

Large-Scale Downy Brome Treatments Alter Plant-Soil Relationships and Promote Perennial Grasses in Salt Desert Shrublands

Merilynn C. Hirsch-Schantz,¹ Thomas A. Monaco,² Christopher A. Call,¹ and R. L. Sheley³

Authors are ¹Graduate Research Assistant and Professor, Wildland Resources Department, Utah State University, Logan, UT 84322, USA; ²Ecologist, USDA, Agricultural Research Service, Forage and Range Research Laboratories, Logan, UT 84322, USA; and ³Ecologist, USDA, Agricultural Research Service, Eastern Oregon Agricultural Research Center, Burns, OR 97720, USA.

Abstract

Because invasive annual grasses can strongly influence soil resource availability and disturbance regimes to favor their own persistence, there is a great need to understand the interrelationships among invasive plant abundance, resource availability, and desirable species prominence. These interrelationships were studied in two salt desert sites where the local abundance of downy brome (*Bromus tectorum* L.) varied spatially and increased more than 12-fold over a 3-yr period. We measured downy brome percentage cover, resource availability, and soil chemical and physical properties within 112 plots per site and found significant negative associations between downy brome abundance and both soil water content ($P < 0.05$; $r = -0.27$ to -0.49) and nitrate accumulation ($P < 0.05$; $r = -0.34$ to -0.45), which corroborated with the direction and strength of multivariate factor loadings assessed with principal component analysis. We then applied factorial combinations of prescribed burning and preemergence herbicide at management-relevant scales (i.e., 6 to 46 ha) as well as biomass removal to smaller plots (12.25 m²) at both sites to determine their impact on downy brome, soil resources, and resident plant species. Burning and herbicide applications, especially when combined, significantly reduced downy brome cover ($P = 0.069$ to 0.015), which in turn increased soil nitrate accumulation and water content in the spring. Furthermore, for one shrubland site that was seeded 6 yr previously, the combination of burning and herbicide treatments significantly increased perennial grass percentage cover in the 2 yr posttreatment ($P < 0.05$). Results not only demonstrate the strong relationships between downy brome abundance, soil resources, and residence species for impoverished salt desert shrub ecosystems, but also suggest that restoration and management efforts must include tactics that facilitate resource use by the residual plant community or establish a greater abundance of species capable of high resource acquisition in the spring.

Key Words: cheatgrass, disturbance ecology, ecosystem resilience, restoration ecology, soil resource dynamics, spatial and temporal variation

INTRODUCTION

Invasive plant species pose a major threat to ecosystems and complicate managerial efforts to improve wildlife habitat, forage productivity, and reduce wildfire risk. Depending on their functional distinctiveness and abundance within an ecosystem, invasive species may largely influence ecosystem processes like plant-soil resource dynamics and disturbance regimes (D'Antonio and Vitousek 1992; Ehrenfeld et al. 2005; MacDougall and Turkington 2005; Strayer et al. 2006). Moreover, when functionally diverse perennial species are lacking and ecological processes are primarily driven by invasive species, a perpetual feedback cycle develops that modifies natural successional pathways (e.g., Beckage et al. 2009). Consequently, there is great need to understand plant-soil relationships of invasive-plant-impacted ecosystems and

explore how rehabilitation actions influence these relationships.

Species composition of a plant community strongly impacts soil resource availability (Fargione et al. 2003; Cleland et al. 2004; Seastedt and Pysek 2011). When plant functional diversity is low it can lead to underutilized soil resources, making ecosystems more susceptible to invasion and eventual dominance by non-native plant species (Davis et al. 2000). Invasive species dominance may also exacerbate fluctuations in resource availability that can occur from year to year, or within a year (Chambers et al. 2007). Resource fluctuations are a result of invasive species differing fundamentally from resident native species in life history traits, including phenological development, primary productivity, and seasonal soil resource acquisition (Evans et al. 2001; Maron and Jeffries 2001; Parker et al. 2012). For example, in low- to mid-elevation zones in the Intermountain Region of western North America, the annual grass downy brome (*Bromus tectorum* L.) is a highly problematic invader that dominates large expanses and is known to promote destructive disturbance regimes and alter plant-soil relationships (Adair et al. 2008; Balch et al. 2013). Where downy brome dominates, mineral nitrogen availability is lower than uninvaded areas (Norton et al. 2004; Schaeffer et al. 2012). However, following autumn senescence, a pronounced pulse of soil nitrogen availability occurs, which is not present where perennial grasses remain dominant (Booth et al. 2003). Conversely, when downy brome is experimentally

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Correspondence: Merilynn C. Hirsch-Schantz, Rangeland Ecology and Management Dept, Oregon State University, Corvallis, OR 97331, USA. Email: hirschm@onid.orst.edu

Current address: Merilynn C. Hirsch-Schantz, Rangeland Ecology and Management Dept, Oregon State University, Corvallis, OR 97331, USA.

