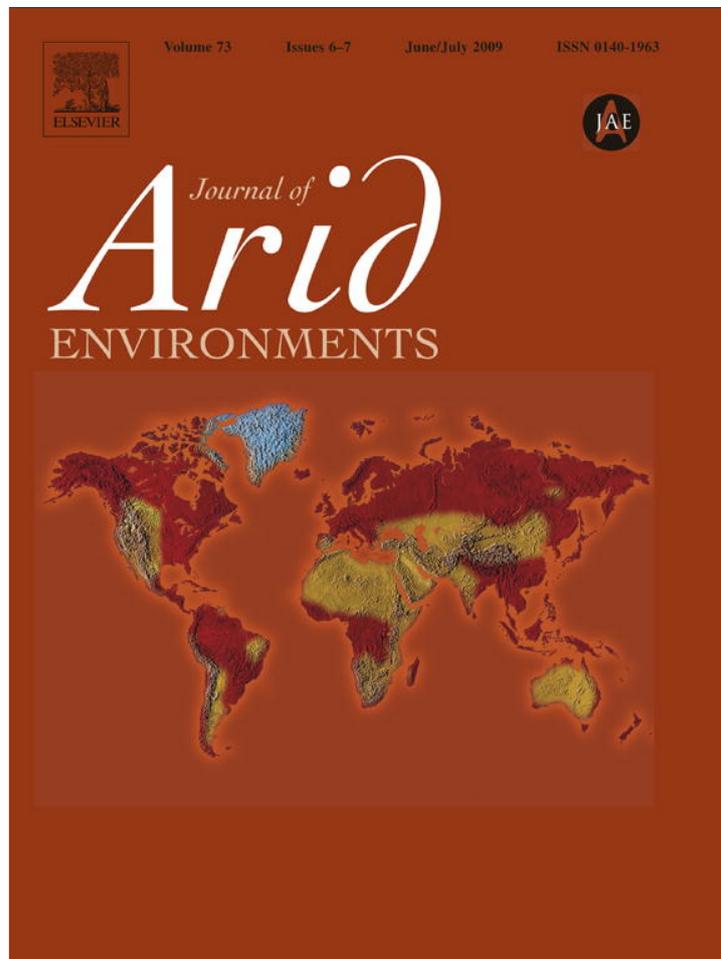


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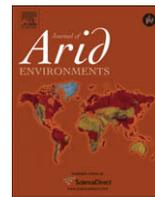
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Effects of fire and environmental variables on plant structure and composition in grazed salt desert shrublands of the Great Basin (USA)

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ABSTRACT

Fire in shrub-dominated portions of the Great Basin, largely fueled by non-native annuals such as *Bromus tectorum*, has become an important structuring force altering vegetation composition and soil characteristics. The extent to which fire affects native species in drier portions of the Great Basin, termed salt desert, is poorly documented. We conducted a survey of grazed salt desert habitat in northwestern Nevada 5 years after wildfires burned 650,000 ha, with the goal of investigating community response to fire and factors correlating with post-fire recovery. We found that recruitment of a dominant shrub, *Artemisia spinescens*, is severely restricted following fire: it occurred in only 2 of the 24 burned sites. The co-dominant shrub, *Atriplex confertifolia*, occurred in most burned sites although on average its percent cover was one-third lower than adjacent unburned sites. Biotic soil crust cover was four times lower, and non-native species cover 5 times higher, in burned sites compared to unburned. Ordination analyses confirmed differences among plant communities in burned versus unburned sites, with environmental variables soil conductivity, plant litter, soil potassium (K^+) and pH explaining 38% of the variance in community composition. However, we found no environmental predictors of recovery for native species in burned sites. Future recruitment is likely to be further limited, as fire frequency in the salt desert is expected to increase with invasion by non-native annual grasses and with global climate change.

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1. Introduction

While fire has long been recognized as an important ecological and evolutionary force in structuring vegetation, human influences on the landscape are resulting in fire regime characteristics that may be outside the evolutionary history of the plants in those habitats. For example, fire frequencies have increased dramatically in the Great Basin following the introduction of *Bromus tectorum* L. (cheatgrass), a non-native annual grass from Eurasia, which has resulted in a conversion of shrubland to annual grassland in a sizeable area of the region (Whisenant, 1990). This fire-driven vegetation shift has resulted in loss of habitat, resources and consequently declining populations of other species such as

American badgers (Eldridge, 2004) and Townsend's ground squirrel (Groves and Steenhof, 1988; Yensen et al., 1992), the latter of which is considered a keystone species for a number of birds of prey in sagebrush steppe habitat (Yensen et al., 1992). However, despite the general consensus that the grass–fire cycle continues to affect ever greater areas, patches of recovering native plant species persist and are regularly observed within the burned matrix (Meyer et al., 1998; M. Zelinski, unpublished data; Whisenant, 1990). These burned patches showing native species recovery are of particular interest to both land managers and ecologists.

The effects of fire in the Great Basin have been well-documented in both sagebrush communities (Klemmenson and Smith, 1964; Pickford, 1932; Whisenant, 1990) and on higher-elevation habitats such as pinyon–juniper (Everett and Ward, 1984; Tausch and West, 1988). Salt desert communities, dominated by drought and salt-tolerant plant species of the chenopod family, have been even less studied although they extend over 22% of the total area of the Great Basin (Wisdom et al., 2003). They tend to occur on soils that have higher salinity and lower rainfall compared to their more mesic upland counterparts (Billings, 1949) and some communities periodically experience periods of soil saturation, all of which have been shown to cause mortality of the dominant shrubs (Ewing and

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Dobrowolski, 1992). Because of the relatively unique characteristics of this community, post-fire recovery patterns may be different from their upland counterparts, but these patterns have not yet been described.

