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Effects of high fire frequency in creosote bush scrub vegetation of the Mojave Desert

Matthew L. Brooks

US Geological Survey, Western Ecological Research Center, Yosemite Field Station, 5083 Foresta Road. El Portal, CA 95318-0700, USA. Email: matt_brooks@usgs.gov

Abstract. Plant invasions can increase fire frequency in desert ecosystems where fires were historically infrequent. Although there are many resource management concerns associated with high frequency fire in deserts, fundamental effects on plant community characteristics remain largely unstudied. Here I describe the effects of fire frequency on creosote bush scrub vegetation in the Mojave Desert, USA. Biomass of the invasive annual grass *Bromus rubens* L. increased following fire, but did not increase further with additional fires. In contrast, density, cover and species richness of native perennial plants each decreased following fire and continued to decrease with subsequent fires, although not as dramatically as after the initial fire. Responses were similar 5 and 14 years post-fire, except that cover of *Hymenoclea salsola* Torr. & A. Gray and *Achnatherum speciosa* Trin. & Rupr. both increased in areas burnt once. These results suggest that control of *B. rubens* may be equally warranted after one, two or three fires, but revegetation of native perennial plants is most warranted following multiple fires. These results are valid within the scope of this study, which is defined as relatively short term vegetation responses (≤14 years) to short fire return intervals (6.3 and 7.3 years for the two and three fire frequency levels) within creosote bush scrub of the Mojave Desert.

Additional keywords: annual grass, *Bromus rubens*, disturbance, ecosystem transformer, fire effects, grass–fire cycle, red brome.

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Introduction

Arid conditions in desert ecosystems associated with low productivity, sparse fuels and very infrequent fire have resulted in native plant and animal species with generally low resilience to fire (Humphrey 1974; Wright and Bailey 1982; Brooks and Minnich 2006; Enright and Thomas 2008; Brooks and Chambers 2011). When plant invasions alter fuelbeds and lead to high fire frequency, the deleterious effects on native species are often a significant management concern (Zouhar *et al.* 2008). The Mojave Desert of North America is one such desert ecosystem that has experienced increased fire frequency as a result of invasive annual grasses, especially in the lower and middle elevation zones dominated by creosote bush scrub (Brooks and Matchett 2006). These altered fire regimes have been cited as a significant threat to natural resources, most notably the federally threatened desert tortoise (*Gopherus agassizii* (Cooper)) (United States Fish and Wildlife Service 1994; Brooks and Pyke 2001; Brooks and Esque 2002) and have prompted significant fire suppression and post-fire revegetation efforts (Zouhar *et al.* 2008).

There are numerous studies that have evaluated the effects of single fires in the Mojave Desert (Bowns 1973; Callison *et al.* 1985; Minnich 1995; Lei 1999; Brooks 2002; Brooks and Matchett 2003; Brooks and Minnich 2006; Abella 2009). These studies collectively indicate that fire effects on perennial vegetation can vary by vegetation type and that total cover of perennial plants can return to preburn conditions within a few decades but species composition may take centuries to reach preburn characteristics. Studies also suggest that the non-native invasive annual grass, red brome (*Bromus rubens* L.), increases in abundance following single fires (Beatley 1966; Brooks 2002; Brooks and Matchett 2003; Brooks and Minnich 2006) and that its presence can promote fire spread (Brooks 1999) and the establishment of an altered fire regime (Brooks and Pyke 2001; Brooks and Esque 2002). The concern about *B. rubens* proliferating following fire in the Mojave Desert dates back to the mid 1900s (Holmgren 1960). Historical photos of burnt landscapes archived in the Caliente Field Office of the US Department of the Interior, Bureau of Land Management, in southern Nevada clearly show *B. rubens* carpeting post-fire landscapes during the initial few years following fires that occurred in the early 1940s. Upon revisiting those sites in 2001, it was observed that *B. rubens* was still the dominant herbaceous vegetation component, both in areas that had not burnt since the 1940s and those that have subsequently reburnt (M. L. Brooks, pers. obs.). Thus, increases in *B. rubens* biomass following fire appear to persist for at least 60 years in the Mojave Desert.

Although there are numerous studies evaluating the effects of single fires as described above, the effects of multiple fires over short time periods on vegetation or any other ecosystem

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response have not been evaluated in the Mojave Desert. This information is specifically needed to evaluate two current assumptions often made by fire managers regarding fire effects. The first is that biomass of *B. rubens* increases in response to frequent fire. The second is that density, cover and species richness of perennial plants each decline in response to frequent fire. These assumptions are based on the common belief that if a single fire has a measureable effect on *B. rubens* and perennial plants in the Mojave Desert, then multiple fires will have some compounding effect on these vegetation components.

