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EARLY POST-FIRE PLANT ESTABLISHMENT ON A MOJAVE DESERT BURN

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ABSTRACT

Fire has become more extensive in recent decades in southwestern United States arid lands. Burned areas pose management challenges and opportunities, and increasing our understanding of post-fire plant colonization may assist management decision-making. We examined plant communities, soils, and soil seed banks two years after the 2005 Loop Fire, located in a creosote-blackbrush community in Red Rock Canyon National Conservation Area in southern Nevada's Mojave Desert. Based on a spring sampling of 20, 0.01-ha plots, live + dead cover of the exotic annual *Bromus rubens* averaged nine times lower on the burn than on a paired unburned area. Perennial species composition shifted from dominance by late-successional native shrubs (e.g., *Coleogyne ramosissima*) on the unburned area, to dominance by native perennial forbs (e.g., *Sphaeralcea ambigua*, *Baileya multiradiata*) on the burn. Species richness of live plants averaged 26% (100 m² scale) and 239% (1 m² scale) greater on the burn compared to the unburned area. Only 5% of *Larrea tridentata* individuals resprouted, compared to 64% of *Yucca schidigera* and *baccata*. Fire and microsite (interspace, below *L. tridentata*, or below *Yucca*) interacted to affect several 0–5 cm soil properties, with higher pH, conductivity, and total P and K on burned *Yucca* microsites. *Bromus rubens* density in 0–5 cm soil seed banks was four times lower on the burn, and its distribution among microsites reversed. Below-shrub microsites contained the most *B. rubens* seeds on the unburned area, but the least on the burned area. Intense fire below shrubs may have increased seed mortality, an idea supported by >3-fold decreases we found in emergence density after heating seed bank samples to 100°C. Our study occurred after a post-fire period of below-average precipitation, underscoring a need for longer term monitoring that characterizes moister years.

Key Words: Colonization window, exotic species, grass-fire cycle, soil seed bank, wildfire.

Wildfire has become widespread in southwestern USA deserts. In a record 2005 fire season in the Mojave Desert, for example, more than 385,000 hectares burned (Brooks and Matchett 2006). This area represents approximately 3% of the entire Mojave Desert. Fueled in large part by exotic annual grasses, these fires burned desert shrublands thought to have only burned infrequently historically (Brooks 1999; Esque and Schwalbe 2002). Burns now occupy significant portions of desert landscapes, posing prominent management

challenges. In addition to such concerns as post-fire soil erosion, burns pose challenges and opportunities for meeting mandates of land management agencies to manage for native species and communities in areas such as national parks and conservation areas. Fires in arid lands have been cited to initiate a “grass-fire cycle,” where fire promotes resurgence of the exotic grasses that fueled the fire to create a frequent-fire regime (D’Antonio and Vitousek 1992). Such a fire cycle threatens the sustainability of many fire-susceptible, infrequently regenerating native species, such as *Coleogyne ramosissima* Torr. (Rosaceae) or *Yucca brevifolia* Engelm. (Agavaceae). However, just as in more mesic regions, deserts contain early successional native species that might benefit from fire (Cave and Patten 1984).

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Improving our understanding of plant colonization on desert burns is important for evaluating future fire hazard, whether natural colonization will meet management objectives for burned sites, or for planning active revegetation if this becomes a management goal. It is possible that opportunities exist for intervention in the grass-fire cycle immediately following a fire if exotic grass competition is temporarily reduced while available nutrients liberated by the fire increase. This time period may serve as a colonization window, which is often a key feature of plant succession in other regions. For example, periodic droughts provided windows for colonization by underrepresented species during a 40-year permanent plot study of succession in New Jersey (Bartha et al. 2003). The post-fire environment, together with the frequent dry years characterizing desert climates, may permit colonization by species not dominant prior to fires (Lei 2001; Brooks 2002).

In addition to precipitation, two of the many factors that may influence plant colonization are soil seed banks and post-fire soil properties. Seed banks can provide propagules of both native and exotic species if emergence requirements are met following disturbance (Warr et al. 1993). Seed bank contributions to plant colonization after wildfires hinge upon the density of seeds surviving fire, their germinability, and post-fire seed deposition and dispersal (Lei 2001). Soil pH often increases after fire through combustion of organic acids or release of base cations. Correspondingly, availabilities of some soil nutrients also frequently increase initially post-fire (Raison 1979). On one hand, pulses of nutrient availability, following precipitation events, are considered important to the functioning of native desert plant communities (Noy-Meir 1973). On the other hand, exotic species often respond with vigorous growth to nutrient additions (James et al. 2006).

We measured plant communities, soil seed banks, and soil properties during the second year after the 2005 Loop Fire in the eastern Mojave Desert. This burn occurred within a National Conservation Area and encompasses a popular tourist and recreation site. The fire burned within and spread across a scenic loop road that receives 900,000 visitors annually (Bureau of Land Management, Las Vegas Field Office, Las Vegas, NV). The area is regarded as a symbol of the "natural" desert landscape surrounding metropolitan Las Vegas, Nevada. Resource managers are concerned about post-fire succession in relation to aesthetics, native community recovery, future fuel loads, and if or how active revegetation should be a management goal. Our objectives were to (1) compare plant species richness, composition, and soil properties between the burn and a matched unburned area, (2) assess resprouting of burned dominant native shrubs, and (3) assay soil seed bank composition and

experimentally test responses of seed bank samples to the fire cues of heat and smoke.