There is a wide array of biological and environmental characteristics of sites that have been demonstrated to help determine post-fire recovery and abundance of native species. These factors include the relative abundance of resprouting species versus obligate seeders, characteristics of the fire itself, and proximity of sites to native seed sources (Brooks et al., 2004). Other factors important for native species recovery are longevity or abundance of seedbank (Valbuena and Trabaud, 2001), species diversity of the matrix surrounding the recovering or reestablishing patch (Longland and Bateman, 2002), and climatic factors and fire intensity (D'Antonio et al., 2000). Interference from quickly recolonizing non-native species can be an important factor for native species recovery (Jessop and Anderson, 2007). The potential productivity of a site, determined in part by innate soil characteristics such as nutrient availability, water-holding capacity (texture) and salinity, is also thought to affect regeneration following fire (Jessop and Anderson, 2007). Soil crusts are recognized as having important effects on plant colonization and growth in arid environments (Belnap and Eldridge, 2001). The extent to which crusts remain intact following fire may therefore contribute to recovery of native plant communities.

Recruitment of some native shrubs after fire has been observed in several salt desert areas (Meyer et al., 1998), but these researchers note that quantitative data are lacking. We were interested in examining first whether common pre-fire native species are recruiting after fire in the salt desert. We then considered whether there were easily measurable environmental parameters that might predict the extent of recovery, or the abundance of native versus non-native species in salt desert habitat following fire. We hypothesized that the extent to which native species regenerate or recover in burned sites may depend on a suite of factors, including the cover of invasive non-natives, fire intensity, and environmental variables such as soil texture and nutrient status, and cover of soil biotic crusts. Dynamics of recovery could be quite different in ungrazed salt desert; our study areas however were grazed before fire and remain grazed. Therefore, our questions and inferences are based within the context of a grazed salt desert system.

2. Materials and methods

In June 2004 we surveyed a total of 24 sites that burned in 1999 plus 10 adjacent unburned sites in salt desert habitat of the Great Basin in the northwestern region of Nevada. Our sampling area encompassed $\sim 27 \text{ km}^2$ across two large watersheds of $\sim 750 \text{ km}^2$ total area. The mean annual precipitation of the area (averaged over the last 55 years) is 20.1 cm, but one watershed ("Rye Patch") has slightly higher annual precipitation than the other ("Sage Valley") (www.wrcc.dri.edu). Fig. 1 shows monthly precipitation levels for the period between the fire (1999) and our sampling (2004), with above-average rainfall the year preceding the fire (National Climatic Data Center, www.ncdc.noaa.gov). The climate is characterized by cold, wet winters (average minimum January temperature 7.9°C) and warm, dry summers (average maximum July temperature 34.6°C). In Sage Valley, sheep grazing has been a long-term use and occurred during the winter months beginning 2 years after the fire. Rye Patch is grazed lightly by cattle also during the winter.

The sites we surveyed burned in July 1999, when an estimated 78 wildfires burned a total of 650,000 ha in northern Nevada. The winters of 1998 and 1999 had above-average rainfall (Fig. 1)

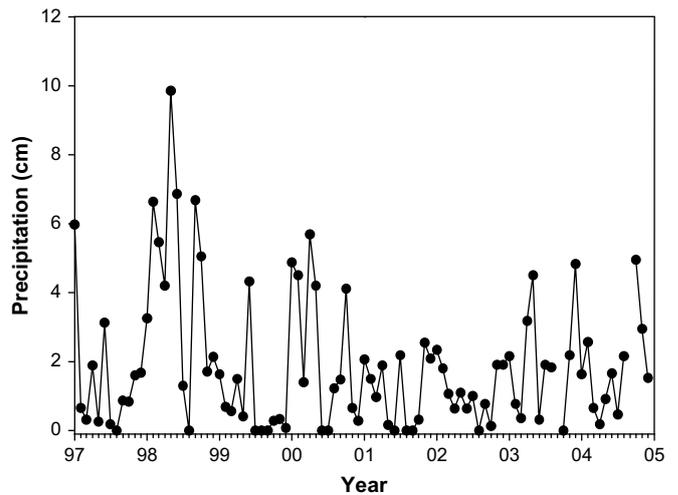


Fig. 1. Mean monthly precipitation (cm) from 1997 to 2005, encompassing wildfire event (1999) and sampling (2004).

resulting in abundant growth of *B. tectorum* which provided the fuel to carry fire. In 2004, we randomly located sites to survey in each watershed using TOPO! software (www.nationalgeographic.com) and a USGS map providing the outline of the burns. We noted the GPS positions of our randomly selected locations and then used a hand-held GPS unit (Garmin GPSMAP76) to find the approximate site location on the ground. Fewer unburned sites were located because across the two watersheds, there was less unburned compared to burned habitat and we wanted to locate all sites within an elevational range that reflected salt desert habitat (i.e., 700–1600 m). Unburned sites were all located within the same regional climate, with the same regional species pool, relief and parent material as the burned sites. Examination of aerial photographs taken before these fires confirmed that species composition of dominant shrubs was similar between burned and unburned areas, and that no obvious discontinuities existed that would cause the fire to stop where it did. In most cases, a fire break (i.e., road) separated burned from unburned sites that we sampled. For these reasons, we are fairly confident that the unburned sites are adequate proxies for what the burned sites looked like before fire. Nonetheless, we emphasize that inference is not based on experimental manipulation, which is virtually impossible with an unplanned large-scale disturbance such as wildfire.

