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VEGETATION RESPONSE TO FIRE AND POSTBURN SEEDING TREATMENTS IN JUNIPER WOODLANDS OF THE GRAND STAIRCASE–ESCALANTE NATIONAL MONUMENT, UTAH

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ABSTRACT.—We compared 3 naturally ignited burns with unburned sites in the Grand Staircase–Escalante National Monument. Each burn site was restored with native and nonnative seed mixes, restored with native seeds only, or regenerated naturally. In general, burned sites had significantly lower native species richness (1.8 vs. 2.9 species), native species cover (11% vs. 22.5%), and soil crust cover (4.1% vs. 15%) than unburned sites. Most burned plots, seeded or not, had significantly higher average nonnative species richness and cover and lower average native species richness and cover than unburned sites. Regression tree analyses suggest site variation was equally important to rehabilitation results as seeding treatments. Low native species richness and cover, high soil C, and low cover of biological soil crusts may facilitate increased nonnative species richness and cover. Our study also found that unburned sites in the region had equally high cover of nonnative species compared with the rest of the Monument. Cheatgrass (*Bromus tectorum*) dominated both burned and unburned sites. Despite the invasion of cheatgrass, unburned sites still maintain higher native species richness; however, the high cover of cheatgrass may increase fire frequency, further reduce native species richness and cover, and ultimately change vegetation composition in juniper woodlands.

Key words: Juniperus osteosperma, *fire, postburn seeding, nonnative species,* Bromus tectorum, *biological soil crusts, regression tree analysis.*

Juniper Woodland Communities

Utah juniper (*Juniperus osteosperma*) occurs on approximately 80% of the more than 780,000 ha that form the Grand Staircase–Escalante National Monument (hereafter referred to as the Monument) in southern Utah. Often associated with pinyon pine (*Pinus edulis*) and big sagebrush (*Artemisia tridentata*), juniper commonly inhabits intermediate areas between xeric shrubland, relatively mesic coniferous forests, and grass-dominated environments on a variety of soil types and geologic formations (West and Van Pelt 1986, Evans 1988, Welsh et al. 1993). In the more xeric portion of its range, at lower elevations in the Monument, juniper stands tend to be more homogeneous, while pinyon increases proportionally with elevation (Welsh et al. 1993). Climate, corresponding with elevation, appears to be the greatest determinant affecting juniper distribution and may greatly influence tree size and stand structure (Peiper 1977, Welsh et al. 1993).

Herbaceous vegetation assemblages associated with juniper woodlands are highly variable and are often influenced by a range of conditions such as elevation, soil characteristics, and land use practices. These conditions are difficult to generalize because juniper woodlands occupy a diverse array of landscapes. Herbaceous composition is also influenced by stand density, with species richness greatest prior to juniper establishment and decreasing as trees become mature and the canopy closes (Peiper 1977, Koniak and Everett 1992). These succession stages portray general patterns observed within natural systems; however, they do not accurately reflect the complexity of how multiple variables, such as the impacts of nonnative plant species, land use practices, and management, drive successional processes and patterns (Everett et al. 1983).

Biological soil crusts are common throughout the Monument, are closely associated with juniper woodlands, and may play a significant role in determining the composition of herbaceous vegetation. Concentrated in the top 1 mm of soil, they primarily affect processes that occur at the soil surface and a few processes deeper

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in the soil. Soil crusts provide several crucial functions in semiarid ecosystems, including soil stability, atmospheric-N fixation, water retention, and germination enhancement (Anderson et al. 1982, West 1990, Belnap 1993, Belnap and Harper 1995). Despite adaptations to severe growing conditions, they are extremely vulnerable to trampling and compaction commonly related to anthropogenic activities (Belnap 1998). Following compaction, Anderson et al. (1982) observed that soil crusts regenerate only 15% of their original area in the first 14–18 years and only an additional 1% during the following 20 years. Such disturbances may reduce nitrogenase activity by 30%–100%, result in decreased water availability to vascular plants, accelerate soil loss through wind and water erosion, and decrease diversity and abundance of soil biota (Anderson et. al. 1982, Belnap 1995, Belnap and Gillette 1998).

Fire

In the Monument the role of fire in juniper woodlands and its effect on vegetation dynamics are poorly understood due to few historical records and limited scientific research. Because of their thin, volatile bark and lack of defense mechanisms, junipers are extremely sensitive to fire. When junipers are exposed to fire, burning is usually complete, leaving little evidence to reconstruct fire histories (Young and Evans 1981, Agee 1993). Within the Monument, fire frequency in juniper woodlands is generally low and the spatial extent of burns is small, both appearing to be highly dependent on stand density and associated vegetation (fuel loads).

Lightning storms in spring and midsummer provide a ready source of ignition. Large fires occasionally occur in mature stands where sufficient fuel loads are present and weather conditions are conducive to fire. Such fires are likely to be high-intensity burns often facilitated by the presence of dead and highly flammable vegetation. Seasonal occurrence of fire in the Monument is greatest from late July through August. A combination of factors occurring at this time of year creates ideal circumstances for fire. First, most herbaceous vegetation is past its phenological peak, becoming dormant or dying. As mortality increases, accumulated litter and standing dead plants provide fuel for fire to spread. Second, weather conditions change dramatically during summer months. Moisture levels, which are at their lowest, result in plant mortality and create an extremely dry and flammable landscape. The combination of frequent lightning, strong winds, and accumulation of dry fuels can create conditions favorable for fire.

Introduction of nonnative plant species further complicates ecological processes and can cause major changes in fire regimes. Nonnative species, such as cheatgrass (*Bromus tectorum*), have already invaded much of the landscape within the Monument (Stohlgren et al. 2001). An important factor contributing to the success of cheatgrass establishment is its tolerance to fire. Hull (1965) estimated that rangeland dominated by cheatgrass is 10–500 times more likely to burn than rangeland dominated by native bunchgrasses, and that the fire season in cheatgrass-dominated rangeland may be extended by 1 to 3 months. The estimated increase in fire frequency is attributed to the accumulation of litter and fine fuels in dense cheatgrass-dominated systems. Arid conditions inhibit decomposition, allowing plant biomass to accumulate over several years. The abundance of cheatgrass seeds in the seedbank and their prolific germination capabilities allow rapid establishment following fire (Stewart and Hull 1949, Knapp 1996).

