



Changes in fire intensity have carry-over effects on plant responses after the next fire in southern California chaparral

José M. Moreno, Iván Torres, Belén Luna, Walter C. Oechel & Jon E. Keeley

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Nomenclature

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Moreno, J.M. (corresponding author, josem.moreno@uclm.es), **Torres, I.** (ivan.torres@uclm.es) & **Luna, B.** (belen.luna@uclm.es): Department of Environmental Sciences, Universidad de Castilla-La Mancha, Toledo, 45071, Spain

Oechel, W.C. (oechel@sunstroke.sdsu.edu): Global Change Research Group and Department of Biology, San Diego State University, San Diego, CA, 92182, USA

Oechel, W.C.: CRI Fondazione Edmund Mach, San Michele all'Adige (TN), 38010, Italy

Keeley, J.E. (jon_keeley@usgs.gov): U.S. Geological Survey, Western Ecological Research Center, Sequoia National Park, Three Rivers, CA, 93271, USA

Keeley, J.E.: Department of Ecology & Evolutionary Biology, University of California, Los Angeles, CA, 90095, USA

Introduction

The energy liberated through combustion during a wildfire is highly variable in space and time. As a fire spreads, fire-line intensity and spread rate will change across the landscape due to variations in fuel quantity and quality, wind and topography (Rothermel 1972). Furthermore, for any given place, similar changes can occur across seasons and years, because of variations in weather, climate and fuel as vegetation develops with time (Rothermel & Philpot 1973). Therefore, variations in the degree of heating to which plants may be exposed during fire are common within a fire (Odion & Davis

Abstract

Question: Do variations in fire intensity within a stand determine changes in fire intensity and plant demographics in a subsequent fire?

Location: San Diego (CA, USA); chaparral dominated by *Adenostoma fasciculatum* (resprouter) and *Ceanothus greggii* (seeder).

Methods: In 2003, a wildfire burned a young (16-yr-old) stand containing a set of experimental plots burned in 1987 with various levels of fire intensity. In 2004, all the 1987 plots were sampled for *Adenostoma* survival and the recruitment of both species. Similar measures were carried out in the adjacent old (75-yr) stand. Fire intensity in 2003 was estimated by a surrogate fire severity measure [minimum diameter of burned branches (branch diameter)].

Results: In the young stand, branch diameter in 2003 was similar to the control plots in 1987, but lower than in the old stand. Fire intensity in 1987 did not significantly affect branch diameter in 2003. Survival of *Adenostoma* in the young stand was very low, much lower than after the 1987 burn and that in the old stand. Fire intensity in 1987 did not affect *Adenostoma* survival. Recruitment in *Adenostoma* increased, and in *Ceanothus* decreased, with increased fire intensity in 1987.

Conclusions: We demonstrate that there is a carry-over effect of fire intensity across a whole fire cycle on plant recruitment of the two dominant species. The 2003 fire partially reversed the relative effects on recruitment caused by elevated fire intensity in 1987. Arguably, this effect was driven by the contrasted relationships of the two species to fire intensity. *Adenostoma* survival in the young stand was much lower in 2003 than in 1987, despite similar branch diameter, and was also lower than in the old stand, despite higher branch diameter in this case. The causes of such mortality are unknown.

2000) and across fires (Hodgkinson 1991; Knapp & Keeley 2006). In general, as heating at the soil surface increases, plant mortality, including seeds, increases, and changes in species composition, dominance and spatial distribution may follow, as shown by numerous studies across many world ecosystems (Segura et al. 1998; Morrison 2002; Govender et al. 2006; Knox & Clarke 2006; Penman & Towerton 2008), including California chaparral (Moreno & Oechel 1991b, 1992, 1993; Rice 1993; Tyler 1996; Odion & Davis 2000; Keeley et al. 2005, 2008).

Nevertheless, given the varying sensitivity of plants to heating in space and time (Wright 1970; Kauffman &

Martin 1991; Drewa et al. 2002; Le Fer & Parker 2005), and the high variability in fire behaviour characteristics and associated heating across scales, from the landscape (Turner et al. 1994) to a few meters (Odion & Davis 2000) or lower (Hiers et al. 2009), anticipating the effects of fire intensity is complicated (Keeley 2009). This topic continues to be a research priority.

An important limitation in our understanding of the role of varying soil surface heating during fires on plant responses in crown fire ecosystems, such as chaparral and similar shrubland ecosystems, throughout the world is that most studies to date are restricted to the first few years after fire. Long-term studies are uncommon and, more importantly, few studies have investigated the effects across a whole fire cycle. Long-term studies are particularly relevant in systems like chaparral, in which recruitment is largely dependent on fire, there being no significant recruitment in the period between fires (Keeley 1992). Hence, the individuals that establish immediately after fire are the ones that contribute to recovery of the community (Hilbert & Larigauderie 1990). Recruitment success, however, can be affected by characteristics of the fire. In particular, high soil surface heating can cause reduced regeneration after fire, a change in the dominant species or alterations in the spatial patterns, which could modify biomass accretion and patterns through time and potentially affect fire behaviour in a subsequent fire (Riggan et al. 1988; Odion & Davis 2000; Hiers et al. 2009).