METHODS

Study Site

This study occurred inside the Loop Drive area of Red Rock Canyon National Conservation Area, managed by the Bureau of Land Management and located 15 km west of the western Las Vegas suburbs in Clark Co., southern Nevada. Precipitation at the Spring Mountain Ranch State Park weather station, 7 km south of the study site, has averaged 30 cm/yr (range = 6–61 cm/yr, coefficient of variation [CV] = 45%) during a 1977–2008 period of record (Western Regional Climate Center, Reno, NV). January daily minimum temperatures have averaged -1°C (range = -6 to 2°C , CV = 12%), and July maximum temperatures have averaged 36°C (range = 33 – 38°C , CV = 2%). We studied the 348-ha Loop Fire, which started from a lightning ignition on July 22, 2005. Maximum temperature on this day was 38°C , and erratic winds gusted up to 80 km/hr during the fire. Typical flame heights were ≥ 2 m and flame lengths were ≥ 6 m (Troy Phelps, Bureau of Land Management, personal communication). Fire managers also noted that the fuel provided by exotic annual grasses facilitated ignition of native shrubs and allowed the fire to burn continuously across the landscape. The fire left fewer than five unburned islands, all < 1 ha in size, within the burn perimeter.

We matched an unburned area immediately adjacent to the west of the burned area that was similar in climate, soils, and vegetation. Based on plot sampling described below, mean elevation of the burned area (1274 m) differed by 54 m from the mean elevation of the unburned area (1220 m). Soils on the burned and unburned areas were both mapped in the county soil survey as $> 90\%$ of the 731 (Purob-Irongold association) and 732 (Purob extremely gravelly loam) types (Lato 2006). These soils are classified as Typic and Calcic Petrocalcids, have alluvium parent material derived from limestone, and occur on fan piedmont landforms. Based on identifying resprouts and burned shrub skeletons on the burned area, both the burned and unburned areas were similarly dominated by *Coleogyne ramosissima*, *Yucca schidigera* Roezl ex Ortgies (Agavaceae), *Yucca baccata* Torr. (Agavaceae), and *Larrea tridentata* (DC.) Coville (Zygophyllaceae).

Plot Sampling

We overlaid a square grid of 315 ha encompassing 91% of the irregularly shaped burn and randomly located ten 10 m \times 10 m (0.01 ha) plots within the grid using randomly selected coordi-

nates in a geographic information system. We located 10 plots in the adjacent unburned area using the same method but in a square grid of 130 ha that the site would accommodate. Each plot contained six, $1\text{ m} \times 1\text{ m}$ subplots located at the four plot corners and centered at 5 m along the southern and northern plot boundaries. We visually categorized areal percent cover of each live perennial species and of live and dead annual species rooted in each subplot using Peet et al.'s (1998) cover classes: 1 = trace (assigned 0.1%), 2 = 0–1%, 3 = 1–2%, 4 = 2–5%, 5 = 5–10%, 6 = 10–25%, 7 = 25–50%, 8 = 50–75%, 9 = 75–95%, and 10 = 95–100%. We measured both live and dead annuals to provide a measure of the recent annual communities on plots. Dead annuals (especially the exotic grasses) also provide the fuel that allows fire to spread between perennial plants. We quantified measurement reproducibility in subplot data by remeasuring a total of three randomly selected subplots on three different plots. Species richness/m² was identical in original and repeated measurements. The maximum difference in cover class between original and repeated measurements was one class. We inventoried whole plots for species not already occurring in subplots and categorized cover of these species on a whole-plot basis. Plants not able to be readily identified to species in the field were collected, pressed, and identified to species when possible. Six vegetative specimens, which occurred on only one plot each, could not be identified to species or genus and were deleted from the data set. Nomenclature, classification of species life forms (e.g., shrub, forb), longevity (e.g., annual, perennial), and native/exotic status in North America followed the PLANTS database (USDA 2007).

We counted the number of individuals of each shrub species on each plot. On a $10\text{ m} \times 40\text{ m}$ (0.04 ha) plot originating at each $10\text{ m} \times 10\text{ m}$ plot, we further counted the number of *Larrea tridentata*, *Yucca baccata*, and *Yucca schidigera* individuals and classified them into one of four categories: unburned alive, burned but crown survived, resprout, or dead (Rogers and Steele 1980).

We collected soil and soil seed bank samples from three interspaces (>1 m from any shrub) and from below the canopies of three each of the largest *Larrea tridentata* and *Yucca* spp. (*Y. baccata* or *Y. schidigera*) adjacent to each plot. In the shrub microsites, we collected a 200-cm³ soil and a 200-cm³ seed bank sample (cores 7 cm in diameter) halfway between the main central stem and the outer canopy edge on both the north and south sides of each shrub. Samples were collected from a 0–5 cm depth, which could include a litter layer (only the below-shrub microsites contained appreciable litter) only for the seed bank samples. We included litter as part of the 0–5 cm seed bank

sampling depth because litter can trap seeds (Warr et al. 1993). We chose this depth for both soil and seed bank sampling because upper soils become hottest during fire and may more strongly reflect post-fire differences than deeper layers (Raison 1979; Patten and Cave 1984). This depth also includes the highest density of viable seeds in desert seed banks and is a maximum depth from which most seeds can emerge or reach emergence depth (Guo et al. 1998). We composited soil and seed bank samples on a plot basis for each of the three microsite types. This resulted in a soil volume of 1200 cm³ each for soil and seed banks for each microsite type on each plot. We also collected separate 200-cm³ samples from each microsite for measuring soil bulk density (2-mm sieving followed by drying at 105°C for 24 hr).

