubs such as *Adenostoma* and *Arctostaphylos* spp. have greatly reduced heat tolerance after they seasonally absorb moisture (Sweeney 1956, Parker and Rogers 1988).

In order to determine natural patterns of plant growth produced by soil heating associated with wildfire, and to describe their scale and intensity, we studied two autumn fires that burned vigorously over a dry, eolian sand substratum in nearly pure stands of *Adenostoma*. By studying natural canopy gaps, as well as gaps created or displaced by reciprocally translocating fuel, we investigated the degree to which preburn canopy can control soil heating, as well as seed and resprout tissue mortality. We also related variation in heating under an unmodified fuel array to changes in seed populations using a spatially explicit approach. Finally, to find out how important the initial patterns of shrub establishment would be to long-term community structure, we monitored survival of seedlings, vegetation change, and measured resprout growth for 4–5 yr, thereby en-

compassing the dynamic portion of the chaparral fire cycle.

## METHODS

### Study sites

The two burn sites (1988, site 1; 1989, site 2) are 7 km apart, near sea level, within Vandenberg Air Force Base in central, coastal California. Unlike most chaparral areas, these sites are on level terrain. Substratum at both sites is the Orcutt Formation, a Pleistocene eolian sand (Dibblee 1950). At site 1, soil is mapped as Tangair sand, a poorly drained soil of light gray sand that formed in old marine terrace deposits (Shipman 1972). Site 2 is located near a mapped border between the Tangair and the very similar Oceano Soil Series. The Oceano Series consists of soils that formed in old coastal sand dunes.

Climate at the two sites is strongly influenced by the prevailing onshore winds. Because the nearby ocean remains cool all year, the temperature regime is mild, especially for a chaparral environment. The mean annual precipitation is 35.3 cm, which is less than generally required to support chaparral. However, the area is often blanketed in fog that reduces evapotranspiration. Based on precipitation records from Vandenberg Air Field, which is within 6 km of the study sites at the same elevation, 90% of the measurable precipitation falls during November–April. The 1988–1989 precipitation totaled only 19.13 cm; during the season following the 1989 burn it was 32.94 cm.

Analysis of aerial photos indicated that neither site had burned in the prior 50 yr (Hickson 1988). We counted annual rings from obligate-seeding *Arctostaphylos* and *Ceanothus* (Keeley 1993) to establish that site 1 had not burned for 75–80 yr, and that stand age at site 2 was 50–53 yr.

Nearly pure stands of *Adenostoma* are common on the Orcutt formation, as they are in most chaparral areas (Davis et al. 1988). Shrubs associated with *Adenostoma* in the study area include the local endemics *Arctostaphylos purissima* (hereafter *Arctostaphylos*), *Ceanothus cuneatus* var. *fascicularis* (hereafter *Ceanothus*), and *C. impressus,* all obligate seeders. The 1.5–2 m tall fuel complex these formed at each site was typical for old age class chaparral (Riggan et al. 1988). There was a mixture of small particle size fuels with live-to-dead and surface-to-volume ratios favorable to combustion of most aboveground phytomass. At site 1, fuel consisted of living *Adenostoma,* with some living and many recently dead *Arctostaphylos.* There were distinct gaps in shrub cover in portions of the burn area at site 1. These mainly resulted from the past death and nearly complete decomposition of *Arctostaphylos* and *Ceanothus.* There was an understory of live but seasonally dry perennial bunchgrasses (*Koeleria macrantha* and *Nassela lepida,* ~10% cover). The fuel bed at site 2 consisted predominantly of living *Adenostoma,*

with some mostly dead individuals of *Ceanothus,* and occasional live *Salvia mellifera* and *Artemisia californica.* The latter are drought-deciduous shrubs that contain high concentrations of volatile terpenes (Muller et al. 1964). Shrubs at both sites supported substantial growth of epiphytic lichens. A complete list of all species found in the field and in seed bank samples is provided in Odion (1995). Nomenclature follows Hickman (1993).

The study site's level topography and sand substratum provide a relatively simple setting for testing heating effects on seeds and seedling establishment. The effects of hill slope processes are negligible. The sand substratum has relatively uniform thermal properties and is much more amenable to seed bank analysis than rocky chaparral substrata.

### Preburn sampling

An L-shaped transect, 24 m on each side, was established before each burn in a nearly pure stand of *Adenostoma.* The transects were oriented so that one arm pointed in the prevailing wind direction (northwest). The L-shaped design was chosen to obtain more observations of sample pairs separated by short distances than are produced by a linear transect, as well as to account for possible directional effects related to fire behavior. Contiguous plots allow for determination of scale and intensity of patterns in variables measured (Hill 1973, Dale and Blundon 1990).

In each of the 47 contiguous 1-m$^2$ plots along each transect, we counted the number and measured the basal area of all *Adenostoma* stems arising from burls, and all individual trunks of other species. Canopy cover was measured along both outer edges of the transect by the line intercept method (Barbour et al. 1980). Cover for each plot is the amount of the total 200 cm along the outer edge of each plot that was intercepted by the canopy of each species.

Live and dead fuel moisture measurements were taken just before the start of each burn in adjacent chaparral. Ten samples, each consisting of several 1–1.5 cm diameter clippings were gathered from several shrubs. Live and dead material from each sample was separated and immediately placed into airtight containers. Samples were returned to the lab, where live and constant dry masses were obtained.

### Burn characteristics and surface heating measurement

Burn parcels were ~75 ha in size and rectangular in shape. The longer side of each parcel was perpendicular to the prevailing northwest wind. At each site, a fire line was ignited along the windward edge at ~1230 under conditions detailed in Table 1. Site 1 was burned on the afternoon of 27 October 1988, and site 2 on 25 November 1989. Flame lengths of 15 m were observed as the fires swept through the transects located 75–100 m from the windward edge of each parcel. The forward rate of

TABLE 1. Weather and fuel conditions at the hour of 1230, when each burn commenced.

| Condition | Site 1 (1988) | Site 2 (1989) |
|---|---|---|
| Air temperature (°C) | 15.6 | 18.3 |
| Relative humidity (%) | 78 | 48 |
| Wind speed (km/h) | 11 | 8 |
| Rainfall previous year (cm) | 32.9 | 19.1 |
| Live *Adenostoma* fuel moisture (% dry mass) | 50.6 | 49.7 |
| Dead *Adenostoma* fuel moisture (% dry mass) | 17.0 | 14.2 |
| Live *Arctostaphylos* fuel moisture (% dry mass) | 58.1 | ... |
| Dead *Arctostaphylos* fuel moisture (% dry mass) | 14.5 | ... |

fire line spread through the transects was 1.2 m/s (4.3 km/h) at site 1 and 1.0 m/s (3.6 km/h) at site 2.

Variation in surface heating was measured using three direct procedures at each site:

1). Twenty-five 30 gauge Chromel Alumel thermocouples (Omega Engineering, Stamford, Connecticut, USA) connected to two underground Campbell CR10 data loggers (Campbell Scientific, North Logan, Utah, USA) were placed horizontally under the litter layer at the mineral soil surface in the first 13 transect plots extending in each direction from the base of the L. Twelve thermocouples were 0.5 m apart in the plot at the base of the L and 2 m in each direction. Thermocouples were 1 m apart in the fourth to seventh plots and 2 m apart in the 7–13th in each direction. When the temperature detected by the northwest thermocouple was >75°C, the data loggers recorded every 5 s, otherwise, they recorded at 30-s intervals. Resolution was 0.1°C. We also established a vertical array of seven thermocouples located at the base of the L. These measured heating at depths of 10, 5, 2, and 1 cm in the soil, and heights of 0, 1, and 3 m above it.

2). Tempilac pyrometers (190–1357°C range, accurate to +55.6°C; Tempil, Plainfield, New Jersey, USA) were placed at 0.5-m intervals along the transect (two per plot) at the soil surface. These consisted of 2 × 5 cm sheet metal copper strips coated with an array of Tempilac thermal paints applied in a series from lowest to highest melting point across the short axis of the strip. Values for each plot are the mean of two pyrometers.

3). At site 1, we placed 12-cm tall, 300 mL metal cans, having 2 cm diameter openings in their lids, on top of the soil in the center of each of the 47 plots in the L-transect. The cans were filled with 200 mL of water. Cans were similarly placed in the 47 plots at site 2, but we used standard 1.06 L paint cans filled to the top, where a 1 cm opening was drilled. This change was made, because, at site 1, 11 cans were found empty and overturned. All empty cans at site 1 were assigned a value of 200 mL evaporated, because it is unlikely they would have overturned until most or all water was lost. At site 2, five cans were found tilted to the side after fire, due to uneven consumption of organic matter beneath. Because these cans were full, some water may have been lost by spilling. Water loss from these cans was therefore given a mean value determined from the two adjacent cans (values from three to five adjacent plots were combined at the block sizes where relationships were strongest). Cans were placed in both burn areas immediately before fire. Openings in the cans were sealed with waterproof tape that melted/burned during the fire. The cans were collected the morning following each fire, when they were resealed. The amount of water lost was determined gravimetrically. This procedure provides an estimate of the heat load impinging on each can (Beaufait 1966).

We also measured the minimum diameter of *Adenostoma* branches remaining after fire. This has been shown to be statistically related to fire severity in *Adenostoma* chaparral (Moreno and Oechel 1989). Diameters of all remaining branches (a variable number) were measured within a 1 × 1 m plot centered on each thermocouple. All branches ≤1 m in any direction of each thermocouple, and all branches in the space directly above each of the transect plots, were also measured. In a few plots at each burn, there were fewer than five stems in the space above the plots, so the next closest stems were measured to obtain a minimum sample of five stems (more, if warranted by variance). These stems were within 0.5 m of the plots at site 1, and 0.75 m at site 2. Because minimum branch diameter is a mean variable, sufficient sample sizes are needed to be representative of an area.

At site 1, 16 cm long steel nails were placed in the four corners of all 47 transect plots and 5 cm away from each thermocouple. The distance the head of the nail protruded above the soil after fire was measured to describe litter consumption.

### Effect of fire on seed populations

Seed survivorship was monitored by comparing preburn and postburn soil seed reserves present in each plot. Nine 5 cm diameter, 7.5 cm deep cores of soil were obtained per plot for preburn seed bank analysis at site 1 (six from along the outside two edges of the plot, and three from the center). At site 2, five cores were taken from around the water cans placed in the center of each plot (i.e., a 25–30 cm diameter circle). At site 1, the preburn samples were collected approximately three weeks prior to the burn, while at site 2 there was a two-week time lag. Six soil cores per plot were collected the day after the fire from site 1 (four from along the outside two edges of the plot, and three

from the center) for analysis of postburn seed banks. At site 2, five samples were collected for postburn analysis. Seed bank cores for each plot were composited, and 350-cm³ subsamples were removed from each homogenized sample.