The use of remote sensing has permitted quantifying how fire severity may be affected by severity of the previous fire (Thompson et al. 2007). While this approach is promising, it also has limitations for understanding the impacts on plant populations since, by relying on wildfires, studies will rarely have detailed information on plant populations across the two fires. Furthermore, fire severity metrics obtained from remote sensing can be too coarse, even for forest ecosystems (French et al. 2008). Moreover, application to shrubland vegetation subject to high-intensity crown fires that kill all above-ground biomass can be problematic (Stow et al. 2007). Indeed, no such study is available for shrubland ecosystems such as chaparral or other Mediterranean-type shrublands.

Nowadays, a main concern for managers is to identify areas of high risk of vegetation regeneration failure due to high fire intensity. To this end, surveys are regularly conducted after fire to identify such areas at risk, which are usually based on fire severity metrics (i.e., surrogates of fire intensity; Keeley 2009). It is then important to understand not only the short-term effects of variations in fire intensity but the longer-term effects, including those across a fire cycle. We need to answer questions such as, to what extent does previous fire intensity alter subsequent fire intensity? That is, is there a carry-over effect of this fire

characteristic onto the next fire? If so, for how long does this effect persist? Additionally, will plant demographics vary as a function of previous fire intensity after subsequent burning? Answering these questions would permit better assessment of the role of varying heating on plants and, ultimately, on ecosystem responses.

This paper reports a unique experiment made possible when the southern California Coyote Fire burned in the summer of 2003 through a *Ceanothus–Adenostoma* chaparral stand containing experimental plots that had been experimentally burned in 1987. In 1987, fuel load had been manipulated before burning to produce different levels of fire intensity in order to determine their effects on the demography of the dominant species in this vegetation (Moreno & Oechel 1991a,b, 1993).

The experiment that we now report evaluates the carry-over effects of variation in fire intensity in the 1987 fire on the next fire in 2003, 16 yr later. We specifically tested whether the experimentally produced changes in fire intensity in 1987 affected fire intensity surrogates in 2003. Additionally, we tested whether differences in fire intensity in 1987 affected plant survival and seedling recruitment of the two dominant plant species.

Based on the results obtained in the 1987 experiment, we hypothesized the following: plots burned with higher fire intensity in 1987 would burn with lower fire intensity in 2003. The reasoning behind this is that, as fire intensity increased in the 1987 burns, *Adenostoma* survival decreased (Moreno & Oechel 1991a), and individuals that resprouted did so later, produced fewer resprouts and grew less during the first few years (Moreno & Oechel 1994). Since this is the dominant species, and contributes the largest portion of the biomass of the system, that would have resulted in lower biomass accumulation during the 16 yr after fire and lower fire intensity in the 2003 fire. We further expected that the reduced fire intensity during the 2003 fire in the high fire intensity plots of 1987 would result in higher survival of *Adenostoma* after 2003. Additionally, seedling recruitment of *Adenostoma* would be higher the higher the fire intensity in 1987, while the reverse would be anticipated for *Ceanothus*. This would be due to the contrasted relationships of these two species to fire intensity in 1987 (Moreno & Oechel 1991b).

Methods

Study site and fire characteristics

The study was carried out at the Sky Oaks Biological Field Station (33°21' N, 116°34' W; 1385 m a.s.l.), San Diego County, California, USA. The vegetation of the south-facing slopes is composed of a chaparral

dominated by *Adenostoma fasciculatum* H. and A. (Rosaceae) and *Ceanothus greggii* Gray (Rhamnaceae). The climate is mediterranean, with cool wet winters and warm dry summers; mean annual precipitation is 419 mm, mean January temperature is 9.6 °C and mean July temperature is 25.4 °C (Oak Grove Remote Automatic Weather Station).

Most of the field station facilities and adjacent land were burned on 17 July 2003, by a 9000-ha wildfire started by lightning (the Coyote Fire, California Department of Forestry & Fire Protection). The burned area included a set of experimental plots burned in 1987, which in 2003 comprised a 16-yr-old chaparral, plus the surrounding old stand, which at this time was 75 yr old.

The exact time when the experimental plots burned is unknown. Therefore, we used a range of meteorological and fuel-moisture conditions comprising low (low air relative humidity and wind) and high (high air relative humidity and wind) conditions during 17 July 2003, to calculate the main fire characteristics using Behave Plus 4.0 (Andrews et al. 2008). Fuel loads were calculated based on the equations provided by Black (1987) for 16-yr-old chaparral. Fuel fractions were assigned using the proportions given by Weise & Regelbrugge (1997) for young *A. fasciculatum* (chamise) (SCAL17) fuel model. The remaining fuel model parameters remained unchanged from the chaparral NFFL 4 model. Weather conditions during the day of burning were taken from Oak Grove RAWs (Western Regional Climate Center: <http://www.wrcc.dri.edu/>), located 16 km away from Sky Oaks Field Station. The 10-h dead fuel moisture ranged between 3.6% and 5.1%. The moisture of the rest of the fuel fractions was adjusted using Behave Plus 4.0. Mean wind speed was 0.6 m·s⁻¹ and mean maximum wind speed was 3.6 m·s⁻¹. These resulted in estimated fire-line intensities of 420–5247 KW·m⁻¹, flame lengths of 2–4 m, and flame depths of 1.1–6.5 m, for mean wind and maximum moisture conditions or mean gust wind and minimum moisture conditions, respectively.

