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PEAK FIRE TEMPERATURES AND EFFECTS ON ANNUAL PLANTS IN THE MOJAVE DESERT

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Abstract. Very little is known about the behavior and effects of fire in the Mojave Desert, because fire was historically uncommon. However, fire has become more frequent since the 1970s with increased dominance of the invasive annual grasses *Bromus rubens* and *Schismus* spp., and land managers are concerned about its ecological effect. In this paper, I describe patterns of peak fire temperature and their effect on annual plants in creosote bush scrub vegetation of the Mojave Desert. Temperatures were monitored among microhabitats and distances from the soil surface, and between spring and summer. Microhabitats ranged from high amounts of fuel beneath creosote bush (*Larrea tridentata*) canopies, to intermediate amounts at the canopy drip line, to low amounts in the interspaces between them. Distances from the soil surface were within the vertical range where most annual plant seeds occur (−2, 0, 5, and 10 cm). I also compare temperature patterns with postfire changes in soil properties and annual plant biomass and species richness to infer potential mechanisms by which fires affect annual plants.

Peak fire temperatures were most affected by the microhabitat fuel gradient, and the effects of fire on annual plants varied among microhabitats. Beneath creosote bushes, lethal fire temperatures for annual plant seeds occurred above- and belowground, resulting in four postfire years of reduced annual plant biomass and species richness due most likely to seed mortality, especially of *Bromus rubens* and native forbs. At the canopy drip line, lethal fire temperatures occurred only aboveground, reducing annual plant biomass for 1 yr and species richness for 2 yr, and increasing biomass of *Schismus* sp., the alien forb *Erodium cicutarium*, and native annuals after 3 yr. Negligible changes were caused by fire in interspaces or between spring and summer.

Fire effects models for creosote bush scrub vegetation must account for patterns of peak fire temperature along the shrub–intershrub gradient. The responses of annual plants to this gradient vary depending on the species composition of the seedling cohort, their microhabitat affinities, and their respective phenologic stages at the time of burning. Fire can temporarily reduce seed densities of *Bromus rubens*, but dominance of *Schismus* sp. may quickly increase above prefire levels.

Key words: Bromus rubens; Erodium cicutarium; *invasive plants; land management; Mojave Desert, California; nitrogen; postfire succession;* Schismus; *soil nutrients; water repellency.*

INTRODUCTION

Fire characteristics and effects remain mostly unstudied in desert shrublands worldwide, primarily because fires were historically uncommon due to limited fuels created by sparse vegetation. Recent invasions by grasses have increased the amount and continuity of fuels, which has increased the frequency of fire, in a variety of ecosystems including deserts (D'Antonio and Vitousek 1992). In the Mojave Desert of North America, fires have become more frequent since the 1970s partly due to increased dominance by invasive annual grasses (Brooks 1999*a*; Brooks, *in press*), which now comprise most of the total annual plant biomass (Samson 1986, Brooks 1998). An annual mean of 144 (50 to 262) fires affected 11 455 ha (1411 to 30 054) between 1980 and 1995 in the Mojave Desert portions of the Bureau of Land Management California Desert District (BLM-CDD). Although 79% of these fires were ≤4 ha (10 acres) and typically occurred along major roads, 11% were >40 ha (100 acres) and 10 fires were >4000 ha (10 000 acres) and most occurred in remote wilderness areas (Brooks, *in press*; BLM-CDD records). Fire is now considered one of the primary threats to the conservation of native plants and animals and the maintenance of ecosystem integrity in the Mojave Desert (Lovich and Bainbridge 1999; Brooks, *in press*; Esque and Schwalbe, *in press*).

Effective management of fire requires an understanding of the mechanisms by which fires affect ecosystems, because management prescriptions designed to mitigate the negative effects of fire can differ greatly depending on the mechanism involved. Peak fire temperatures can greatly influence the ecological effects of fire (DeBano et al. 1998), and in this paper I report peak temperatures during spring and summer fires and

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evaluate their effects on postfire annual plant community characteristics and soil properties in previously unburned creosote bush scrub habitat (Vasek and Barbour 1988) in the Mojave Desert.

Fire temperatures can vary spatially and seasonally due to variable fuel characteristics and environmental conditions (Wright and Bailey 1982, Whelan 1995, Pyne et al. 1996). Temperatures increase with the amount of vegetation (Smith and Sparling 1966, Stinson and Wright 1969), and woody fuels such as those created by creosote bush (*Larrea tridentata*) burn hotter than fine fuels produced by annual plants (Bentley and Fenner 1958). Temperatures are higher within the flames above the surface of the soil (McKell et al. 1962, Smith and Sparling 1966, Bailey and Anderson 1980), and lower within the soil beneath layers of insulating mineral and organic matter (Heyward 1938, Beadle 1940, Hartford and Frandsen 1982). Temperatures during fires in spring and summer often differ due to seasonal variations in atmospheric temperature, relative humidity, and wind speed (Pyne et al. 1996). Fire temperature profiles have been described for mesic and semi-arid grasslands (Bentley and Fenner 1958, Daubenmire 1968, Stinson and Wright 1969, Bailey and Anderson 1980), shrublands (Bentley and Fenner 1958, Smith and Sparling 1966, Bailey and Anderson 1980, Odion and Davis 2000), and forests (Heyward 1938, Beadle 1940, Bentley and Fenner 1958, Bailey and Anderson 1980), but virtually no data exist for desert shrublands (but see Patten and Cave 1984).

Fires can affect annual plants directly by killing seeds and seedlings (Daubenmire 1968, Wright and Bailey 1982) and indirectly by altering soil nutrient levels (DeBano et al. 1998) and water repellency (Osborn et al. 1967, Adams et al. 1970, DeBano 2000). Most annual plant seeds are located in inflorescences within 10 cm above the soil surface in the Mojave Desert (*personal observation*), or within 2 cm below the soil surface in the adjacent Sonoran Desert (Reichman 1984), so the effects of elevated fire temperatures on annual plant seeds should be greatest within this vertical range. The seasonal timing of fire may cause variable seed mortality, with high mortality during spring when many seeds are suspended aboveground or during summer when potentially higher fire temperatures may penetrate deeper into the soil killing more seeds.

Rainfall patterns before fires can influence the amount and continuity of fine fuels affecting fire behavior (McLaughlin and Bowers 1982, Wright and Bailey 1982, Rogers and Vint 1987, Schmid and Rogers 1988, Brooks 1999*a*), and can determine the species composition of aboveground seedling cohorts that are exposed to the most lethal temperatures during fires (Brooks, *in press*). Rainfall patterns after fires can affect postfire plant communities by influencing the germination and growth of annual plants and by affecting mineralization rates of soil nutrients (Patten 1978, Noy-Meir 1979). Thus, the effects of fires on annual plants are influenced by environmental conditions before, during, and after fires, all of which need to be described to accurately evaluate mechanistic relationships.

The desert scrub habitats that dominate the Mojave Desert are characterized by woody perennial shrubs separated by sparsely vegetated interspaces, and creosote bush is the most common dominant or codominant species occurring at −70 to 1500 m elevation (Rowlands et al. 1982, Vasek and Barbour 1988). Woody and fine fuels are highest beneath creosote bushes, intermediate at the canopy drip line, and lowest in the interspaces between shrubs. Heterogeneous fuel distributions often create variable peak fire temperatures (Davis et al. 1989, Odion and Davis 2000), and spatially and seasonally heterogeneous peak fire temperatures should produce variable effects across the landscape.