The primary objective of this study was to evaluate the hypotheses that high fire frequency will result in incremental increases in biomass of *B. rubens* and incremental decreases in density, cover and species richness of perennial plants. An additional objective was to develop recommendations for fire management based upon the results of this study. This study was focussed within the specific context of creosote bush scrub vegetation (Munz 1973) because it: (1) is the most common vegetation association characterising ~70% of the Mojave Desert (MacMahon 2000); (2) occurs within one of the ecological zones where invasive annual grasses appears to have their greatest effects on fire regimes (Brooks and Matchett 2006; Brooks and Minnich 2006); and (3) constitutes the primary habitat for the desert tortoise, which is perhaps the primary species of management concern in the Mojave Desert that is threatened by altered fire regimes (United States Fish and Wildlife Service 1994; Brooks and Esque 2002).

Materials and methods

Study site

The study site is centred on the geographic landmark of Opal Mountain, San Bernardino County, California (USA, UTM 11 482929E, 389022N (NAD27)) at an average elevation of 1036 m above sea level. The site is dominated by creosote bush scrub vegetation (Munz 1973) typical of the low elevation desert shrubland ecological zone of the Mojave Desert (Brooks and Minnich 2006). All perennial plants at this site are native species and the dominant non-native species include *Bromus rubens* L. and the forb red stemmed filaree (*Erodium cicutarium* (L.) L'Hér et Aiton). The closest National Oceanic and Atmospheric Administration (NOAA) weather station was located 32 km SE of the study site in Barstow, California (www.ncdc.noaa.gov, accessed 1 June 2007). Over the past 30 years (1977–2006), the hottest month of the year has been July, which had an average high of 39°C and low of 20°C. The coldest month of the year has been December, which had an average high of 16°C and low of 1°C. Most of the annual rainfall occurred during the winter months of October–April and the long-term average winter rainfall during these months is 109 mm. The Opal mountain study site is also recognised one of ten areas in the Mojave Desert that have experienced high numbers of fires and area burnt since the 1970s (Opal Mountain Fire Cluster #4, described in Brooks and Esque 2002).

The fire season of 1993 was one of the most active since reliable records have been archived in the Mojave Desert (Brooks and Matchett 2006). Two large fires burnt across the study site during the summer of that year (Opal, 243 ha and Opal 2, 3383 ha). These fires burnt over areas that had previously burnt in 1984, 1986 and 1987 (some of which also overlapped) and others that had not previously burnt (R Franklin, pers. comm., Department of the Interior DI-1202 fire reports). The result was a spatial patchwork following the 1993 fires of areas that had burnt zero, one, two and three times since 1984. There have been no subsequent fires at the study site since 1993, allowing for a comparison of vegetation characteristics in areas of differing fire frequency but holding time since last fire constant. This last point was very important because post-fire effects vary depending on the number of years since the last fire and can be influenced by conditions immediately before, during and after the specific year in which the last fire occurred. Although official fire records do not exist before 1980, this particular region did not have extensive burn scars before the 1984 fire (R Franklin, pers. comm.) and probably did not experience much fire through the mid-century when production of fine fuels were likely very low in response to a protracted dry period that extended from 1942 through to 1975 (Hereford *et al.* 2006). Thus, fires were unlikely to have occurred at the study site between the early 1940s and early 1980s and possibly further back in time because *B. rubens* became naturalised in California at the end of the 1800s and may not have become common in the Mojave Desert until the middle of the 1900s (Brooks 2000).

Rainfall was generally above the long-term average in the Mojave Desert since the first fire occurred at the study site in 1984 (Hereford *et al.* 2006). The first burn period (1984–87) followed a 9 year period of particularly high rainfall (1976–1983) and the second burn period (1993) occurred following 2 years of high rainfall (1992–93). Years of high rainfall are necessary for large fires to occur in creosote bush scrub vegetation of the Mojave Desert and are attributed to accumulations of fine fuels created by non-native annual grasses that allow fire to spread across the interspaces between perennial plants (Brooks and Matchett 2006; Brooks and Minnich 2006).