Experimental design

The 1987 plots were placed in an area of ca. 2 ha, in a stand that had not burned since 1929 (59-yr-old stand). Within this area, eight blocks, each with five 5 m × 5 m plots were established. Each plot within a block was randomly assigned one of five different treatments: control fuel load (no changes in fuel load, three plots), high fuel load (addition of 4 kg·m⁻² of brush, one plot) and very high fuel load (addition of 8 kg·m⁻² of brush, one plot). These fuel manipulations produced three different levels of fire intensity, as attested by the amount of water evaporated from containers during the

fire and by measures of temperature at the soil surface or of heat penetration into the soil. From now on, these treatments will be referred to as control (CO), high fire intensity (HI) and very high fire intensity (VHI). In addition, two of the three control plots per block (burned but with no fuel added) received after fire additional amounts of ash and char to simulate the levels falling onto the high and very high fire intensity treatments. This additional ash and char had no effect on plant responses after fire in 1987, and so these plots were used as additional control plots. For further details on the experimental design and results of the 1987 experiment see Moreno & Oechel (1989, 1991a,b, 1993).

Field sampling

In October 2004, the 1987 experimental plots (young, 16-yr-old stand) were located and marked for measurements. As in the 1987 experiments, measurements in all plots were taken in the inner 4 m × 4 m quadrat to reduce the edge effects of the experimental burning. In addition, eight plots of similar size were located in the adjacent old stand, which in 2003 was 75 yr old; similar measurements were carried out on them. Because the 2003 fire was a wildfire, no direct measures of fire intensity were possible; intensity was estimated by using as a fire severity metric post-fire measurement of the minimum diameter of burned branches (branch diameter from now on) in *Adenostoma* skeletons (Moreno & Oechel 1989). In each plot, ten plants were selected at random and up to a maximum of 15 randomly selected branches were measured, from which a mean branch diameter per plot was calculated.

Branch diameter was found to be highly correlated ($r^2 = 0.90$) with water loss from containers in the 1987 experiment (Moreno & Oechel 1989), a measure that reflected very well the heat penetration into the soil (e.g., depth of melting of a 62 °C temperature-sensitive paint, $r^2 = 0.70$; Moreno & Oechel 1991b). In addition, branch diameter was highly correlated with time–temperature residence during fire (i.e., time above 150 °C, $r^2 = 0.62$; Pérez & Moreno 1998). Therefore, branch diameter is a good surrogate for fire intensity (*sensu* Keeley 2009). For consistency, and to avoid mixing terminology, when comparing the two fires we will mainly refer to fire intensity throughout, even though this was based on various measures of temperatures or heat release in the 1987 fires, and on minimum diameter of the burned branches in 2003.

All *Adenostoma* plants within each plot were located and their lignotubers measured following the procedures used in Moreno & Oechel (1989). We measured the length of both the longest and shortest axis of a lignotuber and used the product of the two lengths as an index of size. All

lignotubers were assumed to have been alive prior to fire, with the exception of those that showed evident signs of rotting. Only lignotubers with green shoots were considered to have survived the fire; those that produced no new shoots or had produced shoots but were dead by the time of sampling were considered not to have survived the fire. The percentage of surviving lignotuber area per plot was calculated by dividing the sum of the areas of the lignotubers of all surviving plants by the sum of the lignotuber areas of all *Adenostoma* plants in each plot considered alive before fire. Finally, a count of all seedlings of the two dominant species (*Adenostoma* and *Ceanothus*) within each plot provided a measure of the level of recruitment from germination after fire.

Statistical analyses

The effects of the fire intensity treatments in 1987 on intensity (based on its surrogate branch diameter) of the 2003 fire were tested using a randomized complete-block ANOVA, following the original experimental design in 1987 (Moreno & Oechel 1991b, 1993). Planned comparisons among treatment means (fire intensity in 1987) were carried out by defining two sets of *a priori* contrasts: (1) control fire intensity (CO) vs changed fire intensity (HI and VHI plots); and (2) high fire intensity (HI) vs very high fire intensity (VHI). The percentage of lignotuber area index surviving the 2003 fire was tested using the randomized complete-block ANOVA described above. Differences in survival of size index classes of *Adenostoma* after the 2003 fire in relation to 1987 fire intensity treatments and among the two stands (young, old) were analysed with two-sample Kolmogorov–Smirnov tests. Further, the percentage of lignotuber area index surviving after the 2003 fire in both stands was related to the fire intensity surrogate (branch diameter) in 2003 by means of least squares regression. The effect of the 1987 fire intensity treatments on *Adenostoma* and *Ceanothus* seedling recruitment (seedling density, No. m⁻²) was tested using the ANOVA model mentioned above. Finally, seedling density of both species was related to branch diameter by least squares regression. Data were transformed prior to analysis when required to ensure normality (percentage lignotuber area index to arcsine, and seedling density in *Ceanothus* to log).

