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Flammability Is a Niche Construction Trait: Canopy Architecture Affects Fire Intensity

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abstract: By affecting local fire intensities or the probability of ignition, traits that influence plant flammability may indirectly control selection for fire-related life-history and physiological traits. The retention of dead branches in the canopy has been cited as contributing to plant flammability. No experiment, however, has demonstrated that differences in plant canopy architecture on the scale of observed variation in nature can affect local fire characteristics. I experimentally manipulated canopies of *Adenostoma fasciculatum*, a California shrub that naturally retains dead branches, to mimic degrees of self-pruning in four small-scale (4 m × 6 m) treatments: removal of all canopy dead wood, clipping of all dead wood with wood left as litter, an unmanipulated treatment, and a dead wood addition. Treatment plots were burned in large-scale prescribed fires. Fire temperatures and heat release were significantly higher in Unmanipulated and Addition treatments, demonstrating a significant local effect of dead branch retention. Removal and Clip and Leave treatments did not differ significantly; the observed effect is a result of canopy architecture rather than differences in total fuel load.

Keywords: Adenostoma, *Ceanothus*, evolution, chaparral, Mutch hypothesis, self-pruning.

Many physiological and life-history traits have been interpreted as adaptations to fire. Plants, however, do not simply respond to the selective pressures of wildfire; as fuel, plants may influence the nature of this disturbance. Different vegetation types can behave quite differently as fuels (Rothermel 1972; Philpot 1977; Rundel 1981; van Wilgen et al. 1990; Papio and Trabaud 1991). Even within the same climate, vegetation types of quite different flammabilities can occur adjacent to one another. In California, for example, highly flammable chaparral shrubland often occurs with abrupt boundaries adjacent to the less flammable oak woodland. Similarly, in the Cape of South Africa, patches of relatively nonflammable forest occur within a matrix of flammable fynbos shrubland (Geldenhuys 1994).

Traits such as the retention of dead branches, fine branching patterns that influence the air/fuel mix, and the presence of volatile oils have all been cited as potential flammability-enhancing traits (Rundel 1981; Papio and Trabaud 1991). Ecologists have been intrigued by the possibility that such potential flammability traits may be correlated with other traits interpreted as adaptations to fire. Evidence suggests that in the genus *Pinus*, the retention of dead branches (a trait hypothesized to increase canopy flammability) exhibits an evolutionary correlation with fire-dependent seedling recruitment (Keeley and Zedler 1998; Schwilk and Ackerly 2001).

Many plant communities are maintained by periodic wildfire through fire-dependent seedling recruitment or frequent fires that exclude sensitive competitors (Jackson 1968; Hanes 1971; Hobbs and Gimingham 1987; Robertus et al. 1989; Manders et al. 1992). The observation that vegetation types maintained by fire were relatively flammable prompted Mutch (1970) to suggest that if plants possess reproductive or anatomical mechanisms to persist through fire events, then there may be selection for characteristics that enhance flammability in these plants. The Mutch hypothesis, however, has received a good deal of criticism. One line of criticism argued that the hypothesis does not explain how a more flammable mutant would spread in a population of less flammable conspecifics (Snyder 1984; Troumbis and Trabaud 1989; Bond and Midgley 1995). In response to this criticism, several researchers have proposed individual-based models that describe the conditions under which flammable types can invade a population (Bond and Midgley 1995; Kerr et al. 1999; Schwilk and Kerr 2002). In addition to demonstrating that increased flammability can invade under some conditions, these models have highlighted the effect that flammability traits may have on evolutionary trajectories even when

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such traits evolve as side effects of other evolutionary pressures.