I hypothesized that peak temperatures during fires would be (1) higher beneath creosote bushes than interspaces, and intermediate where shrub canopies and interspaces meet at the canopy drip line; (2) higher above than below the soil surface and intermediate at the soil surface; and (3) higher during summer than spring. I also predicted that annual plant biomass and species richness would vary negatively with peak fire temperature. Postfire soil nutrient levels and water repellency were measured to evaluate their relationships with peak fire temperatures and postfire changes in annual plant communities. The combined data were used to infer potential mechanisms of postfire effects, especially in relation to the postfire dominance of invasive annual grasses.

Methods

Study sites

Three 1-ha sites were studied in the central, southern, and western regions of the Mojave Desert in California (Rowlands et al. 1982), so the results of this study could be generalized across a broad area where fire frequency has increased since the 1970s. Sites were chosen randomly with the requirement that one edge be located within 25 m of an unimproved dirt road to facilitate access. The central Mojave site was located south of Water Valley, San Bernardino County (35°57′45″ N, 117°13′45″ W), at 680 m elevation on a southwest facing alluvial bajada with 0–3% slope, where mean annual rainfall was 117 mm and winter rainfall (October through April) was 84 mm. The southern Mojave site was located at the northwest base of the Ord Mountains, San Bernardino County (35°2′20″ N, 117°53′00″ W), at 1070 m on a north facing alluvial bajada with 0–2% slope, where mean annual rainfall was 118 mm and winter rainfall was 84 mm. The western Mojave site was located 11 km south of California City, Kern County (35°14′30″ N, 117°51′15″ W), at 740 m on an east facing alluvial bajada with 0–3% slope, where mean

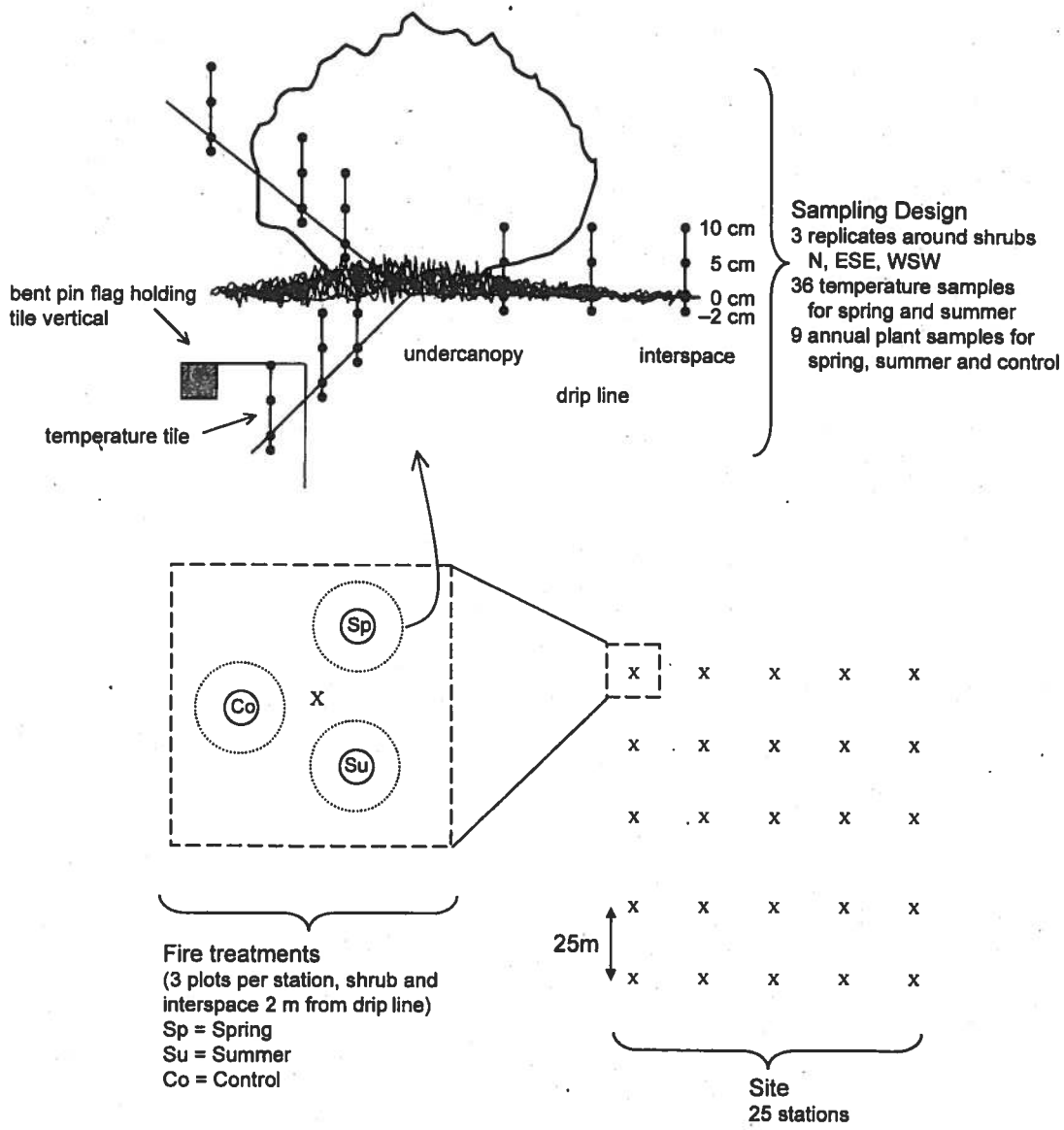

FIG. 1. Diagram of sampling stations, fire treatments, and sampling design at each study site.

annual rainfall was 173 mm and winter rainfall was 149 mm.

Creosote bush scrub vegetation (Vasek and Barbour 1988) dominated each site, with creosote bush comprising 88–94% of the total shrub cover and burrobush (*Ambrosia dumosa*) comprising 3–9%. Absolute shrub cover ranged from 5% to 8%. Cover of individual creosote bushes at the three sites ranged from 12 to 24 m^2 and their mean canopy volume ranged from 10 to 22 m^3. Soil texture ranged from loamy sand beneath creosote bushes to sandy loam in the interspace between them, based on the feel test of moist soil (Brady 1990). There was no evidence of previous fires such as charred shrub stems or charcoal on the soil surface at any of the sites.

Fire treatments

Fire treatment plots were established at 25 stations within each study site (Fig. 1). Spring fire (April or May), summer fire (August or September), and unburned controls were randomly applied to the three creosote bushes (>150 cm diameter) closest to each station during 1996. Each treatment plot included a creosote bush and the interspace within 2 m surrounding it. Fires were ignited using a drip torch to apply flaming diesel–gasoline mix to dried annual plant material just outside of the upwind edge of the treatment plot. A headfire spread throughout the interspace and into each creosote bush. The resulting fire treatments were approximately circular and ranged from 25 to 75 m^2 centered on individual creosote bushes. Each fire

treatment was allowed to extinguish naturally, but the spread of fire away from the treatment plots was controlled using a fine mist of water applied from a backpack pump.

Sampling design

For peak fire temperature, spring and summer fire treatments were sampled at 25 stations within each site (Fig. 1). Peak fire temperatures were also sampled at four heights from the soil surface (−2, 0, 5, 10 cm). For annual plants and soils, the two fire treatments plus the control plots were sampled at five and three randomly chosen stations at each site, respectively. All samples were collected in three microhabitats within each plot: (1) the undercanopy microhabitat beneath each creosote bush midway between the rooting axis and the edge of the canopy; (2) the drip line microhabitat beneath the outside edge of the canopy; and (3) the interspace microhabitat 1 m outside of the drip line (Fig. 1). These microhabitats ranged from high amounts of woody and fine fuels, to no woody fuels plus low amounts of fine fuels. Samples were replicated at 120° intervals to the N, ESE, and WSW of the rooting axis of each creosote bush.