A greater soil volume was collected at site 1, so that different methods could be compared for effectiveness at inducing germination of refractory seed (Odion, *in press*). A treatment involving heat and addition of ground *Adenostoma* charcoal (charate; Keeley and Pizzorno 1986) was found to induce more germination than controls or samples treated to heat alone, and was therefore used for the site 2 samples. Heat treatment consisted of spreading the soil to a depth of 2–3 mm on thin, pliable, aluminum cooking trays and placing them in a forced-air oven at 100°C for 7 min. Soil subsamples (350 cm³) were then spread on sterile sand in 20 cm diameter plastic pots in which 21.3 ± 0.94 g ($n = 11$) of charate was sprinkled. Because of apparent negative germination response detected for a few species (Odion, *in press*), and since little charate is needed to effect seed germination (Keeley and Pizzorno 1986), only one-half as much charate was added to samples from site 2. Charate was not added to postburn samples, as they already contained charred, woody fragments and other byproducts of plant combustion.

Seed bank sampling was also undertaken at 10 of the experimental gap areas. Cores from gap and adjacent understory areas were separated into 0–2.5 and 2.5–7.5 cm depth fractions. Heat and charate were applied to preburn samples. Due to smaller soil amounts available, 175-cm³ subsamples were spread over sand in 16 cm diameter plastic pots. Finally, we collected seed bank samples from each site just before the second growing season. Twenty samples were collected from transect plots selected randomly. For these, we used the same germination treatments we employed on site 1 preburn samples.

The pots were covered with clear plastic to protect seedlings from herbivory, and they were kept moist out-of-doors at Cal-Orchid Nursery in Santa Barbara, where temperature fluctuations were comparable to the field. During each year, potting was completed in late November, at which time all samples were given their first watering. All the samples were exposed to outdoor temperatures from the time of collection through the subsequent growing season to provide natural temperature stratification to overcome secondary dormancy (Bewley and Black 1985). Seedlings were tallied, identified, and removed upon emergence from the samples to provide pre- and postburn seed bank inventories.

*Canopy gaps and manipulation of fuel patterns*

The existence of distinct discontinuities in canopy cover within the burn area at site 1 allowed us to directly assess how shrub canopy may control soil heating and seed and resprout tissue mortality associated with fire. Gaps were approximately circular and had mean diameters 1.7 + 0.56 m before the burn. There were no gaps located along either transect. Twenty gap sites were studied in detail. We inverted the fuel pattern at five of these sites by removing *Adenostoma* canopy adjacent to the gap and piling it loosely in the gap. A $1 \times 0.5$ m plot was located in each natural gap ($n = 15$), each created gap ($n = 5$), as well as the area immediately adjacent to these where natural ($n = 15$), or added shrub canopy ($n = 5$) was present before fire. We placed 300-cm³ water cans and pyrometers in the center of five gap and five adjacent understory plots and the five gap and five understory plots created by reciprocal translocation of fuel. Three pre- and three postburn soil cores were taken for seed bank inventory from near the center of plots where soil heating was measured. Soil heating and seed populations were not measured at the remaining 10 gap and 10 adjacent understory plots. Field seedling densities were, however, measured in all plots. Preburn seed bank samples were not affected by fuel treatment, and gap vs. adjacent understory comparisons of these are based on a sample size of 10. Seed populations were much greater in gaps after fire and lower in understory areas, regardless of whether they were natural or created, so postburn seed bank data from all gaps were combined to obtain a sample size of 10. The same was done for understory areas. For data on field abundance, we compare densities at plots in the 15 naturally occurring gap and understory locations with those in the five experimentally created gaps and understories.

*Seedling and resprout patterns in the field*

At each site, seedling and resprout growth in the field were censused in all plots during mid-spring (late March to late April) of the first four to five postfire growing seasons. The density of all species was tallied. No recruitment of shrub seedlings occurred after year 1, so subsequent mortality was determined by reduction in density of these seedlings.

At site 2, feral pigs (*Sus scrofa*) overturned the sand in portions of plots 3–18, before postburn field densities were measured. Although relatively few seedlings were affected, this may have diminished correlations between postburn seed bank and plant abundance at site 2.

*Data analysis*

Patterns in the initial heat pulse and duration of heating were explored by time-integrating thermocouple data above a range of temperatures, to calculate total heat generated above these thresholds. Semivariogram analysis of heat generation was undertaken to evaluate spatial patterns in thermocouple data based on actual distances among thermocouples. We also performed correlation analysis with these time-integrated data and preburn vegetation attributes.

We chose a contiguous plot layout design, so that

patterns among variables could be studied by evaluating quadrat variance over a range of scales. The quadrat variance analysis method of Hill (1973) combines the quadrats into blocks that, in this case, increase in size by 1 m² each iteration to determine the size that maximizes the difference between adjacent blocks (Dale and Zbigniewicz 1995). Where low-density gaps alternate with high-density patches, the scale of pattern is the mean distance between the center of a patch and the center of its neighboring gap. Correlations among parameters measured in each plot along the transect are similarly calculated using two-term covariance analysis (Hill 1973). This method will slightly overestimate scale of maximum correlation among variables for block sizes $>4\times$ the smallest, so patterns peaking at block sizes of 4–6 m in our study may actually represent a block size 0.25–0.5 m smaller (Dale and Blundon 1990). Standard significance tests cannot be applied to the correlations because of serial autocorrelation in data collected in contiguous plots (i.e., plots cannot be treated as independent observations).

We adopted the L-shaped design of the transects to efficiently deploy a thermocouple array in a layout that allowed us to examine both distance and directional effects in fire behavior and vegetation. The field data revealed no systematic trends along the transect, nor any directional effects in spatial pattern. Thus, for the block variance and covariance analyses, we treated the two arms of the L as a replicate pair of 24-m transects. The two ''subtransects'' are not entirely independent samples, but serve well for studying spatial patterns over short (e.g., $<8$ m) distances.

Individual seedling counts and other comparisons made between gap and adjacent understory plots, etc., were tested for statistical significance using the nonparametric Kruskal-Wallis one-way analysis of variance or a pairwise $t$ test, as appropriate.

The proportion of shrub seedlings surviving over all measured time intervals in each plot was arcsine transformed. Regressions were performed with survival data and herb, shrub, subshrub, and total plant density data, as well as the initial density of the surviving species. Multiple regressions were done with subsets of these variables. Output from stepwise multiple regression was used to identify the best multiple regression models. Logarithmic transformation of density data strengthened many relationships. Survival data were also evaluated as a function of percent cover of *Adenostoma* resprouts after five years at the understory plots adjacent to gap plots ($n = 20$) at site 1. *Adenostoma* resprout success along transects was linearly related to soil heating and other parameters, by ranking it on a scale of one to eight (high to low mortality), based on the eight different possible combinations of the number of live and dead shrubs found in 1-m² plots (1, 2 dead; 2, 1 dead; 3, 3 dead and 1 alive; 4, 2 dead and 1 alive; 5, 1 alive and 1 dead; 6, 2 alive and 1 dead; 7, 1 alive; 8, 2 alive).
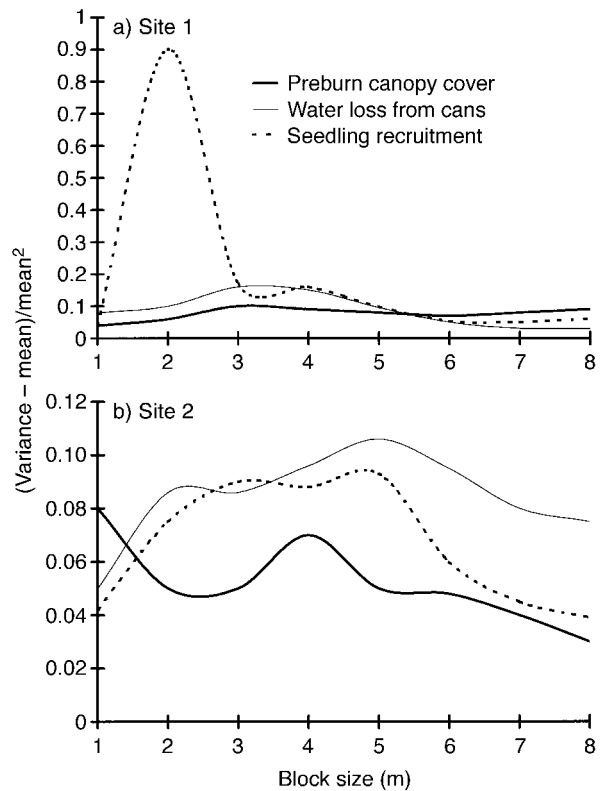


FIG. 1. Variance in data from adjacent plots and blocks of plots (pattern intensity) at (a) site 1 and (b) site 2. Data from postburn variables were rescaled to fit on the same plot with preburn data.

RESULTS

*Spatial patterns in preburn vegetation*

At site 1, preburn shrub cover was nearly continuous along the transect, ranging 65–193%, with a mean of 104.4% (100% maximum per species). *Adenostoma* dominated, with both live and recently dead *Arctostaphylos* scattered among them. At site 2, preburn canopy cover was less continuous, with a mean per plot of 107% and a range of 18–155%. *Ceanothus, Artemisia californica,* and *Salvia mellifera* were present. Areas of especially high cover and fuel loading occurred where shrub canopies intermingled and where *Arctostaphylos* were found. Mean variance in cover between blocks of quadrats $<8$ m² in size, a measure of relative pattern intensity, peaked at a scale of 4 m at site 1 (Fig. 1a). At site 2, variance in canopy cover was relatively high at the smallest block size, dropped as block size increased from 1 m to 2–3 m, then rose to a distinct peak again at 4 m (Fig. 1b).

*Heating patterns*

Temperature–time curves from one arm of the transect at site 2 are representative of the thermocouple data in their entirety and are shown in Fig. 2. With arrival of the flame front, temperatures rose from am-
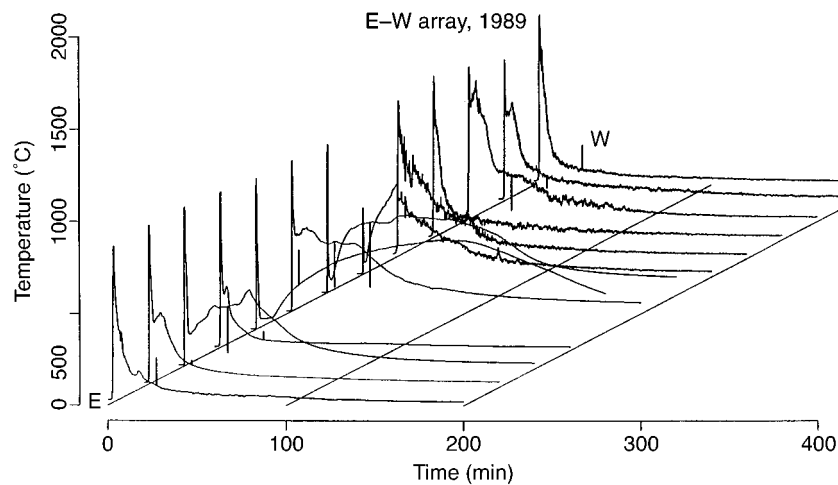
FIG. 2. Continuous temperature measurements from along the thermocouple array (*z*-axis), oriented west (slightly northwest) at site 2.

bient to 775–925°C in 10–15 s. There was a rapid drop to 500–600°C after 3–5 min, as the zone of flaming combustion passed. Like the thermocouples, the Tempilac pyrometers recorded maximum temperatures that were high for a fire in *Adenostoma* chaparral (see DeBano et al. [1979] for comparison). The mean maximum measured at site 1 (mean, 1088°C; SD, 112°C) was higher than at site 2 (mean, 840°C; SD, 65°C). Unlike thermocouples, there was considerable range in maximum temperatures recorded by pyrometers (700–1200°C), suggesting that pyrometers were influenced by temperature duration. This is further evidenced by the positive correlations between maximum pyrometer temperatures and water loss from cans ($r = 0.56$ for site 1; $r = 0.68$ for site 2).

