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### Cover Page Footnote

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# Native Annual Plant Response to Fire: an Examination of Invaded, 3 to 29 Year Old Burned Creosote Bush Scrub from the Western Colorado Desert

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## ABSTRACT

*Creosote bush scrub vegetation typically contains high diversity of native annual plants relative to shrubs, cacti, perennial herbaceous species, or other plant life forms. This vegetation type is also very susceptible to exotic, invasive annual plants, which promote fire by changing fuel properties. The impact of fire on most perennial species is severe but the impact on native annual plants is not well understood. We measured annual species composition in five sites that each contained paired burned and unburned stands in the western Colorado Desert, California. The burned stands at each site ranged in time since fire from 3 to 29 years ago. Annual plant cover, species richness, and soil chemical and physical properties were compared in the paired burned and unburned reference stands. Differences between paired stands at the time of each fire are assumed negligible since shrub cover across fuel breaks did not differ prior to each fire based on aerial photographs. Fires elevated soil pH but otherwise had little effect on other soil properties. In recently burned stands, invasive annual grass abundance increased while native annual plant cover and species richness decreased. However, in older burned stands, annual plant composition did not always differ between paired stands because invasive annual plant abundance was very high in both stands. Thus, while fires can have long-lasting negative impacts to perennial components of creosote bush scrub, invasive species can displace native annual plants regardless of whether or not a site burns, although fire disturbance appears to accelerate invasive plant dominance.*

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## INTRODUCTION

Desert annual plants contribute a large proportion of the plant diversity found in creosote bush scrub vegetation (Jennings 2001). Many desert annuals are attractive wildflowers that can carpet the desert floor when the appropriate conditions are met (Goodpasture and others 2004). Unfortunately, exotic annual plants such as grasses (*Bromus madritensis*, *Schismus barbatus*, and *Schismus arabicus*), red-stem filaree (*Erodium cicutarium*), and Sahara mustard (*Brassica tournefortii*) have invaded and displaced native annual plants in many parts of California's deserts (Minnich 2008). In localized areas, invasive grasses have been especially problematic for fueling wildfires (Brooks and Matchett 2006; Brooks and Minnich 2006). One such area is the western edge of the northern Colorado Desert and southern Mojave Desert in Riverside and San Bernardino Counties, California (Brooks and Esque 2002). Fire is thought to be relatively common here

due to elevated precipitation and anthropogenic nitrogen deposition that promote invasive grasses (Allen and others 2009; Rao and Allen 2010; Rao and others 2010), and also because of increased human ignitions due to its location within a major wildland urban interface (Brooks and Esque 2002; Brooks and Matchett 2006).

Previous studies investigating the response of desert annual plants to fire have reported increases in *Schismus* spp. (Cave and Patten 1984; Brown and Minnich 1986; Brooks 2002) and *E. cicutarium* (Brown and Minnich 1986; Brooks and Matchett 2003). Larger seeded invasive annual grasses, like *B. madritensis* ssp. *rubens*, usually decrease immediately following fire (Brooks 2002; Abella and others 2009), but may return to or exceed pre-fire levels of abundance after several years (Brooks 2002). Species-specific responses to fire by native annual plants have been reported, but due to large differences in species composition between study sites, generalizations are

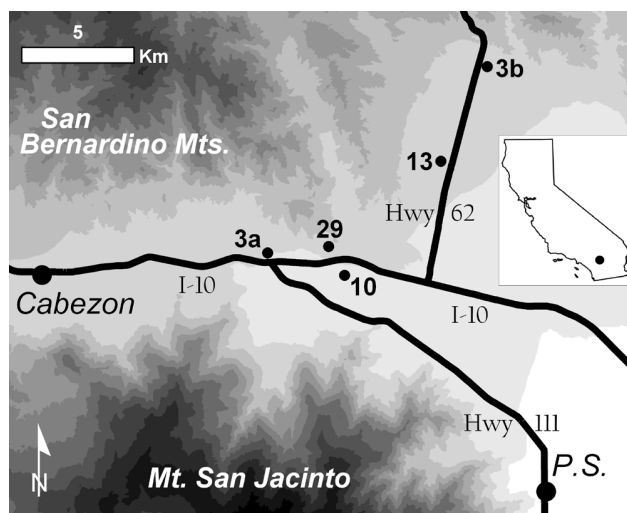
difficult to draw. However, several studies have found an increase in *Plantago ovata* following fire (Brown and Minnich 1986; Cave and Patten 1984; Brooks 2002). Lastly, there is evidence that fire in creosote bush scrub reduces annual plant species richness (Brooks 2002; Steers and Allen, in press), although other types of desert shrublands found at higher elevations in the Mojave and Sonoran Deserts, can have increased native annual plant species richness following fire when fires eliminate *B. madritensis* and no other invasive species become dominant (Brooks and Matchett 2003; Abella and others 2009; Steers, unpublished data).

The goal of this study was to document the impact of fire on native and exotic annual plants by investigating a number of burns that ranged in time since fire. Specifically, we wanted to determine how fire impacts native annual plant diversity. We also wanted to document whether fire promotes invasive annual plant abundance. Annual vegetation was sampled in the field from five sites that had burned from three to almost thirty years since the time of sampling. Our hypotheses were that fire would promote exotic annual plants and decrease native annual species richness in sites of varying age since fire.

## MATERIALS AND METHODS

### Study Area

The study area was located on the western edge of the Coachella Valley in Riverside County, California (figure 1). This valley forms the extreme northwest portion of the Colorado Desert and transitions into the Mojave Desert to the north, and into cismontane vegetation of the California Floristic Province towards the west and south. The primary vegetation in this region is creosote bush scrub (CBS) on the valley bottoms. A rich post-1960 fire chronosequence exists for the CBS vegetation that dominates the valley and eastern reaches of the Banning Pass, and several burned sites have been investigated previously (O'Leary and Minnich 1981; Brown and Minnich 1986). Average precipitation in the city of Palm Spring to the east of the study area is 13.1 cm while to the west, at Cabazon, average precipitation is 39.9 cm (WRCC 2008). Creosote bush scrub reaches its western-most extent in the Banning Pass near the eastern border of Cabazon.