Results

Branch diameter (mean ± SE) per plot in the young stand (all 1987 plots combined) after the 2003 fire was 7.4 ± 0.2 mm, similar to the control plots in 1987 (7.2 ± 0.5 mm; Moreno & Oechel 1989), and much lower than in the adjacent old stand (15.4 ± 0.8 mm). Fire intensity treatments in 1987 did not significantly affect

branch diameter in 2003 ($F_{2,34} = 2.981$, $P = 0.064$; Fig. 1).

Adenostoma adult plant density in the young stand before the 2003 fire was lower the higher the fire intensity treatment in 1987, which reflects the impacts of the fire intensity experiments in 1987. These effects were particularly visible in the reduced number of small size index individuals as fire intensity increased in 1987 (Table 1, Fig. 2a). Survival of *Adenostoma* adult individuals after the 2003 fire was lower (33.6%, all plots combined) in the young stand than in the old stand (55.4%; Table 1). Survival increased with lignotuber size index (Fig. 3), resulting in a reduced frequency of low size index individuals (Fig. 2b). There were no statistically significant differences in the size classes of surviving adult *Adenostoma* plants among plots that burned in 1987 with different fire intensity (K-S two-sample test between CO and HI + VHI: $Z = 0.588$, $P = 0.859$; K-S between HI and VHI: $Z = 1.177$, $P = 0.125$). Differences in the size classes of surviving *Adenostoma* plants among the control and old stand were significant (K-S two-sample test between CO and old stand: $Z = 1.569$; $P = 0.015$; Fig. 3).

Survival on a per lignotuber area index basis after the 2003 fire (% lignotuber area index per plot surviving fire) was higher in the old stand (75 ± 5%) than in the young stand (41 ± 4%, all treatments combined). Fire intensity in 1987 did not significantly affect the percentage lignotuber area index surviving in 2003 ($F_{2,34} = 2.457$, $P = 0.101$;

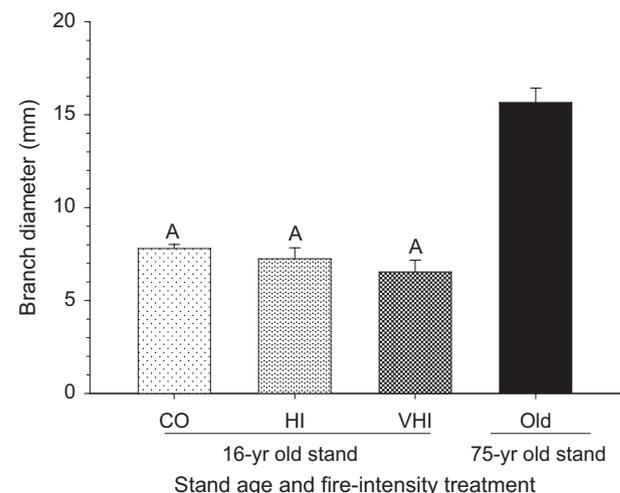


Fig. 1. Mean minimum diameter of burned branches (branch diameter, mm) per plot, a surrogate measure of fire intensity, for plots burned in 2003 after having been burned experimentally in 1987 (young stand, 16 yr old) at control (CO), high (HI) or very high (VHI) fire intensity (see Methods) or by a wildfire in 1928 (old stand, 75 yr old) at the Sky Oaks Biological Station in San Diego, CA. Letters above the bars indicate the result of ANOVA for random blocks ($F_{2,34} = 2.981$, $P = 0.064$). For treatments of the 1987 experimental fire, see Methods and Moreno and Oechel (1991b).

Table 1. Mean (\pm SE) *Adenostoma fasciculatum* adult plant density (No. individuals per 4 m \times 4 m plot) before and after the 2003 fire and survival 1 yr after fire in the young stand (1987 treated plots: control, high and very high fire intensity) and in the old stand.

	Pre-fire density		Post-fire density		Survival (%)	
	Mean	SE	Mean	SE	Mean	SE
Young stand						
Control intensity	27.0	2.3	8.5	1.2	29.3	3.3
High intensity	21.9	3.3	7.5	1.7	33.4	5.1
Very high intensity	13.1	2.0	5.9	1.5	42.2	7.1
Old stand	23.0	2.6	12.8	1.6	55.4	2.4