Management Directives

Prior to the Monument designation, juniper woodlands were managed in part for fuelwood, fence post production, and livestock grazing by the Bureau of Land Management (BLM). Fire, both natural and prescribed, has been used as a tool to maintain or improve rangeland conditions and control juniper expansion. Burned sites have been seeded with native and nonnative grass species to increase forage production for wildlife and livestock. Since the creation of the Monument on 18 September 1996 (Presidential Proclamation 6920), resource managers have had to consider additional objectives when making decisions regarding the maintenance of natural ecosystems, the role of fire, and the restoration of disturbed landscapes. Natural ignited fires have been allowed to burn without suppression whenever possible across the landscape. Postburn rehabilitation activities are evaluated on a case-by-case basis as mandated by the Vegetation Management Objectives of the Monument (USDI 1999). These objectives must take into consideration (1) the structure and diversity of vegetation prior to burning and (2) the presence of noxious weeds in the area and the likelihood of such weeds increasing as a result of the fire. The use of native species in seeding operations is a priority for all Monument projects; however, nonnative species may be used for stabilization of soils or for seeding treatments after burning if the area is threatened by species with high invasive potential (USDI 1999).

In addition to restoring native vegetation and discouraging nonnative species invasion, Monument resource managers must also consider the impact of fire and seeding treatments on biological soil crusts. Evangelista et al. (2001) found that fire in juniper woodlands of the Monument substantially decreased the cover of soil crusts, especially the older and highly developed pedicles that are more vulnerable to heat exposure. The remaining nonliving pedicles, if left undisturbed or untrampled, may stay structurally intact and continue to provide soil stability and increase moisture and nutrient retention (Belnap and Gardner 1993). Within 3 years after a fire, regeneration of new crusts begins rapidly and, as early as 10 years after fire, crusts may occupy an area equal to the total crust cover at preburn conditions. However, when mechanized equipment, such as tractors and drill-seeders, is used for postburn seeding treatments, the nonliving pedicles and surviving biological crusts are destroyed and regeneration of crusts is suppressed (Evangelista et al. 2001).

Management strategies and land use practices over the past century have undoubtedly altered the community structure and ecosystem processes, resulting in the modification of fire regimes (Everett and Sharrow 1985), encroachment of juniper woodlands (Harry Barber personal communication), reduction of native herbaceous vegetation, and invasion of nonnative plant species (Stohlgren et al. 2001). Restoration treatments in the Monument, such as postburn seeding, are designed to restore a natural array of native plant and animal associations (USDI 1999). However, many treatments have not been carefully surveyed and monitored. Monument managers have been unable to distinguish which variables affect the success or failure of postburn seeding. This study examines multiple variables that influence the success or failure of restoration following fire and postburn seeding. The goal of this research is to provide resource managers with scientific data to support and guide decisions that will comply with the objectives outlined in the Monument's Management Plan (USDI 1999), including the protection and promotion of native plant species and soil crusts.

STUDY AREA AND METHODS

Study Area

The Buckskin Mountain study area is in the south central part of the Monument, just south of Highway 89 and east of the Cockscomb Wilderness study area. Elevations of the study area range between 1645 m and 1830 m. Juniper woodlands dominate the area, but patches of big sagebrush and cliff-rose (*Purshia mexicana*) are prevalent. Soils are of limestone parent materials. Surface textures are gravelly, sandy loam with gravelly, sandy loam, and clay loam subsurfaces (Chapman 1996, 1997). Topography of the study area is relatively flat with slopes consistently less than 3%. The Buckskin Mountain study area lies within the Mollie's Nipple grazing allotment. Grazing of domestic cattle is permitted during winter months but is minimal due to the distance from water sources (Chapman 1996).

We examined 3 natural ignition burn sites in the Buckskin Mountain study area (Fig. 1). The burns occurred on 14 July 1996, 20 July 1997, and 1 August 1998. Each site has been subjected to a unique postburn management strategy. The 1996 burn, approximately 140 ha in size, was seeded with native and nonnative seeds the following spring (Table 1). The 1997 burn also covered an area of approximately 140 ha. In October 1997, two different native seed mixes were applied to the east and west sides of the burned area (Table 1). Seeds on the 1996 and 1997 sites were applied using a rangeland drill pulled by a bulldozer (Chapman 1996, 1997). The 1998 burn covered an area of approximately 445 ha. Approximately one-third of this fire overlapped the 1996 burn area. The 1998 burn area received no postburn seeding treatment.

Sampling and Data Analyses

Three multiscale sample plots were randomly established within each burned site, burned/seeded site, and adjacent unburned sites in April and May 2000. Due to logistical constraints, we chose only 2 unburned sites, 1 outside the