The initial heat pulse was followed by gradual reduction of temperatures to <100°C after ~35–45 min among half of the thermocouples. The remaining thermocouples measured renewed heating for a period of one to several hours (Fig. 2). Temperatures among these rose to levels associated with smoldering combustion (Chandler et al. 1983). Location of secondary heating was not well correlated with depth of litter at site 1 ($r = 0.09$), which ranged 2–40 mm and was completely consumed by fire. Considering this, and how prolonged secondary heating was, smoldering fuel must have been dominated by canopy material that became detached with the burning through of shrub branches and fell to the ground before being consumed, as was observed and photographed (Odion 1995). This fire behavior in chaparral was originally described by Craddock (1929). Distribution of smoldering combustion, and, therefore, patterns in total heating, was marked after fire by the white ash produced (see Odion [1995] for photo). Secondary heating was so prolonged that it accounted for the majority of overall heating where it occurred. The amount of smoldering canopy material on and adjacent to water cans, therefore, predominantly determined wa-

ter loss, which varied substantially with location. This variance peaked at a scale of 2–5 m and exceeded that found in preburn canopy cover (Fig. 1).

Soil heating at depth is illustrated by data collected from the vertical thermocouple array at site 2 (Fig. 3). At 2 cm deep, soils reached a maximum of 150°C and were >100°C for longer than 1 h. Maximum soil temperature diminished rapidly with depth, only reaching 51 and 39°C at 5 and 10 cm, respectively. Temperatures remained near these maxima for several hours. The three surface thermocouples from the same plot where the vertical array was located showed no secondary heat pulse. Water loss, minimum remaining branch diameter, and seed mortality data all suggested that much less surface heat flux occurred at this location, compared to where secondary heating did occur.

Thermocouples measuring secondary heating often occurred within 1 m of those unaffected by smoldering combustion (Fig. 2). With the large discrepancy in heat impinging on thermocouples with and without secondary heating, similarity among temperature–time curves, as a function of proximity of sensors, was not evident. The plot for site 1 does indicate a somewhat regular pattern at a distance of 6–7 m. However, there is no evidence of positive spatial autocorrelation over shorter distances at either site (Fig. 4). Poor fits were obtained for standard forms, such as spherical ($r^2 < 0.01$), exponential ($r^2 < 0.01$), or linear ($r^2 < 0.10$) models.

Considered as independent samples, the time-integrated thermocouple data >100°C were significantly positively correlated with preburn canopy cover for the 1-m$^2$ plot in which they were located at site 1 (Table 2). In both burns, the density and/or cross-sectional area of stems arising from lignotubers 0.5–1 m away from thermocouples were significantly correlated with total heat generation >100–500°C (Table 2). No significant correlations were found when stems measured 1–3 m outward were included. Thus, the burning
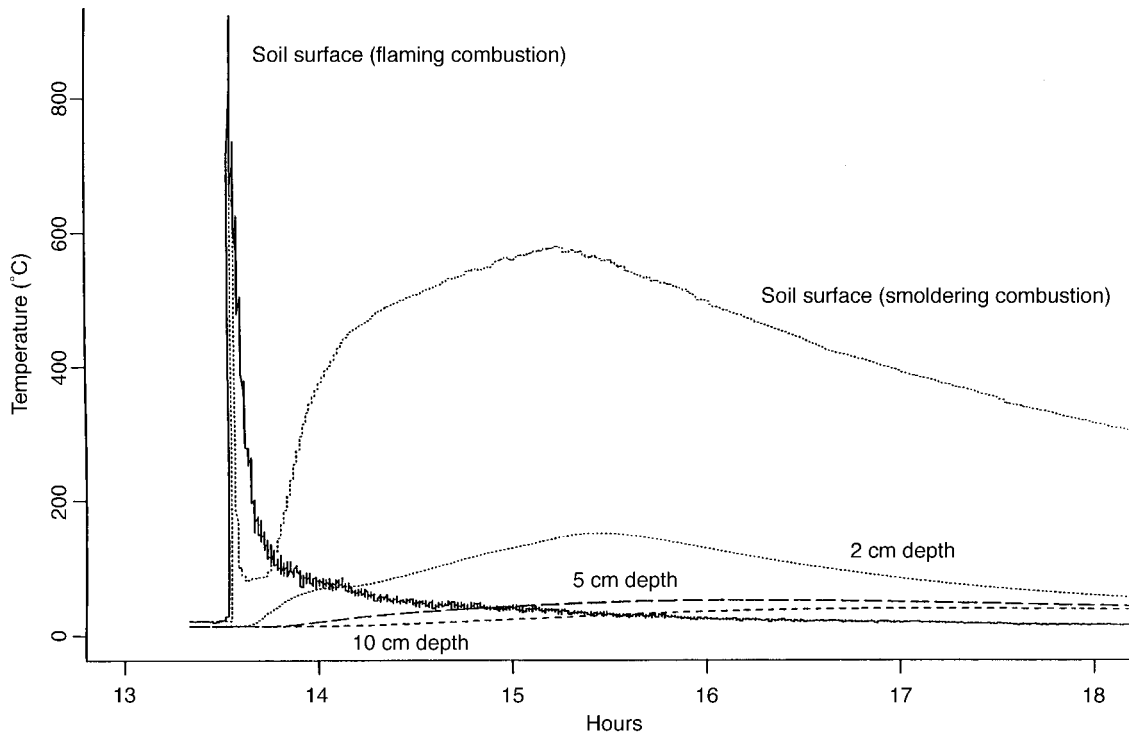
FIG. 3.   Temperature–time curves for two locations in the site-2 burn. The dotted surface curve illustrates secondary heating from smoldering combustion of collapsed canopy at one point. The other surface curve and depth measures are from a second point at the base of the L-shaped transect.

through of branches and collapse of the fuels producing long-duration combustion occurred mainly between 0.5–1 m horizontally from *Adenostoma* lignotubers. There was also a significant correlation between flaming combustion, i.e., heating above 500°C, and the total basal area of stems within 0.25 m at site 2.

### Relationship between preburn vegetation and heating patterns

Two-term local covariance analysis illustrates how water loss from cans and maximum temperature were strongly associated with the preburn canopy at 3–5-m blocks at both sites (Fig. 5a, b). The strength of these relationships diminished with smaller block sizes and, for water loss from cans, also decreased with larger block sizes. Water loss became negatively associated with canopy at block sizes of 7–12 m, however, 24-m transects are not long enough to effectively evaluate spatial associations at this scale. Water loss from cans at canopy gaps was significantly lower than under the adjacent chaparral canopy ($P < 0.05$, $t$ test, Table 3), as well as along the transect. Water loss was greater at gaps where fuel was added than under natural canopy (Table 3).

Mean minimum branch diameter was well correlated with canopy at block sizes $\geq 2$ m at site 1, but was poorly correlated at site 2, where it did not vary as greatly. Differences in preburn branch diameters and

shrubs intermingling with *Adenostoma,* particularly the volatile mesophyllous species at site 2, could account for the discrepancy in canopy vs. minimum branch diameter relationships.

In summary, preburn canopy, can water loss, maximum temperature pyrometers, and minimum branch diameter, and at site 1 depth of litter consumed, all exhibited the same pattern of variation. Further, this was the pattern of variation that developed in two interrelated biological indicators of heating, seed mortality and seedling recruitment in the field.

### Vegetation response to heating effects

After burning, both sites developed into a mosaic of patches of fairly dense seedling and herbaceous resprout growth, especially in gaps, alternating with near barren patches associated with charred *Adenostoma* skeletons (Figs. 6 and 7, Table 4). Seedling patterns mirrored postburn seed distribution; neither resembled the preburn pattern of seed abundance (Fig. 6). Postburn patterns were strongly correlated with heating, as illustrated in Fig. 6b, d, and results from experiments indicate that they were caused by heating.

*Resprouting in relation to preburn vegetation and heating.*—At gaps where fuel was added, only 3.2 (SD = 2.4) herbaceous resprouts/m² were found, compared to 18.3 (SD = 14.4) in naturally occurring gaps ($P \ll$ 0.05, Kruskal–Wallis Test, Table 4). A number of plots
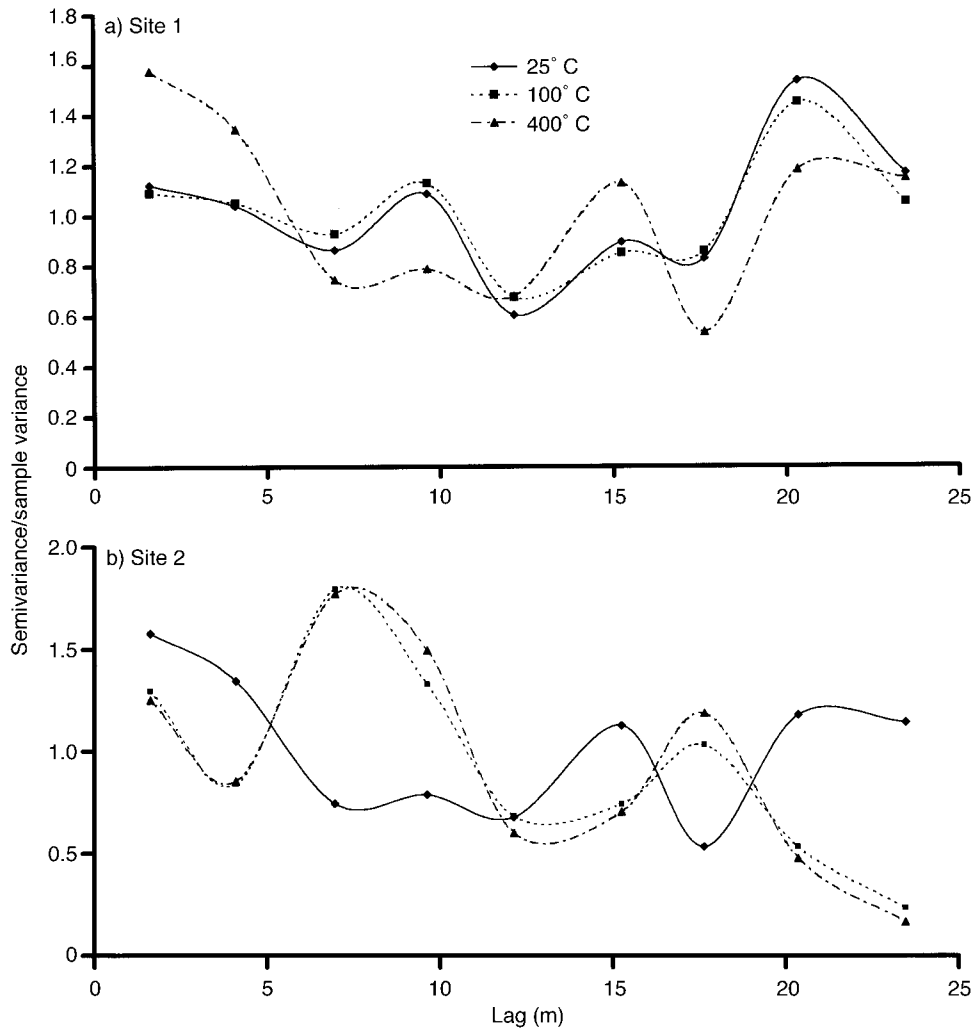
FIG. 4. Variograms of time-integrated thermocouple data for (a) site 1 and (b) site 2. The *x*-axis shows lag distance between sample observations, and the *y*-axis shows semivariance, normalized by sample variance, for temperature records >25°, >100°, and >400°C.