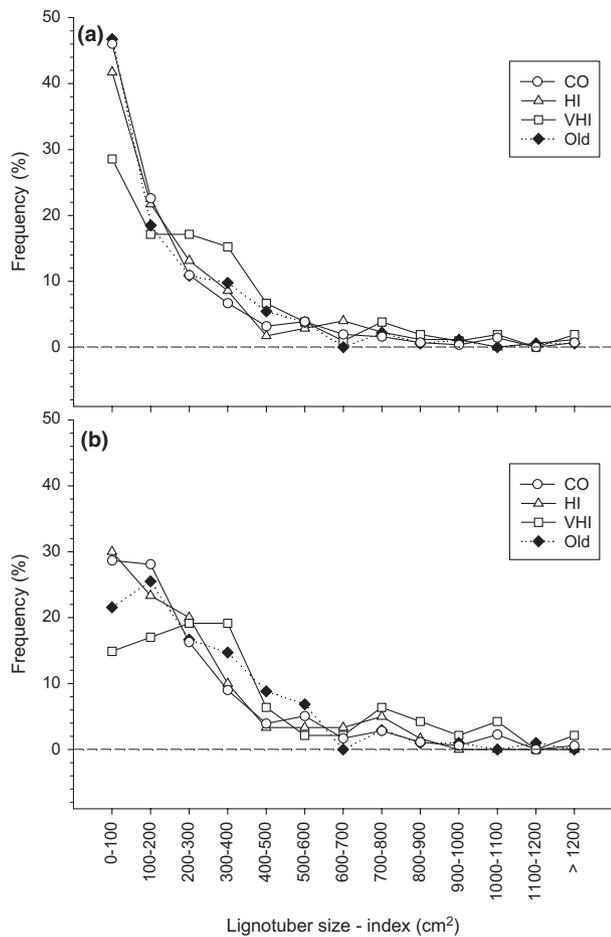


Fig. 2. Lignotuber size index frequency distribution of *Adenostoma fasciculatum* plants (a) before the 2003 fire, (b) after the 2003 fire, in plots burned experimentally in 1987 with a different fire intensity (CO, HI, VHI) (young stand, 16 yr old) or by a wildfire in 1928 (old stand, 75 yr old), at the Sky Oaks Biological Station in San Diego, CA.

Fig. 4). In the young stand, branch diameter in 2003 was a good predictor of the percentage of lignotuber area index surviving, which statistically significantly decreased as

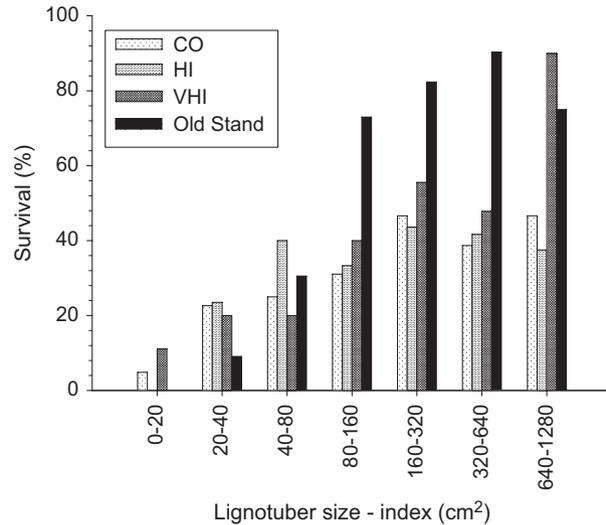


Fig. 3. Survival of adult plants of *Adenostoma fasciculatum* 1 yr after the 2003 fire as a function of lignotuber size index for the plots burned experimentally in 1987 (young stand, 16 yr old) at control (CO), high (HI) or very high (VHI) fire intensity or by a wildfire in 1928 (old stand, 75 yr old) at the Sky Oaks Biological Station in San Diego, CA. Kolmogorov–Smirnov two-sample tests: CO vs HI + VHI ($Z = 0.588$, $P = 0.859$); HI vs VHI ($Z = 0.588$; $P = 0.859$); CO vs old stand ($Z = 1.569$; $P = 0.015$).

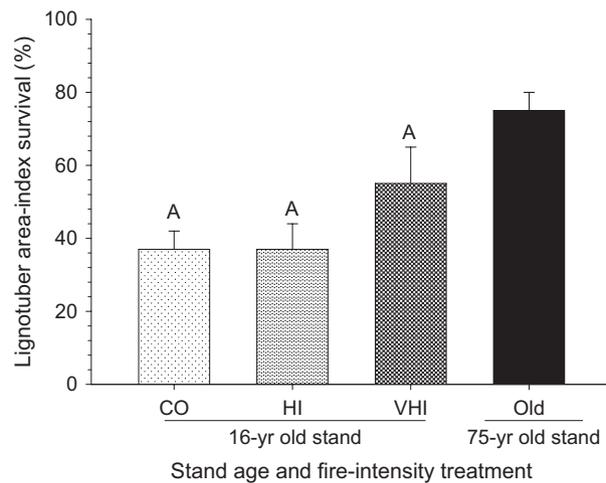


Fig. 4. Percentage of surviving *Adenostoma* lignotuber area index in plots burned in 2003 after having been burned experimentally in 1987 (young stand, 16 yr old) at control (CO), high (HI) or very high (VHI) fire intensity (see Methods) or by a wildfire in 1928 (old stand, 75 yr old) at the Sky Oaks Biological Station in San Diego, CA. Letters above the bars indicate the result of ANOVA for random blocks ($F_{2,34} = 2.457$, $P = 0.101$). For treatments of the 1987 experimental fire see Methods and Moreno and Oechel (1991b).

branch diameter increased ($m = -0.068$, $r^2 = 0.14$, $P = 0.025$). This relationship was not significant in the old stand ($m = 0.047$, $r^2 = 0.26$, $P = 0.198$).