**Figure 1.** Study area on the western edge of Coachella Valley, Riverside County, California, showing study sites (numbers w/dots) that are named after their respective time since fire, as of spring 2008. P.S. represents the city of Palm Springs, I-10 is Interstate 10. Dark colors indicate increasing elevation.

### Site Determination

In the spring of 2006, potential study sites were selected based on stereoscope validation of fire perimeters from a series of aerial photographs of the study landscape, spanning from 1949 to 2005. Aerial photos were obtained from Riverside County Flood Control and Water Conservation District, Coachella Valley Water District, and UC Riverside Science Library. The year when examined aerial photos were taken include the following: 1949, 1957, 1974, 1980, 1984, 1985, 1986, 1987, 1989, 1990, 1995, 1996, 1998, 2000, and 2005. Dates of the fires at each site were first determined from the aerial photos, but historic Los Angeles Times articles via ProQuest® (<http://www.proquest.com>), verbal communication with Richard Minnich (University of California, Riverside), and personal observations for all fires that occurred in 2005 were also used to date the year of fire. At two of the study sites utilized, the year of fire was only narrowed down to a 2 year period. Since fires in desert vegetation are more common following winter seasons with above average rainfall (Brooks and Matchett 2006), the wetter of the two possible burn years is reported in this experiment as the assumed burn year.

Respective unburned reference stands for all of the burned stands were also identified from aerial photographs in the spring of 2006. All paired unburned reference sites existed in similar areas of

shrub cover to pre-fire conditions based on aerial photographs. They were also located opposite fuel breaks (bulldozer lines, dirt roads, or paved roads) to minimize fuel differences at the time of each fire. Over twenty unique sites that had burned were identified in the study area from aerial photography, but after ground-truthing each site in July and August of 2006 only five were selected for this study. Sites dismissed from the study were done so mostly because of a lack of suitable unburned reference vegetation (in other words, unburned vegetation adjacent to burned vegetation did not appear to be separated by a fuel break so differences in fuel between the two areas may have existed at the time of fire). Other reasons for dismissal were because of recent grazing history (determined in the field), irregular soil type (based on NRSC soils maps or percent sand, silt, and clay analyses), or some sites were removed to minimize climatic variation (for example, sites adjacent to Cabazon or to Palm Springs).

The six sites selected for this study ranged in year burned from 1979 to 2005 with a time since fire (tsf) of 3, 3, 10, 13, and 29 years. The names of the sites correspond directly to tsf. The two sites that had burned in 2005 are called '3a' and '3b.'

### Soil Sampling

In August and September of 2006, 6 sampling units were implemented in a stratified random design in both the unburned and paired burned reference vegetation at all six sites. Sampling units consisted of one modified – National Weed Management Association (mod-NAWMA) circular plot (Stohlgren and others 2003). Slope and aspect were measured from the center of each plot using a compass and clinometer. Soil was also collected for chemical and physical analyses. For nutrient analyses, four soil samples per mod-NAWMA plot were taken to 5 cm depth with a 2.5 cm diameter corer and pooled into one composite sample per plot. The four samples were taken at the center and at three edge locations (7.32 m from plot center), at 30, 150, and 270 degrees from plot center. One core with a 5 cm diameter was taken at the center of the plot for bulk density, coarse fraction (>2 mm), and soil texture measures. All soil sampled was taken at a 5 cm depth. Soil pH from the four pooled soil samples taken with the 2.5 cm diameter core was measured using a Fisher Scientific® Model 50 pH meter. The same soil samples were then analyzed for carbon (C)

nitrogen (N),  $\text{NH}_4^+$ , and  $\text{NO}_3^-$  by the University of California, Davis, Analytical Laboratory (<http://groups.ucanr.org/danranlab>) in addition to percent sand, silt, and clay from the 5 cm diameter core.

### Vegetation Sampling

In the winter wet-season of 2006-07, insufficient rainfall prevented the germination of annual plants at the study sites and no vegetation measurements were taken. In the wet season of 2007-08, precipitation was about average and vegetation was sampled throughout March 2008 during peak flowering in each established mod-NAWMA plot. Percent cover by species and species richness were measured in three 1 m<sup>2</sup> (1 x 1 m) quadrats per plot, located 4.57 m from plot center at 30, 150, and 270 degrees. Species richness was measured within each of the three 1 m<sup>2</sup> quadrats per plot and also within each plot (to a 7.32 m radius from plot center). All species nomenclature follows Hickman (1996).

### Data Analyses

Vegetation cover at each of the five study sites was categorized into invasive grass, invasive forb, total invasive (grass + forb), native annual (grass + forb), herbaceous perennial, and native shrub cover at the 1 m<sup>2</sup> scale (in quadrats). For all analyses, shrub data included species in the Cactaceae. Species richness of invasive annuals, native annuals, and shrubs was also calculated at both the quadrat and mod-NAWMA plot scales. These parameters were used to compare the unburned stands of the six study sites with their respective, paired burned stands.

One-way ANOVA was used to compare the soil and vegetative variables between paired unburned and burned stands. When comparing shrub cover, Kruskal-Wallis tests were used instead of ANOVA, since these data were not normally distributed even when transformed. Two-way ANOVA was used to evaluate time since fire related differences in relative exotic grass, exotic forb, and native annual plant cover between paired burned and unburned stands. Lastly, a Detrended Correspondence Analysis (DCA) was performed for the two stands that had most recently burned (3a and 3b). Ordinations representing the other three sites were performed but are not reported because of weak (site 13) or no difference (sites 10 and 28) between paired stands. For each

DCA, only species that were recorded from three or more of the six plots from either paired stand (burned or unburned) were included. In other words, any species that was present in less than three plots per stand was removed prior to conducting the analyses. The DCA utilized mean species coverage values taken at the 1 m<sup>2</sup> scale and were used to compare plots based on their floristic composition as well as to determine which species were more associated with burned vegetation versus unburned (Vamstad and Rotenberry 2010). Analyses were performed using JMP 7.0.2 (SAS Institute Inc.) R v.11 (<http://www.r-project.org/>), and PC-ORD (McCune and Medford, 1999).