Sampling methods

Factors that affect fire temperature.—The day before fire treatments were applied at each site, fuel characteristics of creosote bushes were documented by measuring the volume, percentage of dead fuel volume, and gravimetric moisture content of each creosote bush that was burned. Volume was determined using the formula for a spheroid ($V = 4/3\pi ab^2$) where a was the mean canopy diameter of the major axis and the axis perpendicular to it, and b was the mean height of four measurements taken in each of four quadrates around the rooting axis. The percentage of dead creosote bush volume was estimated visually using modified Braun-Blanquet intervals (Grieg-Smith 1964): 0–5%, 6–25%, 26–50%, 51–75%, 76–99%, and 100%. Gravimetric moisture content of each creosote bush was estimated from a single combined sample consisting of five subsamples (2 g dry mass each) of live leaves and twigs (≤3 mm diameter) collected from the highest point of the shrub canopy and from the outer edge of the canopy drip line along the four cardinal compass directions. These samples were dried at 60°C to a constant mass to determine the ratio of water to dry plant mass, reported as percent fuel moisture.

The day of each fire treatment, fuel characteristics of annual plants were documented by measuring the aboveground dry biomass, percentage of dead fuel biomass, and gravimetric moisture content of annual plants rooted within 10 × 10 cm sampling frames in each microhabitat. Aboveground live biomass was determined by clipping plants at ground level, drying at 60°C to a constant mass, and weighing. Weather conditions were documented by averaging air temperature, relative humidity, and wind speed before and after fire treatments were applied at each site. Fire behavior was documented by measuring flame residency times as the duration of flaming combustion, and measuring flame lengths by visual estimation using the known heights of creosote bushes and the temperature tiles described below as reference scales.

Peak fire temperatures.—During each fire, I measured peak fire temperatures using temperature-indicating paints (Tempilaq, Tempil, Inc., South Plainfield, New Jersey, USA) applied to 15 × 15 cm unglazed ceramic tiles. Nine different paints calibrated to melt at peak temperatures of 52, 66, 79, 93, 107, 121, 177, 232, and 288°C (±1–4%) represented the expected range of temperatures for desert scrub and fine fuels (Wright and Bailey 1982), and were similar to temperatures recorded during a 0.04-ha experimental fire conducted during August 1994 (M. Brooks, *unpublished data*). The paints were placed in four horizontal rows of nine 5 mm diameter dots across the tiles, producing four rows of nine dots each: the first row 1 cm from the bottom edge of the tile, and the others 2 cm higher, 7 cm higher, and 12 cm higher. The bottom edge of each tile was gently worked into the soil and the tile was held vertically with a wire pin-flag bent over its top edge, such that the four rows were situated −2, 0, 5 and 10 cm from the soil surface (Fig. 1). This technique resulted in minimal disturbance of soils and fuels. Conduction of aboveground heat through the tile to belowground was negligible, based on validity tests in which tiles that were completely buried horizontally 2 cm below the soil surface recorded similar belowground peak temperatures as adjacent tiles placed vertically into the soil.

Annual plant community characteristics.—Annual plant samples were collected in 10 × 10 cm sampling plots located 5–10 cm from the temperature tiles at five randomly chosen stations within each site. Sampling was done at the phenologic stage when most annuals reached peak biomass and began to senesce, during spring before treatments were applied in 1996 and during spring from 1997–2000. Sampling plots were repositioned 10 cm from previous samples during each year. Aboveground live biomass was determined by clipping, drying, then weighing all annual plants rooted within each 10 × 10 cm sampling plot. Species richness was determined by counting all species rooted within each plot.

Annual plant sampling focused mostly on invasive alien species. Two categories of alien grasses (*Bromus* [*Bromus madritensis* ssp. *rubens*, *Bromus tectorum* L., and *Bromus trinii* Desv.] and *Schismus* [*S. arabicus* Ness, *Schismus barbatus* (L.) Thell.]), one alien forb (*Erodium cicutarium* [L.] L'Hér), and one category comprised of native annuals were measured. *Bromus* was visually estimated to consist of 90% *Bromus madritensis* ssp. *rubens*, 5% *Bromus trinii*, and 5% *Bromus tectorum* during the 5 yr sampled. *Schismus* could not

be reliably identified to species. Native annuals were estimated to be 95% forbs and 5% grasses of 119 native species sampled.

Soil properties.—Soil nutrient levels were measured during plant sampling in spring 1997, the first postfire year. Cylindrical soil cores (8 cm diameter × 7 cm depth) were collected ~20 cm from the temperature and annual plant sampling points. The cores were analyzed for total Kjeldahl nitrogen and Olson-extractable phosphorous. Compared to total nitrogen, available nitrogen such as NH_4^+ and NO_3^- allows more precise estimates of soil fertility levels, but levels can fluctuate significantly (DeBano et al. 1979, Vitousek and Mellilo 1979) and typically return to prefire levels within the first postfire year (Wright and Bailey 1982, DeBano et al. 1998). Total nitrogen was measured in the current study to estimate the potential effects of fire beyond the first postfire year.

Postfire soil water repellency was measured in September 1996 after the technique described by Krammes and DeBano (1965). Measurements were made at 0, 1, 2, and 3 cm beneath the surface of the mineral soil at the same stations where soil cores were collected.

Data analyses

Rainfall totals across the entire study region were estimated from data reported from 1948 through 2000 at the Daggett airport, Mojave, and Randsburg weather stations operated by the National Oceanographic and Atmospheric Administration in California.[1] The weather stations ranged from 25 to 35 km from the nearest study site. Long-term mean monthly rainfall was calculated using the entire data set, and recent winter rainfall (October to April) was calculated using data from 1990 to 2000.

The significance and magnitude of the variance components for peak fire temperature, annual plant, and soil data were evaluated using a balanced, linear, mixed-model ANOVA. Site was a random effect, and station, treatment, microhabitat, height, and year were fixed effects. The model only included main effects and first order interactions, because higher order interactions were either nonsignificant or contributed ≤1% to the variance of the full model. Differences between main effect levels were evaluated using Fisher's protected least significant difference test (Day and Quinn 1989).

The general linear model (GLM) procedure of SAS statistical software was used to derive the expected mean squares of each variance component (SAS Institute 1985). Variance components for the random factor (site) were derived using the Scheffé model (Ayers and Thomas 1990) as described by Price and Joyner (1997), and fixed factor variance components were derived using model II and tested over their fixed-by-random interactions using the TEST option (SAS Institute 1985).

[1] URL: ⟨www.ncdc.noaa.gov⟩

For peak fire temperature, main effects (and number of levels) were site (3), station (25), fire treatment (2), microhabitat (3), and height (4). The midpoints of each temperature interval were used in statistical analyses, except for the last interval (≥288) which was recorded as 288°C. For annual plant analyses, main effects were site (3), station (25), treatment (3), microhabitat (3), and year (4). Spring and summer fire treatments were compared to unburned controls during each year, rather than to prefire conditions within the burned plots, because of the naturally high variation in annual plant communities among years. For soil nitrogen and phosphorous, main effects were site (3), station (3), treatment (3), and microhabitat (3). For water repellency, main effects were site (3), station (3), treatment (3), microhabitat (3), and depth (4).

Descriptive data were reported graphically as means and standard errors calculated from the mean values from each site ($n = 3$). Fuel characteristics of creosote bushes and weather conditions were compared between spring and summer using paired t tests (df = 2). Annual plant fuel characteristics and fire behavior variables were compared between seasons and among microhabitats using analysis of variance (ANOVA), and post hoc Bonferonni t tests (Sokal and Rohlf 1996). Site-by-microhabitat interactions were used as the error term to calculate F values for seasonal fire treatment (df = 1, 2), and model residuals were used as the error term for the microhabitat variable (df = 2, 12). Significance was defined throughout this paper as $P \leq 0.05$.