A second line of criticism argued that putative flammability traits were in fact emergent properties of communities rather than characteristics of individual plants (Snyder 1984; Troumbis and Trabaud 1989). The evolutionary models cited assume that potential flammability traits have local effects. Flammability, in these models, acts as a "niche-constructing" trait that modifies the local environment (for a discussion of niche construction, see Laland et al. 1996; Odling-Smee et al. 1996). Flammability could affect the local environment by providing fire-cleared gaps that benefit the flammable species (Mutch 1970; Bond and Midgley 1995; Kerr et al. 1999). Such recruitment gaps may provide opportunities for rapid evolutionary change that, although available to flammable and nonflammable types equally, allow higher fitness to become associated with flammability through spatial population structure ("genetic niche-hiking"; Schwilk and Kerr 2002). Conversely, if the characteristics of an individual plant have little effect on its probability of burning or the intensity of fire it experiences, then presumed flammability traits are insulated from selective pressures, positive or negative.

One important plant characteristic that may affect flammability is the retention of dead material. Living plant parts act as a heat sink, and it is the combustion of dead fuels that drives the moisture out of living fuels so that they contribute to the energy release in a fire (Johnson 1992; Bond and van Wilgen 1996). The retention of dead branches in the canopy is one of the most obvious plant traits that is likely to increase flammability by maintaining the important dead fuels in an aerated state and, in the case of tall trees, by increasing the probability of ground fire entering the canopy.

California chaparral shrub species differ dramatically from one another in the degree to which they retain dead branches. The retention of dead branches in the canopy may contribute to the flammability of some shrubs (e.g., *Ceanothus cuneatus*, *Adenostoma fasciculatum*; Rothermel and Philpot 1973), while self-pruning of dead wood may be a mechanism to decrease flammability in others (e.g., *Quercus* spp., *Heteromeles arbutifolia*). Little is known, however, about the potential local effects such traits may