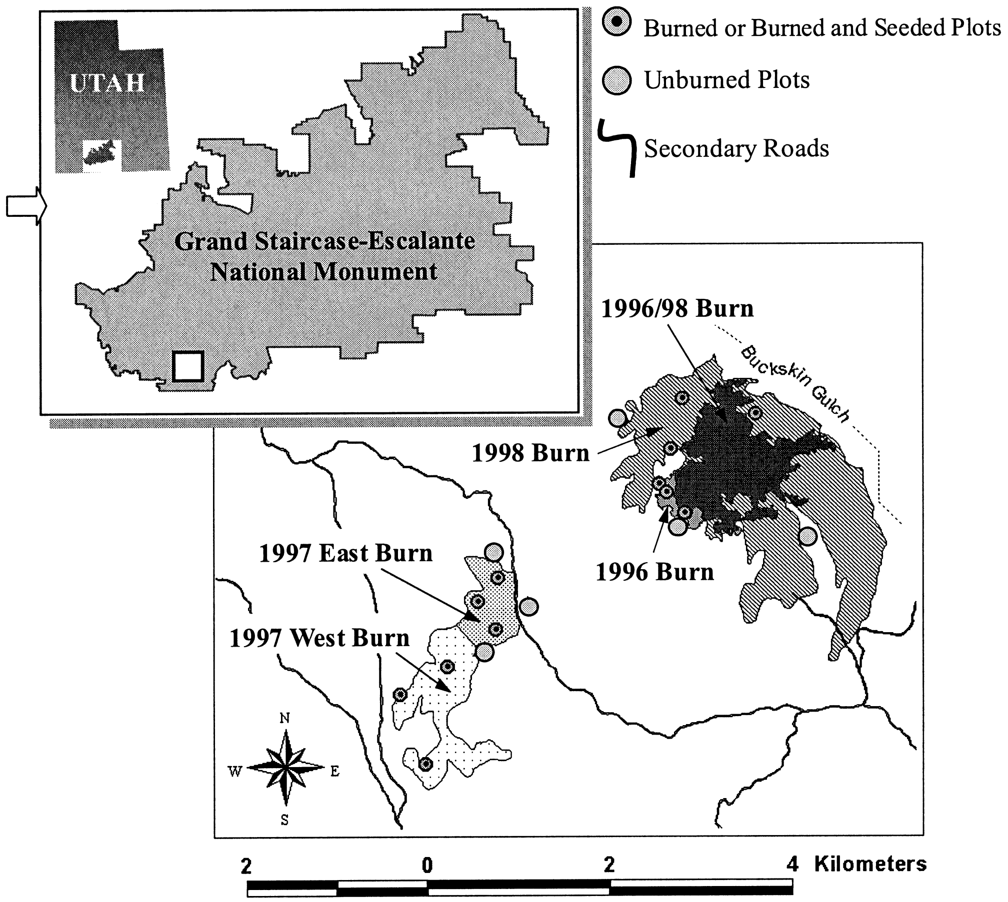

Fig. 1. Map of Buckskin Mountain study area and modified-Whittaker plot location, Grand Staircase–Escalante National Monument, Utah.

perimeter of the 1996/1998 fires and another for each of the two 1997 seeded burn sites. The modified-Whittaker nested vegetation design (Stohlgren et al. 1995) was used to collect species data at multiple spatial scales. Each plot included ten 1-m^2 subplots. In each subplot we recorded percent foliar cover for each species, percent cover of biological soil crusts by developmental stages, and percent bare soil without crusts. A 2.5-cm-diameter soil corer was used to take 5 soil samples at each corner and at the center of each plot at depths of 0–15 cm and combined to be representative of the entire modified-Whittaker plot. Ancillary data, such as UTM location from a global positioning system, elevation from a USGS topographical map, slope, and aspect, were also recorded for each plot.

We identified plant specimens in the field to genus and species. Unknown specimens were collected, pressed, and later identified at Brigham Young University Herbarium in Provo, Utah. Origins of plant species were determined using the National Plants Database (USDA NRCS 2001) and A Utah Flora (Welsh et al. 1993).

Soil samples were analyzed at the Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, Colorado. Samples from each plot were air-dried for 48 hours, after which biotic debris and particles >2 mm were removed using a standard #10 sieve. Samples were then ground using a roller mill and oven-dried at 55°C for 48 hours prior to analyses. Percent total carbon and nitrogen was analyzed using a LECO-1000 CHN Analyzer

TABLE 1. Seed mixes of each burn applied by a mechanized drill-seeder. Nonnative species are highlighted in bold print and species captured in our modified-Whittaker plots are noted with *.

Seed mix for 1996 burn	Seed mix for 1997 East burn	Seed mix for 1997 West burn
cliff-rose (*Purshia mexicana*)	thickspike wheatgrass (*Elymus lanceolatus*)	thickspike wheatgrass (*Elymus lanceolatus*)
four-wing saltbush (*Atriplex canescens*)*	Indian ricegrass (*Stipa hymenoides*)*	Indian ricegrass (*Stipa hymenoides*)*
Wyoming big sagebrush (*Artemisia tridentata*)	needle and thread (*Stipa comata*)*	blue bunch wheatgrass (*Elymus spicatus*)*
kochia (*Kochia scoparia*)	blue bunch wheatgrass (*Elymus spicatus*)*	Lewis flax (*Linum perenne* spp. *lewisii*)*
small burnet (*Sanguisorba minor*)*	Lewis flax (*Linum perenne* spp. *lewisii*)*	four-wing saltbush (*Atriplex canescens*)*
yellow sweetclover (*Melilotus officinalis*)*	Palmer penstemon (*Penstemon palmeri*)*	Wyoming big sagebrush (*Artemisia tridentata*)*
crested wheatgrass (*Agropyron cristatum*)*	cliff-rose (*Purshia mexicana*)*	antelope bitterbrush (*Purshia tridentata*)
	four-wing saltbrush (*Atriplex tridentata*)*	
	antelope bitterbrush (*Purshia tridentata*)	

(Carter 1993). Inorganic carbon from carbonates was determined using a volumetric method described by Wagner et al. (1998) and subtracted from total carbon to find percent total organic carbon. Soil phosphorus content (mg · kg^{-1} of soil) was determined colormetrically from a sodium-bicarbonate extraction (Kou 1996). Additionally, each sample was analyzed for texture based on the standard hydrometer method (Gee and Bauber 1986).

All statistical analyses were conducted using SYSTAT v. 10 (SPSS, Inc. 2001) software, and $P < 0.05$ was used to determine significance in all tests. Variables were first reviewed for normality and log transformations were conducted to skewed data distributions. We calculated the mean number and percent cover of vegetation by species, the percent cover of biological soil crusts by developmental stage, and the total cover of vegetation of each of the 1-m^2 subplots. Two-way analyses of variance (ANOVA) were used with Tukey's means comparison test to compare variables for each burned and associated unburned site for the 1-m^2 subplots. Discriminant analyses were conducted to see if plots in the unburned sites were distinguishable from all plots that were burned or burned and seeded.