At each site, we placed four 30-m transects parallel to each other and separated by 10-m. Along each transect we randomly located four 1-m² plots. In each plot we measured density and cover of all vascular plant species, including the dominant native shrubs, which were mainly *Atriplex confertifolia* (Torrey & Fremont) S. Watson (shadscale) and *Artemisia spinescens* D.C. Eaton in Wats. (budsage), both of which are obligate seeders and do not resprout after fire. Cover was estimated using cover classes (sensu Daubenmire, 1959) and averaged between two observers. We simultaneously noted % cover of rock, bare soil, and soil biotic crusts in all sixteen plots at each site. We counted the number of burned stumps of shrubs in each plot. Because measures of fire intensity are usually only available for prescribed fire, we used a proxy for fire intensity: the diameter of the smallest branch left on the shrub skeleton, a representation of biomass loss where the greater the stem diameter left on the burned shrub, the higher the fire intensity (Moreno and Oechel, 1989; Perez and Moreno, 1998). A broader scale estimate of native shrub density was obtained by walking each of the four 30-m transects and noting every shrub individual of any species in a 1-m width. For each individual found we

measured the length of the major axis of the shrub at the widest diameter, assigning each to a size class: seedling (<10 cm), small (10–30 cm), medium (30–60), and large (>60 cm). At each site we collected three mineral soil samples (each was a composite of two cores measuring 3 cm in diameter and 12 cm depth). We returned these soils to the laboratory and measured texture using a standard hydrometer approach, nutrient cations (exchangeable sodium [Na⁺], magnesium [Mg⁺], potassium [K⁺] and calcium [Ca²⁺]) (measured at UC Davis Soil Analytical Laboratory), total carbon (C) and nitrogen (N) (Carlo Erba Fisons CN analyzer), pH and conductivity.

2.1. Statistical analysis

Because we were particularly interested in recruitment patterns of native shrubs (the dominant feature of these communities) within and between watersheds as a function of fire, we used ANOVA to analyze differences in the average density (number of individuals per square meter) in each size class of shrubs with fire treatment (burned versus unburned), watershed, and size class as fixed main effects. The two dominant native shrub species were analyzed separately. We also analyzed the effect of fire and watershed location on % cover of all groups of species, and all environmental variables, with two-way ANOVA. A separate ANOVA was conducted for each group or variable. We tested assumptions of normality and homogeneity of variance by inspecting residual plots (normal probability plots, histograms, and residual–estimate scatter plots). All analyses were conducted with SYSTAT (SYSTAT 11, 2004).

We used multivariate analyses to examine floristic and environmental gradients in the data, and to assess the relative importance of environmental factors in determining the observed species distributions. We used PC-ORD (v 4.25) to perform a Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA). The two approaches examine community composition in different ways (Clark et al., 1999). DCA is an indirect gradient analysis technique (Hill and Gauch, 1980) that detects gradients in species composition from species abundance data, and relates species directly to the samples or plots where they occur. CCA is a direct gradient analysis technique (ter Braak and Prentice, 1988) that relates species composition to measured environmental variables. We first considered burned and unburned sites together, then subsequently analyzed the burned sites only. A noteworthy characteristic of this system is the depauperate nature of the species pool; overall, we had relatively few species to include in our analyses. When all sites were considered, the matrix consisted of the seven species that had sufficient % cover to be included in the analyses. We separated shrub cover into live and dead. This resulted in a matrix of ten species “classes.” The matrix included: *B. tectorum*; *Halogeton glomeratus* (Bieb.) Mey in Ledeb. (halogeton); *Salsola paulsenii* Litv. (Russian thistle); *A. confertifolia*, *A. spinescens*; native grasses (*Elymus elymoides* [Raf.] Swezey [squirrel tail grass]; plus *Achnatherum hymenoides* (Roem. & Schult.) Barkw. [Indian ricegrass]); *Krascheninnikovia lanata* (Pursh) A. Meeuse & A. Smit (winterfat); and ephemeral annual forbs (including genera such as *Chaenactis*, *Eriastrum*, *Eriogonum* and *Gilia*).

For CCA on all burned and unburned sites, a subset of environmental variables was selected in order to minimize the possibility of false correlations due to the small numbers of observations relative to the number of environmental variables (McCune and Grace, 2002). These included: litter, soil pH, soil conductivity, soil C:N ratio, soil nutrient cations (exchangeable Na⁺, Mg⁺, K⁺ and Ca²⁺), and % sand. CCA was tested using the Monte Carlo simulation algorithm with 150 runs, optimizing column scaling of scores (species) and standardization by centering and normalizing.

For analyses of burned sites only, we separated shrubs by size class in order to extract more information about shrub recruitment following fire. The species matrix included density of the following: *A. confertifolia* (large, medium, small, and seedling size classes), dead *A. confertifolia*, *A. spinescens* (large, medium, and small/seedling size classes), dead *A. spinescens*, *K. lanata*, and native grasses (combined density of *E. elymoides* and *A. hymenoides*). The matrix also included % cover of *B. tectorum*, *S. paulsenii*, and *H. glomeratus*. We combined density and % cover in this matrix by standardizing the data by maximum values in each site (McCune and Grace, 2002). DCA run parameters did not include down-weighting rare species (since so many were “rare” – i.e., <5% cover – in this system) and used 26 segments. For CCA, the subset of environmental variables included for the analysis of burned sites were: soil pH, soil Ca²⁺ and exchangeable Na⁺, soil C:N, % cover of soil biotic crust, fire intensity, and % sand.

As a follow-up to ordination described above, we used linear regression to analyze relationships between various species and some environmental variables. All univariate analyses were conducted with SYSTAT (SYSTAT 11, 2004).