Study design

Twenty-four transects were established to characterise current vegetation in areas of differing fire frequency. All transects were located in areas with evidence of similar creosote bush scrub vegetation before burning. Evidence included adjacent unburnt islands and residual bases of burnt shrubs that could be identified to species. Each transect was 10×60 m (600 m^2) and oriented parallel to the elevation contour. A minimum of two transects were established in each area representing unique combinations of past fires, resulting in a total of six transects of four differing fire frequencies: no fire ($n = 6$), one fire (1993, $n = 6$), two fires (1984, 1993, $n = 2$; 1986, 1993, $n = 2$; 1987, 1993, $n = 2$) and three fires since 1984 (1984, 1986, 1993, $n = 3$; 1986, 1987, 1993, $n = 3$). The average fire return interval was 7.3 years for the two fire frequency level and 6.3 years for the three fire frequency level. Transects were located randomly within each area representing a unique combination of past fires, with the one constraint that they were >50 m from the nearest dirt road. Vegetation sampling was conducted during 1998 and 2007, 5 and 14 years post-fire. These 2 years followed winters when rainfall was 190 and 21% of the long-term average. Rainfall during a single year can have significant effects on annual plant

biomass, but does not typically affect perennial plant density, cover and species richness, which respond more to multi year to decadal rainfall patterns (Webb *et al.* 2009*b*).

Biomass of *B. rubens* was measured within six 1×1-m sampling frames randomly located along the long axis centreline of each 10×60-m transect during April 1998 and 2007. If, during the randomisation process in 2007, the location of a sampling frame fell within 1 m of the edge of a location sampled during 1998, the frame was relocated to another random point along the transect centreline to avoid potential residual effects of biomass sampling from 1998 on sampling in 2007. All live *B. rubens* individuals rooted within the sampling frames were clipped at the soil surface and placed in a paper bag (one pooled 6-m^2 sample per transect). Each sample was oven dried to a constant mass at 60°C and weighed to determine its aboveground live dry biomass (to 0.0001-g precision). No other species within the genus *Bromus* were present at the study site. The area contained very small amounts (0–5 kg ha^{-1}) of another non-native annual grass, Mediterranean split grass (*Schismus* spp.) and large amounts of the non-native forb *Erodium cicutarium* (L.) L'Hér et Aiton. These other two species were not included in biomass sampling because the former was in low abundance and the latter is known to have little to no effect on fire behaviour in the Mojave Desert (Brooks 1999).

Density, cover and species richness of live perennial plants were measured within each 10×60 m transect during late October and early November 1998 and mid October 2007. Density was the number of individuals rooted within each transect and cover was calculated assuming a circular canopy for each plant where the radius was half the average of two measurements, the greatest horizontal diameter and the diameter 90° to the first. Each diameter measurement was recorded to the nearest 10 cm. Species richness was the number of species recorded at two spatial scales: within each 10×60-m (600-m^2) transect and within each of the six 10×10-m (100-m^2) areas within each transect. Sampling was focussed on woody perennial plants, bunchgrasses and cacti. Sampling did not include herbaceous perennials that were present in the study region, but are not optimally sampled during the fall months and are not optimally sampled by the methods used in this study. Common herbaceous perennials that were present in the study area but were not sampled included rattlesnakeweed (*Chamaesyce albomarginata* (Torr. & A. Gray) Small), desert larkspur (*Delphinium parishii* A. Gray), desert trumpet (*Eriogonum inflatum* Torr. & Frém.), desert globemallow (*Sphaeralcea ambigua* A. Gray), Parry's wireletuce (*Stephanomeria parryi* A. Gray) and small wirelettuce (*Stephanomeria exigua* Nutt.). Ideally, these species are sampled during early summer, but resources for this project allowed only for fall sampling of perennial plants.

Data analyses

Two-way analysis of variance (ANOVA) was used to evaluate the effects of two fixed factors, fire frequency (zero, one, two and three times burnt) and post-fire year (1998, 2007) on biomass of *B. rubens* and density, cover and species richness of perennial plants from 24 transects. Where separate measurements were recorded for each of the six subsamples within an individual transect (e.g. species richness and *B. rubens* biomass), the average of those values was used to represent the transect. Bonferroni-corrected *P*-values were used when comparing differences among the four fire frequency levels (Sokal and Rohlf 1995). In the rare case that patterns differed between years, a paired two-tailed Student's *t*-test was used to evaluate statistical significance of the difference (Sokal and Rohlf 1995). Type III sums of squares were used in all analyses and effects were considered significant at $P \leq 0.05$. Prior to using parametric statistics, the frequency distribution and residuals were inspected and generally found to be non-normal and heteroscedastic. Therefore, data were transformed using $v(x + 0.5)$ for density and species richness and $\log(x + 1)$ for cover and biomass (Sokal and Rohlf 1995). Summary statistics are reported as back transformed values.