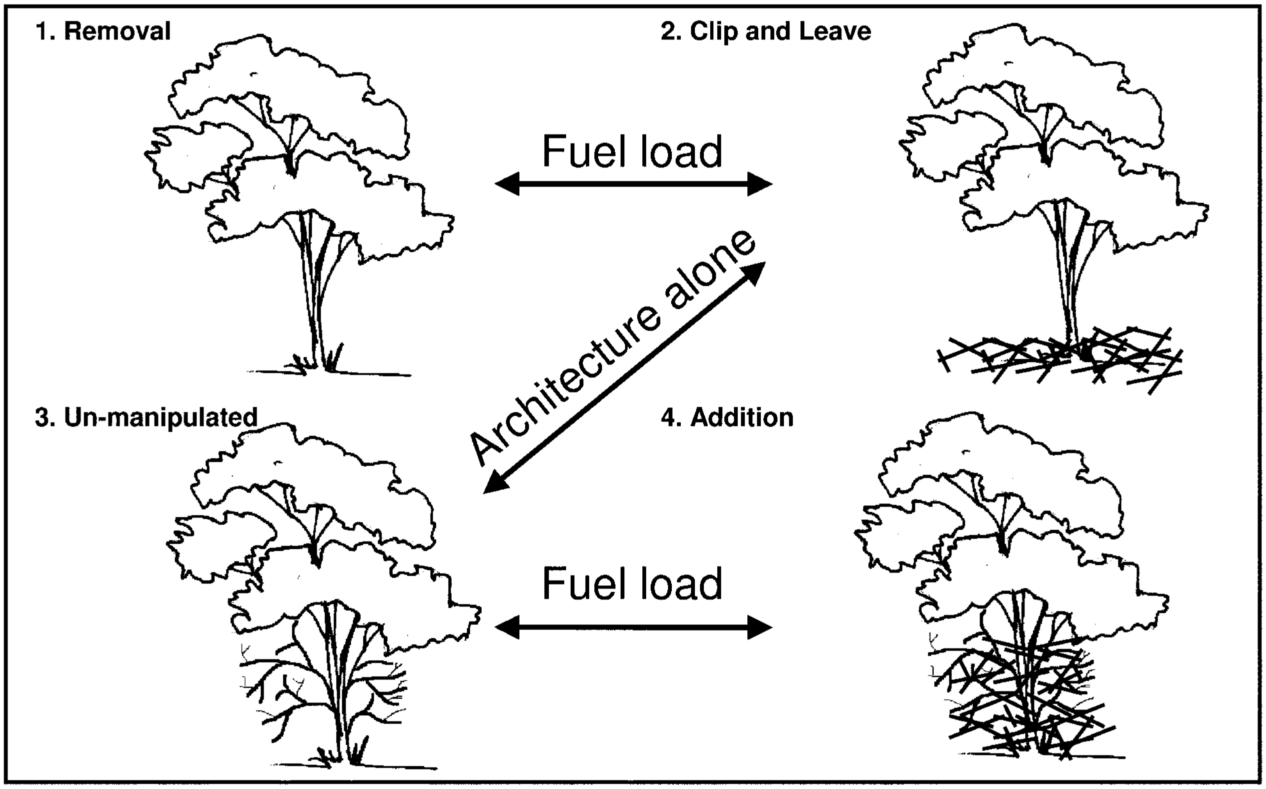

Figure 1: Dead wood clipping treatments and a priori pairwise comparisons. This graphic illustrates the four treatments and indicates the three most important pairwise comparisons for distinguishing the effect of canopy architecture (dead branch retention) from that of total fuel load.

have on fire behavior. Evidence suggests that variation in fire intensity may have profound effects on postfire vegetation dynamics in fire-prone shrublands (Westman et al. 1981; Bond et al. 1990; Moreno and Oechel 1991, 1993, 1994; Rice 1993; Segura et al. 1998), but the degree to which local fire intensity is influenced by traits of individual plants is unknown.

Dead branch retention is a puzzling trait because it is difficult to imagine what the fitness consequences of this trait could be other than through its effects on flammability. Although the potential costs and benefits of dead branch retention are unknown, it is possible that retained dead branches may increase the probability of pathogen infection. Evidence suggests, however, that dead branch retention is correlated with a suite of fire adaptations (Keeley and Zedler 1998; Schwilk and Ackerly 2001). Even if dead branch retention does not carry costs other than a possible increased probability of mortality during fire, correlated interspecific variation in a presumably neutral trait merits adaptive explanation.

To investigate whether the retention of dead branches can indeed affect local fire temperatures and heat release, I experimentally manipulated canopy architecture of *A. fasciculatum* (chamise), an evergreen shrub that naturally retains dead branches, in California chaparral. These treatments were burned in large-scale prescribed fires to gauge the effect of dead branch retention on fire intensity. This experiment had two goals: first, to test the effects of a canopy architecture trait on local fire characteristics and to distinguish the effect of architecture from that of total fuel load; second, if local effects are evident, to discover whether they result in biotic effects such as influencing resprouting ability or seed germination.

Methods

Study Sites

The study sites were located at an elevation of 800–1,000 m in the University of California Hopland Research and Extension Center (HREC), Mendocino County, California (39.026°N, 123.065°W). The two sites (Upper Orchard Basin and Lookout Point) were <2 km apart and both on west-facing slopes that varied in steepness from approximately 20% to 55%. The sites contained nearly monospecific stands of *Adenostoma fasciculatum* with a continuous canopy 1–2 m high. Other species, including *Arctostaphylos manzanita*, *Ceanothus cuneatus*, *Cercocarpus betuloides*, *Heteromeles arbutifolia*, *Quercus* spp., and *Toxicodendron diversilobum*, made up <5% of total cover and did not fall in any of the treatment plots. The dominance of *A. fasciculatum* provided an opportunity to limit the canopy treatments to a single species.

Experimental Design

This study included four prefire shrub canopy treatments (fig. 1): Removal: simulation of self-pruning followed by decomposition by clipping dead branches and removing from the treatment plot; Clip and Leave: simulation of self-pruning with no overall change in total fuel load by clipping dead branches and leaving them as litter; Unmanipulated: no change to dead wood naturally maintained in canopy; and Addition: simulation of increased dead branch retention by adding dead wood to the canopy and litter.