along the transect at site 1 (e.g., 4–8, 15–19, and 41–46) lacked resprouts. These plots had high preburn canopy and soil heating (Fig. 7a). The perennial grass *Koeleria macrantha* was a dominant herb at site 1. The density of *Koeleria* ramets per plot became strongly negatively correlated with total preburn canopy cover ($r = -0.58$) and water loss from cans ($r = -0.67$) as block sizes increased to 3 m (Fig. 8a). The strength of these relationships diminished rapidly as block size increased further, becoming positive as block sizes became relatively large. The geophytes *Dichelostemma capitatum, Calochortus albus, Sanicula laciniata,* and *Erigeron sanctarum* had correlations with heating that were similar to those of *Koeleria,* despite the greater depth their perennating tissue occurs in the soil (Fig. 8a).

*Adenostoma* shrubs experienced 50% mortality along the transect at site 1 (Fig. 7b). The mortality produced

openings that lacked resprouting shrubs at 5–9, 15–20, 35–38, and 44–47 m along the transect. These were areas of greatest preburn canopy cover and soil heating. Results from correlation analyses suggested that heating was a factor in shrub mortality (e.g., $r = 0.48$ for correlation with water loss; see *Methods* for calculation). *Adenostoma* shrubs that died were generally much smaller than those that lived; mean total area of basal stems was 44 $cm^2$/plant, compared to 121 $cm^2$ ($P \ll 0.05$, *t* test).

At site 2, herbaceous resprouts were abundant along the entire transect (Fig. 7c), but were again negatively associated with areas of greatest heating ($r = -0.54$ and $r = -0.61$ for correlations with water loss and total seed mortality, respectively). The negative association between geophytes and heating, as well as preburn canopy, was consistent with that found at site 1: strong at 3–5 m block sizes (Fig. 8b). All *Adenostoma*

TABLE 2.  Correlations (Pearson's *r*) between integrated thermocouple profiles (*n* = 25) and preburn canopy cover, as well as density and basal area of stems arising from *Adenostoma* lignotubers.

| Feature and site | Temperature threshold (°C) | | | | | |
| --- | --- | --- | --- | --- | --- | --- |
| | 100 | 200 | 300 | 400 | 500 | 600 |
| Canopy cover site 1 | 0.40* | 0.33 | 0.29 | 0.23 | 0.27 | 0.26 |
| Canopy cover site 2 | 0.05 | 0.18 | 0.20 | 0.35 | 0.33 | 0.23 |
| Stem density site 1 | | | | | | |
| 0.25-m radius | −0.07 | 0.07 | 0.14 | 0.32 | 0.50 | −0.01 |
| 0.50-m radius | 0.06 | 0.01 | 0.09 | 0.20 | −0.01 | −0.35 |
| 1.00-m radius | 0.37 | 0.29 | 0.42* | 0.39* | −0.08 | −0.22 |
| Stem density site 2 | | | | | | |
| 0.50-m radius | 0.61*** | 0.56*** | 0.44* | 0.08 | 0.09 | 0.04 |
| 1.00-m radius | 0.49*** | 0.40* | 0.28 | −0.11 | −0.06 | −0.04 |
| Stem basal area site 1 | | | | | | |
| 0.25-m radius | −0.10 | 0.00 | 0.07 | 0.25 | 0.51* | 0.05 |
| 0.50-m radius | 0.01 | 0.05 | 0.16 | 0.40* | 0.55*** | −0.07 |
| 1.00-m radius | 0.26 | 0.21 | 0.30 | 0.45* | 0.40* | 0.02 |
| Stem basal area site 2 | | | | | | |
| 0.50-m radius | 0.45* | 0.46* | 0.40* | 0.36 | 0.33 | 0.20 |
| 1.00-m radius | 0.49*** | 0.44* | 0.36 | 0.0 | 0.07 | −0.01 |

*Notes:* Thermocouple data were integrated above increasing temperature thresholds to estimate total heat generation above a particular temperature. Canopy cover values were for the 1-m$^2$ plot in which each thermocouple was located. Stem density and basal area were measured within circular plots of increasing radius that were centered on each thermocouple.
　* $P < 0.05$; *** $P < 0.001$.

along the transect resprouted at site 2, and few instances of mortality were noted within that burn.

*Reduction in germinable seed and seedling recruitment in relation to preburn vegetation and heat.*—Total seed densities (Table 4) were significantly greater before fire and closer to the surface in gap (88% in top 2.5 cm) compared to understory plots (73% in top 2.5 cm). After fire, there was a bigger disparity in total abundance, but not in depth of burial (61% vs. 58% in top 2.5 cm). Seed density along the site 1 and 2 transects was 11,316 and 18,142 seeds/m$^2$ before fire, and 804.9 and 3026 seeds/m$^2$ after, so not only was maximum pyrometer temperature greater along the transect at site 1 vs. site 2, so was seed mortality.

Total mean seedling density in gap plots was 209.9 seedlings/m$^2$ after fire, but was only 28.6 seedlings/m$^2$ in the adjacent understory plots. This is a greater discrepancy than found among postburn seed abundance, due, in large part, to failure of *Helianthemum* to germinate at understory plots in the field. Seedling densities were approximately as low after fire where fuel was added to gaps as they were in natural understory plots, even though seed densities were significantly greater in gaps before fire (Table 4). The greater seed mortality with fuel addition is consistent with water loss data, as an indication of greater heating with this treatment vs. what occurred under the natural canopy next to gaps.

The distribution of seed that survived fire along transects was strongly negatively associated with preburn canopy and water loss from cans at both sites (Fig. 9a, b). These correlations had a distinct negative peak at block sizes of 3–4 m at site 1 and 5 m at site 2. Total density of seedlings in the field was even more strongly negatively correlated with the amount of shrub cover present before fire, and with soil heating, than were postburn seed populations. At site 1, the correlations among cover and can water loss vs. seedling density reached $r = -0.81$ and $r = -0.88$ at block sizes of 3–4 m, respectively, forming a distinct negative peak at this scale (Fig. 9a). At site 2, block size of maximum correlation among these was 5 m, and was equally scale dependent, but not quite as strong ($r = -0.77$ and $r = -0.61$, respectively; Fig. 9b).

*Adenostoma,* with abundant seed close to the soil surface (88% < 2.5 cm in depth) and significantly concentrated under its canopy (Table 4), was the shrub whose seed was most sensitive to heating. Only 2–3% of its seed survived fire along the transects, and its pattern of abundance became negatively associated with preburn canopy (Table 4). Likewise, *Adenostoma* seedlings in the field were four times more abundant in gap vs. understory plots, but the inverse pattern was found where fuel was switched (Table 4). Along transects, *Adenostoma* seedlings were negatively correlated with preburn canopy and water loss. These relationships were strongly scale dependent (4 m) at site 1 (Fig. 10a). At site 2, there was not a distinct negative peak in the correlations; the relationships were moderately strong at scales spanning 2–5 m block sizes (Fig. 10b).

As a result of having more seed at depth (81% of seeds were from 2.5–7.5-cm depths), *Arctostaphylos* seed had better survival with fire (17%), and 8.7 seed-

a) Site 1   Descriptors of soil heating

— Canopy cover vs. water loss from cans
- - Canopy cover vs. maximum temperature
 Canopy cover vs. mimimum branch diameter
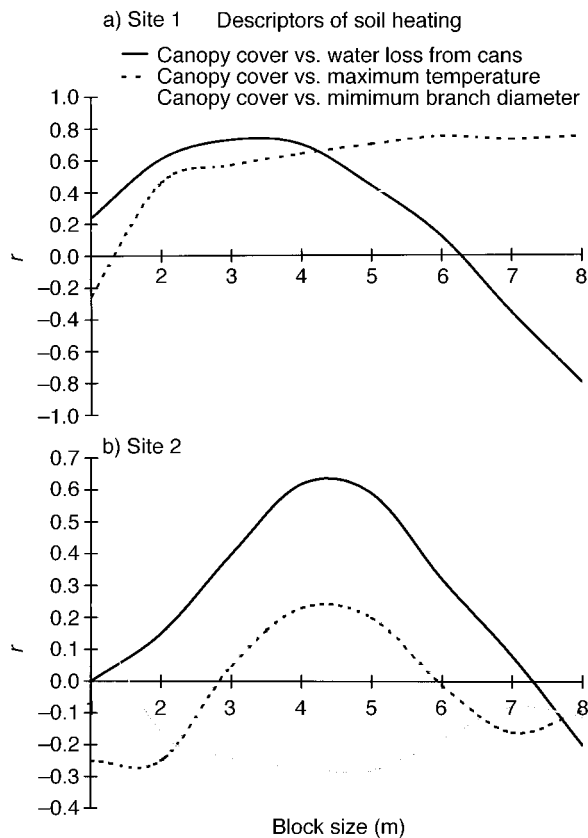
b) Site 2

Block size (m)

FIG. 5. Correlations calculated by two-term covariance analysis among preburn canopy and descriptors of heating as a function of block size along the transects at (a) site 1 and (b) site 2.

lings/m² were recruited in understory plots. Nonetheless, seed of this species was sensitive to high soil heating. The 5.6 seedlings/m² found in fuel addition plots were significantly fewer than the 14.4 seedlings/m² in untreated gap plots. There were strong negative correlations for both postburn seed bank and especially field abundance vs. preburn canopy and water loss from cans. Once again, the strength of these relationships increased with spatial scale ≤4 m (Fig. 11).

*Ceanothus* was unique in having better seedling recruitment at understory vs. adjacent gap plots and no increase in field seedling density with gap creation.

Unfortunately, *Ceanothus* seed densities were not sufficient to determine whether seeds were concentrated under *Adenostoma* canopy and buried relatively deeply, as these data suggest. *Ceanothus* was strongly affected by fuel addition. Only 1.6 seedlings/m² were found where this treatment was undertaken (Table 4). Along transects, *Ceanothus* seedling recruitment was negatively associated with preburn canopy and water loss from cans (Fig. 12a, b). The strength of these associations was much greater at block sizes of 2–4 m at site 1. At site 2, the relationship between preburn canopy and field recruitment strengthened gradually with increasing block size to 5 m, then remained about the same at greater spatial scales.