Results

Bromus rubens *response*

Biomass of *B. rubens* varied significantly among areas of differing fire frequency ($F_{3,40} = 3.86$, $P = 0.0163$). However, this effect was only significant between unburnt (fire frequency = 0) and burnt areas (fire frequency = 1, 2 or 3) and did not vary among areas that had burnt one, two or three times between 1984 and 1993 (Fig. 1). Differences as a result of fire were only apparent in 1998 when biomass was approximately three times higher in burnt than unburnt areas, but not in 2007 when biomass was very low and similar in burnt and unburnt areas (fire × year; $F_{3,40} = 4.06$, $P = 0.0131$). This interaction was associated with excessively high overall productivity of *B. rubens* in 1998 (526 kg ha^{-1}) when rainfall was high, compared with low productivity in 2007 (19 kg ha^{-1}) when rainfall was low ($F_{1,40} = 89.65$, $P < 0.0001$).

Perennial plant response

Density of perennial plants varied significantly among areas of differing fire frequencies ($F_{3,40} = 16.03$, $P < 0.0001$). However, in contrast with what was observed for *B. rubens* biomass, burnt

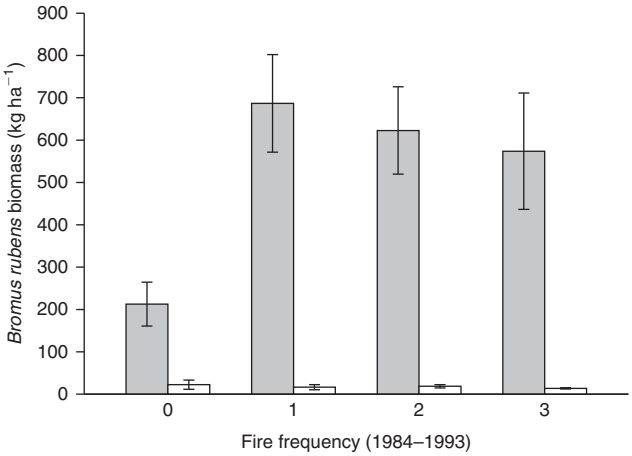

Fig. 1. Effects of fire frequency on aboveground dry biomass of *Bromus rubens* (mean ± s.e.) sampled during April 1998 (shaded bars) and April 2007 (unshaded bars) in creosote bush scrub vegetation near Opal Mountain, San Bernardino County, California, USA.

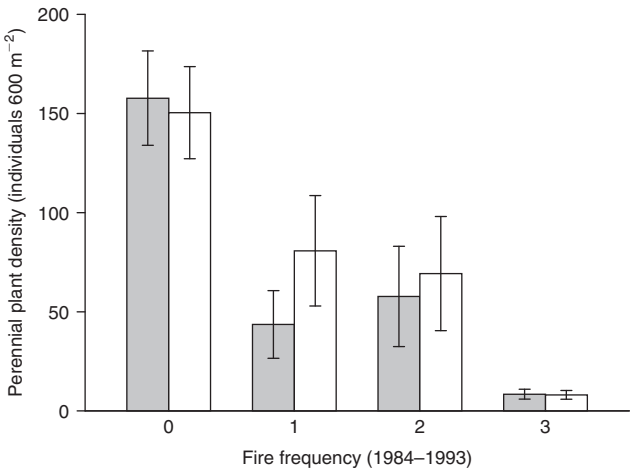

Fig. 2. Effects of fire frequency on density of perennial plants (mean ± s.e.) sampled during October–November 1998 (shaded bars) and October 2007 (unshaded bars) in creosote bush scrub vegetation near Opal Mountain, San Bernardino County, California, USA.

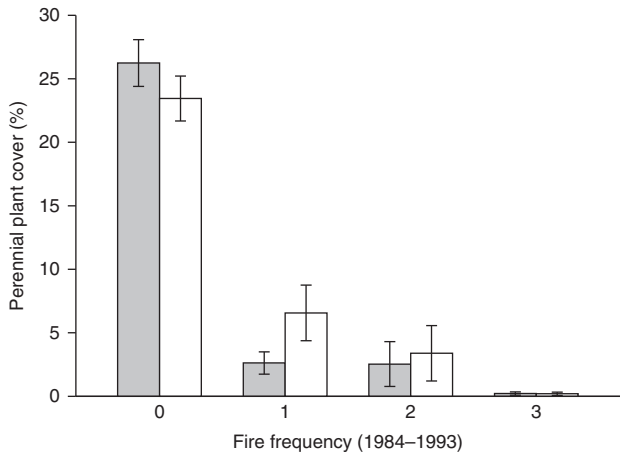

Fig. 3. Effects of fire frequency on percent cover of perennial plants (mean ± s.e.) sampled during October–November 1998 (shaded bars) and October 2007 (unshaded bars) in creosote bush scrub vegetation near Opal Mountain, San Bernardino County, California, USA.