Sampling occurred in 2007 (two years post-fire) in spring (April–May), the time of peak annual plant community growth in the Mojave Desert (Beatley 1966). We did not collect soil seed bank samples during what is considered the optimal time (fall or early winter just prior to germination of winter annuals) in this region. However, as only 6 cm of precipitation fell (as opposed to the long-term average of 23 cm) from September 2006 through March 2007 prior to sampling, emergence of annual plants was limited. Therefore, depletion of soil seed banks through field germination should not have been a major factor affecting the detection of seeds in the greenhouse soil seed bank assay.

Soil Laboratory Analysis

The air dried, <2-mm fraction of soil samples was analyzed for texture (hydrometer method), electrical conductivity and pH (1:1 soil:water), total C and N (Leco C/N analyzer), and extractable P and K (Olsen NaHCO₃ method) following methods in Amacher et al. (2003). Measurement error, based on analyzing a duplicate sample every 10 samples and comparing original and duplicate means, ranged from 0.2% (electrical conductivity) to 6.8% (total N).

Soil Seed Bank Experiment

We assessed responses of seed bank samples to simulated fire exposure in a factorial experiment consisting of heat (two levels: presence or absence of 100°C heating) and liquid smoke (two levels: presence or absence of 10% smoke). Treatments were performed on 240 cm³ soil volumes extracted from microsite/plot composite samples. We conducted heating treatments by placing samples in tins in an electric oven. Samples remained in the oven until the soil reached 100°C for one minute, which required about 10 min, at which time samples were removed from the oven. We

monitored temperature using a probe accurate to 0.1°C and placed directly in the soil. The soil cooled to 65°C within five minutes of being removed from the oven and to 45°C within 10 min. We chose the 100°C treatment to be within the temperature range previously reported to occur in upper soil layers during burns in the Sonoran and Mojave Deserts (Patten and Cave 1984; Brooks 2002). For smoke only samples and after heating for heat × smoke samples, we applied 120 ml (diluted to 10% smoke by volume using tap water) of commercially available liquid smoke (Wright's Brand, Roseland, NJ) to each sample. Liquid smoke contains the same butanol compound contained in air smoke that can affect germination in some species (Flematti et al. 2004). The non-smoke samples received 120 ml of tap water not containing liquid smoke.

After applying treatments, we placed each sample in a 2 cm thick layer on top of 300 cm³ of sterile potting soil in 700-cm³ square plastic pots. We randomly arranged these pots, including six pots containing only potting soil to check for seed contamination (none was detected), on a bench in a greenhouse. This greenhouse did not receive supplemental lighting and was maintained at approximately 28°C during the first three months (summer) of the emergence period and 17°C during the last three months (fall). Samples were watered by an automated misting system that delivered approximately 1.5 cm of water/day. We conducted periodic (at least monthly) inventories during a six-month emergence period; 93% of the total number of emerging seedlings emerged within the first 10 d. We also checked samples every 1–2 d to monitor for potential mass mortality between inventories, which we did not detect.

Data Analysis

Statistical inference is limited to the particular fire that we studied (van Mantgem et al. 2001). We compared live, dead, and total mean cover of *Bromus rubens* L. (Poaceae), a fuel-producing exotic annual grass, and community species richness (per m² and per 100 m²) between the burned and unburned area using two-tailed t-tests. Findings can change based on the scale of analysis for species richness, which is why we examined effects of fire at two different scales. Based on species importance values for live vegetation for each plot, we ordinated species composition using non-metric multidimensional scaling (Sørensen distance, thorough mode) in PC-ORD (McCune and Mefford 1999). We calculated importance values as the average of relative frequency (based on six subplots per plot) and relative cover (with percent cover calculated as the midpoint of a cover class). We tested the hypothesis of no difference in live plant species

composition between burned and unburned areas using multi-response permutation procedures (Zimmerman et al. 1985). We based this analysis on Sørensen distance and performed it in PC-ORD. To examine the fidelity of live species with burn status, we performed indicator species analysis (Dufrêne and Legendre 1997) using species importance values and a Monte Carlo test of significance (1000 permutations). Indicator species analysis combines the relative abundance and frequency of a species within a group to produce an indicator value that ranges from zero (no fidelity) to 100 (maximum fidelity). We analyzed univariate soils data as a split-plot analysis of variance (ANOVA) with burn status as the whole-plot factor and microsite (inter-space, below *Larrea*, or below *Yucca*) as the subplot factor using JMP (SAS Institute 2004). Tukey's test was used for mean separation. *Bromus rubens* comprised 92% of seeds in the seed bank experiment, so we focused the statistical analysis on this species. Log10 transformed *B. rubens* seed counts were modeled using a mixed-model ANOVA (SAS PROC MIXED; REML) with burn status, microsite, heat, smoke, and all two-, three-, and four-way interactions as fixed effects (SAS Institute 1999). This was a partially nested design, so plot nested within burn status and its two- and three-way interactions with microsite, heat, and smoke were treated as random effects.

RESULTS

Relative to longer lived species, live annual cover was low in the unburned area and both live and dead annual cover was low in the burned area. Live annuals averaged only 0.05% (SD = 0.09%) cover in the unburned area (0.4% of the 15% total mean live plant cover), and 0.6% (SD = 0.6%) in the burned area (27% of the 2% total mean live plant cover). Total mean cover of *Bromus rubens* was nine times lower in the burned than in the unburned area, a difference driven by significantly greater ($t = -5.32$, $P < 0.001$) dead cover in the unburned area (Fig. 1). Although live cover was sharply lower than dead cover in both areas, live *B. rubens* cover was significantly greater ($t = 3.09$, $P = 0.006$) in the burned area relative to the unburned area.

