

Plant Community Patterns in Unburned and Burned Blackbrush (*Coleogyne ramosissima*) Shrublands in the Mojave Desert

Prepared by

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Executive Summary

This report is the first product of a larger research project titled “fire behavior and ecological effects in blackbrush (*Coleogyne ramosissima*) shrublands and invasive annual grasslands of the Mojave Desert.” The results contained herein are baseline comparisons of unburned and burned blackbrush vegetation sampled in spring 2001, prior to the application of experimental fire and herbicide treatments that will begin in spring 2002. The significant findings from these baseline comparisons are that:

- species richness in blackbrush vegetation is not low as is generally believed, and is comparable to other vegetation types
- patterns of species richness can vary significantly between 1- and 1000-m² spatial scales, indicating that vegetation monitoring for species diversity in blackbrush should incorporate multi-scale sampling
- total cover 6-14 years postfire recovered to levels in unburned blackbrush, but cover was still reduced for woody perennials and increased for annual forbs, annual grasses, herbaceous perennials, and perennial grasses
- postfire composition of plant communities can vary widely after blackbrush is burned, but fire generally increases species evenness and decreases species richness
- alien annual grasses do not always dominate postfire landscapes, especially when previous years of low rainfall may have reduced their population densities

At the time this report was prepared, a similar manuscript was submitted by the authors for review in the scientific journal *Western North American Naturalist*. This peer-reviewed journal article will possibly be published in 2003, and copies will be available at that time upon request from the authors. Additional information on this and related research is available online at www.werc.usgs.gov.

Abstract. The blackbrush vegetation type is dominated by *Coleogyne ramosissima*, and this dominance is thought to preclude the coexistence of a wide range of other plant species. Fire can remove blackbrush cover, and possibly increase plant species diversity. Fire may also increase the cover and frequency of alien annual grasses, thereby increasing landscape flammability. We tested these predictions in unburned and burned (6-14 years postfire) blackbrush at 3 sites spanning the range of this vegetation type in the Mojave Desert.

Species richness in unburned blackbrush was not especially low, and was similar to values reported for other vegetation types in western North America. Fire reduced blackbrush cover and thus increased species evenness, but decreased species richness. Native species richness and cover decreased, whereas alien richness and cover increased after burning. Most of the increased alien cover was due to the alien annual forb, *Erodium cicutarium*, and not alien annual grasses. After burning, cover of woody perennials decreased, and cover of annual forbs, annual grasses, herbaceous perennials, and perennial grasses all increased. These results indicate that the effects of fire in blackbrush vary between natives and aliens and among plant life forms, that fire effects on species richness must be evaluated at multiple spatial scales, and early successional postfire landscapes are not always dominated by alien annual grasses.

Introduction

The blackbrush vegetation type occurs at the bioregional transition between the Mojave and Great Basin deserts, from California through Nevada, Arizona, and Utah (Bowns 1973). In the Mojave Desert, blackbrush occupies the elevational zone from approximately 4000 to 5000 ft., above the zone dominated by creosote bush (*Larrea tridentata*) and below the zone dominated by sagebrush (*Artemisia* spp.) (Bradley and Deacon 1967, Randall 1972, Beatley 1976). Blackbrush is dominated by the type species, *Coleogyne ramosissima*, which can comprise 90 to 95% of the total plant cover (Shreve 1942). For clarity in this paper, we refer to the vegetation type as blackbrush, and the type species as *Coleogyne*.

Although 185 species of vascular plants have been found growing within blackbrush (Vasek and Barbour 1988), they are never very abundant except at upper and lower elevational ecotones (Bowns 1973, Beatley 1976, West and Young 2000). Beatley (1976) states, "so nearly complete is the dominance of this shrub species that in areas that are not ecotonal there are only a few associated shrub species, and these occur usually as scattered plants in an otherwise pure stand of *Coleogyne*." Thus, species diversity of higher vascular plants is thought to be relatively low in blackbrush, although this has not been verified.

Most accounts describing the dominance of *Coleogyne* in blackbrush indirectly suggest that high cover of this species results in the competitive exclusion of other plant species (Bowns 1973, Beatley 1976, Bowns and West 1976). If this is true, then reduction of *Coleogyne* cover should lead to increased species diversity. Fire has been used to reduce *Coleogyne* cover and promote the growth of more

palatable rangeland species (Bowns 1973), but the effects of fire on plant species diversity are unknown.

Effects of fire on blackbrush appear to be long-term. There is only one report of *Coleogyne* resprouting after fire (Bates 1984), two reports of seedling establishment by *Coleogyne* after fire (Ellison 1950, Lei 1999), and one report of autogenic succession back to blackbrush after fire (Thatcher 1975). In the latter case, fire intensity was likely very low and *Coleogyne* survival very high, resulting in incomplete removal of *Coleogyne* which allowed the direct reestablishment of the blackbrush vegetation type. Most studies report that blackbrush does not reestablish after fire (Bowns 1973, Beatley 1976, West and Young 2000), even after 37 (Callison et al. 1985) to 71 postfire years (Matt Brooks unpublished data). It may have taken centuries for existing blackbrush stands to become established, since they typically occur on very old soils (Webb et al. 1987). In addition, blackbrush is considered a relictual endemic of arid and semi-arid western North America (Stebbins and Major 1965), and very old stands that established hundreds to thousands of years ago may not be able to reestablish under current climatic and fire regimes.

A wide range of species can dominate after *Coleogyne* is removed by fire (Jensen et al. 1960, Bowns 1973, Wright and Bailey 1982, Bates 1984, Callison et al. 1985). Annuals typically dominate during the first few postfire years, and early successional perennial plants dominate after the first few decades (Jensen et al. 1960, Bates 1983, Callison et al. 1985). Although the species composition can be highly variable (Bowns 1973), the alien annual grasses red brome (*Bromus madritensis* ssp. *rubens*) and cheatgrass (*Bromus tectorum*) are often among the most common postfire species (Jensen et al. 1960, West 1983, Callison et al. 1985).

Alien annual grasses can create a continuous cover of fine fuels that persists for years, thereby facilitating the spread of fire in the Mojave Desert (Brooks 1999). Recurrent fire may increase the cover and frequency of alien annual grasses (Whisenant 1990, D'Antonio and Vitousek 1992), promoting additional fires and possibly replacing long-lived native species in the Mojave Desert (Brooks and Esque 2000, Brooks in review). Slow recruitment rates of *Coleogyne* should make this species particularly sensitive to the effects of recurrent fire. Although blackbrush produces the highest cover of all native vegetation types in the Mojave Desert (up to 51%, Beatley 1975), which is partly why it is considered the most flammable (Bowns 1973, Beatley 1976, West 1983), high cover and frequency of alien annual grasses may create even more flammable fuel conditions (Holmgren 1960).

In this study we report plant community characteristics of unburned and burned blackbrush in the Mojave Desert. We predicted that species diversity in blackbrush would be lower than that reported for other vegetation types in southwestern North America, and that fire would increase species diversity by removing *Coleogyne*. We also predicted that fire would increase cover and frequency of alien annual plants, grass species in particular.

Study area

Three study sites were established from the northeast to the southwest Mojave Desert, in the middle of the blackbrush zone between the upper and lower ecotones in each region. The Beaver Dam site (37°11'17" N, 113°56'39" W, 4040 ft.) was in the Bureau of Land Management, St. George Field Office region of southwestern Utah. The Spring Mountain site (36°01'40" N, 115°33'10" W, 4820 ft.) was in the Spring Mountain National Recreation Area of the Humboldt-Toiyabe National Forest in southern Nevada. The Joshua Tree site (34°03'23" N, 116°19'45" W, 4480 ft.) was located at Joshua Tree National Park in southern California. Each site consisted of mature blackbrush and an adjacent burned area located on similar soils and topography. Burned areas were created by a wildfire in 1995 at the Beaver Dam site, a wildfire in 1987 at the Spring Mountain site, and a prescribed fire in 1993 at the Joshua Tree site.