Regression tree analyses were conducted to identify significant independent variables that influence high numbers of nonnative species and cover (the predicted variable) on burned and unburned sites. We chose this approach because regression trees are nonparametric models that incorporate categorical variables (e.g., disturbance type, crust development) and nonhomogeneous data sets (e.g., unbalanced sample sizes, high variability). Additionally, regression trees are able to identify interactions between independent variables, ranking the relative importance of predicted variables in a hierarchical format without inferring cause-and-effect relationships. Finally, regression tree analyses present resource managers with a comprehensive output that describes the relationships of multiple independent variables, thus facilitating the understanding and use of results by a broader array of resource managers and stakeholders (Hansen et al. 1996).

We generated regression trees based on 6 independent variables: (1) number of native species, (2) percent cover of native species, (3) disturbance class (1 = burned; 2 = unburned), (4) total cover of soil crusts, (5) soil nitrogen, and (6) soil phosphorous. Proportion Reduced Error values (PRE), which are similar to R^2 values, were generated to describe the amount of variation explained by the independent variables in the model (Hansen et al. 1996).

RESULTS

1996 Burn Site

We encountered 26 native and 9 nonnative species in our plots within the burn site. Of 35 species detected, 2 natives and 3 nonnatives

TABLE 2. Mean number of vegetation species and percent cover, and biological soil crusts of 1-m^2 subplots within burned and unburned sites. Standard errors in parentheses and significant differences are noted by *.

Indices	Total spp.	Nonnative spp.	Native spp.	Total cover	Nonnative cover	Native cover	Crusts cover
1996 burn / native and exotic seed	4.4 (0.3)	3.0 (0.2)	1.4 (0.2)	17.4 (1.4)	14.8 (1.5)	2.7 (1.0)	1.9 (0.6)
1996/1998 unburned sites	3.7 (0.3)	0.8 (0.08)	2.9 (0.3)	29.6 (5.9)	1.2 (0.4)	28.5 (5.8)	28.4 (5.3)
P-value	<0.1	<0.001*	<0.001*	0.05*	<0.001*	<0.001*	<0.001*
1997 West burn / native seed	3.2 (0.2)	1.6 (0.1)	1.6 (0.2)	25.6 (2.5)	12.2 (1.5)	13.4 (2.5)	0.6 (0.1)
1997 East burn / native seed	4.1 (0.3)	1.1 (0.07)	3.0 (0.3)	27.5 (2.5)	4.7 (0.7)	22.8 (2.6)	3.2 (0.9)
P-value	0.009*	<0.001*	<0.001*	0.59	<0.001*	0.01*	<0.001*
1997 East burn / native seed	4.1 (0.3)	1.1 (0.07)	3.0 (0.3)	27.5 (2.5)	4.7 (0.7)	22.8 (2.6)	3.2 (0.9)
1997 unburned sites	4.0 (0.2)	1.1 (0.08)	2.9 (0.9)	36.9 (4.2)	20.4 (3.3)	16.5 (2.4)	1.3 (0.4)
P-value	0.84	0.76	0.75	0.06	<0.001*	0.080.06	
1997 West burn / native seed	3.2 (0.2)	1.6 (0.1)	1.6 (0.2)	25.6 (2.5)	12.2 (1.5)	13.4 (2.5)	0.6 (0.1)
1997 unburned sites	4.0 (0.2)	1.1 (0.08)	2.9 (0.9)	36.9 (4.2)	20.4 (3.3)	16.5 (2.4)	1.3 (0.4)
P-value	0.004*	0.001*	<0.001*	0.02*	0.03*	0.04*	0.1
1998 burn / natural regeneration	2.9 (0.2)	1.5 (0.1)	1.4 (0.2)	12.7 (1.1)	7.5 (0.8)	5.2 (1.1)	10.4 (2.8)
1996/1998 unburned sites	3.7 (0.3)	0.8 (0.08)	2.9 (0.3)	29.6 (5.9)	1.2 (0.4)	28.5 (5.8)	28.4 (5.3)
P-value	0.07	<0.001*	<0.001*	0.01*	<0.001*	<0.001*	0.02*

were seeded during the postburn treatment. The average number of nonnative species found in our 30 subplots was twice as great as the number of native species (Table 2). Average vegetation cover was 5 times higher for nonnative species than native species. Cheatgrass had the highest average percent cover (8.6%) in burned sites and 42% of total vegetation cover. Crested wheatgrass (*Agropyron cristatum,* a seeded nonnative) had the 2nd highest percent cover (3.9%) and 22% of total vegetation cover. Biological soil crusts averaged 1.9% cover.

Unburned plots had 28 native and 2 nonnative species. In our subplots the number of native species was 3 times greater than nonnative. Average percent cover of native species was almost 25 times higher than average cover of nonnative species (Table 2). Juniper represented 19.8% cover per subplot and 66% of total vegetation cover. Big sagebrush had the 2nd highest ranking of 5.6% cover and 18% of total vegetation cover. Cheatgrass ranked 3rd in cover, but it averaged only 1.2% cover and 14% of total vegetation cover in the unburned plots. Biological soil crusts averaged 28.4% cover in the unburned plots.

Species richness was significantly greater ($P < 0.001$) in 1996 burned plots than in unburned plots. Of the total number of species, 25% were nonnative in burned plots, compared with 6% in unburned plots. Our analyses also revealed that the burned site had significantly higher mean nonnative cover ($P < 0.001$) than the unburned site and, in fact, had the highest mean of all our study sites.

1997 Burn Site

We sampled in each of the 2 seeded treatments (east and west sides). Each side of the burn was considered a separate test site because of variation in the 2 seed mixes and the different responses to seeding treatments. The East site had a total of 26 native species and 4 nonnative species. Of the native species, 7 were seeded in the postburn treatment. Subplots were dominated by native species, averaging almost 3 times more than nonnatives (Table 2). Mean percent cover for native species was almost 5 times higher than for nonnative. Cheatgrass had the greatest average percent cover (9.1%) and 42% of total vegetation cover. Smallflower globemallow (*Sphaeralcea parvifolia,* a native species) ranked 2nd, averaging 7.1% and 26% of total vegetation cover. Biological soil crusts averaged 3.2% of total cover compared with just 1.3% in unburned sites.