areas had a much lower perennial plant density than unburnt areas and density continued to decrease with additional burning. Specifically, density was two times lower in areas that burnt one or two times, and 17 times lower in areas that burned three times, than in those that remained unburnt (Fig. 2). Also in contrast with *B. rubens*, perennial density was affected by fire frequency, as it decreased an additional 500% between areas burnt one or two *v.* three times. Effects as a result of fire did not vary among years (fire × year; $F_{3,40} = 0.42$, $P = 0.7402$). Although average density almost doubled between 1998 and 2007 in areas burnt once, this increase was not statistically different.

Cover of perennial plants was also significantly affected by fire frequency ($F_{3,40} = 16.03$, $P < 0.0001$). Burnt areas had 5 to 100 times lower perennial plant cover than unburnt areas (Fig. 3). The largest difference was between unburnt areas and areas burnt once, with a further decline between areas burnt two *v.* three times and this trend was detected in both 1998 and 2007 (fire × year; $F_{3,40} = 0.42$, $P = 0.7402$). Cover more than doubled between 1998 and 2007 in areas burnt one time (paired *t*-test = 2.77, $P_{\text{two-tailed}} = 0.0392$, 5 d.f.), but not in areas burnt with higher frequency (Fig. 3). This increase in total cover between 1998 and 2007 was owing to cheesebush (*Hymenoclea salsola*Torr. & A. Gray) increasing from 0.5 to 2.1% and desert needlegrass (*Achnatherum speciosa* (Trin. & Rupr.) Barkworth) increasing from 0.1 to 1.3%.

Unburnt areas were dominated by cover of creosote bush (*Larrea tridentata* (DC.) Coville), saltbush (*Atriplex polycarpa* (Torr.) S. Watson) and spiny hopsage (*Grayia spinosa* Hook (Moq.)) and by density of these species plus Cooper's golden-bush (*Ericameria cooperii* (A. Gray) H.M. Hall), Mojave buckwheat (*Eriogonum fasciculatum* Benth.), turpentinebroom (*Thamnosma montana* Torr. & Frém.), white bursage (*Ambrosia dumosa* (A. Gray) Payne) and *H. salsola* (Table 1). Areas burnt once were dominated by cover of *L. tridentata*, rayless golden-head (*Acamptopappus sphaerocephalus*Harv. & A. Gray ex. A. Gray) and *H. salsola*, in addition to density of *Ambrosia dumosa*. Areas that burnt twice were not dominated by any one species in terms of cover, but were dominated by density of *A. dumosa* and *H. salsola*. Areas burnt three times had excessively low cover and density of all species present.

Species richness of perennial plants varied significantly with fire frequency at the 60 m^2 ($F_{3,40} = 21.35$, $P < 0.0001$) and 600 m^2 scales ($F_{3,40} = 11.29$, $P < 0.0001$). At the 60 m^2 scale, there was an exponential decrease in species richness in response to frequent fire, whereas at the 600 m^2 scale the decrease was more linear (Fig. 4). Effects of fire on species richness were similar during 1998 and 2007 at both the 60 m^2 (fire × year; $F_{3,40} = 0.0588$, $P = 0.9910$) and 600 m^2 (fire × year; $F_{3,40} = 0.0219$, $P = 0.9955$) scales.

The total number of species encountered among all transects within a particular fire frequency category also declined with increasing frequency burnt (0, 1, 2 and 3 times) from 22, 20, 16 to 7 total species at the 600-m^2 scale (Table 1). This decline represented 91% of the original number of species remaining following one burn, 73% after two burns and 32% after three burns. Plant life form type was not useful in explaining this decline, although there was not a large amount of variation among life forms with 20 shrubs species, two perennial grasses and one cactus (Table 1).