Species richness of live plants was 3.4 times greater at a 1-m² scale and 26% greater at a 100-m² scale in the burned area compared to the unburned area (Fig. 2). Exotic annuals in the burn comprised 50% of richness/m², but this percentage declined to 18% of richness/100m². Only 7% of richness at both scales in both the burned and unburned areas consisted of native annuals. Native perennial forbs constituted 34–35% of richness at the two scales on the burn, compared to 2–13% on the unburned area.

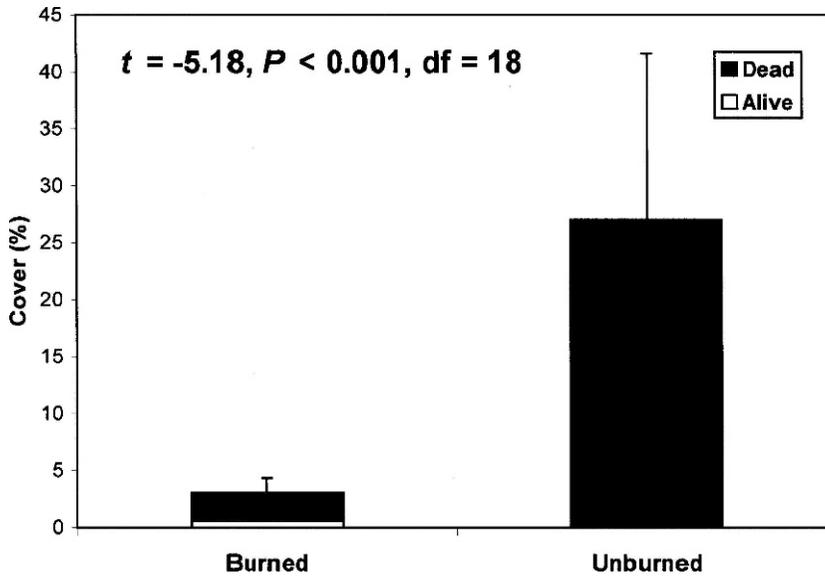


FIG. 1. Areal cover of *Bromus rubens* on a burned and unburned area, Red Rock Canyon National Conservation Area, Mojave Desert. Error bars are one standard deviation for total cover. Total mean cover was compared between the burned and unburned areas using a two-tailed t-test.

Conversely, native perennial shrubs composed 76–79% of richness in the unburned area and only 5–30% in the burned area.

Species composition differed sharply between the burned and unburned areas (Fig. 3). Importance of *Coleogyne ramosissima* and *Yucca baccata* was positively correlated with unburned plots in the ordination. In contrast, species associated with burned plots included the native perennial forbs *Sphaeralcea ambigua* A. Gray (Malvaceae), *Eriogonum inflatum* Torr. & Frém. (Polygonaceae), and *Baileya multiradiata* Harv. & A. Gray ex A. Gray (Asteraceae), the perennial grass *Dasyochloa pulchella* (Kunth) Willd. ex Rydb. (Poaceae), and the exotic annuals *Erodium cicutarium* (L.) L'Hér. ex Aiton (Geraniaceae) and *Bromus rubens*. Consistent with the ordination results, average Sørensen similarities among burned (53%) and unburned plots (47%) were about four times greater than the average similarity between burned and unburned plots (12%). This difference in species composition between the burned and unburned areas was significant based on multi-response permutation procedures (T statistic = -12.1, chance-corrected within-group agreement A statistic = 0.27, $P < 0.001$).

Distributions of individual species also reflected differences between burned and unburned species composition (Fig. 4). Twelve species constituted 71–78% of all relative cover. Based on indicator species analysis, six of these species were significant ($P < 0.05$) indicators for the burn and three for the unburned area.

Resprouting varied between measured shrub species, with only 5% of burned *Larrea tridentata*

resprouting compared to 64% of burned *Yucca baccata* and *schidigera*; Fig. 5). No measured *L. tridentata* and only 3% of *Yucca* in the burned area had crowns that survived the fire. Although we did not measure dead *Coleogyne ramosissima* in the burned area, we found live individuals (three mature individuals presumably avoided by the fire) in only one plot on the burned area and no resprouts. In comparison, live *C. ramosissima* density averaged 4,560/ha (SD = 3,041) in the unburned area.

Several soil properties differed significantly among microsites and between the burned and unburned areas (Table 1). There was a burn \times microsite interaction for four properties (pH, conductivity, P, and K) because the *Yucca* microsite contained higher levels in the burned than in the unburned area compared to the other microsites. Total C varied both with burn status and microsite, being greater on the burn. Total N was higher in *Yucca* microsites than in interspaces but did not differ overall between burned and unburned areas. Soil texture did not differ significantly among microsites or between burned and unburned areas.

In the seed bank experiment, seed density of *Bromus rubens* reversed among microsites with burn status, resulting in a significant burn \times microsite interaction ($F_{2,36} = 47.6$, $P < 0.001$). Seed density was greatest below shrubs on the unburned area, but interspaces contained the most seeds on the burn. Heat also was a significant effect ($F_{1,18} = 101$, $P < 0.001$) that sharply reduced the density of emerging seeds. Therefore, results for the three-way interaction of