Because fire intensity was likely to increase as the flame front moved upslope, treatment plots were positioned in unreplicated blocks of all four treatments along bands of equal elevation. Forty treatment plots were established:

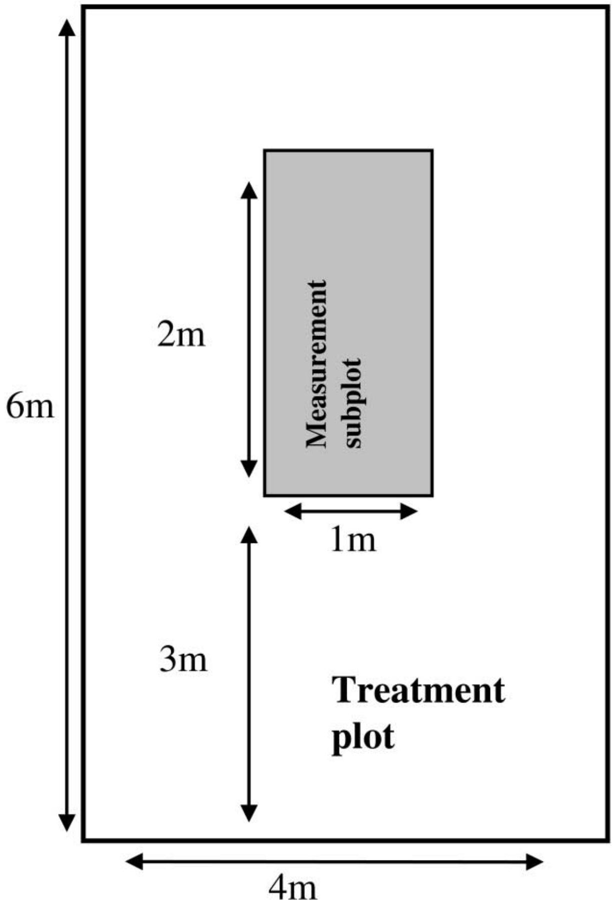

Figure 2: Design of experimental treatment plots. Temperature, heat, and seed germination measurements were taken from the 1 × 2-m subplot in each treatment plot. Subplots were in the uphill portion of the treatment plot, with the top of the subplot 1 m from the uphill side of the treatment plot.

four treatments × five blocks per site × two burn sites (see "Prescribed Fires").

These four treatments were conducted on 4 × 6-m measurement plots (fig. 2). In the clipping treatments (Removal and Clip and Leave), all dead wood was removed from the canopy by cutting dead branches back to the first live leaf or side branch containing live leaves (or cut back to the trunk if there were no live side branches). Wood taken from the Removal treatment plots was added to paired (same block) Addition treatment plots. The larger branches were propped and wired into the canopy of shrubs in the paired Addition plot, but smaller material fell through the canopy and contributed to ground litter. The average amount of wood removed from Removal plots was 1.5 kg m^{-2} (field weight in July and August). Oven dry aboveground biomass for mature chamise chaparral has been reported at around 1.4–1.8 kg m^{-2} (Mooney et al. 1977; Rundel and Parsons 1979). Even allowing for relative moisture contents of 10%–20% for the dead fuels, the dead wood removed in this study apparently represents a significant fraction of the total stand biomass. These four treatments allow an investigation of the possible separate effects of dead branch retention and total fuel load (fig. 1). To control experiment-wide α levels, only three a priori comparisons were chosen as indicated by figure 1: two tests for the effect of fuel load and one test for the effect of canopy architecture alone.