RESULTS

Rainfall patterns

The experimental fire treatments were applied after 6 yr of relatively high winter rainfall (Fig. 2). Accordingly, fine fuel loads during the fires were on the high end of the interannual range due to invasive annual grass fuels that accumulated during consecutive years. In contrast, winter rainfall during three of the four postfire years was below average, which may have slowed postfire recovery of annual plants.

Conditions during the fires

Creosote bush volume and the amount of annual plant biomass did not differ significantly during spring and summer, but annual plant biomass did vary among microhabitats ($P = 0.0040$) where it was significantly higher in the undercanopy and drip line (108 and 45 g dry mass/m²) compared to the interspace (17 g dry mass/m²). Percent dead fuel volume did not differ between seasons for creosote bushes, but was much higher in summer (99%) than spring (29%) for annual plants ($P = 0.0020$). Moisture content was higher in spring than summer for both creosote bushes (27% vs. 16%, $P = 0.0180$) and annual plants (8% vs. 2%, $P = 0.0015$).

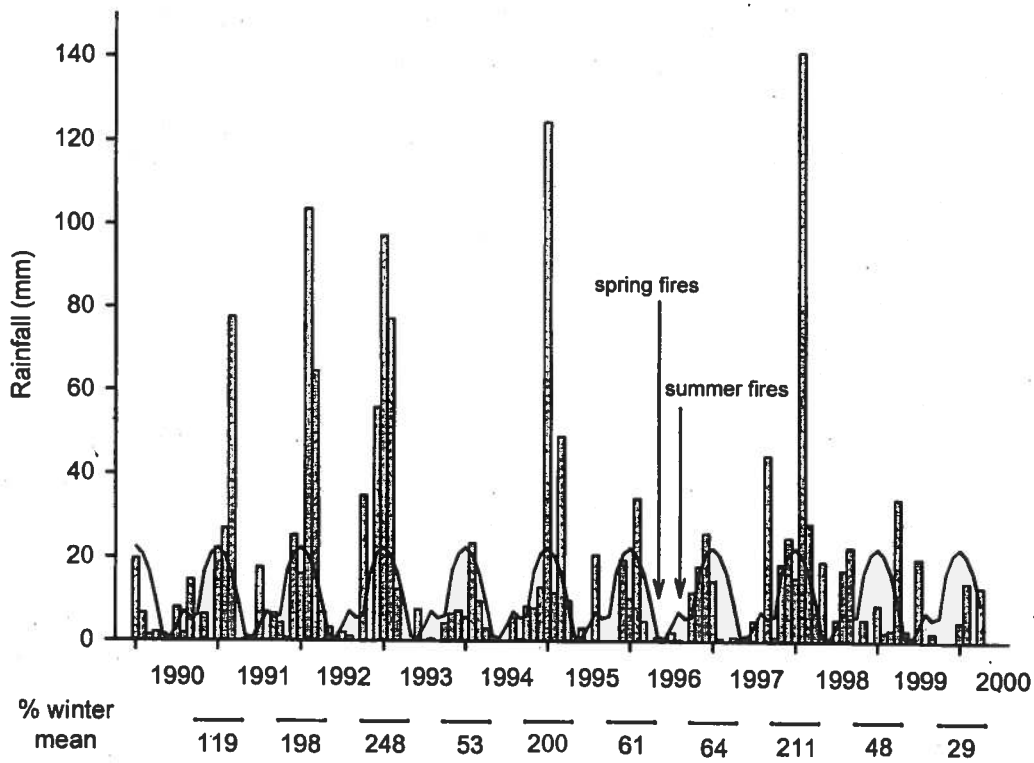

FIG. 2. Monthly rainfall from January 1990 through April 2000 averaged over three weather stations in the central, southern, and western Mojave Desert. The line plot represents the long-term monthly mean from 1948 to 1999. Percentage of mean winter rainfall (October–April) in each year is also shown.

Mean air temperature (32°C), humidity (21%), and wind speed (6 km/h) did not differ significantly between spring and summer fire treatments. Mean residency times were higher within the annual plant layer in the undercanopy (19 s) than the drip line (6 s) and interspace microhabitats (4 s; $P = 0.0002$), and were much higher in the woody fuels within creosote bush canopies (462 s) than the fine fuels in any of the microhabitats ($P < 0.0001$). Flame lengths were also higher in annual plant fuels in the undercanopy (25 cm) than the drip line (15 cm) and interspace (10 cm) microhabitats ($P < 0.0121$), and were much higher within creosote bush canopies (260 cm; $P < 0.0001$). Mean flame residency times and lengths did not differ significantly between spring and summer fire treatments.

Peak fire temperatures

Peak fire temperatures were higher beneath creosote bushes than interspaces and above than below the soil surface. The microhabitat temperature gradient was the most dramatic, due to large differences in the amounts of woody and fine fuels among microhabitats. Peak fire temperature increased dramatically from the interspace to the drip line to the undercanopy microhabitats (Fig. 3), accounting for 77% of the total model variance (Table 1).

Differences in peak fire temperature among distances from the soil surface were greatest in the undercanopy, intermediate in the drip line, and negligible in the interspace microhabitats (Fig. 4). This variation reflected much higher flame residency times and aboveground peak fire temperatures, and greater heat penetration into

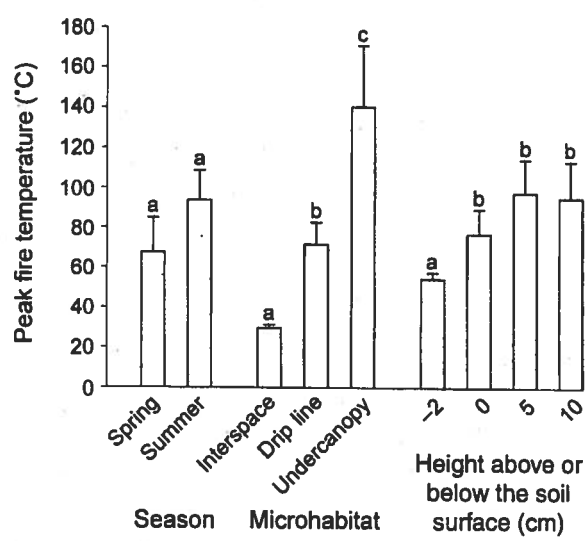

FIG. 3. Peak fire temperatures among seasons, microhabitats, and heights from the soil surface. Different lowercase letters indicate significant differences between levels within each of the three factors (Fisher's least significant test, $n = 3$, $P \leq 0.05$).

TABLE 1. ANOVA results for peak fire temperature.

Source	Variance	%†	Num. df‡	Denom. df§	F	P
Site	60.55	3	2	6	1.18	0.3664
Station	1.44	<1	24	48	0.69	0.8323
Treatment	177.50	10	1	2	7.55	0.1108
Microhabitat	1397.97	77	2	4	58.81	0.0011
Height	64.20	4	3	6	24.98	0.0009
Site × station	2.07	<1	48	5152	8.02	0.0001
Site × treatment	23.50	1	2	5152	90.79	0.0001
Site × microhabitat	23.77	1	4	5152	91.83	0.0001
Site × height	2.51	<1	6	5152	9.93	0.0001
Station × treatment	1.52	<1	24	5152	5.89	0.0001
Station × microhabitat	1.32	<1	48	5152	5.11	0.0001
Station × height	0.54	<1	72	5152	2.10	0.0001
Treatment × microhabitat	37.16	2	2	5152	143.57	0.0001
Treatment × height	4.33	<1	3	5152	16.74	0.0001
Microhabitat × height	8.41	<1	6	5152	32.50	0.0001
Error	0.26					

† Variance expressed as a percentage of the total variance described by all main and first-order interaction effects in the partial ANOVA model.
‡ Numerator degrees of freedom.
§ Approximate denominator degrees of freedom using the Satterthwaite method.

the soil, in the undercanopy than the drip line microhabitat. As a result, soil seed banks at −2 and 0 cm from the soil surface were exposed to mean peak fire temperatures of 87 and 135°C respectively in the undercanopy, and 49 and 66°C in the drip line microhabitats.