Methods

The 3 sites were sampled in spring 2001, during the phenological peak for annual plant biomass; and 6, 8, and 14 years postfire at the Beaver Dam, Joshua Tree, and Spring Mountain sites respectively. At each site we established eight 4-ha plots, 4 in unburned blackbrush and 4 in the previously burned blackbrush.

These plots were established for another study designed to evaluate the effects of 4 fuels management treatments during 2002 (spring burning, summer burning, herbicide application, and untreated control). Results of these treatments will be reported elsewhere.

Within each 4-ha plot we established 2 modified-Whittaker sampling plots (Stohlgren et al. 1995). Each sampling plot was 20 × 50 m (1000 m²), with one 5 × 25 m (100 m²) subplot, two 2 × 5 m (10 m²) subplots, and ten 0.5 × 2 m (1 m²) subplots. Canopy cover of each species was estimated to the nearest 1% in each of the 1-m² subplots. Species richness was measured at 1-, 10-, 100-, and 1000-m² spatial scales, and included all vascular plants, present as seedlings or mature plants, that were rooted within each plot.

Diversity was measured as species richness and evenness of higher vascular plants. Total species richness was calculated as the number of higher vascular plant species at 4 spatial scales in each sampling plot (1, 10, 100, and 1000 m²), which were collectively used as response variables in a two-way multivariate analysis of variance (MANOVA) to evaluate effects of site, fire, and the site-by-fire interaction (Roy's greatest root test statistic, Sokal and Rohlf 1995). We similarly performed separate analyses for native, alien, woody perennial, herbaceous perennial, perennial grass, cacti, annual grass, and annual forb species richness. The list of species that comprised each of these groups is in the Appendix. Raw data were used in these analyses, since they were normally distributed and homoscedastic. Significant effects for these and all other tests were considered at $P \leq 0.05$, and data are reported as averages ± 1 SE.

Species evenness was calculated as Pielou's J' (Ludwig and Reynolds 1988). These data were not normally distributed and transformations did not improve the data structure, therefore the non-parametric median test was used to evaluate the significant effects of site, fire, and the site-by-fire interaction (Sokal and Rohlf, 1995). Patterns of species evenness were also evaluated by visually inspecting the rank-order plots of species cover in burned and unburned areas at each study site.

Total cover was averaged from the ten 1-m² subplots within each sampling plot, and analyzed using analysis of variance (ANOVA) to evaluate effects of site, fire, and the site-by-fire interaction. Cover of aliens versus natives, individual alien species, and various plant life forms were evaluated separately using MANOVA. Alien cover categories included *Bromus madritensis* ssp. *rubens*, *Bromus tectorum*, *Erodium cicutarium*, and other alien species. Life form categories were woody perennials, herbaceous perennials, perennial grasses, cacti, annual grasses, and

annual forbs. Cover data were arcsine transformed prior to analyses.

Frequency was calculated among the ten 1-m² subplots within each sampling plot, and ANOVA was used to evaluate effects of site, fire, and the site-by-fire interaction. Total alien frequency, and frequency of alien annual grasses and *Erodium cicutarium*, were analyzed separately, and data were untransformed.

Results

Plant diversity

Unburned blackbrush. Species richness averaged 11, 20, 30, and 49 species at progressively larger spatial scales in unburned blackbrush (Fig. 1). Richness was much higher for natives (9, 17, 28, and 46 species) than aliens (2, 2, 2, and 3 species), and declined in order from annual forbs, woody perennials, herbaceous perennials, annual grasses, cacti, to perennial grasses (Table 1). Richness varied among sites ($F_{4,16} = 47.26$, $P < 0.0001$), and no single site had the highest richness at

(160%)(Table 1). As a result, there was a decline in the percentage of alien species at progressively larger spatial scales (16, 11, 8, and 6% alien species) (Fig. 2). The percent increase in richness between 1- and 1000-m² also varied among plant life forms: cacti (6,000%), perennial grasses (1000%), herbaceous perennials (943%), and woody perennials (771%), annual forbs (320%) and annual grasses (158%).

Species evenness in unburned blackbrush did not differ significantly among sites ($\chi^2 = 0.9583$, $P = 0.6193$), due to the high dominance of *Coleogyne* cover at all sites (Fig. 3).

Burned blackbrush. Species richness in burned blackbrush was 20, 10, and 14% lower than in unburned blackbrush at the 10-, 100-, and 1000-m² spatial scales (Table 1). Richness did not decline significantly after fire at the 1-m² scale, except at the Beaver Dam site. The effects of burning on richness varied among sites (site-by-fire interaction, $F_{4,16} = 4.34$, $P = 0.0145$), and was strongest at Beaver Dam (Table 1).

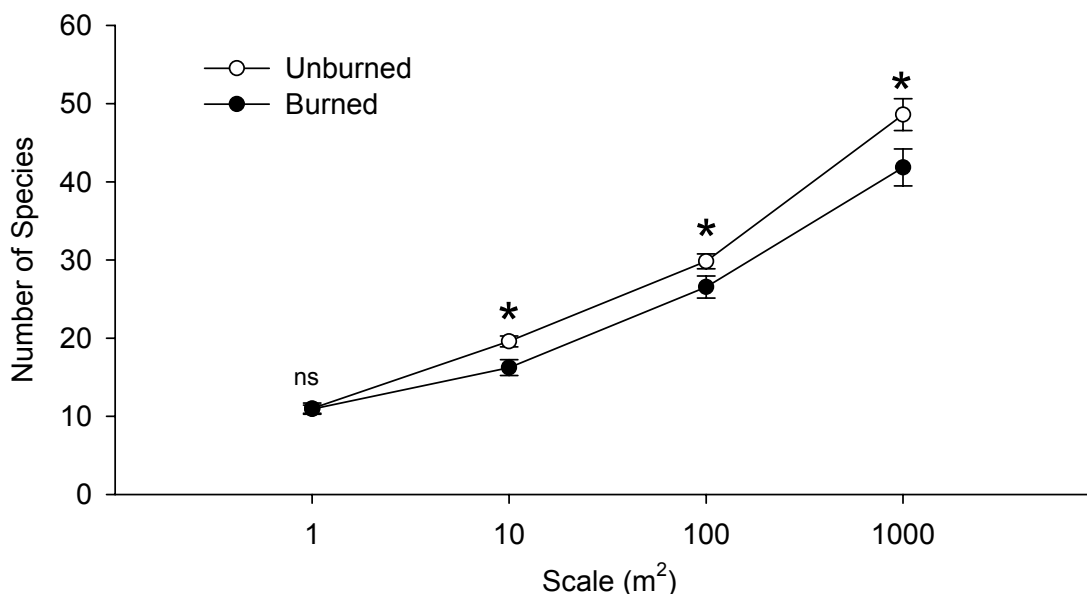


Figure 1. Total species richness in unburned and burned blackbrush averaged over the 3 study sites. * $P \leq 0.05$

all 4 spatial scales. For example, the Spring Mountain site had the lowest richness at 1 m², but the highest at 1000 m².

Species richness increased 446% between the 1- and 1000-m² spatial scales (Fig. 1), but the percent increase differed between natives (497%) and aliens

Effects of fire on species richness differed between aliens and natives, and among plant life forms. Alien richness increased, whereas native richness decreased after fire (Table 1). Accordingly, the percentage of aliens species increased after fire ($F_{4,15} = 28.40$, $P < 0.0001$) (Fig. 2). Richness of annual and perennial

grasses increased, whereas richness of woody perennials and annual forbs decreased after burning (Table 1), but the responses of all life forms varied among sites ($F_{5,15} = 5.98$, $P = 0.0031$).