The West site had 24 native species and 5 nonnative species. Of the native species recorded, 5 were seeded during the postburn treatment. An average of 3.2 species was found, with an equal number of native and nonnative species (Table 2). Mean percent cover was also similar between native and nonnative species. Smallflower globemallow had the highest average percent cover (13.1%) and 51% of total vegetation cover. Broom snakeweed (*Gutierrezia sarothrae*) ranked 2nd in average percent cover (6.2%) and 24% of total vegetation cover. The 3rd-ranking species was cheatgrass, averaging 4.5% and 21% of total vegetation cover. Biological soil crusts averaged 0.6% cover.

Unburned sample plots for both the East and West burns had a total of 28 native species and 3 nonnative species. The mean number of native species found in our subplots was 3 times higher than the mean number of nonnative species found. Average percent cover of nonnative species was slightly higher than native species. Cheatgrass had the highest average percent cover of 19.6% and 51% of total vegetation cover, outranking 2nd-place big sagebrush at 10.8% and 26% of total vegetation.

At the subplot scale there were no significant differences of species richness between the East burn and the unburned plots. Mean percent cover of native species was also similar between the 2 sites; however, mean percent cover of nonnative species was significantly lower in the East burn than in the unburned area. To the contrary, the West burn had fewer total species ($P = 0.004$) and native species ($P < 0.001$) and more nonnative species ($P = 0.001$) compared with unburned plots. There were no significant differences in total percent cover of biological soil crusts between the unburned site and the East ($P = 0.7$) or the West burn site ($P = 0.13$).

Despite similarities in seed mixes of the 1997 East and West sites, the mean total species was significantly greater ($P = 0.009$) on the East site, which also had higher species richness ($P < 0.001$) and mean percent cover ($P = 0.01$) of native species than the West site. Additionally, the East site had lower nonnative species richness ($P < 0.001$) and mean percent cover ($P < 0.001$) compared with the West site. Cover of biological soil crusts was significantly lower in the West sites; however, it should be noted that crust cover was unusually low in the unburned sites.

1998 Burn Site

Five of 30 species found in the burned site were nonnative. The subplots averaged 2.9 species, half of which were native species and half nonnative (Table 2). Mean vegetation cover was slightly higher for nonnative species. Cheatgrass had the highest average percent cover of 7% and 55% of total vegetation cover. Smallflower globemallow had the 2nd highest average of 2.9% and 22% of total vegetation cover. Cover of biological soil crusts averaged 10.4% cover.

Species richness was slightly higher in unburned than in burned plots (Table 2). On average, burned plots had almost twice as many nonnative species as unburned plots ($P < 0.001$) and only half as many native species ($P < 0.001$). Similarly, average nonnative species cover was significantly higher in burned plots ($P < 0.001$), and native species cover significantly lower ($P < 0.001$) than in unburned plots. Biological soil crust cover was almost 3 times greater in unburned than in burned plots ($P < 0.02$).

Comparing Burned and Unburned Sites

We documented several differences between burned and unburned plots. Native species richness, percent cover of native species, and total crust cover were higher on unburned plots than burned plots (Table 3). The 1st regression tree, generated to identify critical factors that influence the number of nonnative species in all plots (burned and unburned sites combined), identified 6 independent variables, or splits, that support nonnative species richness (Fig. 2). In the 1st split, cover of native species is negatively correlated with high nonnative species richness and is predicted to be the most influential variable by the model. Fire or fire and seeding treatments was the 2nd most influential variable we tested, followed by soil C and average number of native species present. The model suggests the highest number of nonnative species occurs when native species cover is low and richness is high, the site is burned, and soil C is high. These variables predict about 63% ($PRE = 0.63$) of the variation.

The 2nd regression tree generated for all plots was conducted to predict the variables that most influence the ratio of nonnative species cover to total vegetation cover (Fig. 3). Our analysis suggests that low native species richness facilitates higher proportions of nonnative cover and that nonnative species will

TABLE 3. Variable means in 1-m² subplots within unburned plots and burned and/or seeded plots. Standard errors are in parentheses and *P*-values of each *t* test are noted with * when significantly different.

Variables	Unburned (n = 60)	Burned or burned and seeded (n = 120)	*P*-value
No. native spp.	2.9 (0.2)	1.8 (0.1)	<0.001*
No. nonnative spp.	1.0 (0.1)	1.8 (0.1)	<0.001*
% native cover	22.5 (3.2)	11.0 (1.2)	<0.001*
% nonnative cover	10.8 (2.1)	9.8 (0.7)	0.65
% *B. tectorum* cover	10.4 (2.0)	7.3 (0.6)	0.14
Sum of crust	15.0 (3.2)	4.1 (0.8)	<0.001*
% soil C	1.1 (0.1)	1.2 (0.1)	0.18
Soil P (mg·kg^{-1} soil)	17.6 (1.2)	17.3 (0.9)	0.83
% nonnative cover of total cover	32.7 (4.3)	55.0 (3.0)	<0.001*