Patterns of peak fire temperatures among microhabitats varied at regional and local scales, as indicated by significant interactions of microhabitat with site and station (Table 1). However, the relatively small magnitude of these interactions compared to the very strong microhabitat effect indicated that patterns of peak temperatures in the microhabitats around creosote bushes were much stronger than variation in these patterns among sites or within sites.

Fire temperature did not differ significantly between spring and summer, although the treatment variable accounted for 10% of the total model variance (Table 1). The lack of a significant treatment effect may have been due to similar environmental conditions during spring and summer, or due to the low statistical power (df = 1, 2) or the relatively large error variance (site × treatment) of the F test. The large error variance was caused by 400% higher peak fire temperatures during summer than spring at one site, but much smaller differences at the other two sites (M. Brooks, *unpublished data*). This difference occurred because the woody fuels in creosote bushes did not burn during spring whereas they did burn during summer at the one site, in contrast to the other two sites where woody fuels burned during both seasons.

Annual plants

Biomass.—Treatment was second only to year in the magnitude of its effect on annual plant biomass (Table 2). Year accounted for almost half of the model variance due to the strong positive relationship between winter rainfall and annual plant biomass (Figs. 2 and 5). Treatments varied significantly among microhabitats (Table 2), and effects were much stronger in the undercanopy than the drip line microhabitat and were

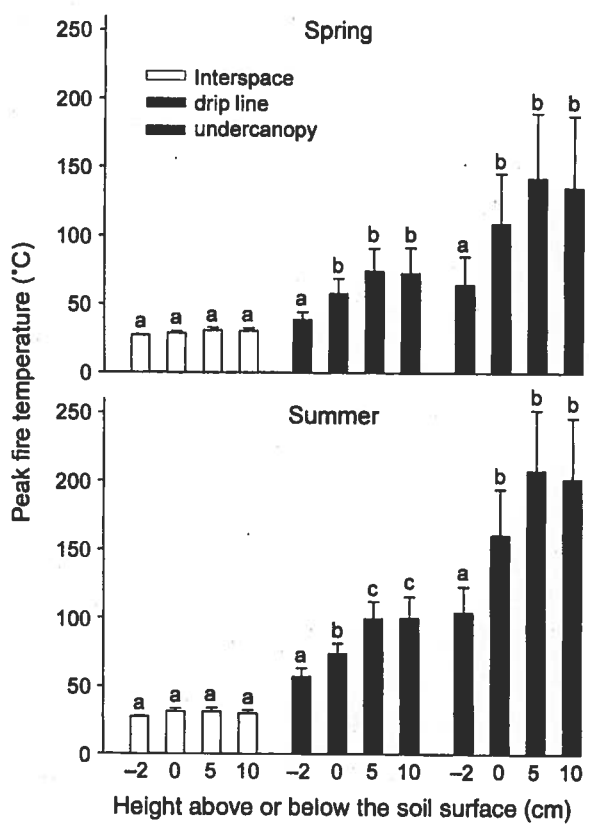

FIG. 4. Peak fire temperatures for three microhabitats and four heights from the soil surface in two seasons. Significant differences are indicated by different lowercase letters, as described in Fig. 3.

TABLE 2. ANOVA results for annual plant biomass.

Source	Variance	%†	Num. df‡	Denom. df§	F	P
Site	1.39	<1	2	6	1.18	0.3664
Station	0.02	<1	4	8	0.04	0.9956
Treatment	93.21	19	2	4	65.57	0.0009
Microhabitat	34.08	7	2	4	65.00	0.0009
Year	219.57	44	3	6	343.46	0.0001
Site × station	0.52	<1	8	1540	0.85	0.5551
Site × treatment	1.42	<1	4	1540	2.32	0.0554
Site × microhabitat	3.10	<1	4	1540	5.16	0.0005
Site × year	0.64	<1	6	1540	1.04	0.3965
Station × treatment	0.94	<1	8	1540	1.53	0.1404
Station × microhabitat	1.26	<1	8	1540	2.06	0.0370
Station × year	0.20	<1	12	1540	0.32	0.9862
Treatment × microhabitat	89.51	18	4	1540	145.80	0.0001
Treatment × year	33.16	7	6	1540	54.01	0.0001
Microhabitat × year	17.71	4	6	1540	28.85	0.0001
Error	0.61					

† Variance expressed as a percentage of the total variance described by all main and first-order interaction effects in the partial ANOVA model.
‡ Numerator degrees of freedom.
§ Approximate denominator degrees of freedom using the Satterthwaite method.

negligible in interspaces (Fig. 5). Interactions between site and station with the other main effects were either not significant or accounted for <1% of the total variance, indicating that patterns of postfire annual plant biomass due to year, treatment, and microhabitat were relatively consistent at regional and local scales.

Responses to fire treatments varied among types of annual plants, which either increased or decreased in biomass depending on microhabitat and postfire year. Spring and summer fires had similar effects on annual plant biomass (Fig. 5), so their combined mean effects were compared with control plots for individual categories of annual plants. In the undercanopy microhabitat, annual plant biomass decreased during all four postfire years (Fig. 5), due to consistent decreases in *Bromus* and native annuals (Fig. 6). In the drip line microhabitat, biomass decreased the first year and increased during the third and fourth postfire years (Fig. 5), due to similar trends in the biomasses of *Schismus*, *Erodium cicutarium*, and native annuals (Fig. 6). Thus,

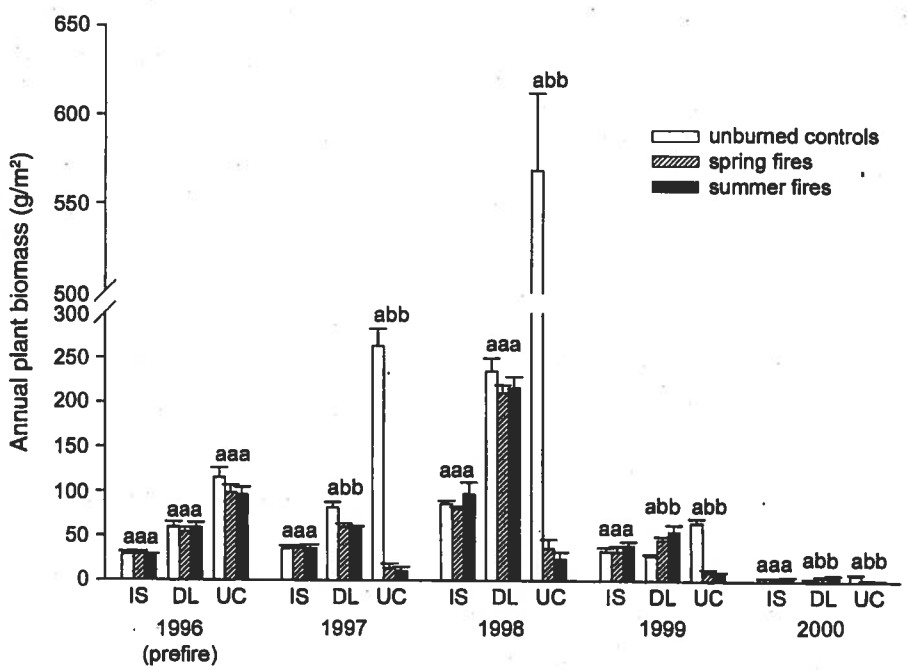

FIG. 5. Biomass of annual plants for three fire treatments and three microhabitats in 1996 (prefire) and 1997–2000 (postfire). Abbreviations are: IS, interspace; DL, drip line; UC, undercanopy. Significant differences are indicated by different lowercase letters, as described in Fig. 3.