Prescribed Fires

The prescribed burns were part of an ongoing study by S. Stephens (University of California, Berkeley) and occurred during the first available weather window following the summer drought, on November 12 and 13, 1999. During the 7 d before the burns, the first significant rain of the year fell, totaling 52 mm (HREC Lambing Pasture station, 335-m elevation). Maximum air temperatures were 18°C on November 12 and 20.5°C on November 13. The fires were ignited along the bottom perimeter of each of the two burn areas and allowed to burn upslope, with

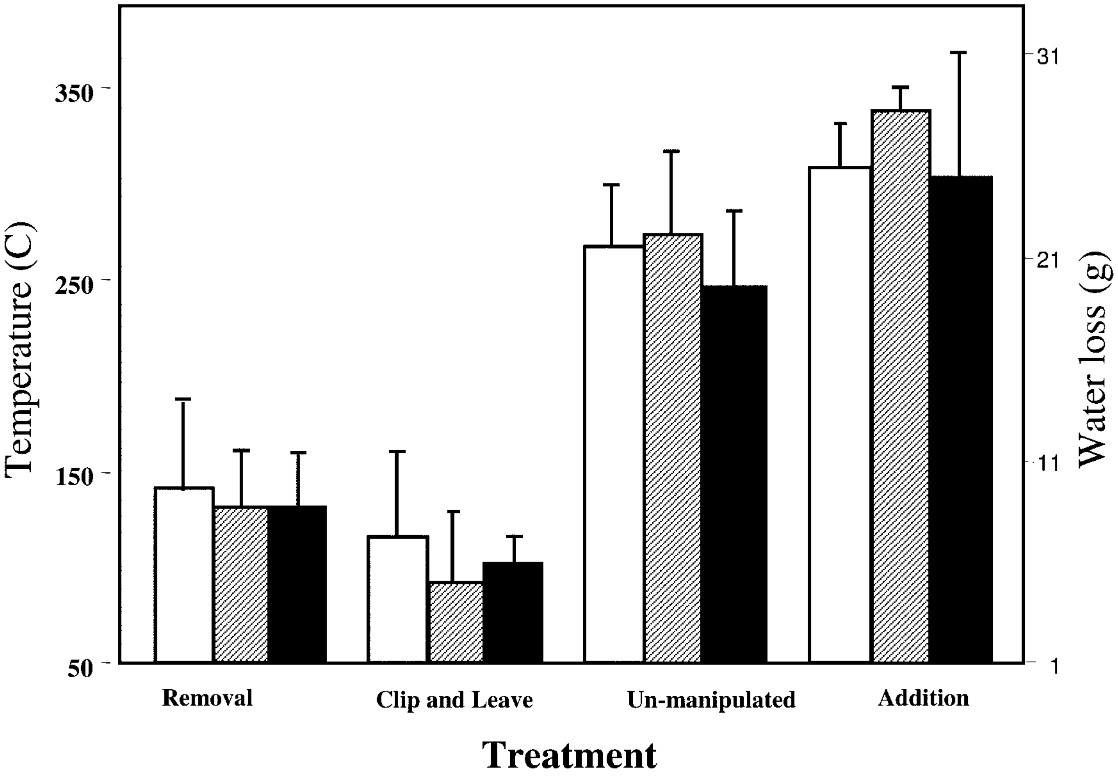

Figure 3: Fire temperatures and heat release. Mean (±SE) pyrometer temperatures at ground surface (*open bars*), temperatures 30 cm above ground (*hatched bars*), and calorimeter water loss (*solid bars*) in four treatments: removal of dead canopy branches from the plot, clipping of all dead branches with wood left as litter, unmanipulated, and dead wood addition. Pairwise significant differences for a priori comparisons are listed in table 1.

Table 1: Temperature pyrometers and calorimeter pairwise comparisons

		Corrected *P* value		
Comparison	Tests effect of	Surface temperature	30-cm temperature	Water loss (g)
Removal versus Clip and Leave	Fuel load	NS	NS	NS
Unmanipulated versus Addition	Fuel load	NS	NS	*
Clip and Leave versus Unmanipulated	Architecture	.0405	.0291	*

Note: For temperature data, significant *P* values are listed after a Bonferroni-style correction of the Kruskal-Wallis pairwise test. To preserve experiment-wide α levels in nonparametric statistics, only three comparisons were investigated (fig. 1). NS = nonsignificant difference.