## RESULTS

### Vegetation of the Study Area

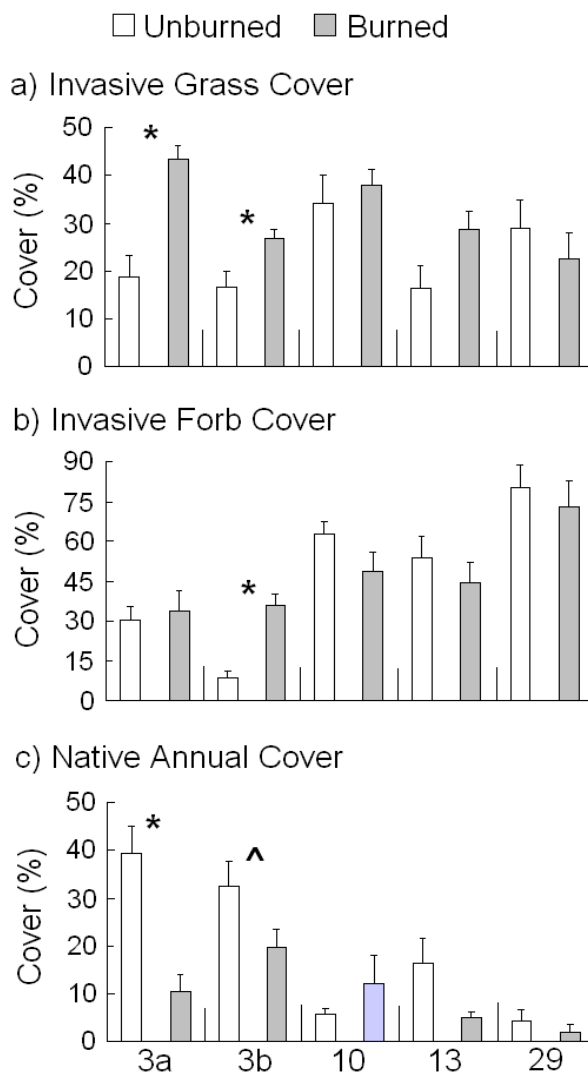
The vegetation of the study area was dominated by *Larrea tridentata*. *Ambrosia dumosa* was usually sub-dominant. Various shrubs and herbaceous perennials were documented in addition to seven exotic annuals and 46 native annual species (appendix 1). Exotic annual plant cover at all study sites was high (figure 2), which can be attributed to the invasive forbs *Erodium cicutarium* and *Brassica tournefortii*, and invasive annual grasses in the *Schismus* spp. complex (almost entirely represented by *S. barbatus*). *Bromus madritensis* ssp. *rubens* was common throughout the study area but was not one of the dominant annual plants, unlike prior years (Minnich 2008).

### Impact of Fire on Soils

Most soil parameters did not differ between burned and unburned reference stands (table 1). Soil pH was greater in burned than unburned stands at the two most recently burned sites (3a and 3b). Other soil parameters, including total N, total C, and extractable nitrogen (NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup>), did not show consistent patterns between paired burned and unburned stands. Percent cover of bare ground in burned stands appeared to increase relative to paired unburned stands with time since fire. Litter cover had an opposite, albeit weak trend, where greater litter cover was found in unburned stands compared to burned stands at more recently burned sites, but differences in litter did not occur between paired stands at older burned sites (table 1).

### Impact of Fire on Annual Plants

When analyzing absolute cover with One-way ANOVA, exotic grass cover was greater in burned than unburned vegetation at sites that had experienced fire three years ago, but not in older burned stands (figure 2). Exotic forb cover was only greater in burned than unburned vegetation at site 3b. Fire reduced native annual cover at the 1 m<sup>2</sup> scale at site 3a and 3b (figure 2).



**Figure 2.** Mean invasive grass (a), invasive forb (b), and native cover (c) of annual plants. Statistical differences between paired stands per site are indicated by \* ( $P < 0.05$ ) or ^ ( $P < 0.08$ ). Numbers below x-axis refer to site names, which also indicate years since burn.

When examining relative cover, recently burned stands had higher relative exotic grass cover but this decreased as time since fire increased, while exotic annual forbs became relatively more abundant as

time since fire increased. Relative cover of native annual plants decreased as time since fire increased (figure 3). Two-way ANOVA showed a significant effect of time since fire on relative exotic forb and native annual plant cover ( $F = 17.8$ ,  $p < 0.0001$ ;  $F = 22.6$ ,  $p < 0.0001$ , respectively), a significant effect of fire on relative exotic grass and native annual plant cover ( $F = 16.4$ ,  $p = 0.0001$ ;  $F = 23.4$ ,  $p < 0.0001$ , respectively) and a significant interaction between time since fire and whether the vegetation was burned or unburned for relative exotic grass, exotic forb, and native annual plant cover ( $F = 4.8$ ,  $p < 0.0048$ ;  $F = 4$ ,  $p < 0.0127$ ;  $F = 7.1$ ,  $p = 0.0004$ , respectively).