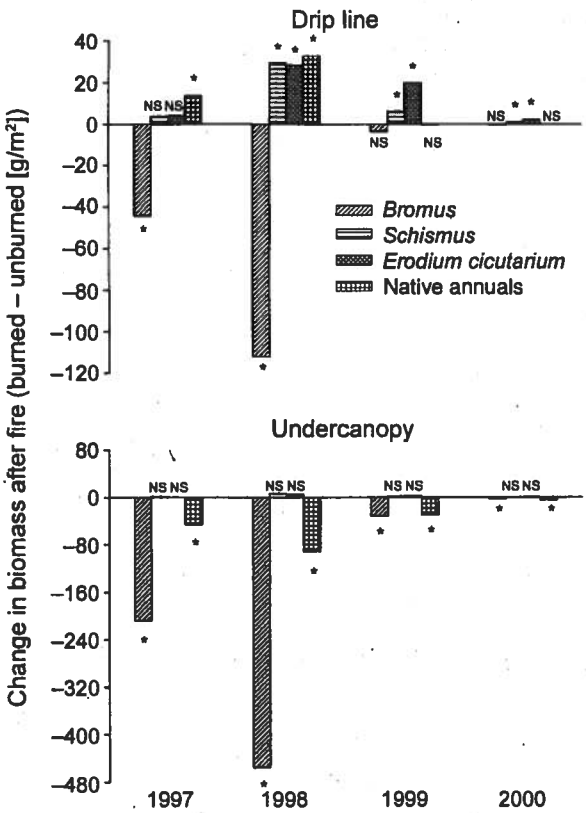

FIG. 6. Change in biomass between burned and unburned plots of four groups of annual plants after fire treatments during four postfire years in the drip line and undercanopy microhabitats.
* $P \leq 0.05$; NS, not significant.

fires caused a decrease in the biomass of *Bromus*, an increase in the biomasses of *Schismus* and *Erodium cicutarium*, and had variable effects on native annual plants depending on microhabitat.

Annual plants in burned plots were often much larger than those in unburned plots, and a random subset of individuals were dried and weighed to estimate the magnitude of this difference. Biomass per individual was 5–20× larger in burned than unburned drip line plots, and 40–100× larger in burned than unburned undercanopy plots during the four postfire years. No difference was observed in the interspace plots. These patterns indicate that increased biomass per individual was highest where decreased total annual plant biomass was highest in the undercanopy microhabitat, suggesting that declines in biomass were not nearly as dramatic as declines in density in response to fire. The most likely explanation for these observations is that high temperatures around creosote bushes killed annual plant seeds, and that the magnitude of this effect was greater in the undercanopy than the drip line microhabitat.

Species richness.—Annual plant species richness was strongly affected by fire treatment, microhabitat, and year (Table 3). Treatment effects varied among microhabitats, and persisted for all four postfire years in the undercanopy, two postfire years in the drip line, and did not have any affect in the interspace microhabitat (Fig. 7). Interactions of site and station with the other main effects were either not significant or accounted for ≤1% of the total variance (Table 3), indicating that patterns of annual plant species richness were similar at regional and local scales.

Spring and summer fire treatments had similar effects on species richness (Fig. 7), so their mean effects were compared with control plots to evaluate the separate

TABLE 3. ANOVA results for annual plant species richness.

Source	Variance	%†	Num. df‡	Denom. df§	*F*	*P*
Site	0.29	<1	2	6	0.18	0.8317
Station	6.47	1	4	8	6.14	0.0147
Treatment	172.96	20	2	4	140.66	0.0002
Microhabitat	401.37	47	2	4	380.86	0.0001
Year	152.11	18	3	6	162.79	0.0001
Site × station	1.05	<1	8	1540	0.67	0.7177
Site × treatment	1.23	<1	4	1540	0.78	0.5364
Site × microhabitat	6.53	1	4	1540	4.16	0.0024
Site × year	0.93	<1	6	1540	0.59	0.7348
Station × treatment	5.81	1	8	1540	3.70	0.0003
Station × microhabitat	12.70	1	8	1540	8.06	0.0001
Station × year	0.54	<1	12	1540	0.34	0.9811
Treatment × microhabitat	52.00	6	4	1540	33.10	0.0001
Treatment × year	20.00	2	6	1540	12.73	0.0001
Microhabitat × year	27.64	3	6	1540	17.59	0.0001
Error	1.57					

† Variance expressed as a percentage of the total variance described by all main and first-order interaction effects in the partial ANOVA model.
‡ Numerator degrees of freedom.
§ Approximate denominator degrees of freedom using the Satterthwaite method.

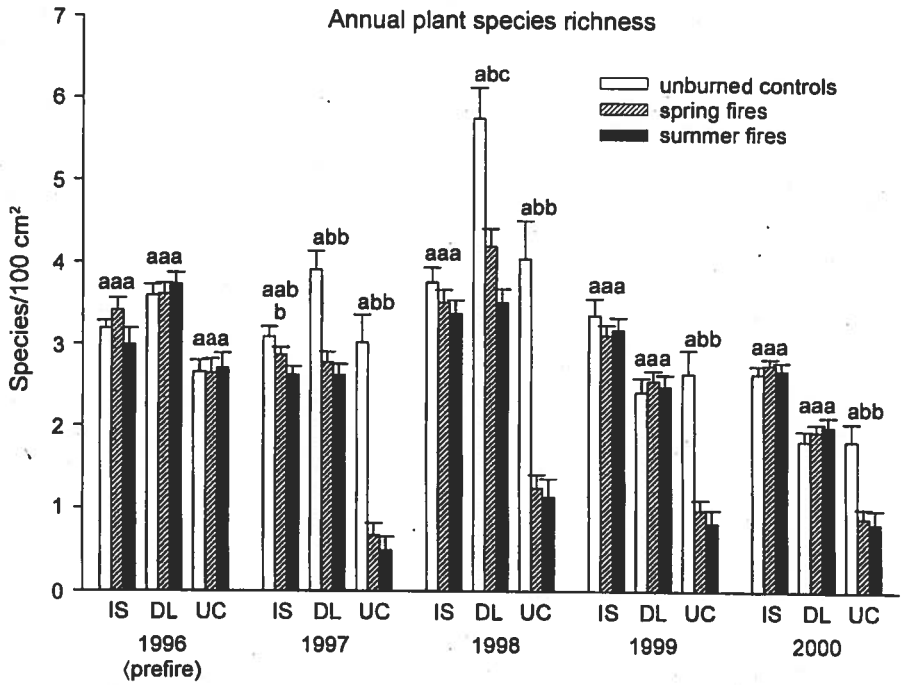

FIG. 7. Species richness of annual plants for three fire treatments and three microhabitats in 1996 (prefire) and 1997–2000 (postfire). Abbreviations are: IS, interspace; DL, drip line; and UC, undercanopy. Significant differences are indicated by different lowercase letters, as described in Fig. 3.

responses of aliens and natives. Fire treatments decreased both alien and native species richness during all four postfire years in the undercanopy microhabitat (Fig. 8). In the drip line microhabitat, alien and native richness decreased during the first 2 yr, but native richness increased beginning the third year.