* Significant pairwise differences (post hoc comparisons $P < .05$).

maximum flame lengths reaching 20 m. All of the Lookout Point plots used in analysis and most of the Orchard Basin site burned in the first prescribed fire on November 12. Three treatment blocks at the Orchard Basin site that were on a slope that did not burn in the first fire were burned in a second fire on November 13. The Orchard Basin fire burn was 5.7 ha, and the Lookout Point burn was 5.9 ha (R. Keiffer, personal communication). Fall prescribed burns should mimic natural fires much better than cooler spring burns and have been used in other ecological studies where preburn data were necessary (e.g., Odion and Davis 2000). Lightning-caused fires are not uncommon in Mendocino County and occur primarily during August (Keeley 1982).

Fire Temperature and Heat Release Measurements

Quantitative assessments of fire intensity are made difficult by both differing definitions of intensity (rate of heat release, total heat release, or time-temperature profile) and limitations in measurement. Foresters use attributes of the flame to obtain indices of intensity (Alexander 1982), but temperature measurements are the most common in prescribed fires (Beadle 1940; DeBano and Conrad 1978; Moreno and Oechel 1991; Perez and Moreno 1998; Odion and Davis 2000). Evaporative water loss from calorimeters provides an integrated measure of total heat release per unit area and has been used successfully to measure intensity in prescribed fires (Moreno and Oechel 1989, 1991; Perez and Moreno 1998). In this study, I used temperature pyrometers and open calorimeters to quantify fire intensity.

Each treatment plot contained a 1 × 2-m measurement subplot in which temperature and heat release measurements were made during the fire (fig. 2). Temperature pyrometers consisted of strips of copper (25 mm × 250 mm × 0.2 mm) painted with 16 temperature-sensitive paints in 50°C increments from 100°C to 850°C (Omegalaq paints, Omega Engineering, Stamford, Conn.). After the paint dried, a second strip of copper was clipped to the painted side of the first so that no blackening of the painted surface would occur (the mass of each sensor was 35–40 g). The temperature-sensitive paints melt and change texture at a specified temperature and therefore provide a rounded-down measure of the maximum temperature the copper reaches. These pyrometers are influenced by temperature duration and therefore provide a somewhat integrated measure of intensity (Odion and Davis 2000). Three sensors were placed in each subplot before the burn: one on the soil surface, one hanging from a wire between two stakes at 30 cm, and one buried 2–3 cm in the soil.

To measure heat release during the fire, open calorimeters were used (Moreno and Oechel 1989, 1991; Perez and Moreno 1998). These consisted of 1-gal-capacity steel cans filled with 2 L of water and with a 1-cm-diameter hole in the lid to allow steam release during the fire. These calorimeters were weighed before and after the burn to determine evaporative water loss as a measure of heat absorbed during the fire.

Pre- and Postfire Measurements

Basal stem diameters of all plants in each subplot were measured before treatment and survival and resprouting success were monitored over the next two growing seasons. After the burns, each 1 × 2-m subplot was fenced and roofed with 1-cm^2 aperture wire hardware cloth at 1 m height to exclude deer and rabbits. Subplots were censused in midspring for two seasons after the fire (April 2000 and April 2001). During the first census, resprouting success was recorded as number and height of resprout shoots on each *A. fasciculatum* lignotuber. The number and species of shrub and herbaceous seedlings were recorded for each subplot. During the second census, shrub seedling species and number were recorded as well as total canopy cover of *A. fasciculatum* resprouts.

Results

Fire Temperature and Heat Release

Because of topography and unpredictable flame fronts, not all of the treatment blocks were in areas that burned. I excluded any plot that was not surrounded on all four sides by burned vegetation after the fires, leaving 29 plots used for analysis (six complete blocks + two blocks in which two and three plots burned). In all plots, the canopy burned and left no leaves or twigs <2 mm in diameter. Amount of canopy consumed varied a great deal among plots. In those plots with dead wood litter, however, only the upper 1–4 cm of litter was ashed.