Burning increased evenness from 0.58 ± 0.04 in unburned to 0.65 ± 0.01 in burned plots, and the effect was strongest at Spring Mountain where there was a 56% increase. Fire increased species evenness by decreasing cover of *Coleogyne*, and increasing the equitability of cover among other species (Fig. 3).

Plant cover and alien frequency

Total plant cover in unburned blackbrush averaged 49% (46-51% range), and was dominated by *Coleogyne* at 26% cover, which comprised 53% of the total cover and 73% of the woody perennial cover (Fig. 3). Total cover in burned blackbrush was 50% (41-51% range), but *Coleogyne* was almost completely removed by fire.

Encelia virginensis, *Erodium cicutarium* and *Baiyla multiradiata*, followed in abundance by *Prunus fasciculatus*, *Gutierrezia sarothrae*, and *Bromus madritensis* ssp. *rubens* (Fig. 3c).

Although total cover returned to prefire levels after 6-14 postfire years, patterns of recovery varied significantly among plant life forms. Cover of woody perennials was 60% lower, and cover of all other plant life forms were 170 to 450% higher, in burned than unburned blackbrush (Table 2). Annual forb cover increased 266% after burning, was higher than that of any other life form in burned areas (21%), and increased significantly after burning at all 3 sites. Responses to fire by other plant life forms varied among sites. Cover of annual grasses only increased significantly at Joshua Tree and Spring Mountain, and cover of herbaceous perennials and perennial grasses only increased significantly at Spring Mountain.

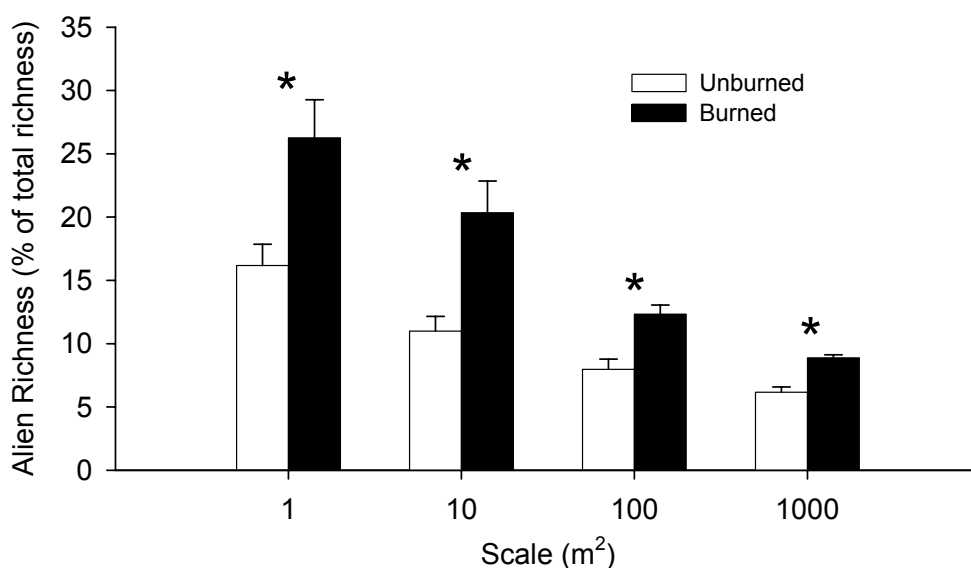


Figure 2. Percent of the total species richness that is comprised of aliens in unburned and burned blackbrush. * $P \leq 0.05$

In the absence of *Coleogyne*, a variety of other species dominated the cover of burned areas. At Beaver Dam, the burned area was dominated by *Erodium cicutarium*, *Gutierrezia sarothrae*, *Thamnosma montanum*, *Astragalus nuttalianus* ssp. *imperfectus*, and *Bromus madritensis* ssp. *rubens* (Fig. 3a). At Joshua Tree, the burned area was dominated by *Mentzelia affinis* and *Bromus tectorum*, followed by *Amsinckia tessellata*, *Chaenactis stevioides*, *Sphaeralcea ambigua*, *Erodium cicutarium*, and *Achnatherum speciosa* (Fig. 3b). At Spring Mountain, the burned area was dominated by

Fire increased cover of aliens 191% ($F_{1,18} = 32.22$, $P < 0.0001$), and decreased cover of natives 26% ($F_{1,18} = 16.15$, $P = 0.0008$) (Fig. 4), and these trends did not differ significantly among sites ($F_{2,18} = 0.13$, $P = 0.74$). As a result, the proportion of the total cover that was comprised of aliens increased from 10% before fire, to 31% after fire ($F_{1,18} = 38.22$, $P < 0.0001$).

The alien plant species that increased the most in cover differed significantly among sites ($F_{4,16} = 4.33$, $P = 0.0146$). At Beaver Dam and Spring Mountain the

Table 1. Species richness of higher vascular plants at 4 spatial scales in unburned (U) and burned (B) blackbrush within each site, and among all sites combined, during spring 2001. Values are averages (± 1 SE; $n = 4$ per site per fire history) and burn effects for each scale are indicated as not significant (ns), negative ($- P \leq 0.05$, $-- P \leq 0.01$, $--- P \leq 0.001$), or positive ($+ P \leq 0.05$, $++ P \leq 0.01$, $+++ P \leq 0.001$); and significant across all scales ($* P \leq 0.05$, $** P \leq 0.01$, $*** P \leq 0.001$).