Manuscript received 24 June 2013; manuscript accepted 12 February 2014.

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disturbed to induce plant mortality, soil nitrogen availability increases for other species in the ecosystem (Adair et al. 2008). While these findings confirm that invasive annual grasses like downy brome have the potential to both alter and strongly control soil resource availability, relatively less is known about how this interrelationship varies within invaded sites, where downy brome abundance varies both temporally and spatially (Stewart and Hull 1949; Evans and Young 1984).

Efforts to reduce the abundance of downy brome often target seed banks, biomass production, and litter accumulation to minimize rapid return of precontrol abundance, resource competition and interference on emerging revegetation species, and wildfire frequency (DiTomaso et al. 2010; Pyke et al. 2010). The primary treatments used to reduce the abundance of downy brome and create an alternative restoration pathway include prescribed burning, preemergence herbicide application, biomass removal, and seeding (DiTomaso et al. 2010; Pyke et al. 2010). Prescribed burning is commonly used to consume seeds in the seed bank and reduce the accumulation of litter that aids annual grass establishment, obstructs herbicide contact with soil, and elevates wildfire risk (Sweet et al. 2008). Burning also increases soil water and mineral nutrients as resource use by fire-damaged plants is reduced, and extractable concentrations of key minerals, including nitrate and phosphate, are elevated after litter is volatilized during combustion (Rau et al. 2007; Johnson et al. 2011). Because emerging downy brome seedlings are a major sink for soil nitrogen in early autumn (Booth et al. 2003), reducing seedling emergence and abundance with soil-active preemergence herbicides can increase the accumulation and availability of mineral nitrogen (e.g., Adair et al. 2008; Davies and Sheley 2011; Hirsch et al. 2012). Livestock grazing, mowing, or general biomass removal can also effectively reduce downy brome abundance by reducing seed production, litter accumulation, and downy brome interference on the performance of residual perennial species (Seabloom et al. 2003; MacDougall and Turkington 2005). These treatments are very costly, although they are often deemed necessary to manipulate ecological processes, alter resiliency of the annual grass-dominated ecological state, and create an alternative restoration pathway (Wisdom and Chambers 2009).

Our current understanding of how large-scale management treatments affect the interrelationships among downy brome abundance, soil resource availability, and desirable species success on invaded sites is limited (Chambers and Wisdom 2009; Sheley et al. 2010). For this reason, we designed a study to characterize the relationships among soil properties and the abundance of downy brome at two salt desert shrubland sites (50–100 ha) in the northeastern Great Basin where the local abundance of downy brome varied both spatially and temporally. Because the distribution of downy brome is highly heterogeneous and varies temporally from year to year (Cleland et al. 2004; Clinton et al. 2010; Hoover and Germino 2012), we tested the following two hypotheses: 1) spatial and temporal variation in downy brome abundance and soil nitrate availability are inversely related, and 2) reducing downy brome abundance by independent and combined treatments of prescribed burning, preemergence herbicide application, and targeted biomass removal will increase soil nitrate availability. Finally, we had a post hoc goal of determining if treatments

would have any noticeable impact on the performance of crested wheatgrass (*Agropyron cristatum* [L.] Gaertn.), which was previously seeded at one of the study sites but resulted in poor establishment. Because our study was conducted at large scales typical of realistic land management in the Great Basin, our results will help refine management strategies that encompass altering plant-soil relationships to yield restoration opportunities.

METHODS

Study Location and Description

Two salt desert shrubland sites, located 5 km south of Park Valley, Utah (Zone 12 N), were chosen for our study. Climate in this region is generally characterized as having cold, wet (snowy) winters and hot, dry summers with an average mean annual precipitation of 27.5 cm. Most of the precipitation within this region occurs during April and May. Between 1991 and 2011, precipitation ranged from 20 to 30 cm per year, and mean annual air temperature during this period was 10°C (NRCS 2011b; USU-CS 2011). Sites were 1 km apart and varied in size from 50 ha (Upper Site: lat 41°46'23.141"N, long 113°17'17.446"W) to 100 ha (Lower Site: lat 41°45'31.482"N, long 113°16'7.842"W). Both sites are classified as semidesert alkali loam (black greasewood) ecological sites (NRCS 1993). Soils are in the Kunzler series and are classified as coarse-loamy mixed, superactive, mesic, durinodic Xeric Haplocalcids (NRCS 2011a). Parent material is derived from alluvium, which has been deposited from the canyons of the Raft River Mountains to the north.