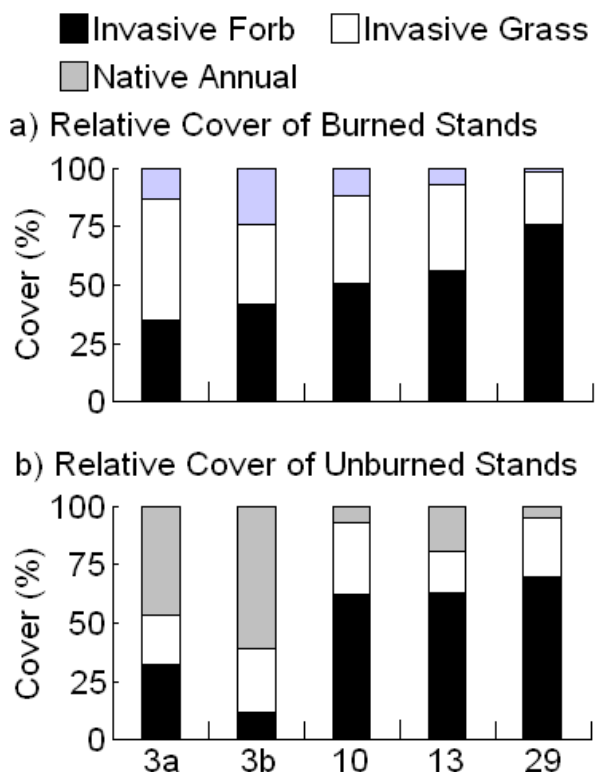
Native annual plant richness at the 1 m<sup>2</sup> scale was also reduced by fire at sites 3b and 13 (figure 4). At the mod-NAWMA plot scale (168.3 m<sup>2</sup>), native annual richness was decreased by fire at sites 3a and 13 (figure 4). Site 3b, with the greatest species richness in unburned plots, surprisingly did not exhibit decreased native annual species richness in the burned stand at the scale of a mod-NAWMA plot. However, many of the species found in plots of the burned stand were only represented by one to a few individuals (Steers, personal observation during field sampling of study site, March 2008).

Ordinations produced with Detrended Correspondence Analysis (DCA) from the two recently burned sites showed a marked effect of fire on annual plant composition. For site 3a, the variance in the species data was 0.6434 and the eigenvalue for axis 1 was 0.35. Eigenvalues for the remaining two axes were less than 0.1 and 0.01, respectively. Thus, axis 1 explained most of the variation among plots. Unburned plots were positively associated with axis 1 while burned plots were negatively associated (figure 5). Thirteen annual plant species were included in the ordination (appendix 1). Species with the strongest positive association with axis 1 (indicative of unburned conditions) were *Bromus madritensis* ssp. *rubens* (axis score = 323), *Pholistoma membranaceum* (275), *Chaenactis fremontii* (194), and *Stephanomeria exigua* (176). Species most negatively associated with axis 1 (burned conditions) were *Erodium cicutarium* (-7 axis score), *Schismus* spp. (-4), *Crassula connata* (24), and *Filago californica* (88). The remaining species had scores ranging from 100 to 151.

**Table 1.** Mean soil and perennial plant parameters in unburned (UB) and paired burned (B) stands (numbers are site names and refer to year since burn; **3a**, and **3b** are two separate 3 year old sites). For each site, bold values indicate the stand with a significantly greater value among paired stands ( $P = 0.5$ ). Aspect and slope were not statistically analyzed.

| Soil and Vegetation Variables           | 3a          |             | 3b          |            | 10         |           | 13          |      | 29          |           |
|---|-------------|-------------|-------------|------------|------------|-----------|-------------|------|-------------|-----------|
|   | UB          | B           | UB          | B          | UB         | B         | UB          | B    | UB          | B         |
| Aspect (deg.)                           | 96          | 92          | 103         | 78         | 163        | 175       | 74          | 95   | 198         | 166       |
| Slope (deg.)                            | 1           | 1           | 2           | 1          | 2          | 2         | 1           | 1    | 4           | 4         |
| Total N (%)                             | 0.10        | 0.10        | 0.08        | 0.05       | 0.09       | 0.08      | <b>0.12</b> | 0.10 | 0.12        | 0.15      |
| Total C (%)                             | 0.84        | 0.89        | 0.76        | 0.56       | 0.99       | 0.75      | <b>1.07</b> | 0.83 | 1.33        | 1.62      |
| NH <sub>4</sub> <sup>+</sup> (ppm)      | 11.9        | 13.4        | 8.3         | 7.7        | 13.0       | 14.1      | 15.6        | 18.0 | <b>16.0</b> | 10.6      |
| NO <sub>3</sub> <sup>-</sup> (ppm)      | <b>28.1</b> | 18.0        | 7.6         | 7.6        | 19.1       | 14.5      | 13.9        | 9.9  | 16.1        | 17.2      |
| Sand (%)                                | 86          | 87          | 87          | 86         | 83         | <b>86</b> | 77          | 80   | 80          | <b>86</b> |
| Silt (%)                                | 12          | 11          | 12          | 12         | 14         | 11        | 19          | 16   | <b>15</b>   | 11        |
| Clay (%)                                | 2           | 2           | 1           | 2          | <b>3</b>   | 2         | 4           | 4    | <b>5</b>    | 4         |
| pH                                      | 7.7         | <b>7.8</b>  | 7.3         | <b>7.6</b> | 7.2        | 7.4       | 7.4         | 7.5  | 7.0         | 7.0       |
| Bulk Density (g · cm <sup>-3</sup> )    | 1.36        | <b>1.61</b> | 1.6         | 1.57       | 1.43       | 1.58      | 1.14        | 1.24 | 1.36        | 1.25      |
| Coarse Fraction (g · cm <sup>-3</sup> ) | 0.14        | 0.16        | <b>0.25</b> | 0.11       | 0.26       | 0.23      | 0.4         | 0.46 | 0.48        | 0.48      |
| Bare Ground Cover (%)                   | 17          | 26          | 41          | 33         | 10         | 10        | 13          | 22   | 5           | <b>12</b> |
| Rock Cover (%)                          | 1           | 3           | 4           | 4          | 2          | 1         | 6           | 2    | 3           | 8         |
| Litter Cover (%)                        | <b>8</b>    | <1          | 3           | 2          | 1          | 1         | <b>3</b>    | 1    | 2           | 3         |
| Live Shrub Cover (%)                    | <b>12</b>   | <1          | <b>8</b>    | <1         | 3          | <1        | 7           | 1    | 7           | 13        |
| <i>Encelia farinosa</i> Cover (%)       | <1          | <1          | <1          | <1         |            |           | <1          | 1    | <1          | <b>13</b> |
| Shrub Richness (1 m <sup>-2</sup> )     | <b>0.4</b>  |             | <b>0.6</b>  | 0.1        | 0.2        |           | 0.4         | 0.4  | 0.2         | 0.5       |
| Shrub Richness (168.3 m <sup>-2</sup> ) | <b>2.3</b>  | 0.5         | <b>5.5</b>  | 2          | <b>2.7</b> | 0.7       | <b>4.3</b>  | 2.3  | <b>6.3</b>  | 1.8       |