	1 m ²		10 m ²		100 m ²		1000 m ²		
	U	B	U	B	U	B	U	B	
All vascular plants									
Beaver Dam **	12.7 (0.28)	10.8 (0.49) -	18.9 (0.46)	14.3 (0.93) --	27.0 (0.89)	20.9 (0.38) ---	42.1 (2.45)	32.4 (1.34) -	
Joshua Tree ^{ns}	12.6 (0.30)	12.9 (0.24) ns	21.9 (1.09)	20.4 (0.95) ns	31.4 (1.55)	28.0 (1.08) ns	47.9 (0.75)	43.6 (2.47) ns	
Spring Mt. ^{ns}	7.8 (0.57)	9.0 (0.30) ns	18.0 (1.08)	14.0 (0.88) ns	31.1 (1.66)	30.8 (1.75) ns	55.8 (2.88)	49.5 (1.77) ns	
Sites combined **	11.0 (0.72)	10.9 (0.52) ns	19.6 (0.70)	16.2 (1.01) ---	29.8 (0.95)	26.5 (1.40) --	48.6 (2.05)	41.8 (2.36) ---	
Aliens									
Beaver Dam ^{ns}	2.9 (0.04)	3.0 (0.01) ns	3.0 (0.00)	3.0 (0.00) ns	3.0 (0.00)	3.0 (0.00) ns	3.1 (0.13)	3.0 (0.00) ns	
Joshua Tree ^{ns}	1.2 (0.11)	1.8 (0.08) ++	1.8 (0.33)	2.1 (0.24) ns	2.0 (0.35)	2.6 (0.13) ns	2.9 (0.32)	3.8 (0.14) +	
Spring Mt. *	1.2 (0.07)	3.3 (0.19) +++	1.6 (0.30)	4.1 (0.06) +++	2.0 (0.29)	4.0 (0.00) +++	2.8 (0.25)	4.3 (0.14) ++	
Sites combined ***	1.8 (0.24)	2.7 (0.20) +++	2.2 (0.23)	3.1 (0.25) +++	2.3 (0.20)	3.2 (0.18) +++	2.9 (0.14)	3.7 (0.17) +++	
Natives									
Beaver Dam **	9.7 (0.32)	7.8 (0.50) -	15.9 (0.46)	11.3 (0.93) --	24.0 (0.89)	17.9 (0.38) ---	39.0 (2.44)	29.4 (1.34) -	
Joshua Tree ^{ns}	11.3 (0.29)	11.1 (0.30) ns	20.1 (0.86)	18.3 (0.73) ns	29.4 (1.52)	25.4 (1.20) ns	45.0 (0.89)	39.9 (2.40) ns	
Spring Mt. ^{ns}	6.6 (0.52)	5.7 (0.46) ns	16.4 (0.83)	9.94 (0.94) --	29.2 (1.49)	26.8 (1.75) ns	53.0 (2.79)	45.3 (1.85) ns	
sites combined ***	9.2 (0.63)	8.2 (0.71) --	17.4 (0.68)	13.2 (1.19) ---	27.5 (1.02)	23.3 (1.34) ---	45.7 (2.08)	38.2 (2.23) ---	
Woody perennials									
Beaver Dam ^{ns}	1.5 (0.04)	1.3 (0.12) ns	3.3 (0.47)	2.8 (0.45) ns	6.3 (0.97)	5.4 (0.13) ns	11.3 (1.42)	8.8 (0.78) ns	
Joshua Tree **	1.2 (0.02)	0.2 (0.07) ---	2.1 (0.16)	0.6 (0.13) ---	5.1 (0.66)	1.6 (0.13) --	10.1 (0.55)	5.8 (0.63) --	
Spring Mt. ^{ns}	2.4 (0.16)	1.3 (0.13) --	5.3 (0.33)	2.5 (0.37) --	10.4 (0.66)	7.5 (0.54) -	17.9 (0.88)	14.8 (0.52) -	
Sites combined ***	1.7 (0.16)	0.9 (0.17) ---	3.6 (0.44)	2.0 (0.34) ---	7.3 (0.79)	4.8 (0.75) ---	13.1 (1.16)	9.8 (1.18) ---	
Herbaceous Perennials									
Beaver Dam ^{ns}	1.2 (0.16)	1.0 (0.09) ns	1.8 (0.20)	1.6 (0.28) ns	3.0 (0.20)	2.8 (0.25) ns	5.9 (0.47)	5.4 (0.24) ns	
Joshua Tree ^{ns}	0.4 (0.05)	0.3 (0.09) ns	1.6 (0.22)	1.6 (0.30) ns	2.6 (0.32)	2.1 (0.24) ns	4.9 (0.52)	4.4 (0.24) ns	
Spring Mt. ^{ns}	0.5 (0.10)	1.1 (0.11) ++	1.8 (0.23)	1.4 (0.16) ns	4.0 (0.74)	4.4 (0.75) ns	9.0 (1.21)	7.4 (0.24) ns	
Sites combined ^{ns}	0.7 (0.11)	0.8 (0.11) ns	1.7 (0.11)	1.5 (0.14) ns	3.2 (0.30)	3.1 (0.38) ns	6.6 (0.68)	5.7 (0.40) ns	
Perennial grasses									
Beaver Dam *	0.1 (0.08)	0.2 (0.07) ns	0.2 (0.06)	0.1 (0.06) ns	0.3 (0.14)	0.9 (0.13) +	0.6 (0.32)	1.8 (0.25) +	
Joshua Tree ^{ns}	0.3 (0.06)	0.3 (0.07) ns	1.3 (0.16)	0.8 (0.18) ns	1.9 (0.13)	2.1 (0.55) ns	2.6 (0.38)	3.6 (0.32) ns	
Spring Mt. **	0.2 (0.04)	0.6 (0.06) ++	0.5 (0.27)	1.0 (0.18) ns	2.0 (0.20)	2.6 (0.32) ns	2.6 (0.38)	3.6 (0.13) +	
Sites combined *	0.2 (0.04)	0.3 (0.06) +	0.7 (0.17)	0.6 (0.14) ns	1.4 (0.26)	1.9 (0.30) +	2.0 (0.34)	3.0 (0.30) +++	

continued...

Table 1 (continued)

	1 m ²		10 m ²		100 m ²		1000 m ²		
	U	B	U	B	U	B	U	B	
Cacti									
Beaver Dam ^{ns}	0.0 (0.00)	0.0 (0.00) ns	0.3 (0.19)	0.0 (0.00) ns	0.9 (0.31)	0.6 (0.24) ns	2.6 (0.72)	1.5 (0.41) ns	
Joshua Tree ^{**}	0.0 (0.01)	0.0 (0.00) ns	0.0 (0.00)	0.0 (0.00) ns	0.8 (0.14)	0.0 (0.00) --	1.3 (0.14)	0.5 (0.20) -	
Spring Mt. ^{**}	0.1 (0.03)	0.0 (0.01) -	0.3 (0.12)	0.0 (0.00) -	1.1 (0.24)	0.3 (0.30) -	3.4 (0.13)	1.1 (0.13) ---	
Sites combined ^{**}	0.0 (0.02)	0.0 (0.00) --	0.2 (0.08)	0.0 (0.00) -	0.9 (0.14)	0.3 (0.13) --	2.4 (0.35)	1.0 (0.19) ---	
Annual grasses									
Beaver Dam [*]	3.3 (0.17)	3.1 (0.11) ns	3.8 (0.18)	3.4 (0.24) ns	4.0 (0.00)	3.4 (0.13) --	4.3 (0.14)	4.0 (0.20) ns	
Joshua Tree ^{ns}	1.2 (0.11)	1.5 (0.12) ns	1.8 (0.31)	1.7 (0.06) ns	1.8 (0.48)	2.3 (0.25) ns	2.5 (0.35)	2.9 (0.24) ns	
Spring Mt. ^{**}	1.1 (0.24)	2.0 (0.07) +++	1.6 (0.16)	2.4 (0.07) ++	1.6 (0.13)	2.3 (0.25) ns	2.4 (0.24)	3.3 (0.14) +	
Sites combined [*]	1.9 (0.31)	2.2 (0.21) ++	2.4 (0.32)	2.5 (0.22) ns	2.5 (0.36)	2.6 (0.20) ns	3.0 (0.29)	3.4 (0.18) ns	
Annual forbs									
Beaver Dam [*]	6.6 (0.32)	5.3 (0.32) -	9.6 (0.24)	6.6 (0.16) ---	12.6 (0.75)	7.9 (0.24) ---	17.5 (0.84)	11.0 (0.74) --	
Joshua Tree ^{ns}	9.4 (0.28)	10.7 (0.40) +	15.1 (0.81)	15.7 (1.02) ns	19.3 (0.78)	19.9 (0.72) ns	26.3 (0.66)	26.5 (1.00) ns	
Spring Mt. ^{ns}	3.5 (0.45)	4.2 (0.26) ns	8.5 (1.00)	6.8 (0.51) ns	12.0 (0.61)	13.8 (0.63) ns	20.5 (1.06)	19.5 (1.36) ns	
Sites combined [*]	6.5 (0.75)	6.7 (0.88) ns	11.1 (0.96)	9.7 (1.33) -	14.6 (1.06)	13.8 (1.51) ns	21.4 (1.19)	19.0 (1.99) --	