Adenostoma seedling density (No. m⁻²) 1 yr after fire was similar in the control plots of the young stand and in the old stand, and lower in both types of plots than in the increased fire intensity plots in the 1987 fire. In the young stand, seedling density of *Adenostoma* significantly increased as fire intensity increased in 1987 ($F_{2,34} = 12.39$, $P < 0.001$; Fig. 5a). *Ceanothus* seedling density 1 yr after fire was much higher in the old stand than in the young stand. In the young stand, *Ceanothus* seedling density was higher in the control plots than in the increased fire intensity plots in 1987 ($F_{2,34} = 6.66$, $P = 0.004$; Fig. 5b).

In the young stand, seedling density of *Adenostoma* was negatively related to branch diameter in 2003 ($m = -0.45$, $r^2 = 0.28$, $P = 0.001$; Fig. 6a); *Ceanothus* seedling density was not related to branch diameter in 2003 ($m = 0.2572$, $r^2 = 0.02$, $P = 0.410$; Fig. 6b). In the old stand, neither

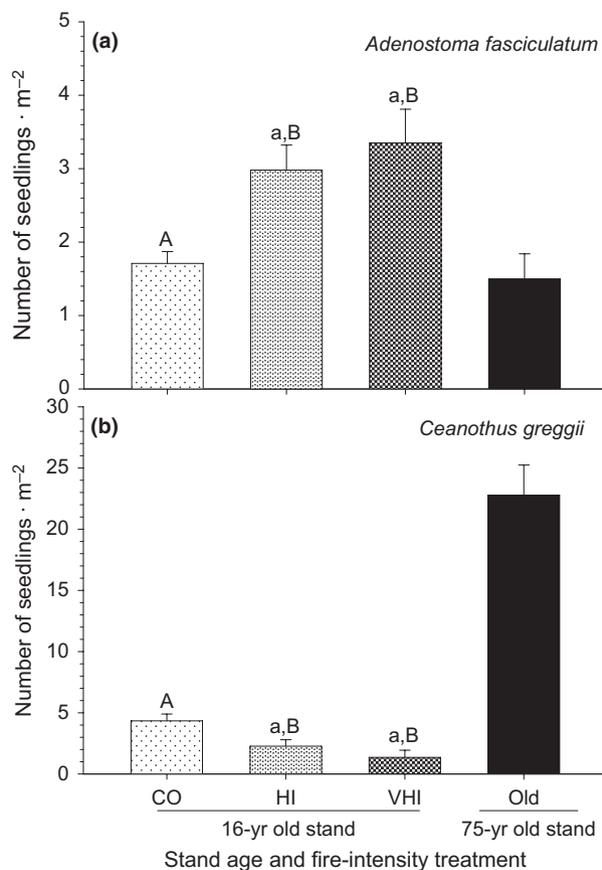


Fig. 5. Seedling density (No. m⁻²) of (a) *Adenostoma fasciculatum*, and (b) *Ceanothus greggii*, 1 yr after the 2003 fire in the plots burned experimentally in 1987 (young stand, 16 yr old) at control (CO), high (HI) or very high (VHI) fire intensity (see Methods) or remained unburned since 1928 (old stand, 75 yr old) at the Sky Oaks Biological Station in San Diego, CA. Letters above the bars indicate the result of *a priori* contrasts based on ANOVA for random blocks (*Adenostoma*: $F_{2,34} = 12.39$, $P < 0.001$; *Ceanothus*: $F_{2,34} = 6.66$, $P = 0.004$). Different letters for a given contrast indicate statistically significant differences ($P \leq 0.05$).