*Helianthemum scoparium,* a subshrub, was the most abundant plant in the field after fire and had high seed bank densities (6819 seeds/m² at site 2 before fire). At gaps prior to fire, 53% of *Helianthemum* seed was in the 2.5–7.5 cm depth fraction, and 75% was in the deeper fraction at adjacent understories. After fire, 94% of seeds were below 2.5 cm at understory plots. Although shallowly buried seed were killed with fire, there was not a strong negative relationship between postburn seed abundance and water loss from cans. However, seedling recruitment in the field exhibited particularly strong, scale-dependent relationships (3–5 m) with both water loss and preburn canopy (Fig. 13a, b). Furthermore, the density of *Helianthemum* seedlings in gaps was 82.1 seedlings/m², but only 3.1 seedlings/m² at adjacent understory plots, even though postburn seed abundance was only twice as great in gaps (Table 4). Although *Helianthemum* did not flower the first year after fire, samples collected after the first growing season contained germinable seed densities of 41 and 439 seeds/m² in sites 1 and 2, respectively. These densities were approximately one-third as great as those found in postburn samples collected immediately after fire. *Helianthemum* is the only species in which we documented that some surviving seed failed to germinate the first year after fire. Apparently, only the most shallowly buried *Helianthemum* seed, the distribution of which was strongly affected by soil heating, was able to germinate and/or emerge in the field. More deeply buried seed, whose pattern of abundance was not strongly affected by fire, remained dormant and/or

TABLE 3. Measurements taken at natural and artificially created gap and adjacent understory areas.

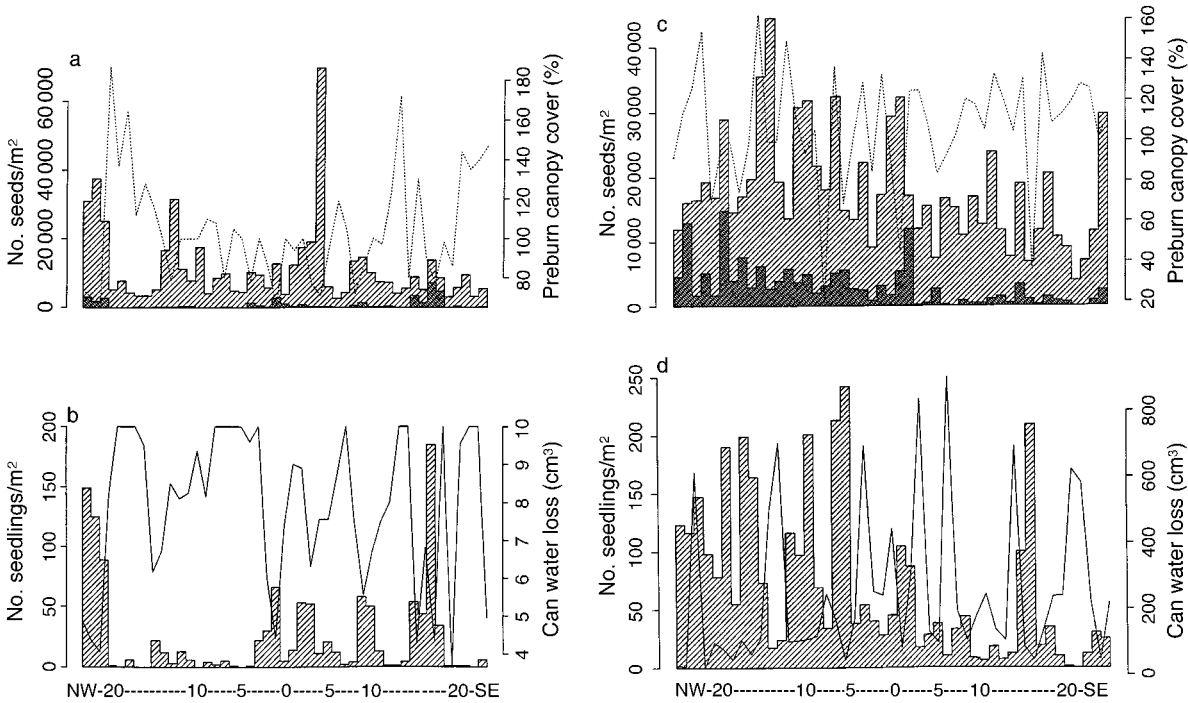| Measure | Type | N | Gap Mean (1 SD) | Understory Mean (1 SD) |
|---|---|---|---|---|
| Gap diameter (m) | Natural | 5 | 1.68 (0.56) | ... |
| | Created | 5 | 1.42 (0.56) | ... |
| Can water loss (mL) | Natural | 5 | 84 (10) | 116 (33) |
| | Created | 5 | 111 (20) | 193 (10) |
| Maximum temperature (°C) | Natural | 5 | 1127 (67) | 1116 (152) |
| | Created | 5 | 927 (109) | 1149 (88) |

Fig. 6. Total density of readily germinable seed and seedlings in each of 47 contiguous 1-m² plots. (a) Site 1, preburn readily germinable seed (sum of control, heat, and heat and charate treatments; see *Methods*) and postburn readily germinable seed (darker, embedded bars). (b) Site 1, field seedling recruitment during the first growing season following fire. (c) Site 2, preburn readily germinable seed based on heat and charate treatment, and postburn readily germinable seed (darker, embedded bars). (d) Site 2, field seedling recruitment during first growing season following fire. Preburn canopy cover and water loss from cans are shown for each transect by dotted and solid lines, respectively.

failed to emerge (Table 4). As a consequence, fuel addition to gaps reduced average *Helianthemum* density by a factor of seven (Table 4).

The second most abundant species following fire, *Navarretia atractyloides,* an opportunistic annual, had seed concentrated near the soil surface; only 8% of seed was at soil depths >2.5 cm. *Navarretia* seed was found to be concentrated in gaps before and after fire (Table 4), and seedlings in the field were abundant in gap plots (58.3 seedlings/m²). However, where fuel was added to gaps before fire, only 1.6 seedlings/m² were found. *Navarretia* postburn seed bank and field seedling distributions along transects exhibited strong scale-dependent negative relationships with preburn canopy and water loss from cans (Fig. 14a, b).

*Shrub seedling survival*

Survival of *Adenostoma* ranged 7–11% over four to five years along transects and in gap plots (Fig. 15a). No seedlings survived in understory plots, but only 13 occurred there initially. Survival in gap plots was found to be significantly negatively affected by the density of *Helianthemum scoparium* ($r = -0.51$, $P = 0.05$).

*Arctostaphylos* survival was 15–16% along the site 1 transect and at understory plots (Fig. 15b), which was significantly greater than the 11% that occurred in gap plots (*t* test, $P < 0.05$). Survival of *Arctostaphylos*

from year 1 to year 2 in gap plots was negatively related to density of all seedlings occurring there ($r = -0.59$, $P = 0.03$). The data suggested a relationship with seedlings of the most abundant species, *Helianthemum* ($r = 0.50$, $P = 0.07$). Survival in understory plots was inversely related to the combination of initial *Arctostaphylos* density and *Adenostoma* resprout cover after five years ($r = 0.41$, $P = 0.01$). The relationship between survival and resprout cover alone was fairly strong ($r = -0.44$, $P = 0.06$).

Of the two *Ceanothus* at site 1 that were combined for analyses of soil heating effects, *C. impressus* had only 21% survival, half of that found among *C. cuneatus.* Therefore, the two species were separated for analysis of survival in relation to location, initial density, and abundance of other plants. There were no factors we could identify from our data explaining survival of *C. impressus,* since it was found in few plots. For *C. cuneatus* (Fig. 15c), survival in understory plots was positively associated with *Adenostoma* resprout cover over the first two years ($r = 0.63$, $P = 0.01$), but negatively related to resprout cover from year 2 to year 5 ($r = -0.43$, $P = 0.38$). After five years, survival of these seedlings was inversely related to the combination of its initial density and the cover of *Adenostoma* resprouts ($r = -0.62$, $P = 0.01$). At site 2, initial densities of *C. cuneatus* were much greater than at site
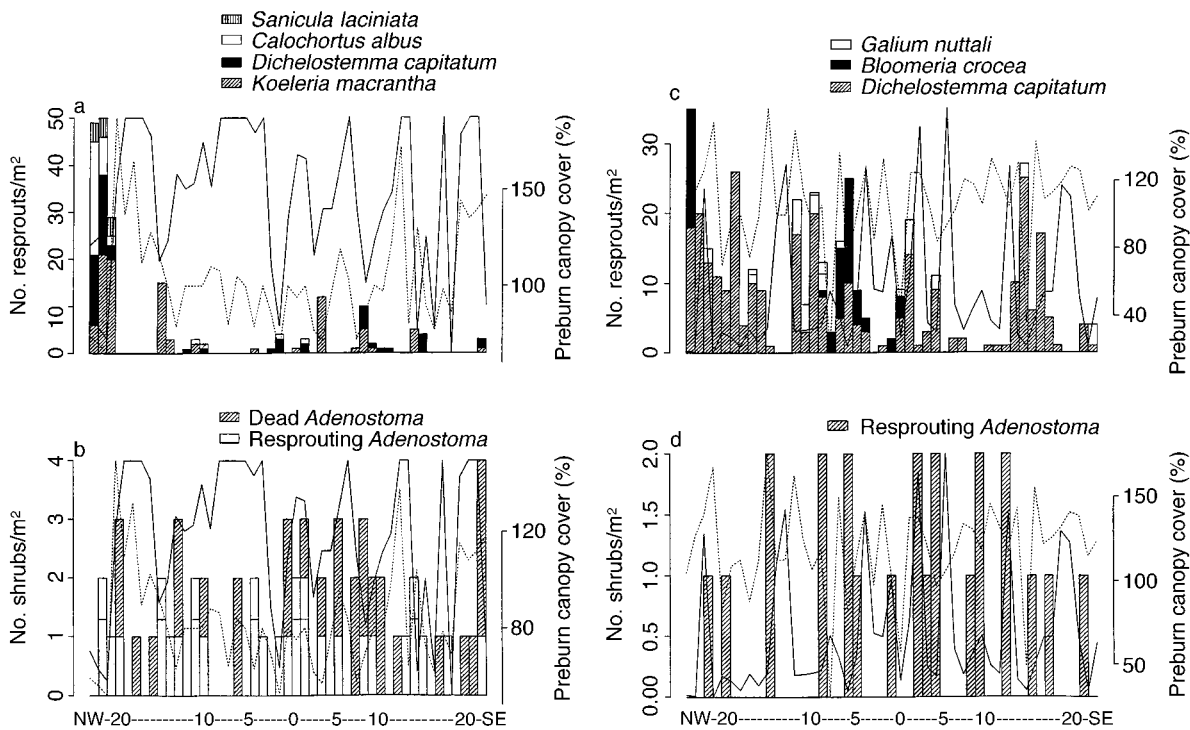
FIG. 7. Density of resprouts in each of 47 contiguous 1-m² plots. (a) Site 1, herbaceous resprouts. (b) Site 1, resprouting and dead *Adenostoma fasciculatum.* (c) Site 2, herbaceous resprouts. (d) Site 2, resprouting *Adenostoma* (no mortality occurred). Preburn canopy cover and water loss from cans (a measure of heating) are shown for each transect by dotted and solid lines, respectively (scale for water loss from cans not shown).