3. Results

Non-native species comprised only 5% cover in the unburned sites we surveyed (Fig. 2a). Total native species, including all shrubs, herbs and grasses, made up ~16% cover in sites that were unburned (Fig. 2b). Virtually all of the unburned sites in this study were dominated by two native shrub species: *A. confertifolia* and *A. spinescens*, with large amounts of open space in between shrubs. Together the shrubs made up the majority of total native cover (~14%) in unburned sites in both watersheds (Fig. 2c). We observed no native grasses in unburned sites in one of the watersheds and in only one unburned site in the other watershed; native grass cover was never greater than 5% in any single plot (Fig. 2f). Another occasional native perennial species in unburned sites was the shrub *K. lanata* (Fig. 2d shows *K. lanata* cover added to the cover of the two dominant shrubs).

In contrast to the unburned sites, *A. spinescens* was almost completely absent from burned sites. It did not occur in any of the burned sites in Rye Patch and occurred in only one of the 13 burned sites in Sage Valley (Fig. 3). *A. confertifolia*, on the other hand, appears to be recruiting continuously based on size distributions in both watersheds since the 1999 fire (Fig. 3). In fact, *A. confertifolia* recruitment appears to be greater in burned than unburned sites: we encountered no *A. confertifolia* seedlings at all in unburned sites in Sage Valley, and an average of only 1.6 seedlings per site in Rye Patch. These differences were statistically significant (watershed × burn × size interaction term, $F_{4,150} = 2.549$, $p = 0.036$ for *A. confertifolia*; $F_{3,120} = 18.396$, $p < 0.001$ for *A. spinescens*). Where *A. confertifolia* and *A. spinescens* were found in burned sites, 85% of *A. spinescens* were in small size classes; nearly half of the *A. confertifolia* (45%) were in medium size classes. Densities of *A. confertifolia* were much greater in the unburned and a lower proportion were in the large size class (Fig. 3). In addition to these differences in shrub frequencies, % cover of the two native shrubs (summed together) was significantly lower in burned compared to unburned sites, as expected ($F_{1,30} = 87.211$, $p < 0.001$; Fig. 2c).

Percent cover of non-native species in burned sites was 5 times greater than in unburned sites ($F_{1,30} = 34.979$, $p < 0.001$), with *B. tectorum*, *S. paulsenii*, and *H. glomeratus* in roughly equal proportions of cover (Fig. 2a). There were large differences between the watersheds in cover of some non-native species, however; in particular, *B. tectorum* cover was only 12% in Rye Patch burned sites versus 32% in Sage Valley. Annual herbs had higher % cover in Rye Patch compared to Sage Valley ($F_{1,30} = 4.851$, $p = 0.035$) but were

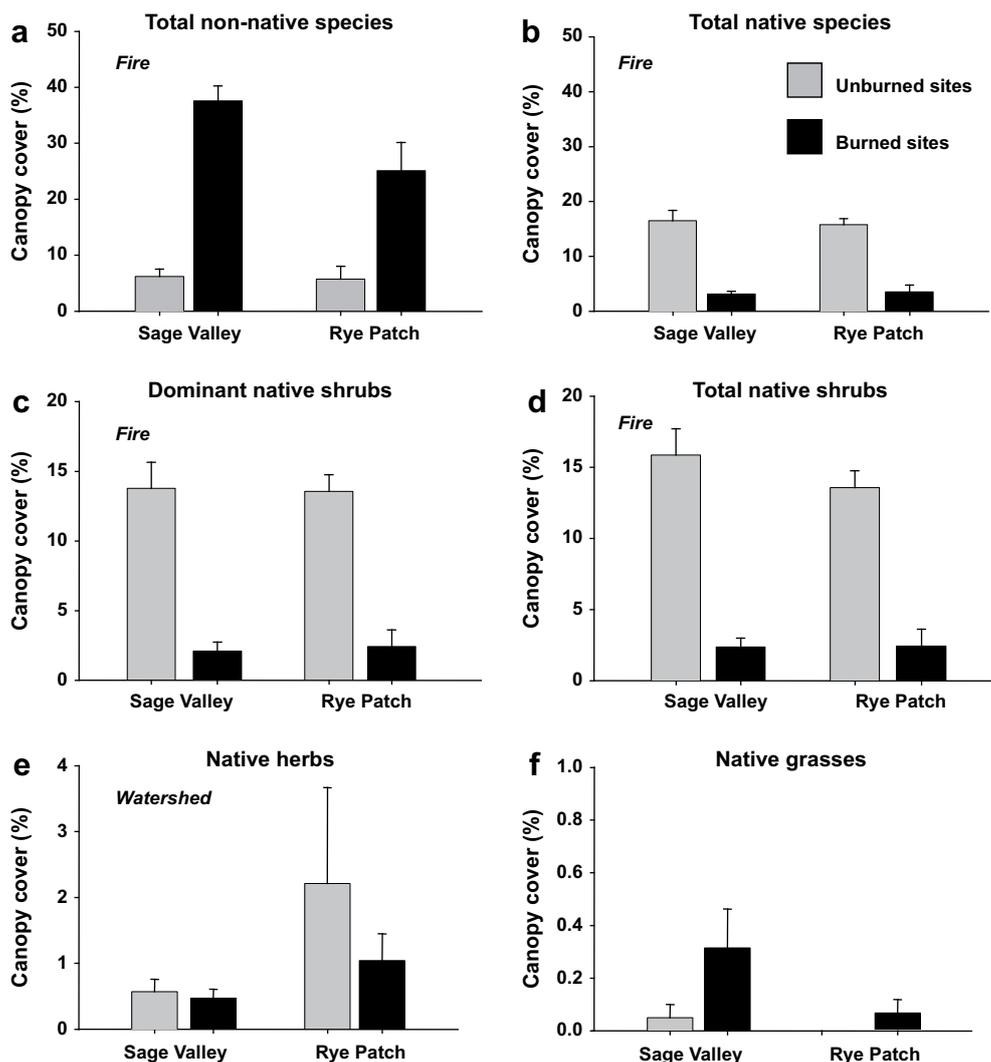


Fig. 2. Percent cover of main groups of species by watershed and burn treatment: a) total non-native species (*B. tectorum*, *S. paulsenii* and *H. glomeratus*); b) total native species (*A. confertifolia*, *A. spinescens*, *K. lanata* [shrubs]; *E. elymoides*, *A. hymenoides* [perennial grasses] and a mix of annual herbs); c) dominant native shrubs *A. confertifolia* and *A. spinescens*; d) dominant shrubs from panel c) plus *K. lanata*; e) native annual herbs including *Chaenactis*, *Eriastrum*, *Eriogonum* and *Gilia* spp.; and f) native perennial grasses *E. elymoides*, *A. hymenoides*. “Fire” or “Watershed” in each panel indicates significant main effects of those factors.