Discussion

Biomass of *B. rubens* was significantly higher in burnt than unburnt landscapes at our study site, a result consistent with other studies from the Mojave Desert (Brooks and Matchett 2003; Brooks and Berry 2006; Brooks and Minnich 2006). As *B. rubens* is the primary fuel that carries fire in the Mojave Desert (Brooks 1999), the chances of repeat burning are greater in burnt than unburnt areas (Brooks *et al.* 2007). However, fire increased biomass of *B. rubens* regardless of whether the area had previously burnt or not, indicating that the maximum strength of this feedback cycle was manifested after a single fire and did not continue to increase following multiple fires.

The positive effect of burning on *B. rubens* biomass was apparent during spring 1998 (5 years post-fire) but not spring 2007 (14 years post-fire). This could be interpreted as evidence

Table 1. Density and cover of perennial plant species in areas of differing fire frequency (1984–93)
Relative values are reported from vegetation sampling during two years (1998, 2007) and all species are shrubs unless otherwise indicated.

Species	Fire frequency (number of times burnt)							
	0		1		2		3	
	Density[A]	Cover[B]	Density	Cover	Density	Cover	Density	Cover
Species that only occurred in areas burnt 0 times								
Lycium cooperi	L, L	L, L	NP, NP	NP, NP	NP, NP	NP, NP	NP, NP	NP, NP
Pleuraphis rigida (grass)	L, L	L, L	NP, NP	NP, NP	NP, NP	NP, NP	NP, NP	NP, NP
Additional species in areas burnt 0 and 1 times								
Acamptopappus sphaerocepalus	L, L	L, L	L, L	L, M	NP, NP	NP, NP	NP, NP	NP, NP
Atriplex polycarpa	H, H	H, H	L, L	L, L	NP, NP	NP, NP	NP, NP	NP, NP
Ericameria cooperi	H, H	L, L	L, L	L, L	NP, NP	NP, NP	NP, NP	NP, NP
Tetradymia spinosa	L, L	L, L	L, L	L, L	NP, NP	NP, NP	NP, NP	NP, NP
Additional species in areas burnt 0, 1 and 2 times								
Chrysothamnus teretifolious	L, L	L, L	L, L	L, L	L, L	L, L	NP, NP	NP, NP
Ephedra nevadensis	M, M	M, M	L, L	L, L	L, L	L, L	NP, NP	NP, NP
Eriogonum fasciculatum	H, H	L, L	L, L	L, L	L, L	L, L	NP, NP	NP, NP
Grayia spinosa	H, H	H, H	L, L	L, L	L, L	L, L	NP, NP	NP, NP
Krascheninnikovia lanata	L, L	L, L	L, L	L, L	L, L	L, L	NP, NP	NP, NP
Lycium andersonii	M, M	L, L	L, L	L, L	L, L	L, L	NP, NP	NP, NP
Salazaria mexicana	L, L	L, L	L, L	L, L	L, L	L, L	NP, NP	NP, NP
Tetradymia stenolepsis	L, L	L, L	L, L	L, L	L, L	L, L	NP, NP	NP, NP
Thamnosma montanum	H, H	L, L	L, L	L, L	L, L	L, L	NP, NP	NP, NP
Additional species in areas burnt 0, 1, 2 and 3 times								
Achnatherum speciosa (grass)	M, M	L, L	L, L	L, L	L, L	L, L	L, L	L, L
Ambrosia dumosa	H, H	L, L	H, H	L, L	H, H	L, L	L, L	L, L
Atriplex spinosa	L, L	M, M	L, L	L, L	L, L	L, L	L, L	L, L
Hymenoclea salsola	H, H	M, M	H, H	L, M	H, H	L, L	L, L	L, L
Larrea tridentata	H, H	H, H	L, L	M, M	L, L	L, L	L, L	L, L
Opuntia basilaris (cactus)	L, L	L, L	L, L	L, L	L, L	L, L	L, L	L, L
Xylorhiza tortifolia	M, M	L, L	L, L	L, L	L, L	L, L	L, L	L, L