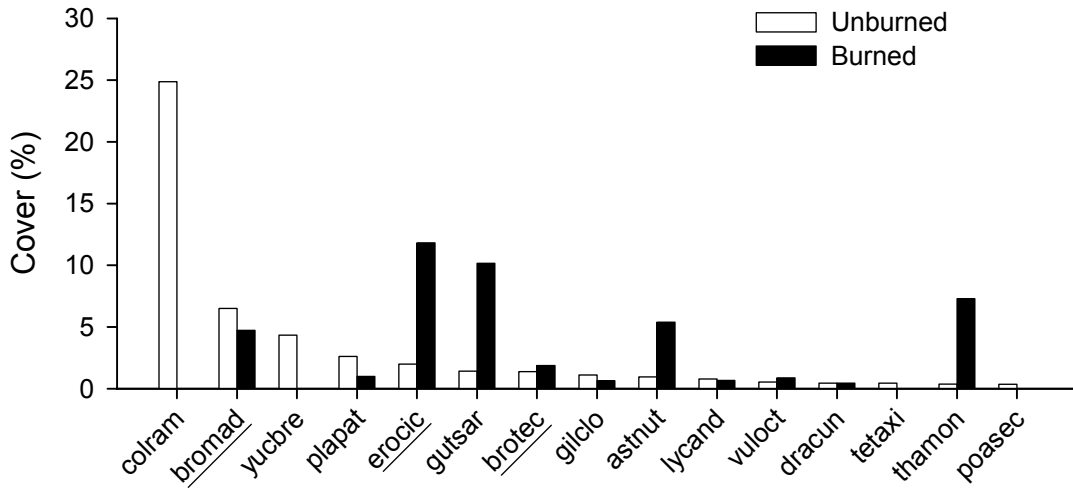
Table 2. Percent cover of higher vascular plants in unburned (U) and burned (B) blackbrush within each study site, and among all sites combined, during spring 2001. Values are averages (\pm 1 SE; $n = 4$ per site per fire history) and burn effects for each group are indicated as not significant (ns), negative ($- P \leq 0.05$, $-- P \leq 0.01$, $--- P \leq 0.001$), or positive ($+ P \leq 0.05$, $++ P \leq 0.01$, $+++ P \leq 0.001$); and significant across all groups ($* P \leq 0.05$, $** P \leq 0.01$, $*** P \leq 0.001$).

Alien species

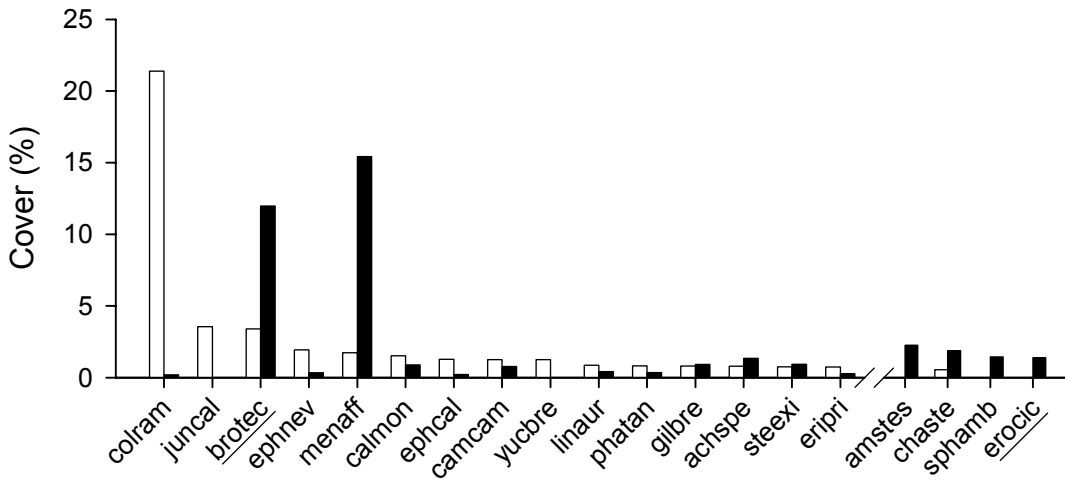
	<i>Bromus madritensis</i> <i>spp. rubens</i>		<i>Bromus tectorum</i>		<i>Erodium cicutarium</i>		Others			
	U	B	U	B	U	B	U	B		
	Beaver Dam ^{**}	6.5 (2.24)	4.7 (0.22) ns	1.4 (0.29)	1.9 (0.36) ns	2.0 (0.20)	11.8 (3.48) ++	0.0 (0.00)	0.0 (0.00) ns	
Joshua Tree ^{ns}	0.4 (0.18)	0.8 (0.34) ns	3.4 (0.63)	12.0 (2.10) ++	0.0 (0.01)	1.4 (1.06) ns	0.3 (0.18)	0.3 (0.08) ns		
Spring Mt. ^{**}	1.0 (0.11)	1.9 (0.17) ++	0.0 (0.01)	1.0 (0.11)+++	0.2 (0.08)	7.8 (2.38) ++	0.0 (0.03)	0.6 (0.13) ++		
Sites combined ^{***}	2.6 (1.07)	2.5 (0.51) ns	1.6 (0.48)	5.0 (1.63)+++	0.7 (0.28)	7.0 (1.84)+++	0.1 (0.07)	0.3 (0.09) ++		
	Life forms ^a									
	Woody perennials		Herbaceous perennials		Perennial grasses		Annual grasses		Annual forbs	
	U	B	U	B	U	B	U	B	U	B
Beaver Dam ^{ns}	32.4 (2.94)	20.5 (3.73) -	0.7 (0.09)	0.7 (0.11) ns	0.4 (0.33)	0.1 (0.08) ns	8.7 (2.44)	7.7 (0.58) ns	8.6 (0.34)	20.2 (4.10) +
Joshua Tree [*]	30.6 (4.15)	1.9 (0.86) ---	0.7 (0.22)	2.1 (0.91) ns	1.0 (0.31)	2.3 (0.54) ns	4.1 (0.65)	13.1 (2.21) ++	12.9 (1.18)	31.2 (3.66) ++
Spring Mt. [*]	41.4 (1.57)	19.4 (3.72) --	0.3 (0.05)	5.2 (0.99)+++	0.3 (0.13)	1.9 (0.64) +	1.0 (0.10)	3.0 (0.22)+++	2.2 (0.28)	11.5 (1.99)+++
Sites combined ^{***}	34.8 (3.04)	13.9 (3.04) ---	0.6 (0.09)	2.7 (0.70)+++	0.6 (0.17)	1.5 (0.38) +	4.6 (1.22)	7.9 (1.42)+++	7.9 (1.38)	21.0 (3.00)+++

^aCacti are excluded because of minimal cover and no statistically significant differences.

A. Beaver Dam



B. Joshua Tree



C. Spring Mountain

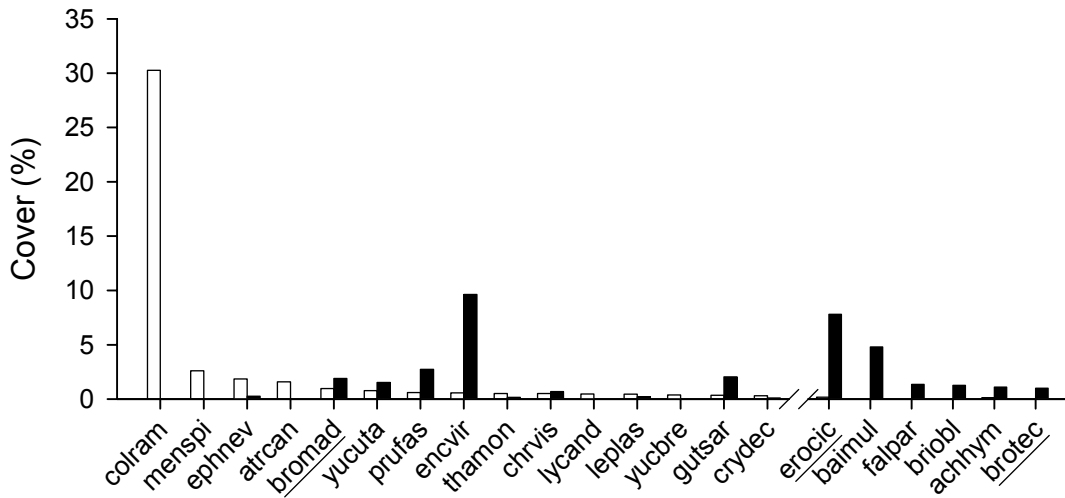


Figure 3. Percent cover distribution of species in unburned and burned blackbrush. Species were arranged along the abscissa in their rank order of cover dominance in the unburned plots. Additional species were added to the right of an axis break if any of the top 15 species in burned plots were not among those plotted for the unburned plots. Alien species are underlined. Species codes are listed in the Appendix.