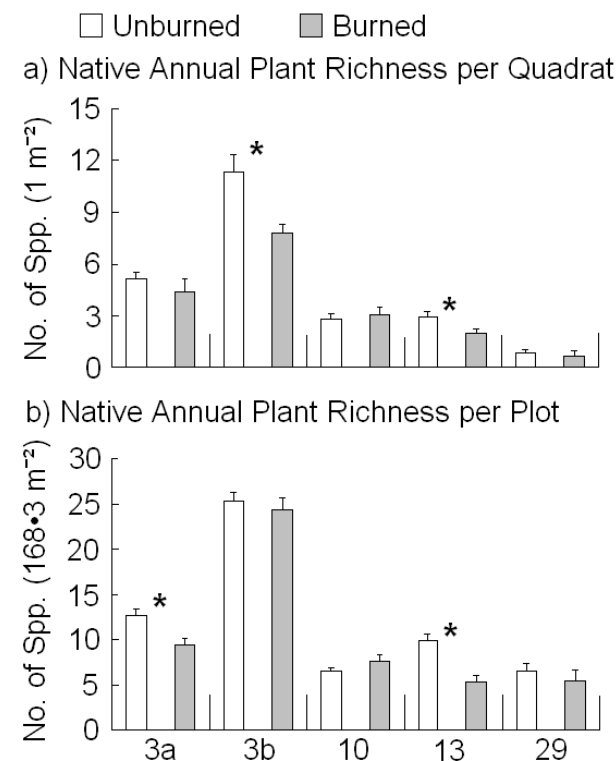
At site 3b, the variance in the species data was 1.1029 and the eigenvalue for axis 1 was 0.4116. Eigenvalues for the remaining two axes were 0.1099 and 0.0307, respectively. Again, axis 1 explained most of the variation among plots. Unburned plots were positively associated with axis 1 while burned plots were negatively associated (figure 5). Twenty four annual plant species were included in the ordination. Species with the strongest positive association with axis 1 (indicative of unburned conditions) were *Cryptantha barbiger* var. *fergusoniae* (323 axis score), *Chorizanthe brevicornu* (305), *Pholistoma membranaceum* (302), *Vulpia octoflora* (291), and *Bromus madritensis* ssp. *rubens* (248). Species most negatively associated with axis 1 (burned conditions) were *Plantago ovata* (-130), *Erodium cicutarium* (-83), *Pectocarya heterocarpa* (0), *Lepidium lasiocarpum* (41), *Malacothrix glabrata* (48), and *Schismus* spp. (71). All other species had scores ranging from 105 to 239, which are indicative of unburned conditions (figure 5).



**Figure 3.** Relative cover of invasive annual forbs (black), invasive annual grasses (white), and native annual plants (grey) in paired unburned and burned stands. Numbers below x-axis refer to site names, which also indicate years since burn.

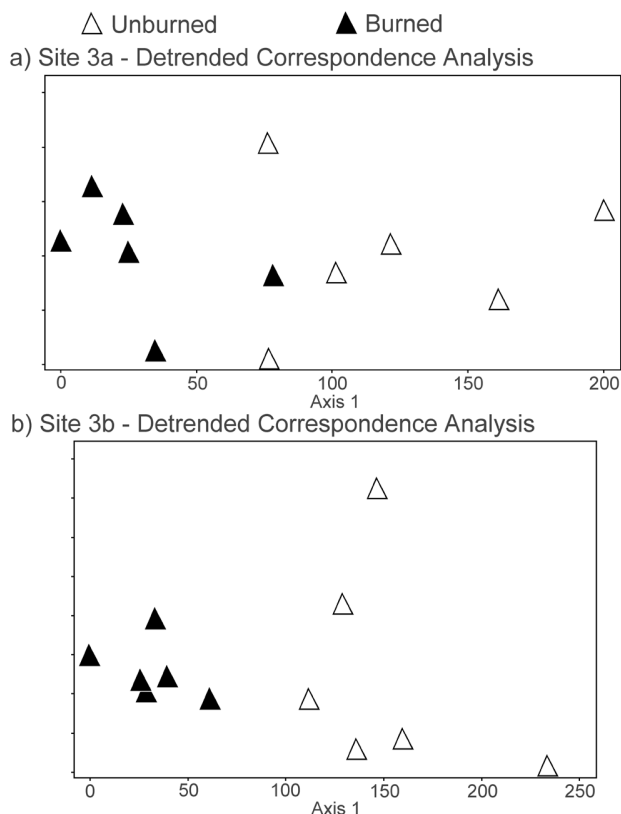
**Impact of Fire on Perennial Plants**

Live shrub cover was decreased by fires that had occurred three years prior to sampling (table 1). However, shrub cover did not show differences between burned and unburned vegetation by 10 years or more after fire. The increase in shrub cover in the two oldest burned stands (13 and 29) was due to recruitment by *Encelia farinosa* (table 1). Shrub cover was very low in both unburned and burned stands at site 10 (table 1); thus, no difference was detected at the 1 m<sup>2</sup> scale. Shrub richness was also compared between paired burned and unburned stands. At the 1 m<sup>2</sup> scale, only sites 3a and 3b experienced decreased shrub richness in the burned stands (table 1). However, at the larger, mod-NAWMA plot scale, shrub richness was reduced in burned stands compared to unburned reference stands at all five study sites (table 1).