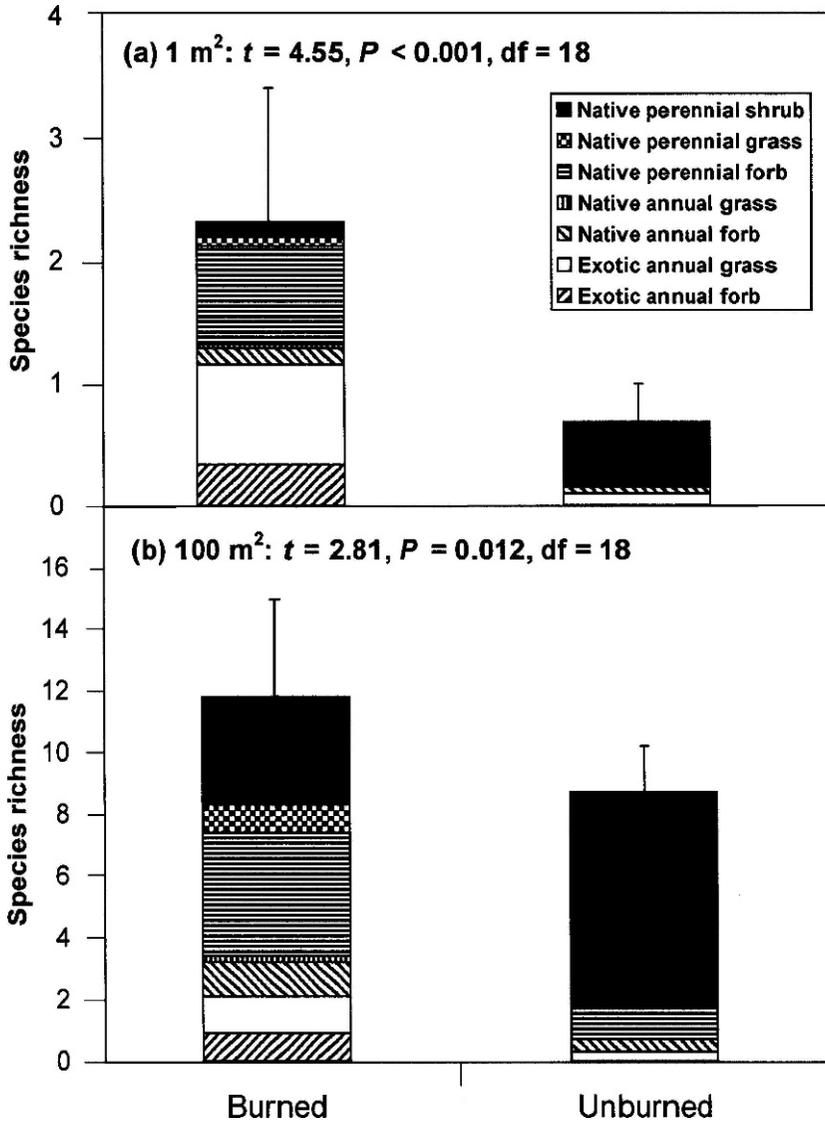


FIG. 2. Plant species richness on a burned and unburned area, Red Rock Canyon National Conservation Area, Mojave Desert. Error bars are one standard deviation for total mean richness. Total mean richness was compared between the burned and unburned areas using a two-tailed t-test.

burn status × microsite × heat ($F_{2,36} = 11.5, P < 0.001$) are presented in Fig. 6.

DISCUSSION

Study Assumption and Context

An assumption of this study is that differences between burned and unburned areas result primarily from the fire and not from pre-existing vegetation or environmental differences. The adjacent burned and unburned areas demonstrated a priori similarity in mapped soil type (Lato 2006) and dominant vegetation type. Plot sam-

pling corroborated this similarity, with mean elevation differing by only 54 m, soil texture nearly identical differing by only 1–2% in sand, silt, or clay (Table 1), and similar dominant shrub composition. Pre-existing *Larrea tridentata* density was probably higher in the burned area (Fig. 5). Because of this, we did not statistically compare post-fire *L. tridentata* density between burned and unburned areas, as instead we focused on the proportion of burned individuals that resprouted.

Annual precipitation was 134% of average in 2004 preceding the fire and 169% of average in the fire year of 2005. These high-precipitation