Canopy architecture manipulations had a significant effect on temperatures recorded by the pyrometers at the surface and 30 cm above the soil surface (fig. 3; Kruskal-Wallis rank test, $N = 29$, $P = .002$ [surface], $P < .001$ [30 cm]). Very few buried pyrometers reached the minimum temperature (100°C), and there were no significant differences among treatments for these sensors. Clip and Leave and Removal treatments had significantly lower surface temperatures than did the Unmanipulated or dead wood Addition treatments (table 1). Although the distribution of the data required nonparametric statistics, these results are supported by ANOVAs that indicate no block or site effect and significant treatment effects (surface temperatures $P = .002$, 30-cm temperatures $P < .001$).

Calorimeter water loss per plot was significantly correlated with temperature measurements ($P = .011$ for 30-cm sensors). Water loss showed significant differences among treatments (ANOVA $P = .012$). Post hoc comparisons revealed significant differences ($P < .05$) between clipping and nonclipping treatments (fig. 3).

Plant Response

Extensive sprouting of *Adenostoma fasciculatum* was observed in all treatments. Postfire shrub seedlings included *A. fasciculatum*, *Arctostaphylos* spp., and *Ceanothus cuneatus.* Several *Heteromeles arbutifolia* seedlings were found during the second census. Seedling densities of herbaceous species (*Emmenanthe penduliflora* being the most common) were highly variable and unrelated to site or treatment. The census results revealed no relationship between treatments and *A. fasciculatum* seedling density. Resprouting success of *A. fasciculatum* adults was nearly 100% and was not related to treatment or fire temperature.

Only one demographic variable showed a treatment effect. The plots with the highest number of *C. cuneatus* seedlings were the Unmanipulated and Addition plots.

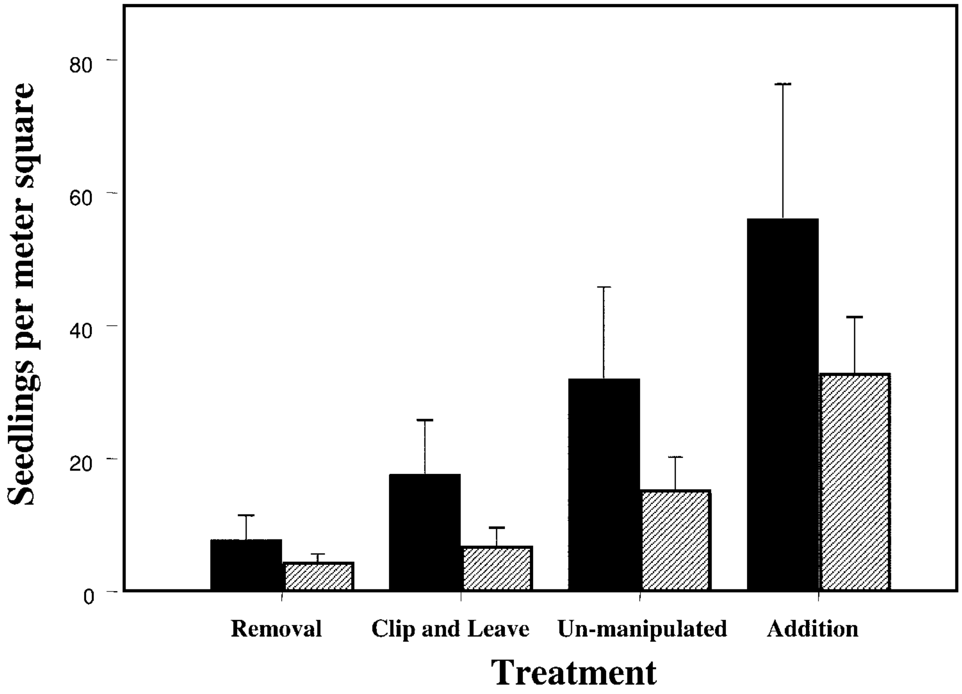

Figure 4: *Ceanothus cuneatus* seedlings in first year after fire. Mean (±SE) number of *C. cuneatus* seedlings per square meter at first census, April 2000 (*solid bars*), and at second census, April 2001 (*hatched bars*).