**Figure 4.** Mean species richness of native annual plants at each of the six study sites, in unburned and burned stands of CBS at the 1 m<sup>2</sup> quadrat (a) and mod-NAWMA plot (b) scales. \* indicate significant differences between paired stands ( $P = 0.05$ ).





**Figure 5.** Ordinations of mean annual plant cover in burned and paired unburned plots from sites 3a and 3b using detrended correspondence analysis.

## DISCUSSION

### Impact of Fire on Soils

The lack of elevated  $\text{NH}_4^+$  and  $\text{NO}_3^-$  in the two most recently burned stands was surprising, but may be explained because post-fire increases in these sources of N could be ephemeral and sampling soils three years after the burn may have missed any increase had it existed (Raison 1979). Soil pH increased after fire, which is consistent with other studies from different vegetation types (Raison 1979). In general, it appears that fires do not result in long-lasting effects on the soil parameters measured. However, the high cover of bare ground in the oldest burned stands may be indicative of higher soil erosion rates due to a desertification-like process (*sensu* Belnap 1995) that results when a site burns. Fires greatly reduced long-lived perennials, like *Larrea tridentata*, *Ambrosia dumosa*, and *Krameria greyi*, which are important for accumulating windblown soil and organic matter. Because the study area is affected by high winds (Rao and others 2011) and because *Encelia farinosa*, which became dominant, is not effective at accumulating organic matter in its

understory because of its architecture (Muller 1953), increased bare ground cover may be a result.

### Impact of Fire on Vegetation

Fire increased exotic annual grass cover within the first three years after a fire (sites 3a and 3b), due almost entirely to *Schismus* spp, which has also been documented in other cases (Cave and Patten 1984; Minnich and Dezzani 1998; Brooks 2002). Fire also significantly increased exotic forb cover at site 3b, due to a non-significant increase in *Brassica tournefortii* and a significant increase in *Erodium cicutarium* (Steers 2008). Again, post-fire increases in *E. cicutarium* have been documented in other cases (Brown and Minnich 1986; Minnich and Dezzani 1998; Brooks and Matchett 2003). No other studies to our knowledge have reported a fire response by *B. tournefortii*; however, it appears this species is capable of responding positively. *Bromus madritensis* ssp. *rubens* typically decreases immediately following fire (Brooks 2002; Abella and others 2009) but no difference was detected in three year old burned stands in this study. This lack of response may be because this species was too infrequent and scarce for statistical analyses. Recent droughts have decreased *B. madritensis* across the landscape of the study area (Minnich 2008). At all other sites with 10 year or older burned stands, invasive annual vegetation did not differ between paired burned and unburned stands. The lack of difference between older paired stands was primarily because invasive plant abundance was very high in both paired stands. Had these older burned stands been sampled when they first burned, it is possible that significant differences could have been apparent.

Unfortunately, as invasive species become more abundant in new portions of the desert it is highly likely they will reduce native annual components of the vegetation. However, the ability of invasives to dramatically decrease native annual components of the vegetation in unburned conditions may be limited to regions of the desert where other factors positively associated with invasive annual plant abundance are elevated, such as nitrogen deposition, precipitation, and wind (Brooks and Esque 2002; Brooks and Matchett 2006; Brooks and Berry 2006; Rao and others 2010; Rao and others 2011). Other regions of the desert that are currently less impacted by these environmental factors may not suffer from invasives

and fire to the same extent as our study area, which has high wind and N deposition that disperse invasives and increase their productivity, coupled with precipitation amounts to produce sufficient fuel in many years (Rao and others 2010; Rao and others 2011) and elevated ignition sources (Brooks and Esque 2002).

Unfortunately, sites with the highest native annual plant abundance and richness experienced some of the largest relative increases in invasive plants once burned, and some of the greatest losses in native annual plant abundance and richness. Decreased annual species richness has been noted previously (Brooks 2002), but where *Schismus* spp. and *Erodium cicutarium* are less abundant or absent, fires can actually increase annual species richness immediately after fire (Abella and others 2009; Steers, unpublished data). Impacts to native annuals from fire, which have been observed under shrubs, have been attributed to lethal temperatures (Brooks 2002), but post-fire decreases in abundance and species richness of native annuals can also result from invasive plant competition (Brooks 2002; Steers and Allen 2010; in press).

Species responses to fire in the recently burned stands (3a and 3b) can be interpreted from DCA ordinations (Vamstad and Rotenberry 2010). In general, annual plant species that were not impacted or responded positively to fire were those species that seemed to be associated with inter-shrub spaces while species associated with the areas under shrubs were typically more impacted (R. Steers, personal observation during field sampling of study sites, March through April 2008). For example, *Bromus madritensis* ssp. *rubens*, *Phacelia distans*, and *Pholistoma membranaceum* were indicative of shrub understories and were associated with unburned plots. *Erodium cicutarium*, *Plantago ovata*, *Loeflingia squarrosa*, *Pectocarya* spp. and *Schismus* spp. were typical of intershrub spaces and were more closely associated with burned plots in the DCA. Post-fire increases in *Plantago ovata* have been documented previously (Brown and Minnich 1986; Cave and Patten 1984; Brooks 2002) but responses by the other annual species found in this study, besides exotic annuals, are largely unreported in the literature. Based on this study, it appears that once exotic annuals become abundant, native annuals decline, with or without fire, although fire can amplify this outcome. Lastly the impact of fire on perennial

components of the vegetation was severe and long-lasting, similar to findings from other studies (Abella 2009).