[A]Density (individuals/600 m^2); H = >10; M = 5 to 10; L = <5; NP = not present
[B]Cover (%); H = >2; M = 1–2; L = <1; NP = not present

that the effects of the last fire in 1993 lapsed sometime between 5 and 14 years post-fire. However, the more likely interpretation is that exceedingly low productivity in spring 2007, following a winter with 21% of average rainfall (Barstow, California, weather station; www.ncdc.noaa.gov) did not produce enough biomass to record a difference between burnt and unburnt areas compared with spring 1998, which followed a winter with 190% of average rainfall. In addition, *B. rubens* biomass was ~200% higher in burnt than unburnt areas only 2 years earlier during spring 2005 (M. L. Brooks, pers. obs.) when productivity was high following a winter rainfall season with 263% of average rainfall (www.ncdc.noaa.gov). Cover of *Bromus* spp. was also higher in burnt than unburnt areas 6–14 years post-fire in blackbrush communities of the Mojave Desert (Brooks and Matchett 2003) and in burnt than in unburnt areas 3–5 years post-fire in creosote bush scrub of the north-western Sonoran Desert (Brown and Minnich 1986). It should be noted that during the first few years following fire in the Mojave Desert the dominance of *B. rubens* can, in some cases, be reduced compared with adjacent unburnt areas, probably because of the combined effects of fire induced seedbank mortality and subsequent low rainfall levels (Brooks 2002). However, the present study and others mentioned above suggest that these initial effects are often reversed after the first few post-fire years and *B. rubens* can dominate landscapes for many decades following fires.

Perennial plant density, cover and species richness all declined appreciably after only one fire in this study and continued to decline to a lesser degree after two and three fires. This pattern was also reported for species richness at a creosote bush scrub site that burnt twice in a short period in the Colorado Desert of California (Steers 2008). Analyses of plant life forms can often provide insights into why certain species decline in abundance with increasing fire frequency, however, this approach was not useful in the current study because 20 of the 23 species were all the same life form (shrubs). In addition, the two perennial grasses present at the study site, which represent a life form that is generally resilient to fire (Pyke *et al.* 2010), responded very differently to fire frequency. *A. speciosum* remained present even after three fires, whereas big galleta (*Pleuraphis rigida* Thurb.) occurred only in unburnt areas. Lack of resilience to fire by *P. rigida* may have been because of the legacy of past disturbances in this region of the Mojave Desert (e.g. livestock grazing) and the fact that the study site is at the edge of its geographic range and environmental conditions (especially summer rainfall) may not be ideal for this species.

Perennial cover increased 2-fold during the 9 year interval between samplings in 1998 and 2007, but only in areas that had

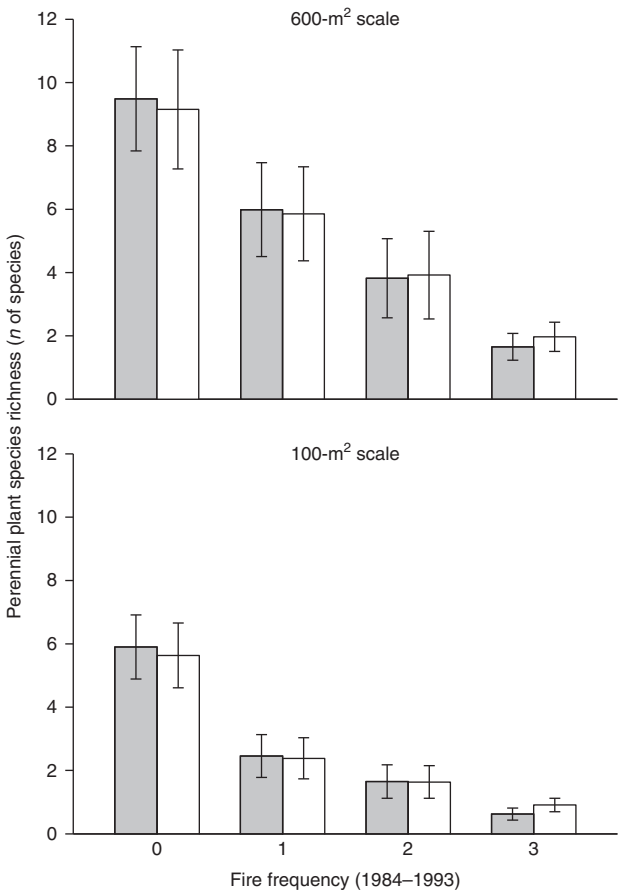

Fig. 4. Effects of fire frequency on species richness of perennial plants (mean ± s.e.) sampled during October–November 1998 (shaded bars) and October 2007 (unshaded bars) in creosote bush scrub vegetation near Opal Mountain, San Bernardino County, California, USA.

burnt once, where the increase was due primarily to two species, *H. salsola* and *A. speciosa*. These species tend to establish early following fire by either re-sprouting or re-establishing from seed in burnt areas of the Mojave Desert and adjacent desert regions (O'Leary and Minnich 1981; Brown and Minnich 1986; Brooks and Minnich 2006) and are among the primary species that initially establish following a wide range of disturbance types (Webb *et al.* 2009*a*). However, the lack of recovery of these species in areas burnt three times in the present study suggests there may be limit to their resilience.