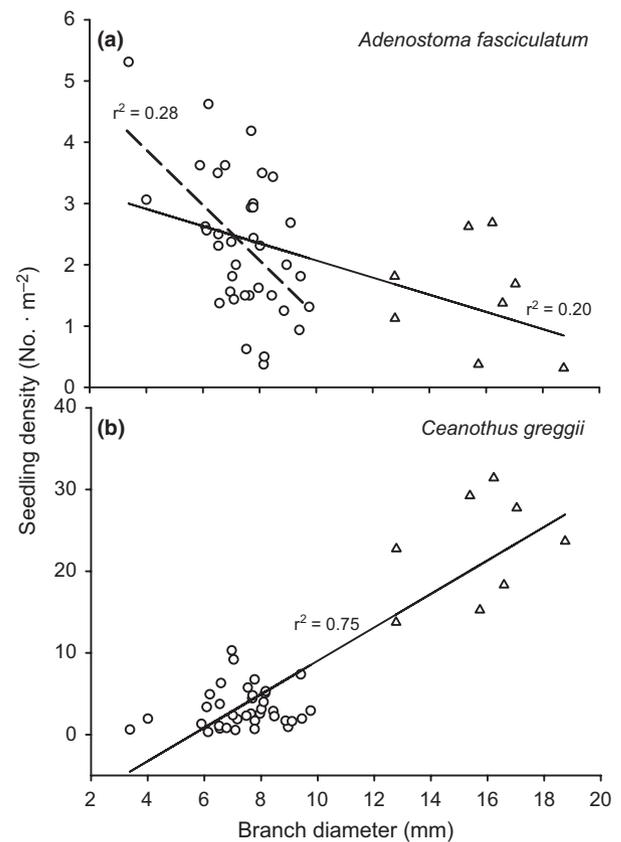


Fig. 6. Relationships between the density (No. m⁻²) of (a) *Adenostoma fasciculatum*, and (b) *Ceanothus greggii*, 1 yr after fire, and branch diameter (mm) (a surrogate measure of fire intensity) for the plots burned experimentally in 1987 (young stand, 16 yr old; circles) and in the adjacent old stand (75 yr old; triangles) at the Sky Oaks Biological Station in San Diego, CA. Only significant relationships are shown: *A. fasciculatum* ($r^2 = 0.28$, $P = 0.001$ for the young stand; $r^2 = 0.20$, $P = 0.002$ for both stands combined); *C. greggii* ($r^2 = 0.75$, $P < 0.001$ for both stands combined).

Adenostoma nor *Ceanothus* seedling density were significantly related to branch diameter in 2003 ($m = -0.105$, $r^2 = 0.06$, $P = 0.574$; $m = 1.181$, $r^2 = 0.13$, $P = 0.375$, respectively). Similar analysis including both stands together resulted in significant relationships for *Adenostoma* ($m = -0.144$; $r^2 = 0.20$, $P = 0.002$) and *Ceanothus* ($m = 2.0511$, $r^2 = 0.75$, $P < 0.001$; Fig. 6).

Discussion

Variation across plots in fire intensity created by the experimental fires of 1987 did not significantly affect fire intensity surrogate (branch diameter) when these plots were burned again by a wildfire (Fig. 1). Despite large differences in the fire intensity and impact produced during the 1987 experimental burning, 16 yr later these differences were not sufficient to significantly affect fire intensity in

the various plots. Several factors could have contributed to this result. Assuming that conditions were stable while the plots were burning, changes in fire intensity were expected in 2003 due to differences in biomass among plots. Indeed, during the first years after the 1987 fire, biomass was lower in the plots burned with high fire intensity than in the control ones (Moreno & Oechel 1994). However, 16 yr may have been sufficient to equalize biomass in the various plots, independent of how severely they had burned. This could be explained by the fact that *Adenostoma* is dominant in the stand, and that the mortality caused by increasing fire intensity in 1987 was concentrated in the smaller size individuals, whose contribution to the overall biomass of the stand would have been small as the years passed. That is, a high impact at the demographic level does not necessarily translate into a similar impact for other ecosystems properties (Riggan et al. 1988).

An additional explanation is that the size of the plots was too small to affect fire behaviour and intensity in a way detectable with our branch diameter metric. Fire intensity can vary at very small scales (>1 m) due to differences in fuel load (Davis et al. 1989; Hiers et al. 2009) or canopy structure (Schwilk 2003). Heating patterns at scales of 4–5 m can emerge in relation to pre-fire patterns of canopy configuration (Odion & Davis 2000). Yet, it is possible that the fire intensity recorded in the plots was influenced by conditions of surrounding areas as well as biomass and its configuration within plots. Any moving fire produces a flame front of variable flame length and flame depth. Modelled flame depths varied from more than 1 m to several meters, depending on wind and moisture. Flames of this magnitude were probably large enough to produce a combustion environment that could have, in part, overridden the biomass existing within the plots. All surrounding areas of the plots were burned in 1987 at control fire intensity; hence they were expected to have equal or higher biomass than the plots burned with high intensity. While the effect of the neighbouring areas on branch diameter within the plots cannot be estimated with any accuracy, it is possible that larger plot sizes would have revealed significant effects of fire intensity in 1987 on branch diameter and subsequent fire intensity in 2003 (Fig. 1).

Our results show that survival of *Adenostoma* was not significantly different among plants of various lignotuber size indices across different 1987 fire intensities. Additionally, fire intensity in 1987 did not affect the percentage of surviving lignotuber area of *Adenostoma* after 2003. Notwithstanding, fire intensity in 2003 was a significant factor in determining the percentage of surviving lignotuber area of *Adenostoma* in the young stand, which experienced high mortality. No such relationships were found in the old stand. This leads us to conclude that fire intensity can be important for *Adenostoma* survival, and that variations

within a burn can have a significant impact. Yet, the variability across the two burns due to changes in fire intensity in the previous fire was not statistically significant, suggesting that any carry-over effects of the variations in fire intensity in 1987 over *Adenostoma* survival were short-lived. The unnatural fuel structure created by the treatments in 1987 probably caused variations in fire intensity that were much larger than those that usually occur under normal conditions. If such large variations did not produce a significant carry-over effect, it is unlikely that normal (i.e., smaller, see variability of branch diameter in Fig. 1 for any treatment) variations in fire intensity within a stand in a wildfire will produce significant effects. This means that the carry-over effects of variations in fire intensity on *Adenostoma* plant survival in a normal fire are probably not very important.