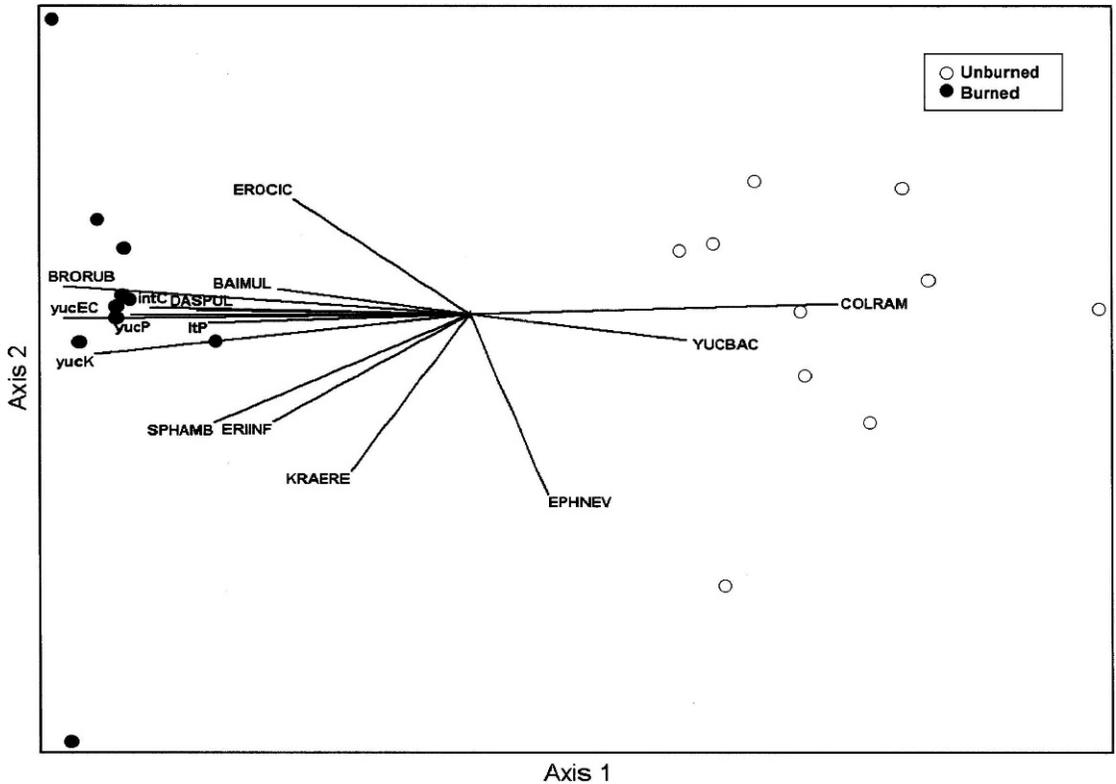


FIG. 3. Non-metric multidimensional scaling ordination of plant species composition on a burned and unburned area, Red Rock Canyon National Conservation Area, Mojave Desert. The lengths of vectors are proportional to correlations with ordination axes, and only vectors with r^2 values ≥ 0.3 are shown. Vectors for species are abbreviated as the first three letters of the genus and species: BAIMUL = *Baileya multiradiata*, BRORUB = *Bromus rubens*, COLRAM = *Coleogyne ramosissima*, DASPUL = *Dasyochloa pulchella*, EPHNEV = *Ephedra nevadensis*, ERIINF = *Eriogonum inflatum*, EROIC = *Erodium cicutarium*, KRAERE = *Krameria erecta*, SPHAMB = *Sphaeralcea ambigua*, and YUCBAC = *Yucca baccata*. Vectors for soils are shown as microsite (int = interspace, It = *Larrea tridentata*, yuc = *Yucca* spp.) and variable (C = total carbon, EC = electrical conductivity, K = potassium, and P = phosphorus).

years resulted in accumulation of annual plant biomass flammable after senescence (Brown and Minnich 1986). Precipitation has been below average since the fire, averaging 65% of average in 2006 and only 14% of the January-May mean in 2007 up to the sampling time for this study (Western Regional Climate Center, Reno, NV). Annual plant production has been negligible since the fire, and our results may be different had different weather patterns occurred after the fire. This observation underscores a need for longer term monitoring, particularly given the high interannual variability characterizing Mojave Desert climates (Beatley 1966).

Bromus rubens

Total mean cover (live + dead) of *Bromus rubens* was sharply lower on the burned than the unburned area (Fig. 1). Furthermore, *B. rubens* density in the soil seed bank of the burn was only 28% of the density on the unburned area (Fig. 6).

Seed density also reversed among microsites, with greater density in interspaces in the burn but greater density below shrubs in the unburned area. Below-shrub microsites, where *B. rubens* is most abundant aboveground in unburned areas, likely burned more intensively due to greater fuel accumulation than in interspaces (Brooks 2002). This intense burning probably killed seeds, an idea supported by results of our experimental 100°C heating that sharply reduced emergence from samples. It is important, however, to determine temperature thresholds for seed mortality of *B. rubens* in comparison with other species. If *B. rubens* has a higher or lower threshold, this could influence its ability to exclude other species after fire. We detected 12 species other than *B. rubens* in seed bank samples, but the low abundance of these species (only 8% of the total seeds detected) precluded making these comparisons.

Our finding that *Bromus rubens* was reduced after fire concurs with Brooks (2002), who found

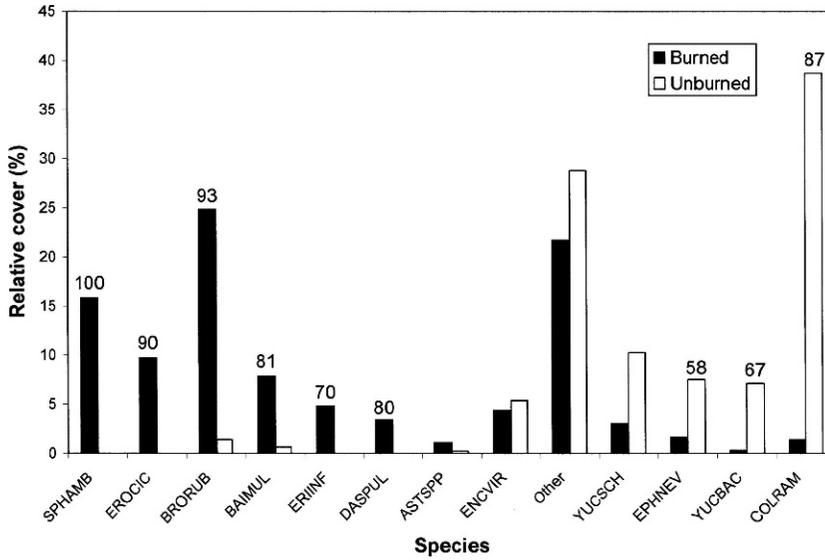


FIG. 4. Mean relative cover and indicator values (top of bars and only given for species that were significant indicators at $P < 0.05$) of the 12 most dominant species on a burned and unburned area, Red Rock Canyon National Conservation Area, Mojave Desert. ASTSPP = *Astragalus* spp., BAIMUL = *Baileya multiradiata*, BRORUB = *Bromus rubens*, COLRAM = *Coleogyne ramosissima*, DASPUL = *Dasyochloa pulchella*, ENCVIR = *Encelia virginensis*, EPHNEV = *Ephedra nevadensis*, ERIINF = *Eriogonum inflatum*, EROIC = *Erodium cicutarium*, SPHAMB = *Sphaeralcea ambigua*, YUCBAC = *Yucca baccata*, and YUCSCH = *Yucca schidigera*.