1 (Fig. 15c), and survival after four years was only 24%.

Because *Ceanothus* and *Arctostaphylos* were the only shrubs to emerge in areas of more prolonged heating, they selectively replaced *Adenostoma* that were killed with fire at site 1. However, where resprouting by *Adenostoma* was vigorous, seedlings of the two shrubs suffered high mortality. *Arctostaphylos* additionally had high mortality in gaps as a function of total seedling densities. As a result, abundance in gap vs. understory plots after five years was comparable among the obligate seeders. The pattern of seedlings for each shrub species along transects was little changed after 4–5 yr in terms of presence vs. absence, but each species abundance was reduced in areas where they were most common.

### DISCUSSION

It has been well-documented that postburn plant growth from sources in the soil will be strongly influenced by the soil heating that occurs with fire (e.g., Beadle 1940, Wright et al. 1976, Shea et al. 1979, Auld 1986, Bond et al. 1990, Hodgkinson 1991, Moreno and Oechel 1991a, b, Bradstock and Auld 1995, Schimmel and Granström 1996). We have quantified the natural spatial variation in the intensity of this disturbance process and the patterns of plant growth that result. By

relating regeneration to soil heating patterns determined by the fuel array, we evaluate the importance of the predisturbance community in structuring the one that follows. Through this work, we demonstrate a strong mechanistic link between pattern and process in this system, an important but rarely quantified relationship in ecology.

### A model for the establishment of within-stand vegetation patterns in chaparral after fire

Our major finding is that the pattern of heating imprinted into the soil by smoldering combustion effectively determined the spatial arrangement of seeds and resprout tissues that survived, regardless of their preburn distribution. Heat-induced patterns in surviving seed and resprout tissue emerged essentially unchanged in the regenerating vegetation, and were persistent through community regrowth over the time period when most of the vegetation dynamics of the fire cycle occur.

We found that relationships among naturally occurring patterns of canopy, soil heating, and regenerating vegetation consistently grew in strength as a function of block size, becoming strong and peaking at a scale of 3–5 m. Each of these variables exhibited a pronounced pattern of heterogeneity at this scale. Because regrowth following fire is from sources onsite at the

TABLE 4. Seedling and resprout (perennial herb) densities (mean no. individuals/m², with 1 SD in parentheses) measured in pre- and postburn seed bank samples and in the field at experimental gap and adjacent understory plots.

| | Gap plot | | | |
| --- | --- | --- | --- | --- |
| | Seed bank | | Field | |
| Species | Preburn | Postburn | Untreated | Fuel added |
| **Shrubs** | | | | |
| *Adenostoma fasciculatum* | 158.1 (360.2)* | 85.5 (225.4) | 8.9 (5.2)* | 0.4 (0.9)† |
| *Arctostaphylos purissima* | 97.0 (210.3) | 55.9 (145.8) | 14.4 (9.6) | 5.6 (5.1)† |
| *Ceanothus* spp. | NA | NA | 4.8 (2.6)* | 1.6 (1.6)† |
| **Subshrubs** | | | | |
| *Helianthemum scoparium* | 1209.3 (1147.7) | 326.7 (607.6)* | 82.1 (46.5)* | 13.0 (20.3)† |
| **Perennial herbs** | | | | |
| *Dichelostemma capitatum* | 0 | 0 | 11.2 (15.1)* | 2.8 (5.2)† |
| *Koeleria macrantha* | 0 | 0 | 2.8 (2.2)* | 0.4 (0.8) |
| All geophytes | 0 | 0 | 18.3 (14.4)* | 3.2 (2.4)† |
| **Annual herbs** | | | | |
| *Lotus strigosus* | 97.1 (182.3)* | 14.7 (46.5)* | 17.2 (17.2)* | 1.6 (2.6)† |
| *Navarretia atractyloides* | 5577.7 (3991.1)* | 582.2 (873.7)* | 58.2 (41.4)* | 1.6 (2.6)† |
| **All seedlings** | | | | |
| 0–2.5 cm seed bank | 19358.4 (12223.6)* | 2569.7 (1537.5)* | ... | ... |
| 2.5–7 cm seed bank | 3118.6 (1824.8) | 1647.5 (1353.3)* | ... | ... |
| Field | ... | ... | 209.9 (87.3)* | 34.0 (26.6)† |

*Note:* Sample sizes vary because more plots were studied in the field after fire than were included in seed bank sampling, and because fuel was added to five gaps and removed to create five gaps (see *Methods*).
\* *P* < 0.05, Kruskal-Wallis test, indicating significant gap vs. understory difference.
† *P* < 0.05, Kruskal-Wallis test, indicating significant treatment effect (within-plot-type comparison).

time of the fire, and because patterns of heating will be controlled by the fuel array provided by dominant shrubs, our results support a model in which local species distributions after fire in *Adenostoma* chaparral are directly linked to the physical and chemical properties of shrub canopies present before fire, through their antecedent effect on patterns in seeds and resprouts.

Through their combustion characteristics, there is much potential for dominant species to structure vegetation patterns that follow fire. In shrub vegetation, the fuel array is inherently heterogeneous (Countyman and Philpot 1970). Variable heating has been consistently measured in relation to this (e.g., Craddock 1929, Sampson 1944, McArthur 1967, DeBano et al. 1979, Tarbes 1980, Anfuso 1982, Hobbs et al. 1984, Hobbs and Atkins 1988, Davis et al. 1989). Effects of this variation will differ depending on where regeneration sources are located and how they are insulated from heating. For example, in Mediterranean-type shrublands in South Africa and Australia, seed of shrubs and small trees that are ant dispersed occur at depths of 5–10 cm, and high soil heating is needed to induce their germination (Auld 1986, Bond et al. 1990, and Hodgkinson 1991). Seedling recruitment is therefore positively associated with fire intensity. Although this is the opposite of what we found, it exemplifies how fine-scale patterns in fire-prone shrublands may be maintained/developed across fire cycles by the same mechanistic processes.

### Soil heating and resprouting

Adding fuel to gaps reduced the abundance of the perennial grass *Koeleria macrantha.* There was a strong negative correlation between water loss from cans and the abundance of its resprouts ($r = -0.67$). Research on lethal temperatures for grasses describes how their resilience to heating increases with decreasing moisture content (Wright 1970). As temperatures approach 90°C, the lethal duration for desiccated *Stipa comata* is 60 s. With regenerative tissue near the soil surface, perennial grasses, even in their most desiccated state, will be vulnerable to heating in chaparral fires.

Unlike *Koeleria,* the bulbs of *Dichelostemma,* and *Calochortus,* and the tubers of *Sanicula laciniata* and *Erigeron sanctarum,* are found at soil depths of 10–20 cm, where they are protected from high temperatures. Nonetheless, their resprouts were reduced in abundance by a factor of six as a result of fuel additions, and their distributions were strongly negatively correlated with heating. In our study, the soil temperature at 10 cm remained at ~39°C for several hours at a location where surface heating was not prolonged (Fig. 3). Geophytes may have been exposed to such temperatures for as much as 10–12 h, where heating was prolonged. Moist vascular tissue would be killed by this length of exposure to temperatures in this range (see Wright and Bailey 1982: Fig. 2.4). Thus, the evidence strongly

TABLE 4. Extended.

| | Understory | | |
| --- | --- | --- | --- |
| Seed bank | | Field | |
| Preburn | Postburn | Untreated | Fuel removed |
| 506.3 (614.4)* | 44.1 (99.2) | 0.9 (1.6)* | 5.6 (6.7) |
| 132.5 (139.1) | 70.6 (154.8) | 8.7 (12.9) | 12.8 (16.6) |
| NA | NA | 9.7 (8.7)* | 8.0 (2.8) |
| 806.4 (1096.5) | 200.2 (400.9)* | 3.4 (4.0)* | 33.6 (45.6) |
| 0 | 0 | 1.2 (1.2)* | 3.2 (3.0) |
| 0 | 0 | 24.4 (44.4)* | 6.4 (7.2) |
| 0 | 0 | 4.4 (1.8)* | 4.4 (1.2) |
| 226.5 (225.5)* | 238.5 (440.7)* | 1.3 (2.4)* | 2.4 (2.2) |
| 1111.6 (1763.2)* | 97.1 (182.7)* | 0.7 (0.5)* | 5.2 (17.4) |
| 7981.01 (6327.5)* | 964.2 (1863.9)* | ... | ... |
| 3070.9 (1732.4) | 706.1 (500.1)* | ... | ... |
| ... | ... | 28.6 (28.3)* | 79.2 (86.0) |
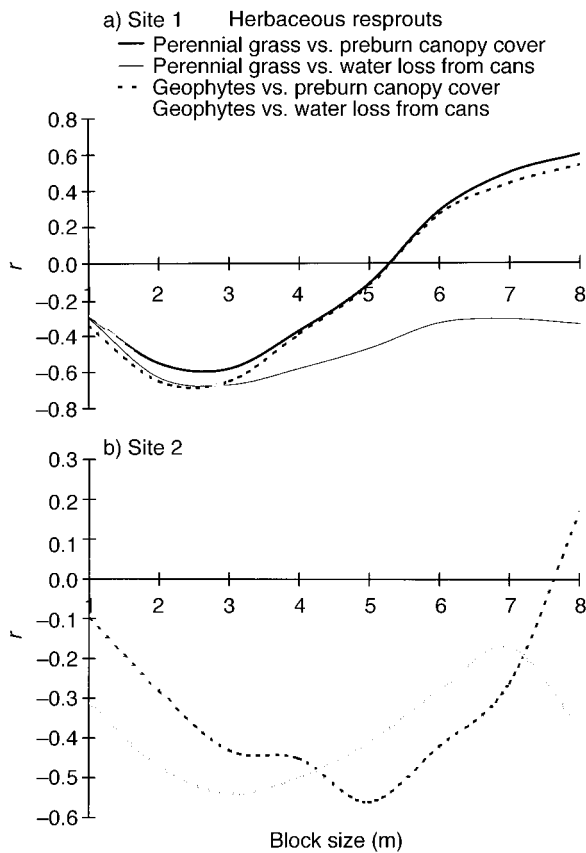


FIG. 8. Correlations calculated by two-term covariance analysis for resprouts vs. preburn canopy cover and water loss from cans, as a function of block size, along the transects at (a) site 1 and (b) site 2.
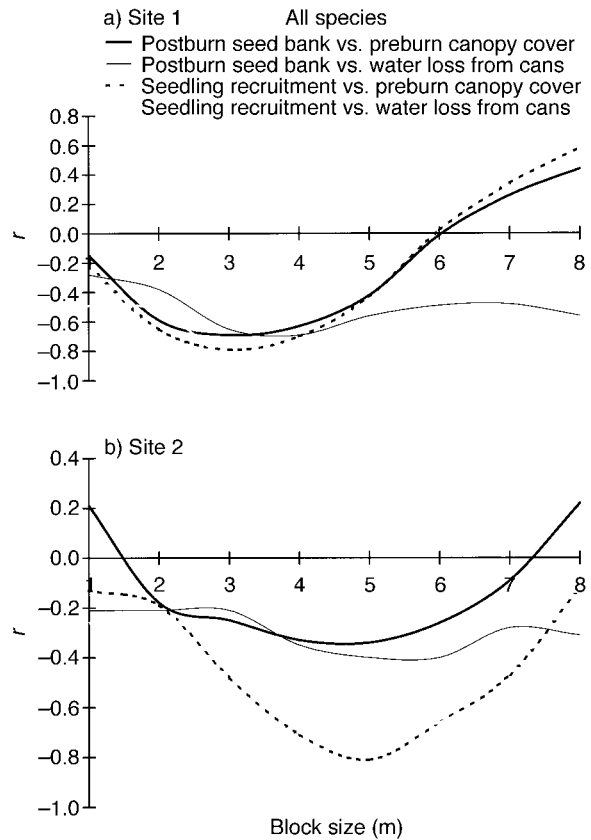


FIG. 9. Correlations calculated by two-term covariance analysis for postburn seed bank and field seedling recruitment of all species vs. preburn canopy cover and water loss from cans, as a function of block size, along the transects at (a) site 1 and (b) site 2.

suggests that the distribution and abundance of canopy material that collapsed during fire is what produced associated patterns in these resprouts.