This difference was not significant in the first census, although it was by the second (Kruskal-Wallis $P = .018$; fig. 4).

Discussion

The fire intensity results demonstrate that variation in dead branch retention may indeed influence local fire temperatures and heat release. The absence of a temperature difference between Removal and the Clip and Leave treatments indicates that the temperature effect is a result of canopy architecture and not merely of total fuel load. In addition, these treatments resulted in significant biotic effects. The ability of an individual plant to influence the local nature of fire suggests that flammability may be subject to selective pressures created by this changed environment.

Removing dead branches resulted in lower local temperatures, but the addition of dead wood did not significantly increase temperatures or heat release. There are two possible explanations for this result. First, not all of the wood added to Addition plots was added to the canopy; the finest material (small dead twigs clipped from branches in the Removal plots) fell through the canopy and contributed to a litter layer that did not fully combust. Second, the response of fire temperature to dead wood addition may saturate, and natural state *Adenostoma* may already be near maximum flammability.

Natural fires (such as those ignited by August thunderstorms) are likely to occur during warmer conditions and result in more intense burns than these prescribed fires. The degree to which canopy architecture influences local fire intensity in hotter burns is unknown. Fire temperatures observed in this study were low compared with the range of temperatures recorded for chaparral fires (Moreno and Oechel 1989, 1991). Water loss from calorimeters (ranging from 0 to 45 g), however, was in the range reported for southern California chaparral burns (5–75 g in identical calorimeters in a study by Moreno and Oechel 1989).

For dead branch retention to have evolutionary feedbacks, the trait must influence not only fire temperature but also the severity of the fire's effects on survival, resprouting, or seed germination. Because these treatments of *Adenostoma fasciculatum* canopies had no effect on *A. fasciculatum* survival or seedling establishment, the study did not reveal any direct evolutionary feedback effects. Although this study does not provide evidence of the effect of fire intensity on *A. fasciculatum* performance, it is likely that this species may exhibit a humped-shaped response to fire intensity. Although dependent on fire for seedling regeneration, *A. fasciculatum* may be susceptible to very intense fires; previous studies have shown that intense fires can reduce *A. fasciculatum* resprouting ability (Moreno and Oechel 1993; Odion and Davis 2000) and germination (Moreno and Oechel 1991). Fire temperatures were higher in those previous studies than in this current study.

Ceanothus cuneatus had enhanced seedling recruitment under greater fire intensity (fig. 4), which may be a result of increased stimulation of dormant seeds by heat (Quick and Quick 1961; Keeley 1987; Odion and Davis 2000). Species in the community may face selective pressures determined by the dominant species' niche construction effects (see Kerr et al. 1999). If hotter fires do indeed favor *C. cuneatus* seedlings, dead branch retention in *A. fasciculatum* may play a role in aiding the establishment of a potential competitor. This could result in a negative feedback mediated through niche construction, while dead branch retention in *C. cuneatus* would provide an adaptive benefit.

Flammability has often been viewed as an emergent property of an entire community (Philpot 1977; Snyder 1984; Troumbis and Trabaud 1989). When traits of individual plants have been examined, research has focused on the easily measurable small-scale structural and chemical combustibility of plant material (Mak 1988; Papio and Trabaud 1990; Fonda et al. 1998). This study reveals the potential importance of architectural traits on flammability in an ecological context. Rather than simply responding to the ecological effects of fire, plants may be actively shaping their environment and, in doing so, influencing the nature of fire that they and their offspring experience.

Acknowledgments

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