that *B. rubens* biomass declined after prescribed fires at three Mojave Desert sites. In that study, *B. rubens* was significantly decreased for four years after fire in shrub microsites and for two years in interspaces. Other studies have reported varying patterns of *B. rubens* abundance after fire. For example, no clear trend in cover of this species was apparent in a 1–37 yr time-since-fire chronosequence in the northeastern Mojave Desert (Callison et al. 1985). Similarly, Cave and Patten (1984) found that post-fire *B. rubens* abundance varied between wildfire and prescribed fire in the upper Sonoran Desert. As Brooks and Matchett (2003) note, longer term patterns of post-fire *B. rubens* abundance can hinge upon climate, disturbance (e.g., grazing),

and other factors. It is unclear how much time is needed after wildfire for *B. rubens* to return to pre-fire levels, or which combinations of factors (e.g., native community composition, soil properties) could result in higher or lower post-fire *B. rubens* abundance.

Native Perennial Species Composition

Although resprouts of perennial shrubs currently contribute little to plant cover on the burn, this contribution may increase over time as existing resprouts grow, particularly for *Yucca baccata* and *schidigera*. Our finding that these two *Yucca* species vigorously resprout concurs with Minnich’s (1995) findings in Joshua Tree

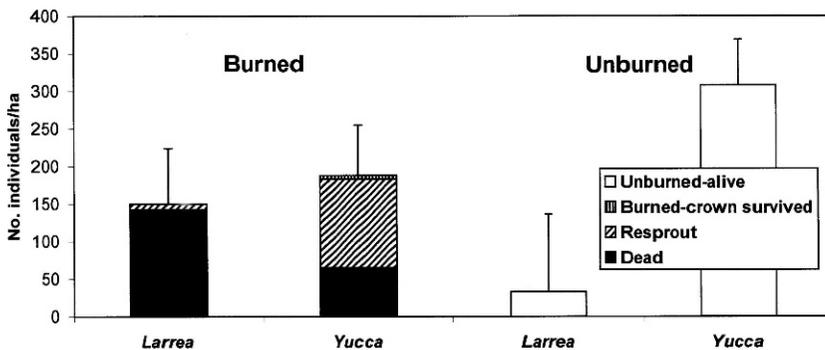


FIG. 5. Density of *Larrea tridentata* and *Yucca* spp. (*schidigera* and *baccata*) on a burned and unburned area, Red Rock Canyon National Conservation Area, Mojave Desert. Error bars are one standard deviation for total mean density.

TABLE 1. SOIL PROPERTIES AMONG MICROsites ON A BURNED AND UNBURNED AREA, RED ROCK CANYON NATIONAL CONSERVATION AREA, MOJAVE DESERT. Means without shared letters differ at $P < 0.05$ (one-way ANOVA, Tukey's Test). Microsite abbreviations: INT = interspace, LT = below *Larrea tridentata* canopy, and YUC = below *Yucca baccata* or *schidigera*) canopy. ¹The means for all burn \times microsite levels are presented, even though some of the variables did not have a statistically significant interaction. We present all of the means because the effect sizes may have biological significance, although we acknowledge that the post-hoc test was made more conservative by the inclusion of the additional means. ²Electrical conductivity. ³Bulk density, calculated as the oven-dry mass of soil (<2 mm) contained in a core of known volume, which included volume of the >2 mm fraction. ⁴Bulk density, calculated the same as above except that volume of the >2 mm fraction was not included.

Variable	Burned			Unburned			Factor effects		
	INT	LT	YUC	INT	LT	YUC	Burn	Microsite	B \times M ¹
	Mean (coefficient of variation %)						Prob. > F		
pH	7.5b (3)	7.5b (2)	7.9a (3)	7.6b (1)	7.6b (1)	7.7b (1)	0.7219	<0.0001	0.0065
EC (dS/m) ²	0.5c (18)	1.5b (53)	2.9a (26)	0.4c (27)	0.7c (17)	0.7c (23)	<0.0001	<0.0001	<0.0001
P (mg/kg)	15c (30)	32bc (21)	94a (21)	16c (37)	21bc (21)	36b (70)	<0.0001	<0.0001	<0.0001
K (mg/kg)	190d (11)	426b (22)	754a (21)	182d (37)	411bc (30)	324c (32)	0.0007	<0.0001	<0.0001
C (% wt.)	4.4bc (13)	5.1ab (14)	5.9a (13)	2.0d (71)	3.4c (49)	3.7c (65)	0.0017	<0.0001	0.3336
N (% wt.)	0.09bc (64)	0.15ab (24)	0.18a (18)	0.06c (21)	0.15ab (35)	0.17a (45)	0.3287	<0.0001	0.5761
Sand (% wt.)	53 (6)	55 (5)	53 (8)	56 (13)	56 (16)	55 (12)	0.3716	0.3591	0.8451
Silt (% wt.)	34 (6)	33 (9)	34 (10)	32 (20)	32 (23)	33 (20)	0.5415	0.4925	0.8319
Clay (% wt.)	13 (18)	13 (10)	14 (12)	13 (21)	12 (18)	12 (12)	0.2334	0.5162	0.6243
BD (g/cm ³) ³	0.70ab (15)	0.58b (13)	0.64b (8)	0.78a (11)	0.62ab (7)	0.67ab (10)	0.0103	0.0028	0.6462
BD (g/cm ³) ⁴	0.83ab (16)	0.66c (11)	0.73bc (8)	0.89a (7)	0.70bc (8)	0.77ab (9)	0.0151	0.0004	0.9314