not significantly different in burned compared to unburned sites ($F_{1,30} = 0.932$, $p = 0.340$) (Fig. 2e). Native grasses occurred in many more burned than unburned sites, but their % cover was not significantly different between burned and unburned sites ($F_{1,30} = 1.431$, $p = 0.241$). Native grass cover in burned sites was on average < 1%, making this group a very small component of the total cover in these sites (Fig. 2f). Overall, the total cover of native species (shrubs, herbs, and grasses) was significantly reduced by fire ($F_{1,30} = 111.6$, $p < 0.001$) (Fig. 2b).

Biotic soil crusts comprised a large proportion of total cover in unburned sites (40% and 23% in Rye Patch and Sage Valley, respectively). Crust cover was significantly lower in burned sites, amounting to 13% in Rye Patch and 5% in Sage Valley ($F_{1,30} = 33.547$, $p < 0.001$). The average cover of crust in Rye Patch, across both burned and unburned sites, was significantly greater than the average cover across all Sage Valley sites ($F_{1,30} = 8.947$, $p = 0.006$) (Table 1). Percent cover of bare ground was similar for the two watersheds ($F_{1,30} = 0.080$, $p = 0.780$), with bare ground comprising ~12–15% cover in unburned sites, increasing to about 40% in both watersheds in burned sites ($F_{1,30} = 13.908$, $p = 0.001$) (Table 1).

Soil cations generally differed between the two watersheds, and some were different between burned and unburned sites, with several showing an interaction between watershed and fire (Table 1). Only exchangeable Na^+ was similar across the two watersheds and did not differ between burned and unburned (Table 1). Soil pH and K^+ were higher in burned compared to unburned sites across both watersheds. Rye Patch had almost twice the Ca^{2+} and K^+ as Sage Valley. Rye Patch sites also had greater total soil C and N pools, neither of which differed between burned and unburned sites. Soil conductivity and Mg^{2+} both showed a watershed \times fire interaction: conductivity was higher in burned sites in Rye Patch but there was no difference in Sage Valley, whereas soil Mg^{2+} concentrations were lower in burned sites in Sage Valley but similar in Rye Patch. The sites were different with respect to their soil texture, where sites that burned in Sage Valley had higher sand and less clay compared to the unburned counterparts, and sites that burned in Rye Patch had lower sand and more clay compared to their unburned counterparts. Percent cover of rock at the soil surface did not differ between burned and unburned sites, however. Instead, all sites across Sage Valley were generally rockier (~32%) compared to those in Rye Patch

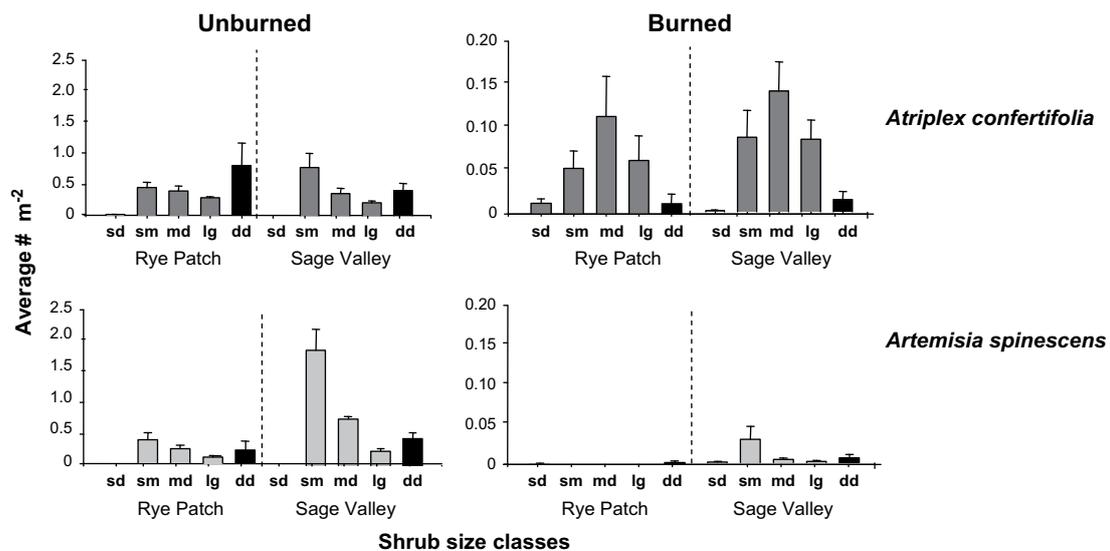


Fig. 3. Average shrub size distribution of a) *Atriplex confertifolia* and b) *Artemisia spinescens* in unburned and burned sites across both watersheds: sd (seedling) < 10 cm diameter; sm (small) 10–30 cm diameter; md (medium) 30–60 cm diameter; lg (large) > 60 cm diameter; dd = dead individuals. Note the different scales on the y-axes.