Resprouting by *Adenostoma* is from a specialized lignotuber (Anfuso 1982). Despite this feature, *Adenostoma* mortality with fire has been observed to be as great as 85% (Barro and Conard 1991). The 50% mortality we found at site 1 was high for an autumn burn. Mortality was correlated with soil heating, and was highest for small individuals. This agrees with previous research by Rundel et al. (1987) and Moreno and Oechel (1991*b,* 1993), who concluded that, after factoring out seasonal effects, *Adenostoma* develop greater heat tolerance as they become larger. Moreno and Oechel (1993) also report that *Adenostoma* lignotuber size was positively correlated with depth of burial. This has been documented for other shrubs in fire-prone environments (Beadle 1940, Wright et al. 1976). The absence of small *Adenostoma* shrubs at site 2 may explain the lack of mortality there.

### Soil heating and seeds

Based on laboratory studies (Wright 1931, Sampson 1944, Sweeney 1956, Keeley 1987, etc.), heat tolerance

a) Site 1    *Adenostoma fasciculatum*

-- Seedling recruitment vs. preburn canopy cover
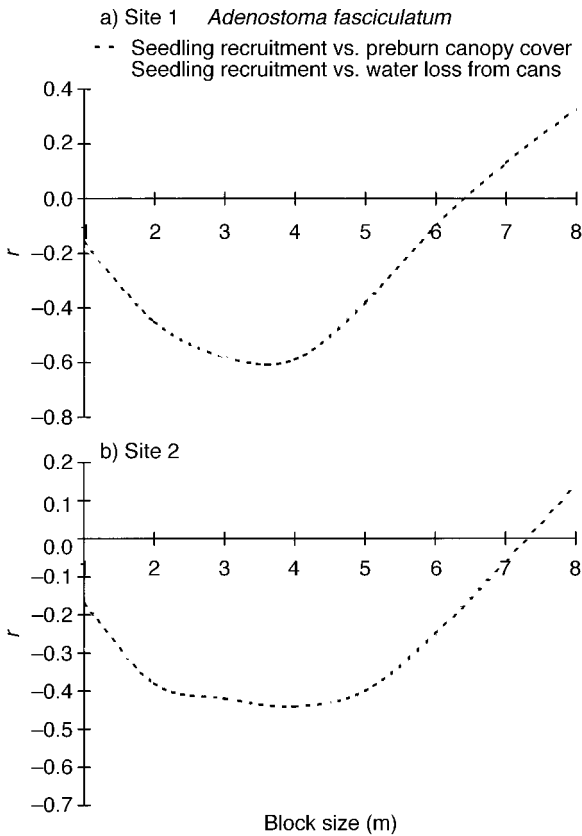 — Seedling recruitment vs. water loss from cans



b) Site 2



FIG. 10. Correlations calculated by two-term covariance analysis for *Adenostoma fasciculatum* field seedling abundance vs. preburn canopy cover and water loss from cans, as a function of block size, along the transects at (a) site 1 and (b) site 2.

of unmoistened seed for a 5-min duration is similar among chaparral species. Seeds appear to be less sensitive to heating duration than to maximum temperature. For example, seeds of many species can tolerate 2–4 hours of 80–100°C (Wright 1931, Keeley et al. 1985). This is 20–40× the total heat produced in 5 min at 170°C, which is generally lethal. The initial flame front in a chaparral fire will induce lethal heating down to a depth that will vary with soil thermal conductivity. Deeper penetration of lethal temperatures will be a function of subsequent combustion of collapsed fuel on the soil surface. The effects of addition of fuel to gaps illustrate this. Survival of seeds was especially low at these locations (none in the 0–2.5 cm depth fraction).

The ability of obligate seeders to maintain sizable seed populations at depth explained their superiority in establishing in areas of greater soil heating. For example, *Arctostaphylos,* with ~80% of its seeds below 2.5 cm, had 17% survival along the site 1 transect. The depth distribution of seeds of *Ceanothus* spp., was unclear in our samples, but they apparently had a high proportion at depth, because, unlike other species, they

Site 1    *Arctostaphylos purissima*

— Postburn seed bank vs. preburn canopy cover
— Postburn seed bank vs. water loss from cans
-- Seedling recruitment vs. preburn canopy cover
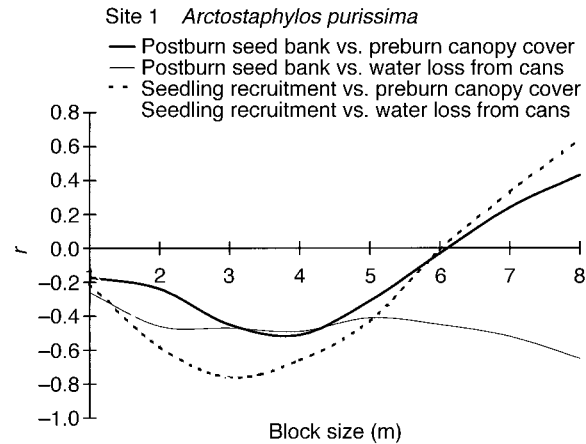 — Seedling recruitment vs. water loss from cans



FIG. 11. Correlations calculated by two-term covariance analysis for *Arctostaphylos purissima* postburn seed bank and field seedling abundance vs. preburn canopy cover and water loss from cans, as a function of block size, along the transect.

a) Site 1    *Ceanothus*

-- Seedling recruitment vs. preburn canopy cover
 — Seedling recruitment vs. water loss from cans
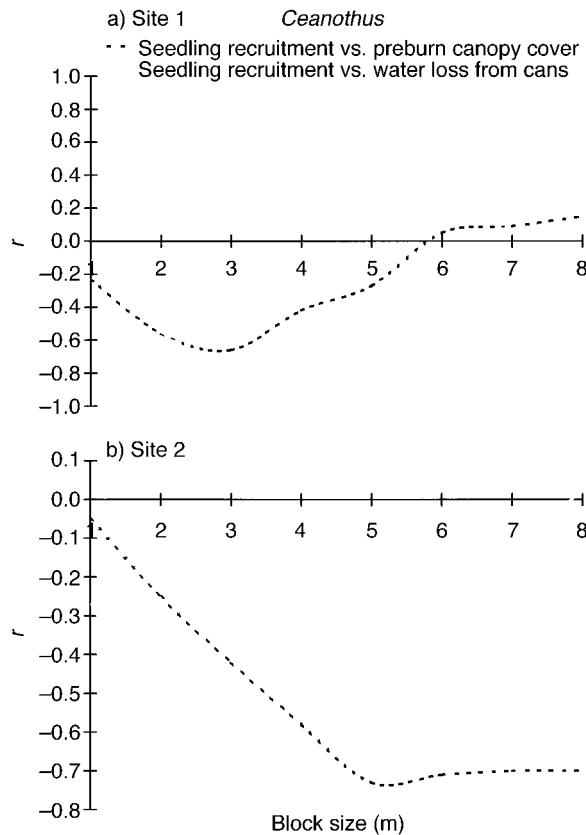


b) Site 2



FIG. 12. Correlations calculated by two-term covariance analysis for *Ceanothus* field seedling abundance vs. preburn canopy cover and water loss from cans, as a function of block size, along the transects at (a) site 1 and (b) site 2. At site 1, densities of *Ceanothus impressus* and *Ceanothus cuneatus* are combined.
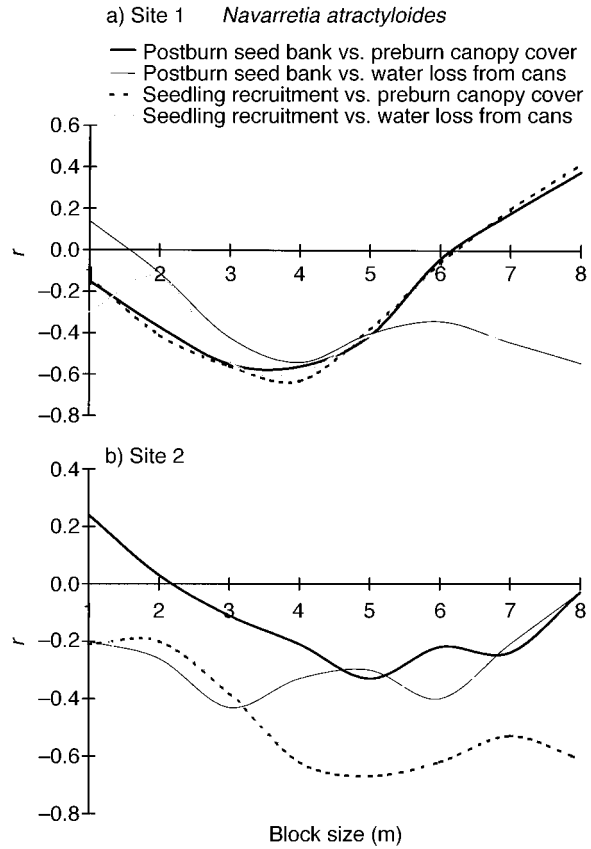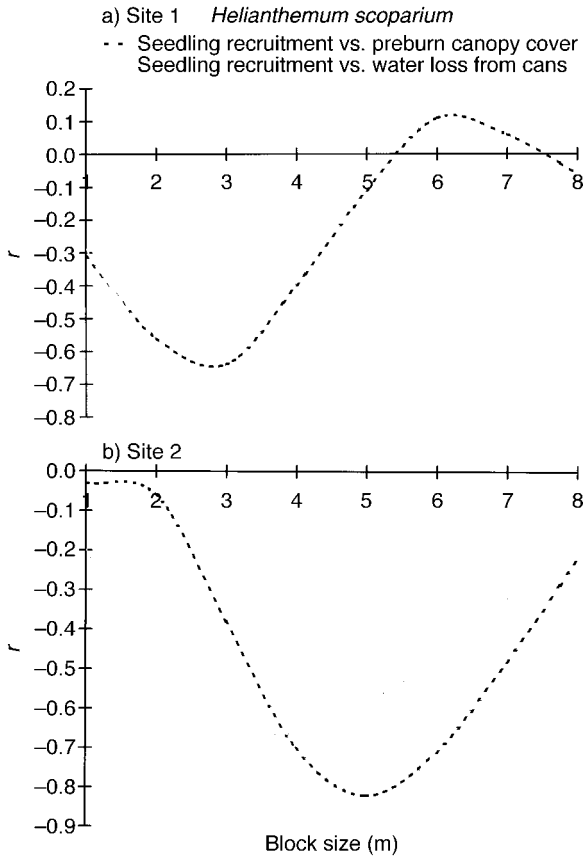
FIG. 13. Correlations calculated by two-term covariance analysis for *Helianthemum scoparium* postburn seed bank and field abundance vs. preburn canopy cover and water loss from cans, as a function of block size, along the transects at (a) site 1 and (b) site 2.