increase in alien cover was mainly due to *Erodium cicutarium*, whereas at Joshua Tree the increase was mainly caused by *Bromus tectorum* (Table 2). Cover of the relatively uncommon alien species *Salsola tragus*, *Bromus trinitii*, and *Schismus* spp. collectively increased after fire, due to their strong positive response at the Spring Mountain site. *Bromus madritensis* ssp. *rubens* cover increased slightly at Spring Mountain, but the overall effect of fire across all sites was not significant.

Total frequency of aliens did not increase significantly due to fire ($F_{1,18} = 1.57$, $P = 0.2266$), but there was a significant site-by-fire effect ($F_{2,18} = 4.01$, $P = 0.0363$), and alien frequency did increase significantly from 54 to 78% at Spring Mountain ($F_{1,6} = 14.99$, $P < 0.0083$). Responses varied among alien

overall combined frequency of the alien annual grasses *Bromus madritensis* ssp. *rubens* and *Bromus tectorum* did not differ significantly ($F_{1,18} = 0.79$, $P < 0.4410$) between unburned 79% (± 7) and burned 84% (± 5) areas.

Discussion

Diversity patterns in unburned blackbrush

Species richness of unburned blackbrush was not lower than other vegetation types in western North America, as we had predicted it would be. In the current study we reported 11 total plant species/1 m², which is comparable to 7 species/1 m² reported in ponderosa pine and shortgrass steppe, 8 in tallgrass prairie, 9 in aspen, and 12 in mixed grasslands (Stohlgren et al.

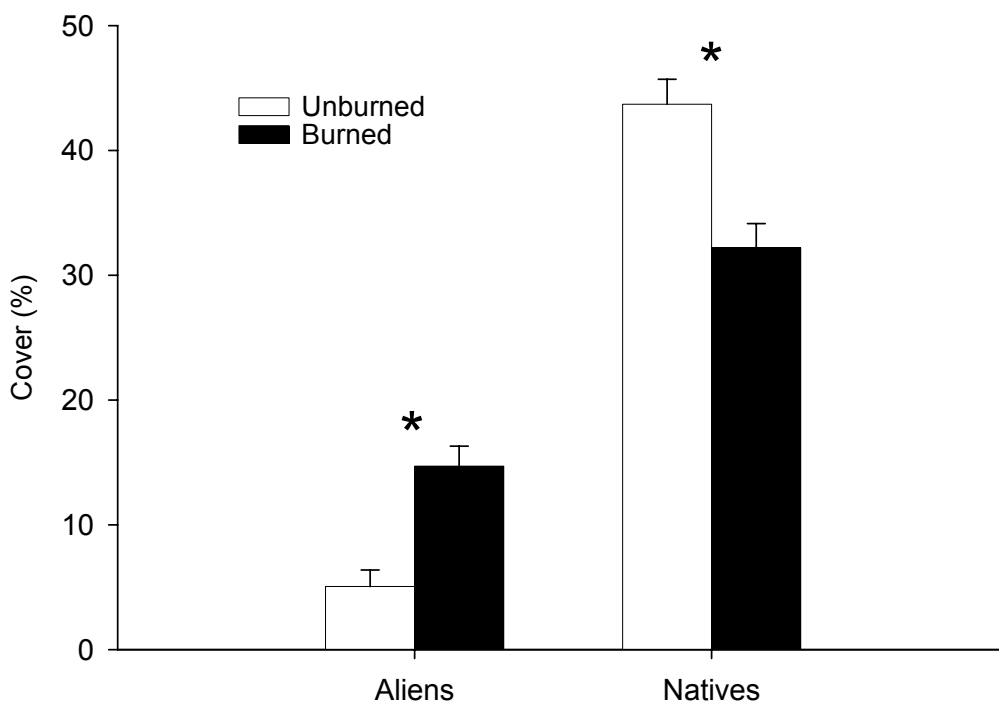


Figure 4. Percent cover of alien and native species in unburned and burned blackbrush. Alien and native species are listed in the Appendix. * $P \leq 0.05$

species, with *Erodium cicutarium* frequency increasing the most from 37% in unburned to 67% in burned areas ($F_{1,18} = 30.69$, $P < 0.0001$). The response of *Erodium cicutarium* frequency to burning varied among sites ($F_{2,18} = 10.44$, $P = 0.0010$), with increases from 1 to 29% at Joshua Tree ($F_{1,6} = 5.22$, $P = 0.0623$), 13 to 75% at Spring Mountain ($F_{1,6} = 32.89$, $P = 0.0012$), and 96 to 98% at Beaver Dam ($F_{1,6} = 0.20$, $P = 0.6704$). The

1999a). We reported an average of 7 woody perennial species/100 m² (10 at Spring Mountain), which compares closely with 6 woody perennial species/100 m² reported in pinyon/juniper/sagebrush, 8 in creosote bush/bursage, and 8-10 reported for unburned blackbrush near our Spring Mountain site (Lei and Walker 1995). We reported 47 total species/1000 m², compared to 38 species/1000 m² in chaparral (Schluter

and Ricklefs 1993), 45 species in the Colorado rocky mountains (Stohlgren et al. 1999a), 50 species in Mediterranean regions with similar rainfall as the sites in the current study (150mm, Rosensweig and Abramsky 1993), and 65-70 species in semiarid grasslands and shrublands (Schluter and Ricklefs 1993). We also reported 46 native species and 3 aliens species/1000 m², which compared favorably with 32 native species and 3 alien species in rocky mountain grasslands (Stohlgren et al. 1999b). Thus, species richness of higher vascular plants, woody perennial species, and alien species was similar in blackbrush compared to other major vegetation types.

Species richness increased logarithmically between the 1- and 1000-m² scales, but this increase was much higher for natives than aliens. This pattern suggests that native richness was more closely related to increased environmental heterogeneity at successively larger spatial scales. Apparently, the spatial distribution of the few alien species in this study were influenced more by environmental heterogeneity at the smaller scales, whereas the distribution of the many native species were affected more equitably by heterogeneity at all scales. The increase in richness at higher spatial scales also varied among plant life forms. Perennials increased proportionally more than annuals, indicating that the former were responding more to environmental variation at successively higher spatial scales. Heterogeneity at 1-m² was due to the shrub-intershrub gradient, and at 1000-m² by the microtopographic gradient from finer textures soils of rainfall runoff areas (hummocks) to coarser textures soils of run-on areas (washlets)(Brooks 1999). These results demonstrate that different spatial scales can produce different relative estimates of species richness between natives and aliens, and among plant life forms in blackbrush.

The single year of plant community data reported in this study should be sufficient to evaluate general diversity patterns in blackbrush. Winter rainfall from October through March ranged from 88 to 111% of the 30-year average at the study sites, resulting in a moderately diverse display of native annuals (Matt Brooks, personal observation). These rainfall estimates are based on data from the closest weather stations to each site that had complete weather data to calculate 30-year averages (1 to 3 stations/site, National Climatic Data Center). There may have been some annual plant species that remained dormant as seeds and were not detected, but this would have only caused species richness to be underestimated, and not affect the conclusion that species richness in blackbrush was comparable to other vegetation types.