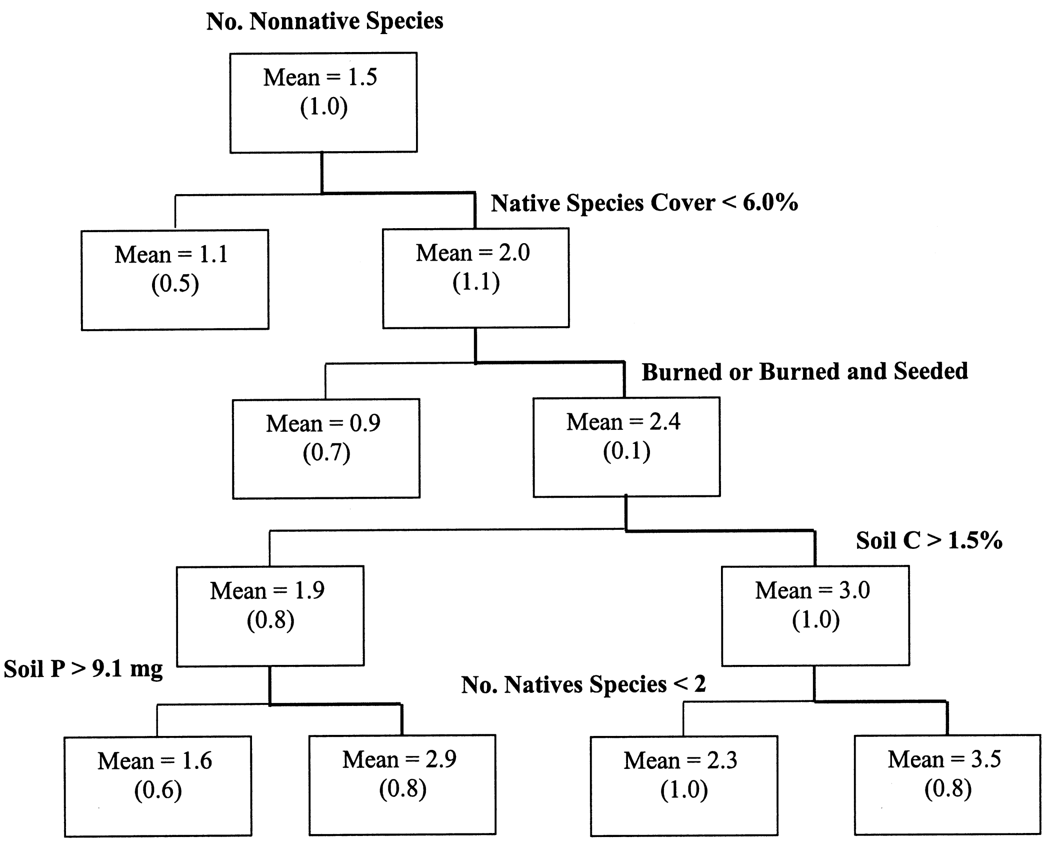

Fig. 2. Regression tree analysis for predicting the mean number of nonnative species in 1-m² subplots of burned and unburned sites. The number of species and percent cover are expressed as means, standard deviations are in parentheses, and *PRE* = 0.63. Bold lines highlight the predicted conditions for the greatest number of nonnative species.

take advantage of soil C supplies and may compete for soil P more efficiently than native species. This model was able to explain 67% (*PRE* = 0.67) of the variation.

Discriminant analysis showed that burned plots could be distinguished from unburned plots in 83% of the cases, based on soil C, cover of biological soil crusts, soil crusts by developmental stages, cover and richness of nonnative plant species, and cover and richness of native plant species (Wilks' lambda = 0.60; P < 0.0001). This justified the use of

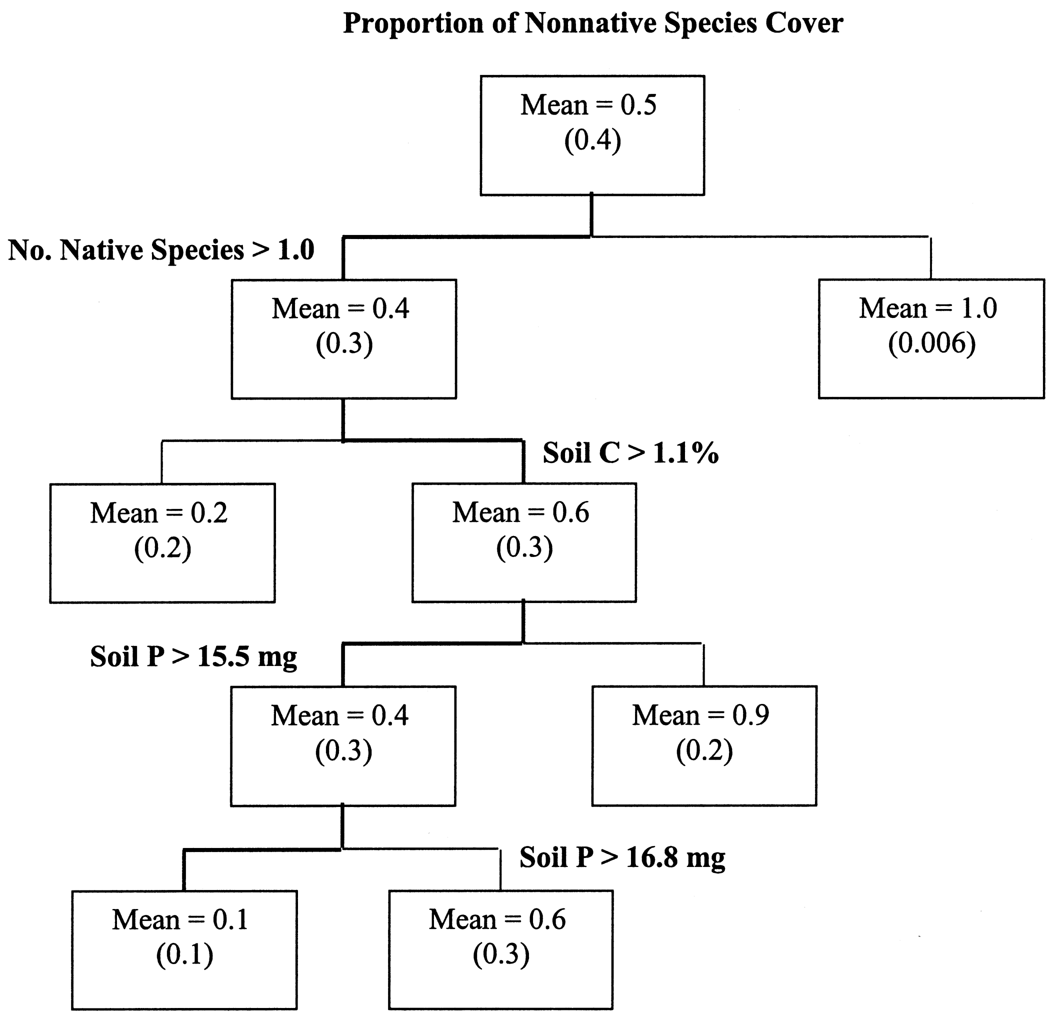

Fig. 3. Regression tree analysis for predicting the mean percent cover of nonnative species in 1-m^2 subplots of burned and unburned sites. The number of species and percent cover are expressed as means, standard deviations are in parentheses, and *PRE* = 0.67. Bold lines highlight the predicted conditions for the greatest percent cover of nonnative species.

regression tree analysis on these 2 largely distinct groups.