Recovery of perennial cover after fire in the Mojave Desert can follow a curvilinear increase to 35, 60 and 75% of unburnt reference cover 10, 20 and 30 years post-fire (fig. 15.9 by Webb *et al.* 2009*a*). Although the short-term rate of recovery at our study site was somewhat similar to the rate reported by Webb *et al.* (2009*a*), these values should be considered only as estimates for recovery rates in the Mojave Desert. Variables such as fire weather conditions before and after burning, fire behaviour and resilience of the plant species that are present can all contribute to high variation among sites in vegetation responses to fire (Fites-Kaufman *et al.* 2006; Pyke *et al.* 2010).

Although perennial plant cover or density may recover within a few decades to a hundred years following disturbances such as fire in the Mojave Desert, recovery of species composition to unburnt reference conditions may take centuries (Webb *et al.* 2009*a*). In addition, initial recovery of cover is typically driven by only a few short-lived species, *H. salsola* and *A. speciosa* as an example in the present study. Full recovery of species composition is hindered by slow recruitment and growth rates of long lived Mojave Desert species (Bowers *et al.* 1995) and the suppressive effects of other types of disturbance (e.g. livestock grazing, off highway vehicles, drought) (Lovich and Bainbridge 1999; Webb *et al.* 2009*b*).

It is important to note that this study period focussed on vegetation responses to fire frequency during the first 14 post-fire years. This is a relatively short period considering that historical fire return intervals in creosote bush scrub before invasion by non-native annual grasses were on the order of centuries (Brooks and Minnich 2006). Although a trend towards recovery of perennial cover was detected only following single fires in this study, results do not rule out eventual recovery following multiple fires. In addition, the average fire return interval for the two and three fire conditions in the current study ranged from 6.3 to 7.3 years, which is similar to a minimum of 5 years reported for fire regimes altered by *B. tectorum* in the Great Basin (Whisenant 1990) and 10 years reported for fire regimes altered by *B. rubens* in the Colorado Desert of western North America (Brown and Minnich 1986). These fire return intervals are among the shortest in the deserts of North America and it would be useful to understand post-fire dynamics following a range of fire return intervals, not just the extreme end of the potential spectrum. Additional research is needed that simultaneously incorporates fire frequency, time since fire and fire return interval to better understand patterns of post-fire recovery in the Mojave Desert.

It is also important to emphasise that the present study was focussed on the creosote bush scrub vegetation type that typifies the low-elevation desert shrubland zone of the Mojave Desert (Brooks and Minnich 2006). Although this vegetation type and ecological zone are the most common in the Mojave Desert, there are many other vegetation types and ecological zones that differ enough in their potential resilience to fire that the results of the present study should not be applied to them. Examples include blackbrush scrub, sagebrush scrub, pinyon–juniper woodland, desert chaparral and riparian woodland, shrubland and grassland vegetation types of the middle elevation, high elevation, desert montane and riparian ecological zones (Rowlands *et al.* 1982; Brooks and Minnich 2006).

Conclusions and management implications

Post-fire abundance of *B. rubens* peaked after a single fire and did not increase in response to multiple fires, suggesting that post-fire management efforts designed to reduce *B. rubens* abundance may be equally warranted after a single or multiple fires. In addition, the abundance and diversity of perennial species declined with each successive fire, thus, areas that have only burnt once may have a greater capacity to recover their perennial species composition than areas where multiple fires have significantly depleted perennial populations. Areas burnt once may, therefore, need only to be protected from additional burning and other significant disturbances to eventually recover

to pre-burn conditions, whereas repeatedly burnt areas may require active revegetation actions such as seeding of perennial species.

Although post-fire management of creosote bush scrub may include *B. rubens* control and perennial plant revegetation, the most effective strategy to prevent an altered fire regime is to prevent fire from occurring in the first place. Thus, the first lines of defence against altered fire regimes should include: (1) vegetation management strategies that minimises the dominance of *B. rubens* and other non-native invasive plants that facilitate fire spread; (2) law enforcement activities that reduce the frequency of anthropogenic sources of ignitions; and (3) fire suppression plans that result in quick responses to fires and limit the size of fires. In addition, decisions to actively control invasive species or to revegetate perennials should not just consider the specific short-term effects on the targeted species, but should more importantly consider the ultimate multi-trophic and ecosystem level effects of these management actions (Brooks 2007).

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