Effects of fire on blackbrush community structure

Fire removed virtually all *Coleogyne* cover, which is consistent with most other reports (Jensen et al. 1960, Bowns 1973, Beatley 1976, Callison et al. 1985, West and Young 2000). The loss of *Coleogyne* as the single dominant species, and its replacement by 2 to 5 other co-dominant species 6-14 years postfire, resulted in increased species evenness, but decreased species richness. Decreased richness after *Coleogyne* removal, and the finding that species richness in blackbrush was similar to other vegetation types, were not consistent with the assertion that *Coleogyne* has a strong negative effect on the number of other coexisting species (Bowns 1973, Beatley 1976, Bowns and West 1976). Thus, the cover dominance of *Coleogyne* does not prevent the coexistence of a wide range of other plant species.

Loss of *Coleogyne* cover is not the only effect of fire, and therefore not the only potential factor related to postfire plant community patterns. Fire can also kill mature plants and seeds, and alter soil characteristics (Whelan 1995). It is likely that many native plant species recover slowly after blackbrush fires, because they evolved in a desert ecosystem where fire was infrequent. Reduced species richness 6-14 years postfire may be due to slow recovery of these native species, especially the woody perennials.

Alien species are often invasive, and respond rapidly to increased availability of limiting resources created by disturbances such as fire (Grime 1977, Chapin et al. 1986). It is therefore not surprising that fire increased alien richness and cover, as we predicted it would in this study. The one site where alien richness, and cover of either *Bromus tectorum* or *Bromus madritensis* ssp. *rubens*, did not increase significantly after fire was at Beaver Dam, where moderate levels of past and current cattle grazing may have allowed aliens to establish relatively high levels of richness and annual grass cover prior to burning. The other two sites had not been grazed by livestock for many decades, and had much lower levels of alien richness and cover. These results suggest that relatively undisturbed blackbrush may be somewhat resistant to invasion by alien species, and the effects of fire on previously disturbed blackbrush may not affect dominance of alien annual plants if disturbance levels are already high.

Although aliens richness and cover were consistently higher in burned than unburned blackbrush, no single alien plant life form or species dominated all sites. Alien annual grass cover increased the most after fire at Joshua Tree, whereas the alien annual forb *Erodium cicutarium* increased the most at the other two sites. Frequency of alien annual grasses did not differ between burned and unburned areas,

indicating that the continuity of annual grass fuels was not affected by burning 6-14 years postfire. These results do not support the conclusions of others that alien annual grasses are typically among the most dominant postfire species in burned blackbrush (Jensen et al. 1960, West 1983, Callison et al. 1985), and that their increased dominance after fire may increase landscape flammability (Holmgren 1960). However, these results are from a single year of annual plant sampling and must be interpreted cautiously.

Annual plant cover can vary dramatically among years of contrasting rainfall, especially for alien species in the Mojave Desert (Brooks 1999, 2000). Before plants were sampled in the current study, 2 of the previous 3 winter rainfall seasons experienced less than half of the long-term average rainfall in the Mojave Desert. In 1999 rainfall ranged from 16 to 54%, in 2000 rainfall averaged 30 to 68%, and in 2001 rainfall averaged 88 to 111% of the 30 year average at rainfall stations near the three study sites (1 to 3 stations/site, National Climatic Data Center). It is probable that the seedbank of alien annual grasses, *Bromus* spp. in particular (Brooks 2000), was depleted during this drought. The dominance of alien annual grasses reported in the current study was therefore on the low end of the interannual range. It is likely that a few years of high rainfall would increase cover, and possibly frequency, of alien annual grasses, and thus increase landscape flammability (Rogers and Vint 1987, Schmid and Rogers 1988, Brooks 1999).

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Appendix. Higher vascular plant species sampled in unburned (U) and burned (B) blackbrush within each study site during spring 2001 (x = present). Six-letter codes are provided for the species listed in figure 3.

	code	Beaver Dam		Joshua Tree		Spring Mt.	
		U	B	U	B	U	B
Aliens							
Annual grasses							
	<i>Bromus madritensis</i> ssp. <i>rubens</i>	bromad	x	x	x	x	x
	<i>Bromus tectorum</i>	brotec	x	x	x	x	x
	<i>Bromus trinii</i>		x				
	<i>Schismus arabicus</i>			x	x		
	<i>Schismus barbatus</i>						x
Annual forbs							
	<i>Erodium cicutarium</i>	erocic	x	x	x	x	x
	<i>Salsola tragus</i>					x	x
Natives							
Woody perennials							
	<i>Acamptopappus spheroccephalus</i>		x		x	x	x
	<i>Ambrosia eriocentra</i>						x
	<i>Artemisia dracunculus</i>						x
	<i>Artemisia tridentata</i>					x	
	<i>Atriplex canescens</i>	atrcan				x	
	<i>Chrysothamnus nauseosus</i>		x	x			x
	<i>Chrysothamnus paniculatus</i>						x
	<i>Chrysothamnus viscidiflorus</i> var. <i>stenophyllus</i>	chrvis	x	x		x	x
	<i>Coleogyne ramosissima</i>	colram	x	x	x	x	x
	<i>Coleogyne ramosissima</i> (seedling)		x	x	x	x	
	<i>Encelia virginensis</i>	encvir	x	x		x	x
	<i>Ephedra californica</i>	ephcal			x	x	x
	<i>Ephedra nevadensis</i>	ephnev	x	x	x	x	x
	<i>Ephedra torreyana</i>		x				
	<i>Ephedra virida</i>		x	x		x	x
	<i>Eriogonum fasciculatum</i> var. <i>polifolium</i>				x	x	
	<i>Fallugia paradoxa</i>	falpar					x
	<i>Grayia spinosa</i>		x		x		
	<i>Gutierrezia sarothrae</i>	gutsar	x	x	x	x	x
	<i>Hymenoclea salsola</i>		x		x		x
	<i>Juniperus californicus</i>	juncal			x	x	
	<i>Juniperus osteosperma</i>						x
	<i>Krascheninnikovia lanata</i>		x				x
	<i>Lycium andersonii</i>	lycand	x	x	x	x	x
	<i>Lycium cooperi</i>				x	x	x
	<i>Menodora spinescens</i>	menspi					x
	<i>Pinus monophylla</i>						x
	<i>Prunus fasciculatus</i>	prufas	x	x			x
	<i>Psilotrophe cooperi</i>						x
	<i>Purshia mexicana</i> var. <i>stansburyana</i>		x				x
	<i>Purshia tridentata</i> var. <i>glandulosa</i>						x
	<i>Salazaria mexicana</i>				x	x	
	<i>Salvia dorrii</i>				x	x	x
	<i>Symphoricarpus longiflorus</i>						x
	<i>Tetradymia axillaris</i> var. <i>longispina</i>	tetaxi	x		x		
	<i>Thamnosma montanum</i>	thamon	x	x			x
	<i>Thermophylla pentachaeta</i> var. <i>belenidium</i>						x
	<i>Viguiera parishii</i>						x
	<i>Yucca brevifolia</i>	yucbre	x	x	x	x	x