We document that the overall survival of *Adenostoma* plants was much lower after the 2003 fire than after the 1987 fires. Survival of *Adenostoma* in the control fire intensity plots of the young stand was low in spite of the low fire intensity recorded. This low survival contrasts with results obtained in the 1987 experimental burns under control fuel load and mild weather conditions typical of early spring. Those burns resulted in low, and similar, fire intensity, unlike the 2003 fire, but resulted in very high survival (above 95% in most size classes), with mortality restricted to small lignotuber size index individuals (Moreno & Oechel 1991a, 1993). The high mortality after the 2003 fire applied to individuals of all sizes. This also contrasts with survival in the old stand, which was higher than in the young stand even though fire intensity as indexed by branch diameter was much higher. Survival in the young stand was lower than in a 24-yr-old stand (68% survival), despite similar branch diameter, and even lower than in a 3-yr-old stand (42% survival) (Keeley & Brennan 2012). The cause of this much lower survival is unknown but, as discussed above, it was not related to changes in fire intensity in 1987. Whether the time of burning in a previous fire (early spring in the 1987 fire) affects the survival of *Adenostoma* with time (for as long as 16 yr) needs to be investigated.

Observed carry-over effects on seedling recruitment of both *Adenostoma* and *Ceanothus*, with higher recruitment of *Adenostoma* and lower recruitment of *Ceanothus*, are more relevant if we take into account higher mortality with higher fire intensity among *Adenostoma* plants in 1987. This pattern may have influenced *Adenostoma* seed availability 16 yr later. As for *Ceanothus*, more plants emerged in the high fire intensity plots than in the other two types of plot in 1987. Nevertheless, seed availability may have been influenced by small plot size, which was within the range of the ballistic mechanisms of dispersal from outside the plots (Evans et al. 1987). Hence, seed availability in all

plots more likely reflected seed production in the control plots, since this is the intensity at which the whole stand burned. The exact cause of this carry-over effect is unknown, but it points to the contrasting sensitivity of two species to fire intensity (see Fig. 6). This finding rests on the assumption that the climate conditions after the fire did not change recruitment among plots burned with different fire intensity in 1987, and is supported by the fact that the year after fire was not at any particular extreme.

The contrasted sensitivity of the two species to fire intensity is further shown by the recruitment levels in the old stand. The *Adenostoma* seed bank was probably much larger in the old than in the young stand (Zammit & Zedler 1988), yet its overall recruitment was similar in both stands. The opposite pattern was found for *Ceanothus*, whose recruitment was much higher in the old stand than in the young one, even though *Ceanothus* does not accrue seeds in the seed bank with age (Zammit & Zedler 1988). It is worth noting that branch diameter was a significant factor in recruitment across stands that differed so much in time since the last fire (16 and 75 yr). In the case of *Ceanothus* this variable accounted for 75% of the variance in recruitment across both stands. Comparison with germination obtained after the 1987 burns in the control plots (at that time they were 59-yr-old stands, so not much different to the 75-yr-old stand now), which burned with low intensity, reflect well these contrasting patterns: emergence of *Adenostoma* was much higher and that of *Ceanothus* much lower (Moreno & Oechel 1991b, 1992).

Our study documents that the effects caused by changes in fire intensity on seedling recruitment can be reversed in part in a next fire. Hence, the lower germination of *Adenostoma* in 1987, caused by increasing fire intensity, resulted in elevated recruitment after the 2003 fire. The relationship was the reverse for *Ceanothus*. This, to our knowledge, is the first time that a compensatory mechanism for the effects of a characteristic of fire, such as fire intensity, on plant populations is documented. This response appeared to be related to the contrasting sensitivity of these two species to fire intensity (see Figs. 5,6). Since changes in fire intensity are probably related to growth and biomass accumulation after fire, the period during which this mechanism operates was probably at the limit, since, as discussed earlier, there were no carry-over effects on fire intensity. This is important since, even though the probability of burning for young stands is low (Keeley & Fotheringham 2003), recurrent fires beyond the first few years following very severe fires would not favour the more heat-tolerant species (*Ceanothus*), but would tend to restore the losses caused by such fires by increasing recruitment of *Adenostoma*. Nevertheless, considering that some of the treatments implemented in 1987 produced variations in fire intensity above normal, no large differences in

recruitment are to be expected across a fire cycle due to fire intensity, even if fires occurred at relatively short intervals beyond a few years (Zedler et al. 1983; Keeley & Brenan 2012). Changes in fire intensity could affect other vegetation components, like herbs, including non-native species, which have also been shown to be sensitive to such changes (Moreno & Oechel 1991b; Keeley et al. 2008; Keeley & Brenan 2012), but these were not investigated here.

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