(~13%). Using the minimum diameter of stem left on shrub skeleton as a proxy for fire intensity, Sage Valley had higher average values and thus a higher fire intensity than Rye Patch (Table 1).

Non-native plant cover increased as soil biotic crust cover decreased in burned sites, although that relationship was only marginally significant in Rye Patch, the watershed with greater crust cover overall ($r^2 = 0.26$, $p = 0.10$ for Rye Patch; $r^2 = 0.02$, $p = 0.55$ for Sage Valley). However, this relationship did not appear to be negative across the full range of crust cover values. Across the Sage Valley sites, when one site with extensive cover of soil crust was removed from the analysis, there was actually an increase in non-native species cover as crust cover increased ($r^2 = 0.11$) noting however, that these sites were at the lower end of the crust cover scale (i.e., between 0 and 4% cover of soil crust). Crust cover was not correlated with native cover except in unburned sites where there was a weak negative relationship (data not shown) most likely reflecting the decline of crusts underneath native shrub canopies (D'Antonio and Haubensak, unpublished data).

3.1. Ordination analyses

The results of the ordination analyses showed that species composition varied considerably between burned and unburned sites, and between watersheds (Fig. 4). The burned sites fall into different portions of ordination space than the unburned sites, with no overlap in a transitional middle area. The burned sites fall on the lower end of the first axis and are associated with invasive annuals, while the unburned are on the upper end of the first axis and are associated with native species and shrubs. DCA eigenvalues support this separation of sites (0.61 and 0.19 for Axes 1 and 2, respectively), with a cumulative r^2 of 0.76.

The CCA results showed that there are strong correlations among species composition across all burned and unburned sites, and the environmental variables we measured. Eigenvalues were fairly high for Axis 1 and moderate for Axis 2 (0.42 for Axis 1, $p = .007$ and 0.22 for Axis 2, $p = .01$), explaining 38% cumulative percentage variance in species composition. Axis 3 had a much lower eigenvalue of 0.09, explaining only 5% of the variance. The species–environment correlations were 0.84 for the first axis and 0.77 for the second. Monte Carlo tests on eigenvalues and

species–environment correlations for both axes were significant ($p < 0.05$). Axis 1 was most strongly conditioned by litter and conductivity, which are inversely related to each other (-0.51 and 0.47 , respectively). Axis 2 was strongly associated with multiple variables, but most strongly with K^+ and pH (0.65 and 0.60, respectively).

When burned sites were considered alone, the DCA eigenvalues indicate strong differences in species distributions among sites

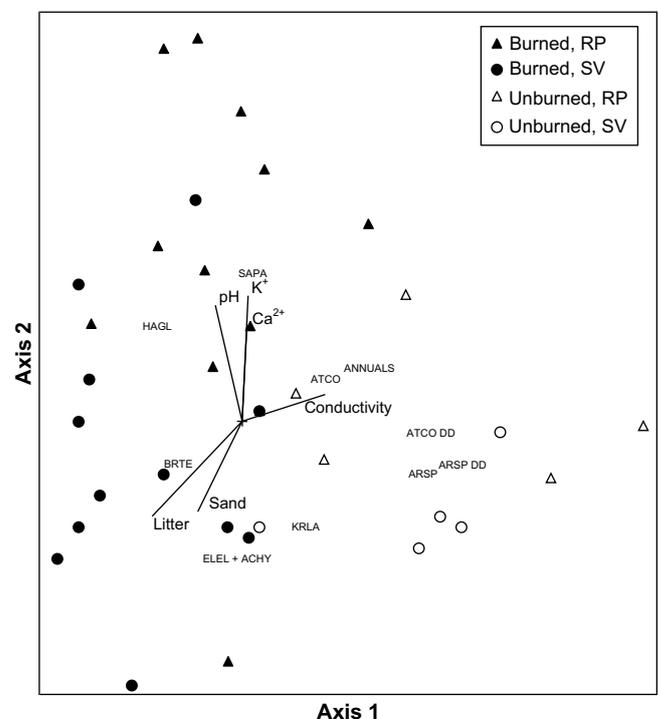


Fig. 4. Canonical correspondence analysis biplot relating plant communities to soil and environmental variables. BRTE = *Bromus tectorum*; ATCO = *Atriplex confertifolia*; ELEM = *Elymus elimoides*; ACHY = *Acnatherum hymenoides*; ARSP = *Artemisia spinescens*; HAGL = *Halogeton glomeratus*; SAPA = *Salsola paulsenii*; KRLA = *Krascheninikovia lanata*; ANNUALS = various ephemeral annuals; DD = dead individuals. Only environmental variables with axis correlation absolute values >0.4 are shown.

Table 1

Soil and environmental parameters measured in burned and unburned sites across both watersheds. Means are presented, with one standard deviation in parentheses. "W" and "F" in last column indicate significant main effects of watershed and fire, respectively; "W × F" indicates a significant interaction between the two factors ($p < 0.05$). Total soil N and C in mg/g soil; soil cations in meq/100 g soil.