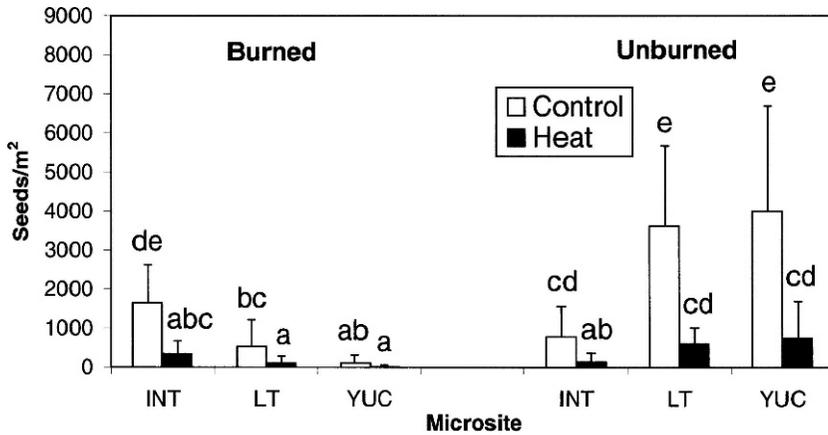


FIG. 6. Emergence density of *Bromus rubens* among treatments performed on 0–5 cm soil seed bank samples from a burned and unburned area, Red Rock Canyon National Conservation Area, Mojave Desert. Error bars are one standard deviation. Means without shared letters differ at $P < 0.05$ and were compared using Tukey's test.

National Park in the southwestern Mojave Desert, where 80–84% of *Yucca schidigera* resprouted after fire. The relatively low (5%) proportion of resprouting for *Larrea tridentata* that we recorded is lower than Minnich (1995: 17%) and two studies in the Sonoran Desert (Rogers and Steele 1980: 23%; McLaughlin and Bowers 1982: 37%). This proportion is similar, however, to Brown and Minnich's (1986) 3% resprout frequency at another site in the Sonoran Desert. Differences in resprouting frequency among studies could be related to differences in fire intensity, site factors (e.g., soils, prevalence of herbivory), or climate (O'Leary and Minnich 1981; Gibson et al. 2004). Our study site also was situated near the upper elevational limit for *L. tridentata*, possibly limiting resprouting compared to other studies.

Relative to the unburned area, fire converted a late-successional shrub community dominated by high cover of *Coleogyne ramosissima* to a community with the perennial cover component dominated by forbs. Dominant native perennials colonizing the burn, such as *Baileya multiradiata*, *Sphaeralcea ambigua*, *Eriogonum inflatum*, and *Dasyochloa pulchella*, have previously been reported as colonizers after fire or other disturbances (e.g., road abandonment, land clearing). For example, *B. multiradiata* exhibited a density 1.7 times greater than the next highest species (among 35 species) one year after fire in the upper Sonoran Desert (Wilson et al. 1995). Similarly, *S. ambigua*, the most abundant perennial on the burn in our study, had the third highest density among all burn colonizers in Wilson et al.'s (1995) study. Brooks and Matchett (2003) found that these two species also had greater cover on burned than unburned areas in the Mojave Desert. Fifty to seventy years after agricultural field abandonment at 20 sites in the eastern

Mojave Desert, Carpenter et al. (1986) found that cover of *S. ambigua* was three times greater on abandoned fields than off field. *Dasyochloa pulchella* and *E. inflatum* also had greater cover on disturbed than undisturbed areas in Mojave Desert studies of succession on a cleared borrow pit (Vasek 1983) and a pipeline corridor (Abella et al. 2007). These observations suggest that the major native perennial colonizers of the burn in our study are early colonizers of several disturbance types.

Colonization Windows and Revegetation Approaches

Brooks (2002) proposed that reduced *Bromus rubens* immediately following fire may offer a colonization window for actively revegetating native species on desert burns. Although the effectiveness of this window may depend on precipitation, we found that several native perennials colonized the burn even during the period of below-average precipitation characterizing our study. Despite this colonization, total live native plant cover remained more than seven times lower on the burned than the unburned area. Although active revegetation (e.g., seeding) can be expensive and prone to failure (Lovich and Bainbridge 1999), managers may wish to attempt revegetation of desert burns for several reasons. Revegetation may improve aesthetics, reduce fugitive dust, increase animal forage, and provide competition with exotic plants (DeFalco et al. 2007). Based on several studies, natural reestablishment of late-successional species such as *Coleogyne ramosissima* or *Larrea tridentata* will require long time periods, often longer than 30 yr and possibly longer than 100 yr (Callison et al. 1985; Lei 1999; Lovich and Bainbridge 1999). A potential concern about reestablishing these late-

successional shrubs is that *B. rubens* is most abundant below their canopies, facilitating fuel accumulation (Brooks 2002). Therefore, reestablishing these shrubs may need to occur in combination with *B. rubens* control treatments. A complementary approach to test, in addition to revegetating with late-successional species, could be augmenting establishment of early colonizing native species (e.g., *Baileya multiradiata* and *Sphaeralcea ambigua*). In a Mojave Desert seeding study, *B. multiradiata* established at a density of 3 plants/m², second most among 12 seeded species (Walker and Powell 1999). If native species could be established in a post-fire colonization window, this early successional vegetation type can persist for more than 30 yr (Carpenter et al. 1986; Abella et al. 2007). Although these species are not thought to form the fertile islands most conducive to *B. rubens* establishment, it is unclear whether this vegetation type can depress *B. rubens* resurgence. In combination with experiments, longer term monitoring of natural post-fire colonization patterns may provide insight into these types of practical questions. However, short-term data on initial colonization patterns such as provided by this study also are crucial, as managers often must plan revegetation activities soon after a fire.

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