We combined and analyzed all burned plots for the number of nonnative species (Fig. 4). Richness of nonnative species for all subplots is greatest when the percent cover of native species is low, soil C is high, and the number of native species is high. This model was able to predict 62% (*PRE* = 0.62) of the variation.

Our 4th regression tree was generated to identify variables that contribute to percent cover of nonnative species on unburned sites. Percent cover of biological soil crusts was negatively correlated with cover of nonnative species and was identified as the most influential variable we tested (Fig. 5). This was followed by soil C and native species richness. This model was able to explain 44% (*PRE* = 0.44) of the variation.

We also used regression tree analyses to model the percent cover of nonnative species for both burned and unburned sites. Percent cover of native species and percent cover of soil C were the best predictors for burned sites and crust cover was the best for unburned sites. These models were weak, predicting only 32% and 29% of the variation, respectively.

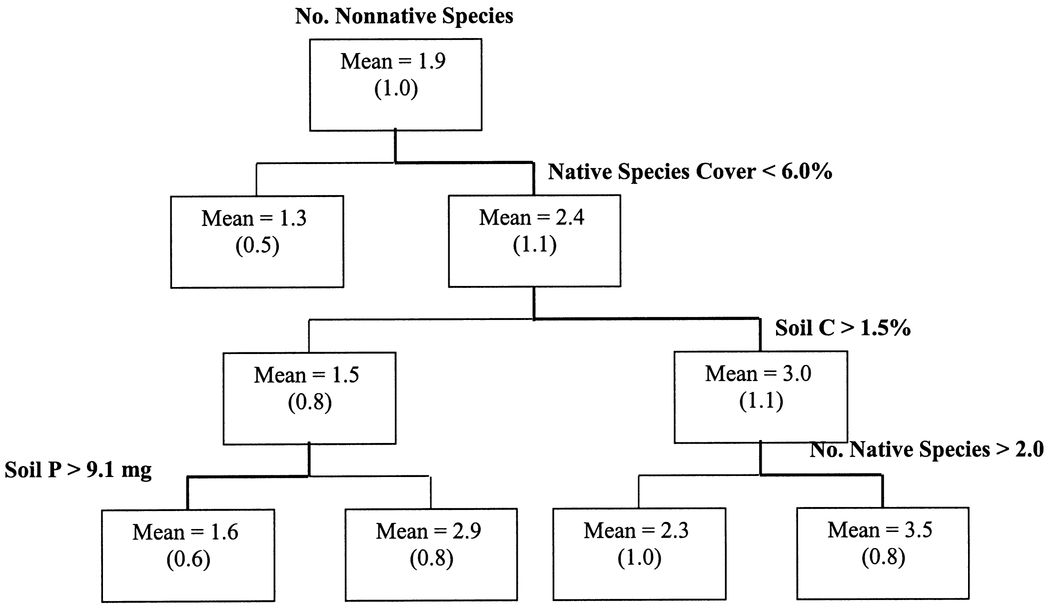

Fig. 4. Regression tree analysis for predicting the mean number of nonnative species in 1-m^2 subplots of burned or burned and seeded sites. The number of species and percent cover are expressed as means, standard deviations are in parentheses, and *PRE* = 0.62. Bold lines highlight the predicted conditions for the greatest number of nonnative species.

DISCUSSION

Role of Site Factors in Postfire Recovery

Site factors (e.g., soil nutrient content, native plant cover) greatly affect restoration efforts and are at least as important as postburn seeding in restoration results. Variability of restoration results among burns was exemplified by the West and East treatments of the 1997 burn. Both sites received similar postburn seeding treatments of native species (Table 1), yet responses were significantly different (Table 2). Seeding treatment on the East side was the most successful of all burn sites, resulting in a more natural array of vegetation than in the control sites. The West side, however, showed no more improvement from rehabilitation efforts than the 1998 burn and, in many cases, remained high in nonnative species richness. Further evidence of variability of sites can be found with the 1997 unburned sites, which had greater mean cover of nonnative species than all burned sites and lower soil crust cover than the East burn, which was mechanically seeded.

Our study examined patterns of succession and identified the interaction of several important factors influencing recovery. However, despite physical similarities (e.g., soil type, slope, aspect, elevation) among all of our sites, a number of other variables also appear to play significant roles in dictating successional trends following fire and the success of postburn rehabilitation. These variables may greatly affect native and nonnative plant species richness and cover. Negative effects, such as increased nonnative species richness and proportional cover, decreased native species richness and cover, and decreased soil crust cover, can still be strongly associated with burning and restoration activities (Table 3).

Site Factors and Nonnative Plant Invasion

We did not expect to find the high presence of nonnative species in so many unburned sites. Nonnative species cover was actually significantly higher, on average, in unburned plots than burn sites, and 5 times greater than average across the Monument (Stohlgren unpublished work). Mean crust cover and native