	Rye Patch		Sage Valley		
	Burned	Unburned	Burned	Unburned	
<i>Soil variables</i>					
Total soil N	0.07 (0.01)	0.05 (0.003)	0.05 (0.002)	0.05 (0.004)	W
Total soil C	0.64 (0.09)	0.63 (0.13)	0.37 (0.02)	0.39 (0.1)	W
Exchangeable Na ⁺	1.0 (0.15)	1.0 (0.49)	0.70 (0.13)	0.58 (0.08)	
Mg ⁺	2.2 (0.11)	1.9 (0.12)	1.8 (0.09)	2.1 (0.17)	W × F
Ca ²⁺	15.6 (1.71)	13.4 (2.01)	8.4 (1.00)	7.0 (0.80)	W
K ⁺	3.0 (0.20)	2.3 (0.24)	1.8 (0.12)	1.7 (0.15)	W, F
<i>Soil texture</i>					
% sand	64.2 (2.29)	71.4 (2.38)	79.1 (2.00)	70.9 (4.06)	W × F
% silt	30.7 (1.99)	25.0 (1.66)	18.9 (1.66)	25.9 (3.41)	
% clay	5.2 (0.43)	3.4 (0.93)	2.1 (0.47)	3.4 (0.79)	W × F
pH	7.6 (0.2)	7.4 (0.2)	7.3 (0.2)	7.1 (0.1)	W, F
Conductivity	0.71 (0.14)	1.31 (0.13)	0.52 (0.27)	0.57 (0.11)	W × F
<i>Plot variables</i>					
Litter (% cover)	22.6 (3.08)	23.6 (5.39)	33.2 (2.52)	21.0 (2.37)	W × F
Biotic crust (% cover)	9.0 (4.58)	40.4 (8.16)	2.1 (1.29)	23.4 (3.72)	W, F
Rock (% cover)	13.3 (4.17)	15.6 (3.93)	20.1 (5.76)	44.4 (11.11)	W
Bare ground (% cover)	39.0 (1.70)	12.0 (0.90)	38.0 (1.50)	15.0 (3.20)	F
Burned stump (#/m ²)	3.3 (0.32)	n/a	5.7 (0.31)	n/a	
Fire intensity ^a	6.5 (0.50)	n/a	7.9 (0.40)	n/a	W

^a Diameter of smallest stem left on shrub skeleton (mm) as an estimate of mass loss, a proxy for fire intensity (Moreno and Oechel, 1989; Perez and Moreno, 1998).

(Axis 1 = 0.53, Axis 2 = 0.31; cumulative $r^2 = 0.67$). The two watersheds (and sites within watersheds) assume distinct positions in ordination space, demonstrating large differences in species composition. For example, *S. paulsenii* was distributed unevenly across sites, with three of the sites within one watershed containing almost 60% of the total abundance. *A. spinescens* was completely absent from the burned sites, with the exception of one site in Sage Valley. Despite strong differences among sites, the results of the CCA suggest no strong correlations between the species and the particular environmental variables we measured. The eigenvalues were low (0.30 and 0.19 for Axes 1 and 2, respectively), and the Monte Carlo test results corroborated the weak relationship ($p > 0.05$ for both axes).

4. Discussion

Grazed salt desert plant communities following fire have dramatically lower plant cover, are more invaded by non-native species, and are more heterogeneous with respect to both dominant native and non-native species across sites compared to the adjacent unburned habitat. Our data show that 5 years following a major wildfire, cover of one of the native shrub species in burned sites is approximately 30% of that in unburned sites, while the other dominant shrub species is absent. This suggests that recovery of native species in these habitats is occurring slowly, even while there are virtually no detectable differences in soil parameters between burned and unburned sites that might help explain species distribution following fire. However, floristic change may take many decades in arid regions (Whisenant and Wagstaff, 1991), and others have reported post-fire regeneration lags in other salt desert species (e.g., greasewood [Rickard and McShane, 1984]). While we do not have good estimates of rates of recovery following fire in salt desert, some researchers have noted rapid change in

vegetation following grazing cessation (e.g., Alzerreca-Angelo et al., 1998); others have observed similar rates of vegetation change (again, following grazing) as we report here (e.g., Turner, 1971; West, 1979). Our results certainly suggest that recruitment of at least one of the co-dominant shrubs, *A. confertifolia*, is occurring. The years between the fires and our sampling had lower than average annual rainfall (in particular, 2001 and 2002; see Fig. 1), which has likely limited recruitment for these native species. *A. confertifolia*, in particular, has been shown to exhibit high rates of mortality and reductions in cover during drought years (Chambers and Norton, 1993; Turner, 1971).

We estimate that a larger recruitment event occurred for *A. confertifolia* approximately 2–3 years following the 1999 fire due to the high frequency of medium-sized individuals which appear to be 3–4 years old based on preliminary examination for growth rings. Nonetheless, the occurrence of small individuals and seedlings suggests that recruitment is continuing to occur. At this rate, we estimate that it would require at least two more major recruitment events for densities to return to pre-burn levels, assuming burns do not recur in this area.

We did not find evidence that the other co-dominant shrub in this community, *A. spinescens*, is recruiting into these sites. We encountered seedlings in only one of the 24 burned sites sampled across the two watersheds, suggesting that this species may be lost from the community for an indefinite period after fire. *A. spinescens* can be highly susceptible to the effects of grazing (Chambers and Norton, 1993), with its relative cover increasing in the absence of grazing (Alzerreca-Angelo et al., 1998; Whisenant and Wagstaff, 1991). Grazing is thus very likely contributing to the lack of *A. spinescens* in our burned sites. We have separate evidence from these sites that *A. spinescens* cover is negatively correlated with *B. tectorum* cover (D'Antonio and Haubensak, unpublished data), so that sites with high *B. tectorum* abundance may have less *A. spinescens* recruitment. However, there is evidence that *B. tectorum*, too, is limited by water availability (Meyer et al., 2001), so perhaps interference from *B. tectorum* would be minimized under drought conditions. Compounding the effects of grazing and competition on *A. spinescens* recovery may be its lack of efficient long-range dispersal. Although we could find no specific information on its dispersal, it likely resembles other sagebrush taxa which generally lack efficient long-range dispersal mechanisms (Marlette and Anderson, 1986; Young and Evans, 1989). *A. confertifolia*, on the other hand, has a persistent seedbank which may play a role in stand reestablishment following fire (Meyer et al., 1998). The seedbank profile of *A. spinescens* has apparently not been studied, but limited evidence from the seedbank of the adjacent shrub-steppe community suggests that the seeds of native perennial species are rare, with *B. tectorum* and other introduced annual seeds outnumbering them by orders of magnitude (Humphrey and Schupp, 2001). The local extirpation of *A. spinescens*, then, may be explained by this suite of factors, including the removal of seed-bearing individuals (by fire) coupled with grazing, competition with non-natives, lack of efficient long-range dispersal, and a transient or non-existent seedbank.