Soil properties

Soil nitrogen was significantly affected by fire ($F_{2,4}$ = 13.05, P = 0.0372), and the effects of spring and summer fires were similar. The effect of fire was only significant in the drip line microhabitat where soil nitrogen increased from 0.09% in unburned controls to 0.14% in burned plots. Soil phosphorous and water repellency were not significantly affected by fire treatments.

DISCUSSION

When the experimental fires were conducted during 1996 there were 150 wildfires in the Bureau of Land Management California Desert District, compared to the annual mean of 144 from 1980–1995, and fine fuel loads produced by annual plants were similar to those described in creosote bush scrub habitat during other years preceded by high rainfall in the Mojave Desert (Samson 1986, Brooks 1995, 1998, 1999*b*). In addition, fire treatments closely approximated the typical behavior of fires in creosote bush scrub, spreading with low intensity through interspaces and flaring up as it reached creosote bushes (Brooks 1999*a*). Hence, conditions across the Mojave Desert were generally conducive to burning and fire behavior was typical for creosote bush scrub vegetation, so the results should apply well to years in which most fires occur in this region. A major exception was interspace fuel, which was low compared to unburned areas adjacent to where fires have previously occurred (M. Brooks, *unpublished data*). Typical interspace fire temperatures in the Mojave Desert may therefore be higher than those reported in the current study.

Peak fire temperatures

Only one other study has documented peak fire temperatures in desert shrublands of North America (Cave 1982, Patten and Cave 1984). This study was conducted during summer at a Sonoran Desert site dominated by bursage (*Ambrosia deltoidea*), paloverde (*Cercidium microphyllum*), and saguaro cactus (*Carnegiea gigantea*). Peak fire temperatures at −2 cm from the soil surface were 61°C in interspaces, 60°C beneath bursage, and 57°C beneath paloverde trees in the Sonoran Desert study, compared to 28°C in interspaces, 49°C in the drip line, and 87°C beneath creosote bush canopies in the current Mojave Desert study. Interspace fire temperatures were higher in the Sonoran than the Mojave study because fine fuel loads were higher (70 compared to 20 g dry mass/m²). In contrast, undercanopy fire temperatures were higher in the Mojave study because of the greater woody biomass of creosote bush compared to bursage, and the fact that fires only burned

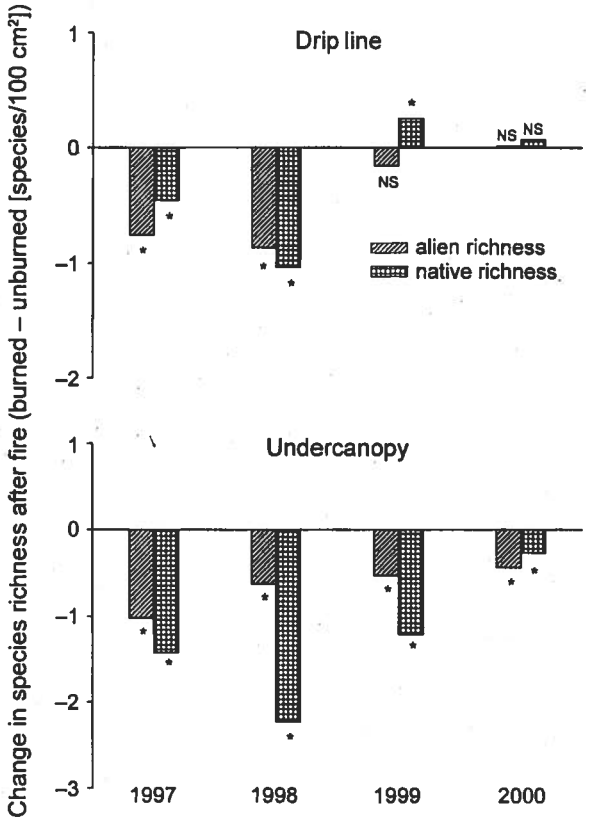

FIG. 8. Change in species richness between burned and unburned plots for alien and native annual plants after fire treatments during four postfire years in the drip line and undercanopy microhabitats.
* $P \leq 0.05$; NS, not significant.

the litter beneath paloverde trees and rarely consumed their woody biomass (Cave 1982). These results demonstrate the variation in peak fire temperatures that can occur among desert sites with differing fine fuel loads and dominant woody species.

Peak fire temperatures varied horizontally and vertically within fires, and this variation may explain postfire patterns of annual plant biomass which were most likely caused by differential seed mortality. Fire temperatures >100°C kill most plant seeds, and fire adapted perennial seeds with thick or hard seed coats cannot tolerate temperatures >150°C (Daubenmire 1968, Wright and Bailey 1982). Although lethal temperatures for desert plant seeds are unknown, they should be no higher than the range listed above. These potentially lethal temperature thresholds were often reached above- and belowground in the undercanopy microhabitat, aboveground in the drip line microhabitat, and were never reached in the interspace microhabitat. These data suggest that both the standing crop of seeds and the soil seedbank were exposed to potentially lethal fire temperatures in the undercanopy microhabitat, whereas only the standing crop was exposed in the drip line.

Annual plants

Biomass of annual plants did not consistently decrease with increasing fire temperature as predicted, but rather increased or decreased depending on microhabitat. This variation was related to patterns of potentially lethal fire temperatures, and the differential exposure of annual plant species to these temperatures based on the distance of seeds from the soil surface and their microhabitat distributions.

The ability of annual plant seeds to survive fire is related to their vertical distance from the soil surface at the time of burning. Seeds contained in the inflorescences of annual plants are typically suspended 5–10 cm above the surface of the soil in the Mojave Desert (*personal observation*), and at these heights seeds are exposed to potentially lethal temperatures during fires (Bentley and Fenner 1958). The chances of seeds surviving a fire are greatly enhanced once they have dispersed to ground level (Daubenmire 1968) or beneath the surface of the soil, which usually occurs between late May and early summer in the Mojave Desert (*personal observation*).

Prefire microhabitat distributions of annual plants can also influence the exposure of local populations to lethal fire temperatures. Prefire surveys indicated that *Bromus* biomass was three times higher, *Schismus* biomass was seven times lower, and *Erodium cicutarium* was five times lower in the undercanopy compared to the drip line microhabitat (M. Brooks, *unpublished data*). Native annual plant biomass was similar in these two microhabitats. Assuming the species composition of seedlings reflected the underlying composition of the soil seedbank, then *Bromus* seeds were at greater risk of mortality whereas *Schismus* and *Erodium cicutarium* seeds were at lower risk of mortality, due to the higher exposure to lethal temperatures in the undercanopy than the drip line microhabitat. This difference may partly explain the lack of recovery of *Bromus* during the first four postfire years, compared to the quick recovery of *Schismus* and *Erodium cicutarium* by the second postfire year.

Responses of annual plant biomass to fire were similar to the results of another study from the Sonoran Desert, where biomass of *Bromus rubens* decreased, biomass of *Schismus* and of two native species (*Plantago* spp. and *Calandrinia cilata*) increased, and biomass of *Erodium cicutarium* remained unchanged in undercanopy and interspace microhabitats one year after burning (Cave 1982, Cave and Patten 1984). In the current study, similar decreases in *Bromus rubens* biomass and increases in *Schismus*, *Erodium cicutarium*, and native annual biomass were observed in the drip line and undercanopy microhabitats. The major difference was the lack of a fire effect on annual plants in the interspace microhabitat in the current study, possibly due to the much lower amounts of interspace fine

fuels and lower fire temperatures at the Mojave than the Sonoran sites.