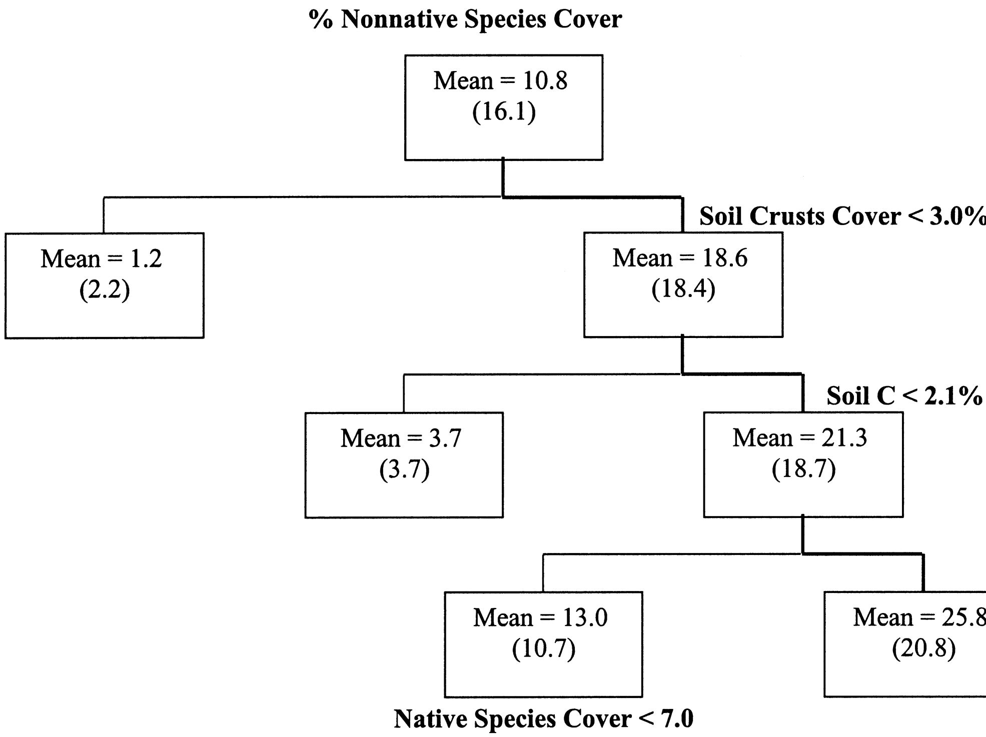

Fig. 5. Regression tree analysis for predicting the mean percent cover of nonnative species in 1-m^2 subplots of unburned sites. The number of species and percent cover are expressed as means, standard deviations are in parentheses, and $PRE = 0.44$. Bold lines highlight predicted conditions for the greatest percent cover of nonnative species.

species richness and cover remained significantly higher on unburned sites. One possible explanation for the high presence of nonnative species may be related to complex site factors not examined by this study (e.g., climatic variability, additional nutrient content of soils). Additionally, livestock grazing and other management activities are likely to have influenced sites. For example, postburn seeding activities may attract domestic cattle to burn sites, accelerating trampling of soil crusts and grazing of native species, which may also explain the high nonnative species richness and cover in adjacent unburned sites.

Perhaps the most surprising result of this study is the domination and extent of cheatgrass, which ranked as the highest species cover on 4 of our study sites and 3rd on the other 2 sites. In other parts of the Monument, we found that over 80% of our 360 modified-Whittaker plots had cheatgrass. Nonnative species richness averaged 2.9 species $\cdot$ 1 m^{-2} in unburned sites, almost 3 times more than we found in our plots across the Monument (Stohlgren unpublished work).

We suspect that the burn areas provide ideal conditions for germination of nonnative species, especially cheatgrass, thus facilitating local seed production and invasion into our unburned sites. Due to the short period between the fires and our field sampling, our study cannot provide any insight on how cheatgrass may affect future successional trends. However, examination of the 1998 fire pattern provides evidence that cheatgrass can increase fire frequency and spatial extent, creating more favorable conditions for its dominance. In a natural condition it is unlikely that the fire would have been able to carry across the 1996 burn, which resulted in a 2-year fire interval between burns. Cheatgrass is successfully outcompeting native plant species and other nonnative species in this area and appears to be dominating much of the unburned woodlands. Until other means of controlling invading species are identified, we can expect this positive feedback loop between invading plants and reoccurring fire.

Need for Experimentation

Controlled experiments will be needed to isolate the effects of fire, restoration, and grazing from high background variation. This was a "natural" and unplanned experiment, basically an observational survey or case study after a series of events. Having detailed pretreatment data and a factorial experiment is the only way to isolate the effects of fire from site effects and high spatial variation. The variability expressed in Table 2 suggests that several replicate study areas will be required in multiple study areas. There should be considerable distance between burned and unburned plots to reduce the effects of source-sink dynamics and propagule pressure effects in the invasion process.

Despite the limitations of our observational study, some differences between burned and unburned sites are obvious (Table 3). A simple analysis clearly shows that restoration efforts can have either positive or negative results. Seeding with native species in the right habitat and conditions can have positive effects on native richness and cover after some fires, as seen in the 1997 East burn. Seeding with nonnative species is not beneficial to native species richness and cover. For example, nonnative species cover in the 1996 burn (native and nonnative species seeded) was over 10 times greater than in unburned sites. Likewise, natural regeneration may preserve soil crusts to a greater extent than drill seeding, but burned areas are still vulnerable to nonnative plant invasion (Table 2). Thus, controlled experiments should be targeted to assess techniques that revitalize crusts and promote native species richness and cover. We conclude that the preservation of native plant diversity and biological soil crusts in the Monument will become increasingly difficult due to the spread of invasive plant species. We found no evidence to suggest that the invasion of the Monument by nonnative species can be curtailed easily; however, as seen in the 1997 East burn, rehabilitation efforts can have positive results.

Management Implications

Our results support many of the existing paradigms regarding postburn succession (Miller and Tausch 2001) and nonnative plant invasion (D'Antonio and Vitousek 1992, Stohlgren et al. 2001). This study has highlighted the complexity and variability of these systems and some of the multiple variables that may affect recovery from fire, successional trends, and rehabilitation efforts.

We offer 3 recommendations to resource managers concerning postburn rehabilitation. First, because soil crusts are so fragile and invasive plant seeds permeate the system, minimize postburn disturbance such as mechanized seeding and livestock trampling (Evangelista et al. in press). We suggest alternative rehabilitation techniques, such as aerial seeding, over tractors and drill-seeders. Second, if a fire occurs, use native species when reseeding (Table 2). Third, long-term monitoring and predictive models may be used to assess changes in species distributions and crust development, and to guide future management actions. Though successional trends in juniper are fairly well understood in natural settings, there is little understanding of how fire management, land use, and nonnative species invasion change the long-term dynamics of a system. Without detailed monitoring and consideration of multiple site factors, managers can expect to continue having unpredictable results to management practices.

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