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**Appendix 1.** Species frequency during March 2008 sampling of creosote bush scrub vegetation of the study sites. Frequency of perennial and annual species found in the six mod-NAWMA plots per stand per site, with values varying from 0 to 6. Numbers refer to site names, which also indicate years since burn, UB = unburned stand, B = paired burned stand.

| Family                       | Species                         | 3a |   | 3b |   | 10 |   | 13 |   | 29 |   |
|------------------------------|---------------------------------|----|---|----|---|----|---|----|---|----|---|
|                              |                                 | UB | B | UB | B | UB | B | UB | B | UB | B |
| <b>HERBACEOUS PERENNIALS</b> |                                 |    |   |    |   |    |   |    |   |    |   |
| Asteraceae                   | <i>Stephanomeria pauciflora</i> |    |   |    | 1 |    | 2 | 1  | 4 |    | 1 |
| Cucurbitaceae                | <i>Cucurbita palmata</i>        |    |   |    | 1 |    |   |    |   |    |   |
| Euphorbiaceae                | <i>Chamaesyce polycarpa</i>     |    |   |    | 1 |    |   |    |   | 1  | 4 |
|                              | <i>Ditaxis neomexicana</i>      |    |   |    |   |    |   |    |   | 1  | 1 |
|                              | <i>Stillingia linearifolia</i>  |    |   |    |   |    |   |    | 1 |    |   |
| Liliaceae                    | <i>Dichelostemma capitatum</i>  |    |   | 1  | 2 |    |   |    |   | 3  |   |
| Nyctaginaceae                | <i>Mirabilis bigelovii</i>      |    |   | 1  | 3 |    | 1 | 5  | 3 | 3  | 6 |
| Poaceae                      | <i>Pleuraphis rigida</i>        |    |   |    |   |    |   |    |   | 1  |   |
| <b>SHRUBS AND CACTI</b>      |                                 |    |   |    |   |    |   |    |   |    |   |
| Asclepiadaceae               | <i>Asclepias subulata</i>       |    |   |    |   |    |   |    | 1 |    |   |
|                              | <i>Acamptopappus</i>            |    |   |    |   |    |   |    |   |    |   |
| Asteraceae                   | <i>sphaerocephalus</i>          |    |   |    |   |    |   |    | 1 |    |   |
|                              | <i>Ambrosia dumosa</i>          | 6  |   | 6  | 6 | 3  |   | 5  | 5 | 6  | 1 |
|                              | <i>Bebbia juncea</i>            |    |   |    |   |    |   |    | 2 |    |   |
|                              | <i>Encelia farinosa</i>         | 1  | 1 | 4  | 4 |    |   | 6  | 5 | 5  | 6 |
|                              | <i>Hymenoclea salsola</i>       |    |   | 1  |   |    |   |    | 1 |    | 1 |
| Cactaceae                    | <i>Echinocereus engelmannii</i> | 1  |   |    |   |    |   |    |   | 1  |   |
|                              | <i>Ferocactus cylindraceus</i>  |    |   |    |   |    |   |    | 1 | 6  | 2 |
|                              | <i>Mamillaria tetrancistra</i>  |    |   |    |   |    |   |    |   | 1  |   |
|                              | <i>Opuntia basilaris</i>        |    |   |    |   |    |   |    |   | 1  |   |
|                              | <i>O. bigelovii</i>             |    |   |    |   |    |   |    |   | 3  | 1 |
|                              | <i>O. echinocarpa</i>           |    |   | 2  |   |    |   |    |   | 2  |   |
| Ephedraceae                  | <i>Ephedra californica</i>      |    |   | 5  |   | 1  |   | 1  |   | 1  |   |
| Fabaceae                     | <i>Psoralea arborescens</i>     |    |   | 3  | 1 |    |   |    |   |    |   |
| Krameriaceae                 | <i>Krameria grayi</i>           |    |   | 4  |   | 6  |   | 4  |   | 6  |   |
| Liliaceae                    | <i>Yucca schidigera</i>         |    |   | 2  |   |    |   |    |   |    |   |
| Polygonaceae                 | <i>Eriogonum fasciculatum</i>   |    |   |    |   |    |   | 1  |   |    |   |
| Rutaceae                     | <i>Thamnosma montana</i>        |    |   |    |   |    |   | 1  |   |    |   |
| Zygophyllaceae               | <i>Larrea tridentata</i>        | 6  | 2 | 6  | 1 | 6  | 4 | 6  |   | 6  |   |
| <b>INVASIVE FORBS</b>        |                                 |    |   |    |   |    |   |    |   |    |   |
| Asteraceae                   | <i>Sonchus oleraceus</i>        |    |   |    |   |    |   |    |   | 1  |   |
| Brassicaceae                 | <i>Brassica tournefortii</i>    | 6  | 6 | 6  | 6 | 6  | 6 | 6  | 6 | 6  | 6 |
| Geraniaceae                  | <i>Erodium cicutarium</i>       | 6  | 6 | 6  | 6 | 6  | 6 | 6  | 6 | 6  | 6 |
| <b>INVASIVE GRASSES</b>      |                                 |    |   |    |   |    |   |    |   |    |   |
| Poaceae                      | <i>Bromus diandrus</i>          |    |   |    |   |    |   | 1  |   |    |   |
|                              | <i>B. madritensis</i>           | 4  |   | 6  | 5 | 1  |   | 6  | 2 | 4  | 1 |
|                              | <i>Hordeum murinum</i>          | 1  | 1 |    |   |    |   |    |   |    |   |
|                              | <i>Schismus spp.</i>            | 6  | 6 | 6  | 6 | 6  | 6 | 6  | 6 | 6  | 6 |
| <b>NATIVE ANNUALS</b>        |                                 |    |   |    |   |    |   |    |   |    |   |
| Asteraceae                   | <i>Chaenactis fremontii</i>     | 6  | 6 | 6  | 6 | 1  | 1 | 3  | 1 | 3  | 4 |
|                              | <i>Eriophyllum wallacei</i>     |    | 1 | 1  | 1 |    |   |    |   |    |   |
|                              | <i>Filago californica</i>       | 6  | 6 | 1  |   | 6  | 6 |    |   | 6  | 4 |
|                              | <i>F. depressa</i>              |    |   | 6  | 6 |    |   |    |   |    |   |