	code	Beaver Dam		Joshua Tree		Spring Mt.	
		U	B	U	B	U	B
<i>Yucca utahensis</i>	yucuta	x	x			x	x
Herbaceous perennials							
<i>Arabis pulchra</i>		x		x		x	x
<i>Astragalus bernardianus</i>				x	x		
<i>Astragalus lentiginosus</i>							x
<i>Baileya multiradiata</i>	bailmul	x				x	x
<i>Calochortus flexuosus</i>		x	x			x	x
<i>Calochortus kennedyi</i>				x			
<i>Castilleja angustifolia</i>		x				x	x
<i>Caulanthus crassicaulis</i>						x	x
<i>Chamaesyce albomarginata</i>				x	x		
<i>Chamaesyce fendleri</i>						x	x
<i>Chenopodium incanum</i>						x	
<i>Cymopterus multinervatus</i>		x	x				
<i>Delphinium nuttalianum</i>		x	x				
<i>Delphinium parishii</i>				x	x	x	x
<i>Dichelostemma capitata</i>		x	x	x	x		
<i>Eriogonum inflatum</i>							x
<i>Eriogonum plumatella</i>				x	x		
<i>Erioneuron pulchellum</i>			x			x	x
<i>Gaura coccinea</i>			x				
<i>Lepidium fremontii</i>		x	x			x	
<i>Linum lewisii</i>							x
<i>Lomatium mohavense</i>				x			
<i>Lomatium nevadense</i>						x	
<i>Mirabilis bigelovii</i>				x	x		
<i>Mirabilis multiflorus</i>		x	x			x	x
<i>Oenothera californica</i>					x		
<i>Penstemon palmeri</i>							x
<i>Penstemon sp.</i>						x	
<i>Phlox longifolia</i>		x	x				
<i>Phoradendron juniperinum</i>				x			
<i>Prenanthesella exigua</i>						x	x
<i>Senecio multilobatus</i>						x	x
<i>Sphaeralcea ambigua</i>	sphamb	x	x	x	x	x	x
<i>Stephanomeria pauciflora</i>						x	x
<i>Streptanthus cordatus</i>			x			x	
<i>Tricardia watsonii</i>		x					
Perennial grasses							
<i>Achnatherum hymenoides</i>	achhym	x		x	x	x	x
<i>Achnatherum speciosum</i>	achspe		x	x	x	x	x
<i>Aristida purpurea</i>			x			x	x
<i>Elymus elymoides</i>			x	x	x	x	x
<i>Pleuraphis rigida</i>				x	x		x
<i>Poa secunda</i>	poasec	x	x	x	x		
Cacti							
<i>Echinocerus engelmannii</i>		x	x	x		x	
<i>Echinocerus triglochidiatus</i>						x	
<i>Escobaria vivipara desertii</i>						x	x
<i>Opuntia acanthocarpa</i>		x	x				
<i>Opuntia basilaris</i>		x		x	x	x	x
<i>Opuntia echinocarpa</i>				x	x	x	
<i>Opuntia erinacea</i>		x	x				
<i>Opuntia seedling</i>							x

	code	Beaver Dam		Joshua Tree		Spring Mt.	
		U	B	U	B	U	B
Annual grasses							
<i>Poa bigelovii</i>		x	x				
<i>Poa</i> unknown 1 (annual)					x		
<i>Vulpia microstachys</i>		x	x				
<i>Vulpia octoflora</i>	vuloct	x	x			x	x
Annual forbs							
<i>Amsinckia tesellata</i>	amstes	x	x	x	x		
<i>Anisocoma acaulis</i>				x			
Asteraceae unknown 1				x			
Asteraceae unknown 2 (annual)							x
<i>Astragalus nuttalianus</i> var. <i>imperfectus</i>	astnut	x	x				
<i>Baileya pleniradiata</i>		x	x				
<i>Brickellia oblongifolia linoides</i>	briobl					x	x
<i>Calyptridium monandrum</i>	calmon			x	x		
<i>Camissonia campestris</i>	camcam			x	x	x	x
<i>Camissonia</i> unknown species 1					x		
<i>Camissonia</i> unknown species 2				x			
<i>Centrostegia thurberi</i>				x	x		
<i>Chaenactis fremontii</i>			x				
<i>Chaenactis stevioides</i>	chaste			x	x		
<i>Cirsium neomexicanum</i>							x
<i>Claytonia perfoliata</i>		x					
<i>Coreopsis bigelovii</i>					x		
<i>Cryptantha circumcissa</i>				x	x	x	x
<i>Cryptantha decipiens</i>	crydec	x	x		x	x	x
<i>Cryptantha micrantha</i>				x	x		
<i>Cryptantha nevadensis</i>						x	x
<i>Cryptantha pterocarya</i>		x	x	x	x	x	x
<i>Cryptantha recurvata</i>						x	x
<i>Descurainia pinnata</i>		x	x	x	x	x	x
<i>Draba cuneatus</i>	dracun	x	x			x	x
<i>Eriastrum diffusum</i>				x	x	x	
<i>Erigeron divergens</i>		x	x			x	x
<i>Eriogonum</i> annual unknown 1		x		x	x		
<i>Eriogonum</i> annual unknown 2				x	x		
<i>Eriogonum nidularium</i>						x	x
<i>Eriogonum pusillum</i>						x	x
<i>Eriogonum reniforme</i>				x			
<i>Eriophyllum pringlei</i>	eripri			x	x		
<i>Eriophyllum wallacei</i>		x		x	x		
<i>Eschscholzia minutiflora</i>		x				x	
<i>Filago depressum</i>					x		
<i>Gilia brecciarum</i> ssp. <i>brecciarum</i>	gilbre			x	x		
<i>Gilia clokeyi</i>	gilclo	x	x			x	x
<i>Ipomopsis polycladon</i>						x	x
<i>Langloisia setosissima</i>		x			x	x	x
<i>Lappula redowski</i>						x	x
<i>Layia glandulosa</i>				x	x		
<i>Lepidium lasiocarpum</i>	leplas	x	x			x	x
<i>Lesquerella tenella</i>		x	x				
<i>Linanthus aureus</i>	linaur			x	x		x
<i>Linanthus bigelovii</i>		x		x	x		x
<i>Linanthus demissus</i>		x				x	x
<i>Loeseliastrum schottii</i>				x	x		
<i>Macheranthera canescens</i>						x	x

	code	Beaver Dam		Joshua Tree		Spring Mt.	
		U	B	U	B	U	B
<i>Macheranthera canescens</i> var.			x				
<i>leucanthemifolia</i>							
<i>Malacothrix glabrata</i>		x		x	x		
<i>Mentzelia affinis</i>	menaff			x	x	x	x
<i>Mentzelia nitens</i>				x	x		x
<i>Mimulus bigelovii</i>				x	x	x	x
<i>Monoptilon belloides</i>		x					
<i>Nama demissus</i>				x	x	x	x
<i>Nemacladus glanduliferus</i>						x	x
<i>Nemacladus longiflorus</i> var. <i>breviflorus</i>		x		x	x		x
<i>Nemophila menziesii</i>				x	x		
<i>Nyctaginaceae</i> unknown 1					x		
<i>Oenothera deltoidea</i>						x	x
<i>Oxytheca perfoliata</i>						x	
<i>Oxytheca trilobata</i>					x		
<i>Pectocarya platycarpa</i>					x		
<i>Phacelia distans</i>							x
<i>Phacelia fremontii</i>		x	x			x	x
<i>Phacelia tanacetifolia</i>	phatan			x	x		
<i>Phacelia vallis-mortae</i>		x	x			x	
<i>Plantago patagonica</i>	plapat	x	x			x	x
<i>Rafinesquia neomexicana</i>			x	x	x		
<i>Salvia columbariae</i>				x	x		
<i>Silene antirrhina</i>		x	x				
<i>Stephanomeria exigua</i>	steexi		x	x	x	x	
<i>Streptanthella longirostris</i>		x				x	x
<i>Syntripappus fremontii</i>		x	x				
Unknown species 1		x					
<i>Uropappus lindleyi</i>		x		x			
<i>Vicia ludoviciana</i>		x	x				
<i>Yabea microcarpa</i>		x					