FIG. 14. Correlations calculated by two-term covariance analysis for *Navarretia atractyloides* postburn seed bank and field abundance vs. preburn canopy cover and water loss from cans, as a function of block size, along the transects at (a) site 1 and (b) site 2.

did not have improved seedling recruitment with fuel removal. In contrast, *Adenostoma,* with only 12% of its seeds in below 2.5 cm, had only 3% of seeds surviving fire. Only 8% of *Navarretia atractyloides* seed was below 2.5 cm in depth, and only 10% survived fire in the areas of lowest soil heating, which were preburn gaps.

Seed bank samples clearly demonstrated that there was also much *Helianthemum* seed below 2.5 cm in depth (~60%). Patterns of germinable seed in postburn samples were not as strongly associated with soil heating as with most species, indicating that seed was able to survive in areas of high heating. The field distribution of *Helianthemum* was, however, as strongly negatively related to soil heating as species with shallowly buried seed, and recruitment was nil with fuel addition. The inability of this species to establish seedlings in areas of greater soil heating was, in large part, because approximately one-third of its seed bank that survived fire remained dormant in the field, based on comparison of samples collected right after the fire and one year later. The most likely reason is that some surviving

seed must have been too deeply buried to receive temperature stratification to overcome secondary dormancy (Brits 1986). Field densities were much lower than the postburn seed bank minus the portion that remained dormant, suggesting there was also seed that germinated but failed to emerge. Emergence of the epicotyl is dependent on endosperm carbohydrate reserves, and the maximum depth from which emergence can occur has been shown to be allometrically related to seed size over a range of families and genera (Bond and van Wilgen 1995: Fig. 5.12). *Helianthemum* seeds are tiny. They are probably unable to emerge from depths much greater than ~2–3 cm.

No seedlings of other woody species emerged from samples collected the second year; their seed banks were apparently exhausted as a result of fire, and there was no new input until two to four years after fire. Thus, unlike counterpart shrublands in Australia and South Africa, it appears that little or no seed of chaparral shrubs is buried too deeply to receive sufficient heat under typical burning to overcome dormancy. Whether annual seed banks are exhausted with fire remains a question. It is possible that the annuals that
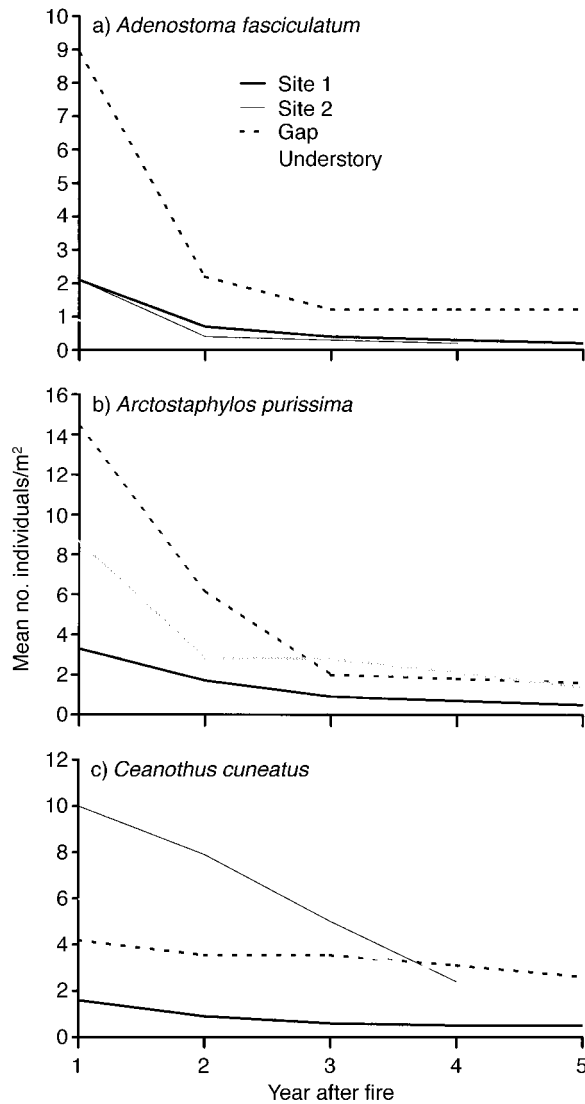
FIG. 15. Survivorship curves for three shrub species in plots along the transects at site 1, site 2, and the gap and understory locations at site 1. No shrub recruitment occurred after year 1; changes in abundance reflect mortality. *Arctostaphylos purcissima* did not occur at site 2.

emerged the second year came from seed that remained dormant during the first year. Annuals may also have emerged from seed produced during year 1 that were readily germinable. Both readily germinable and refractory seed have been found in *Helianthemum,* as well as the chaparral annual *Camissonia hirtella* (Keeley 1991).

*Community development following fire*

*Survival of shrub seedlings.*—Sampson (1944), Horton and Kraebel (1955), and Keeley and Zedler (1978), among others, have documented that the highest numbers of chaparral seedlings die during the first year following fire, as we found. The summer drought is the

predominant cause (Frazer and Davis 1988). It has been hypothesized that selection for traits maximizing seedling survival has occurred to a greater extent among obligate-seeding species (Frazer and Davis 1988, Moreno and Oechel 1992), and seedlings of obligate-seeding *Ceanothus* spp. have been shown to be more tolerant of water stress during summer drought compared to *Adenostoma* seedlings (Jacks 1984, Frazer and Davis 1988, Tyler and D'Antonio 1995). Our research provides evidence both supporting and refuting this hypothesis. We found *Ceanothus* survival was relatively high in comparison to *Adenostoma.* Conversely, survival of *Arctostaphylos* (all locations at site 1 combined, survival = 10.7%) during the course of five years was lower.

Moreno and Oechel (1992) found a positive effect of herb cover on *Adenostoma* seedling survival. Unlike in our study, herbs at their site were mainly fire-following annuals, and subshrubs were not important. We found no relationship between herb cover and *Adenostoma* survival, but did find that *Helianthemum* negatively affected the survival of *Adenostoma* seedlings. We also observed that *Arctostaphylos* was negatively affected by total plant density, which was dominated by *Helianthemum. Helianthemum* is one of the most widespread and abundant fire-following plants in chaparral. It may influence shrub seedling regeneration over a broad area.

*Changes in shrub relative abundance.*—*Adenostoma* may appropriate space through many fire cycles, whereas the space that obligate seeders occupy will be available for seedling establishment following the next fire. A dominance shift from one regeneration mode to the other with fire will have important long-term consequences. Twenty-five of the original 50 *Adenostoma* shrubs present in transect plots died during the fire at site 1. This mortality created large gaps in resprouting shrubs from 16–20 and 5–10 m from the base of the L-transect in the northwest direction, and from 11–13 and 20–22 m in the northeast direction (Fig. 7b). In the vacated space, there were 10 *Adenostoma,* 23 *Arctostaphylos,* 22 *C. cuneatus,* and 9 *C. impressus* after five years. There was also a decrease in *Adenostoma* at the 15 understory locations adjacent to preburn gaps. Four adult shrubs perished there and were replaced by obligate seeders. However, *Adenostoma* seedlings continued to survive after 5 yr in five of the 15 gaps (mean, 2 seedlings/gap). Thus, there was a decrease in *Adenostoma,* where soil heating was high, and an increase at gaps. This illustrates how local variation in heating associated with fire allows different species and regeneration modes to be favored at different sites within the same burn area. This helps explain the coexistence of shrub regeneration modes that may have evolved in response to different fire regimes (Keeley and Zedler 1978).

At site 2, all *Adenostoma* survived fire, but there were 2.4 *Ceanothus cuneatus*/m² established after four

years. No change in relative abundance of shrubs appears to have occurred there because of fire.

### Management implications

Patterns of variation in heating during fire may be significantly more pronounced in chaparral as a function of length of time since fire. Fuel will accumulate within and under the canopy of long-lived shrubs, and gaps will form where obligate seeders die (Keeley 1992), increasing the heterogeneity of the fuel array. These conditions have been hypothesized to favor obligate seeders (Keeley and Zedler 1978), and we found that gaps clearly provided increased opportunities for obligate seeders. Despite this, *Adenostoma* remained dominant in the stand where gaps were important. This species has been shown to be stable over a range of fire intervals (Minnich and Bahre 1995). Gaps may also be critical to the maintenance of seed populations of opportunistic species (Zammit and Zedler 1994), and seeds of most species may be concentrated in gaps, as we found. We also found that development of canopy gaps was important to regeneration of all species from seed, as well as herbaceous resprouts, regardless of their preburn distribution. Finally, chaparral shrubs that do not establish seedlings after fire (called ''fire persisters'' because of their high rate of resprout success) require long fire-free periods for seedling establishment (Keeley 1992). Zedler (1995) evaluated risks to shrubland species from a long fire interval and could find no evidence of significant risk. Thus, it appears diversity and equitability in the postfire flora and overall community resilience may be promoted by a relatively long chaparral fire interval.

On the other hand, it has been documented that especially short fire intervals (<5 yr) can destroy chaparral (Zedler et al. 1983, Haidinger and Keeley 1993). The shallow-rooted and quickly curing grass and weed vegetation that replaces chaparral under such type conversion will ignite more easily over a longer portion of the year (Bradshaw et al. 1983), and it will allow for much greater landslide activity and sediment production in chaparral watersheds, where runoff is typically impounded for highly valued water diversions (Rice et al. 1969). In addition, it has also been documented that local extinctions of obligate seeders may occur under a regime of relatively short fire intervals (Nieuwenhius 1987).

Managing chaparral for optimum biodiversity and watershed values appears to be counter to managing it for human safety. With relatively long fire intervals, acutely combustible high heat yield fuel would exist over extensive areas at any given time. In addition, dry season fires are clearly better from a biological standpoint (Parker and Rogers 1988), but it is difficult and dangerous to undertake hazard reduction burning during the dry season. Effectiveness of such burning can also be questioned; analyses indicate that it is not feasible to prevent large fires from occurring in many chaparral landscapes (Zedler 1995, Moritz 1997). At the interface between human development and chaparral vegetation, desirable management from biological and slope stability perspectives argues not for relatively short rotation hazard reduction burning, but for improving characteristics of the built environment (defensible space, structures, landscaping, safe evacuation means, etc.), in efforts to reduce the perils of fire posed by living near chaparral.

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