**Appendix 1 (cont).** Species frequency during March 2008 sampling of creosote bush scrub vegetation of the study sites.

|                 |                                       |   |   |   |   |   |   |   |   |   |   |
|-----------------|---------------------------------------|---|---|---|---|---|---|---|---|---|---|
| Asteraceae      | <i>Lasthenia californica</i>          |   | 1 |   |   |   |   | 1 | 1 |   |   |
|                 | <i>L. coronaria</i>                   |   |   | 1 | 2 |   |   |   |   |   |   |
|                 | <i>Malacothrix glabrata</i>           | 6 | 6 | 6 | 6 | 6 | 5 | 4 | 2 | 2 | 3 |
|                 | <i>Rafinesquia neomexicana</i>        | 2 |   | 6 | 5 |   |   | 3 |   |   |   |
|                 | <i>Stephanomeria exigua</i>           | 5 | 3 |   | 1 |   |   |   |   | 1 | 2 |
|                 | <i>Stylocline gnaphaloides</i>        | 1 |   | 4 | 4 |   |   |   |   |   |   |
| Boraginaceae    | <i>Cryptantha angustifolia</i>        |   |   |   | 3 |   |   |   |   |   |   |
|                 | <i>C. barbiger a var. fergusoniae</i> | 2 |   | 6 | 6 |   |   | 6 | 4 | 1 | 6 |
|                 | <i>C. circumscissa</i>                |   |   | 3 | 3 |   |   |   |   |   |   |
|                 | <i>C. decipiens</i>                   |   |   | 1 |   |   |   |   |   |   |   |
|                 | <i>C. maritima</i>                    |   |   | 5 |   |   |   | 1 |   |   |   |
|                 | <i>C. micrantha</i>                   | 1 |   | 3 | 5 |   |   |   |   |   |   |
|                 | <i>C. nevadensis</i>                  |   |   | 1 |   |   |   |   |   |   |   |
|                 | <i>Pectocarya heterocarpa</i>         | 3 | 4 | 6 | 6 | 2 | 6 | 4 | 6 | 1 |   |
|                 | <i>P. linearis</i>                    | 6 | 5 | 6 | 2 | 6 | 6 | 6 | 6 | 4 | 3 |
|                 | <i>P. platycarpa</i>                  |   |   | 4 |   |   |   |   |   |   |   |
|                 | <i>P. recurvata</i>                   | 3 | 1 | 6 | 6 |   |   | 6 | 6 | 3 | 1 |
| Brassicaceae    | <i>Lepidium lasiocarpum</i>           |   |   | 6 | 4 |   |   | 1 | 1 | 1 |   |
|                 | <i>Tropidocarpum gracile</i>          |   |   |   |   |   |   | 1 |   | 4 | 1 |
| Campanulaceae   | <i>Nemacladus longiflorus</i>         |   |   |   | 1 |   |   |   |   |   |   |
| Caryophyllaceae | <i>Loeflingia squarrosa</i>           | 2 | 5 | 6 | 5 |   | 4 |   |   |   |   |
| Crassulaceae    | <i>Crassula connata</i>               | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 4 | 6 | 6 |
| Fabaceae        | <i>Lotus strigosus</i>                | 6 | 4 | 4 | 5 | 6 | 6 |   |   | 2 | 1 |
| Hydrophyllaceae | <i>Emmenanthe penduliflora</i>        |   |   |   | 3 |   |   |   |   |   |   |
|                 | <i>P. distans</i>                     | 1 |   | 6 | 6 |   |   | 3 |   |   |   |
|                 | <i>Pholistoma membranaceum</i>        | 6 |   | 6 | 3 |   |   | 6 |   | 5 |   |
| Lamiaceae       | <i>Salvia columbariae</i>             |   |   | 1 |   |   |   | 1 |   |   |   |
| Loasaceae       | <i>Mentzelia sp.</i>                  |   |   | 2 | 1 |   |   | 1 |   |   |   |
| Onagraceae      | <i>Camissonia californica</i>         |   |   | 5 | 6 |   |   |   |   |   | 1 |
|                 | <i>C. pallida</i>                     | 6 | 6 | 6 | 6 | 2 | 3 | 1 |   |   | 1 |
| Papaveraceae    | <i>Eschscholzia minutiflora</i>       |   |   |   | 2 |   |   |   |   |   |   |
| Plantaginaceae  | <i>Plantago ovata</i>                 | 1 |   |   | 6 |   |   |   |   |   |   |
| Poaceae         | <i>V. octoflora</i>                   | 6 | 1 | 6 | 5 | 4 | 3 | 1 |   |   |   |
| Polemoniaceae   | <i>Eriastrum diffusum</i>             |   |   | 3 | 3 |   |   |   |   |   |   |
|                 | <i>Eriastrum sp.</i>                  |   |   | 3 | 3 |   |   |   |   |   |   |
|                 | <i>G. maculata</i>                    |   |   | 2 |   |   |   |   |   |   |   |
|                 | <i>Linanthus bigelovii</i>            |   |   | 1 |   |   |   |   |   |   |   |
|                 | <i>Loeseliastrum schottii</i>         |   |   | 3 | 2 |   |   |   |   |   |   |
| Polygonaceae    | <i>Chorizanthe brevicornu</i>         | 1 | 2 | 6 | 6 |   |   | 4 | 1 |   |   |
|                 | <i>C. watsonii</i>                    |   |   |   | 2 |   |   |   |   |   |   |
|                 | <i>Pterostegia drymarioides</i>       |   |   | 2 | 3 |   |   |   |   |   |   |
| Portulacaceae   | <i>Calyptidium monandrum</i>          |   |   | 6 | 6 |   |   |   |   |   |   |