In our study, a dramatic environmental change that occurred with fire was a decrease in the cover of biotic crusts and an increase in the amount of bare ground. Others have reported similar decreases in crust cover with fire (Hilty et al., 2004; Johansen et al., 1984, 1993). There is evidence that crust cover, when intact, inhibits invasion by non-native species (Deines et al., 2007; Evangelista et al., 2004; Kaltenecker et al., 1999; Serpe et al., 2006). The loss of crust by itself may represent a long-term loss since most crusts and their associated organisms take from 14 to 250 years to accumulate (Belnap and Eldridge, 2001) although there is some evidence that algae may recover more quickly (Johansen et al., 1984). However,

our data also suggest this loss may have larger community-level implications (i.e. invasion by non-native species). Across the burned sites in one watershed that we sampled, 26% of the variation in exotic species cover was explained by crust cover. Our data also suggest that *B. tectorum* is not the only non-native species responding to the grass–fire cycle in this system: *S. paulesenii* and *H. glomeratus* increased in similar proportions as *B. tectorum* following fire. Whether they contribute to fuel loads on a similar scale has not been evaluated.

Although our data suggest that fire decreases crust cover and increases bare ground, we did not detect clear and consistent differences in soil characteristics between burned and unburned sites that were associated with plant community composition. The ordination analyses suggest that soil conductivity is associated with plant community structure, with burned sites having lower conductivity overall compared to unburned sites. The burned sites also had less litter cover. These same analyses also suggest that soil pH and K^+ were associated with differences among plant communities, but only with respect to watershed location rather than differences between burned and unburned sites. It is likely that 5 years after fire, any alterations to soil nutrient status may be undetectable. Other studies that have documented increases in soil nutrient cations following wildfire in semi-arid systems (e.g., Blank et al., 1994; DeBano and Klopatek, 1988; Sturgis, 1993) have typically observed those changes in the brief one or two-year window following fire. There is no clear evidence in the literature that those changes persist for more than several years.

4.1. Variability across the landscape

The results of our ordination analyses suggest that no single factor or small subset of factors explains community composition 5 years after fire. DCA eigenvalues consider the gradients in species composition based on abundance data, whereas CCA eigenvalues relate the species composition to measured environmental variables. In general, the DCA eigenvalues were higher than CCA eigenvalues, indicating that species composition is markedly different between sites but that much of this variation is not explained by the environmental variables that were measured (Clark et al., 1999). While soil variables such as conductivity and pH showed some associations with community composition across all sites regardless of fire, there were virtually no relationships among these variables and community composition in burned sites considered separately. There are several factors that may contribute to the lack of a clear relationship. First, some of the variables we measured were relatively homogeneous across burned sites; pH in particular had a coefficient of variation of ~3%. Second, small plot or sample size can also affect detection of these patterns. Third, there are unmeasured variables or gradients that likely affected community composition 5 years after fire, including seedbank profiles or distance from burn perimeter. However, although we did not find simple predictive variables for community recovery, the ordination analyses confirm a high degree of separation among plant communities in burned sites. Both native and non-native species were spread unequally among all sites following fire. In some sites, total native species cover was close to that of unburned (~14%), while in others native species were nearly undetectable (0.01% cover). The cover of non-native species was similarly variable. For example, 60% of the total abundance of *S. paulesenii* was found in three burned sites in one watershed alone. The variability that we observed is consistent with a mosaic of vegetation patches that has become characteristic of the Great Basin flora since the introduction of *B. tectorum* and increased fire frequencies (Knapp, 1996).

Although the two watersheds had similar post-fire cover of native species (approximately 5% total cover of shrubs), the drier watershed had much higher cover of non-native annual cover (nearly 40% versus ~25%). While these watersheds may have had different levels of abundances of non-native species before the fire, this post-fire difference could also be due to water availability, soil factors we did not measure, or different grazing regimes. For example, the weedier watershed is grazed by sheep during the winter and spring, while the wetter watershed is grazed by cattle but at a low stocking density. These differences in timing and use by livestock may be an important contributor to variability over the landscape that can affect post-fire recovery and dominance by non-native species such as *B. tectorum*. Eiswerth and Shonkwiler (2006) found that grazing burned sagebrush-dominated sites nearby our sites, even after a 2-year post-fire rest period, promoted the occurrence of *B. tectorum*. Also, spring grazing has been shown to have much greater negative impacts on vegetation than grazing at other times of the year in the salt desert shrub ecosystem (Whisenant and Wagstaff, 1991). We also noted that the drier watershed may have had a higher fire intensity, which would also contribute to differences in post-fire abundance of non-native versus native species (Brooks et al., 2004).

4.2. Conclusions

The results of this study suggest that 5 years after fire at least one of the native shrubs, *A. confertifolia*, is recruiting in these grazed sites. At the same time, most burned sites are dominated by a mix of non-native annual species, and total native species cover and density are relatively low. While limited occurrences of native species restricted our ability to analyze patterns of recovery and relate them to environmental variables, we nonetheless noted a marked absence of the other co-dominant shrub, *A. spinescens*, in burned sites. Fire will likely recur in these areas, due not only to invasive species like *B. tectorum* but also to global warming which is predicted to increase the fire interval (McKenzie et al., 2004). Thus, future recruitment of native species in salt desert habitat could be expected to be further limited.

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