Invasive annual grasses

Spring fires are thought to be more effective than summer fires at controlling invasive annual grasses if applied when seeds have high moisture content and are suspended aboveground within inflorescences (Rasmussen 1994). For example, a fire during spring in the Great Basin desert resulted in 400–1000% lower *Bromus* densities the following year (Pechanec and Hull 1945). However, the seasonal timing of fire had little effect on alien grass biomass in the current study, and actually increased the biomass of *Schismus* in the drip line microhabitat during the first four postfire years. One explanation is that low rainfall during the winter prior to the experimental fires prevented many *Schismus* seeds from germinating, leaving most of them buried in the soil and protected from lethal fire temperatures. Another possibility is that the seeds from *Schismus* plants had dispersed to the soil surface before the fire treatments were applied. Detailed studies of seedbank dynamics are needed to determine the fate of invasive annual grass seeds during desert fires.

Rates of postfire recovery by *Bromus* can be highly variable. For example, during the first few postfire years density and biomass of either *Bromus rubens* or *Bromus tectorum* decreased in burned compared to unburned sites in the Mojave (Baldwin 1979), Sonoran (Cave 1982, Cave and Patten 1984), and Great Basin deserts (Hassan and West 1986, Rasmussen 1994), but they also increased at burned sites in the Sonoran (Loftin 1987) and Great Basin deserts (West and Hassan 1985). Regardless of what happens during the first few years, *Bromus rubens* and *Bromus tectorum* eventually return to or exceed prefire dominance during subsequent years in the Mojave (Beatley 1966, Hunter 1991; Brooks, *in press*), Sonoran (Tratz 1978, Brown 1984), and Great Basin deserts (Callison et al. 1985, Rasmussen 1994). However, years of drought can delay reestablishment of *Bromus* by causing local population declines, especially at low elevations where particularly hot and dry conditions often kill seedlings before they reproduce (*personal observation*). Recolonization by *Bromus* may also take longer where interspace densities are low and seeds must disperse from adjacent unburned shrubs.

Species richness

The results of this study indicate that high fire temperatures can temporarily reduce small scale plant species richness in desert shrublands, but they contrast with studies from semi-arid chaparral shrublands. Desert fires can kill a high proportion of the seedbank which is concentrated beneath shrubs (Young and Evans 1978, Hassan and West 1986, Price and Joyner 1997), and may ameliorate undercanopy and drip line microhabitats that are favored by many native annual plants (Shreve 1931, Went 1942, Muller 1953, Halvorson and Patten 1975, Nelson and Chew 1977, Shmida and Whittaker 1981), thereby decreasing species richness. In contrast, chaparral fires kill relatively few seeds since relatively few are present beneath shrubs (Davis et al. 1989), and expose undercanopy soil creating a regeneration niche for opportunistic species and obligate seeders (Keeley and Zedler 1978, Zammit and Zedler 1994, Odion and Davis 2000), thereby enhancing species richness. At the small scale represented by the shrub–intershrub gradient, fire can therefore decrease plant diversity in desert shrubland and increase plant diversity in chaparral shrubland.

The effects of fire on annual plant diversity can also differ at landscape scales between desert and chaparral shrublands. In deserts, postfire landscapes are dominated by invasive annual plants and have low species diversity (Brooks 1998). In chaparral, postfire landscapes can also be dominated by invasive annuals, but they also contain pyrogenic endemic plants, which only grow after fire and help increase the species diversity of burned sites (Hanes 1977). Desert landscape mosaics of burned and unburned sites should therefore have lower species diversity than completely unburned landscapes, whereas chaparral landscape mosaics should have higher species diversity than completely unburned landscapes. Even if desert shrubs recover, the native annual species that typically grow beneath them may not readily recolonize because desert annuals have relatively slow rates of dispersal (Ellner and Shmida 1981, Venable and Pake 1999). Over time, bioturbation may bring deeply buried seeds to the surface and overland flow of water may disperse seeds en masse (Mott and McComb 1974), but abundant aliens with superior dispersal and reproductive abilities such as *Bromus rubens* are likely to establish sooner and possibly preempt later colonization of native annuals through competitive exclusion (Brooks 2000*a*).

Soil properties

Soil nitrogen only increased in the drip line microhabitat, possibly because temperatures at or below the soil surface were below the 200°C threshold where nitrogen volatilizes (White and Klemmedson 1973), although aboveground temperatures approached this critical level in the undercanopy microhabitat. Aboveground nitrogen in plant tissues may have been added to the ashbed at a greater rate in the drip line than the undercanopy microhabitat, because less of this nitrogen was volatilized there. These results do not preclude the possibility that transient forms of nitrogen such as ammonium or nitrate changed after fire, but they do indicate that fires can change the total pool of nitrogen beneath creosote bush drip lines.

Increased soil nitrogen was associated with increased annual plant richness and biomass beginning the second and third postfire years in burned than unburned drip line plots. This 1-yr lag period may represent the

time required for a partially depleted seedbank in the drip line microhabitat to recover. Further studies of seedbank dynamics are needed to resolve the relationships between seed mortality, soil nitrogen increases, and postfire annual plant community characteristics.

Soil water repellency was not significantly affected by fire treatments in the current study. Negligible effects of fire on soil water repellency were also reported from fires in the Sonoran Desert (Cave 1980, Patten and Cave 1984) and Great Basin (Salih et al. 1973), but a slight downward shift in the water repellent zone was observed beneath creosote bushes in the Mojave Desert (Adams et al. 1970). The resinous leaves of creosote bush are a potential source of hydrophobic material and the surface litter beneath them can be strongly hydrophobic (*personal observation*). However, translocation of hydrophobic compounds downward in the soil profile typically occurs at soil temperatures above 175°C (DeBano and Krammes 1966, DeBano 1981, 2000), and these temperatures were rarely achieved beneath the soil surface in the current study. Although the formation of subsurface water repellent soils after fires have been attributed to decreased densities of annual plants in the Mojave Desert (Adams et al. 1970), other covarying factors such as seed mortality and soil nutrient changes may more accurately explain these changes.

Management Implications

Spatial variation in peak fire temperature caused by heterogenous fuels is a critical factor that should be considered when evaluating the effects of desert fires on annual plants. Characteristics of the plant community should also be considered such as the species composition of the seedling cohort, their microhabitat affinities, and their respective phenologic stages at the time of burning. More information is needed regarding the ecology of desert annual plants, especially lethal temperature thresholds, before detailed fire effects models can be developed. In addition, peak fire temperatures and fire effects need to be described for other desert plant communities where fires periodically occur in the Mojave Desert, such as blackbrush scrub, sagebrush scrub, pinyon–juniper woodlands, and desert perennial grasslands.

Effects of fire on *Bromus rubens* and *Schismus* are of particular concern for land managers in the Mojave Desert because these species provide most of the fuels that allow desert fires to spread (Brown and Minnich 1986, Brooks 1999*a*) and they can outcompete native annual plants for limiting resources (Brooks 2000*a*). The affinity of *Bromus rubens* for undercanopy microhabitats in arid and semi-arid shrublands (Brooks 2000*b*) make this species especially susceptible to mortality from high temperatures during fires. *Schismus* is typically found in interspaces and drip line microhabitats (Brooks 2000*c*) where relatively low fire temperatures are much less of a threat to seed survival. Compared to *Schismus*, the seeds of *Bromus rubens* mature later during the spring and remain longer within the inflorescences exposing them to especially lethal aboveground temperatures during summer (Brooks 2000*a, b*). Hence, the threat of seed mortality during fires in desert shrublands is generally higher for *Bromus rubens* than for *Schismus*.

Fire may reduce dominance of *Bromus rubens* during the first few postfire years, especially if interspace densities are low and fire spread is homogenous leaving few unburned shrub islands. These few years of low alien densities may be enough for native plants introduced as seeds to become established. However, the use of fire to control alien annual grasses in the Mojave Desert needs to be evaluated further, and is currently justifiable only in highly disturbed areas where native plants have already been negatively affected by aliens and the fires that they cause.

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