Vegetation is typically dominated by the shrubs *Sarcobatus vermiculatus* [Hook.] Torr. (black greasewood), *Artemisia tridentata* ssp. *wyomingensis* [Beetle & Young] S. L. Welsh (Wyoming big sagebrush), and *Ericameria nauseosa* [Pall. ex Pursh] G. L. Nesom & Baird ssp. *consimilis* [Greene] G. L. Nesom & Baird (rubber rabbitbrush) in the absence of recurring wildfires. Furthermore, the herbaceous understory is composed of *Achnatherum hymenoides* [Roem. & Schult.] Barkworth (Indian ricegrass) and *Elymus elymoides* [Raf.] Swezey (bottlebrush squirreltail). However, this region has experienced frequent wildfire and exotic annual plant invasions in the past 30 yr. For example, a large wildfire burned this region in 1983, which provided suitable conditions for invasive annual species expansion that fueled additional wildfires in 1999 and 2004. Consequently, when the study was initiated in 2008, both sites were dominated by downy brome, with minor occurrences of exotic annual species, including *Halogeton glomeratus* [M. Bieb.] C. A. Mey. (halogeton), *Sisymbrium altissimum* L. (tumble mustard), and *Salsola kali* L. (Russian thistle). Following the 2004 wildfire, the upper site was seeded with *Agropyron cristatum* [L.] Gaertn. (crested wheatgrass), but the seeding was deemed unsuccessful (K. Spackman, personal communication, May 2008), even though it did establish patchily in areas.

Experimental Design

To apply treatments at large scales typical of realistic land management in the Great Basin, we used a factorial experiment

with two levels of burning (no burn and burn), herbicide application (no herbicide and herbicide), and mowing (no mow and mow). Treatments were applied using a split-plot block design with two replications per site. Burning was the whole-plot factor, with treated areas that ranged in size from 12 to 46 ha. Herbicide was the split-plot factor, with treated areas that ranged in size from 6 to 26 ha. The cost of applying these land treatments was \$30 ha⁻¹ for burning and \$40 ha⁻¹ for herbicide application. Within each split-plot factor, a total of 14 smaller 3.5 m × 3.5 m sampling plots were randomly located within downy brome-dominated patches. Mowing was applied to seven randomly assigned sampling plots.

Burning was implemented on 4 November 2009 by igniting the perimeter of whole plots with propane torches, and allowing the prevailing wind to carry the fire. Fire was contained within the plots by disking 10-m-wide buffers around plot perimeters 1 wk before burning. Immediately behind the burning front, an 8-person burning crew ignited patches that failed to burn, paying close attention to burn the previously established sampling plots. On the day of burning, air temperature averaged 6.9°C, with a high of 17.3°C and a low of -0.5°C, wind speed averaged 8.7 kph (ESE), and relative humidity averaged 75%. Given the conditions of this autumn fire, it was estimated that only 75% of units burned.

The preemergence herbicide imazapic, which inhibits aceto-hydroxyacid synthase in plants, was applied aerially on 18 November 2009 from a PA-36 Pawnee Brave agricultural aircraft (Piper Aircraft, Vero Beach, Florida, USA) that was affixed with a 15-m boom. Herbicide application rate was 78 g · ai · ha⁻¹, carried in 22 L · water · ha⁻¹, and was sprayed at 7.6 m above the surface at 160 kph. When herbicide was applied, about 50% of the downy brome plants had emerged on areas that had not burned. On the day of herbicide application, air temperature averaged 1.6 °C, wind speed averaged 17.7 kph (WSW), and relative humidity averaged 53%. The first measurable precipitation event following application was on 21 November 2009.

The mow treatment was applied on 25 June 2009 using a 60-cm diameter motorized push mower. Plots were mowed at a height of 5 cm, when the target plant, downy brome, was primarily between the boot stage (prior to the emergence of the seed head from the sheath of the flag leaf) and seed head emergence.

Sampling Approach

Soils and plant cover attributes were measured in early May prior to applying treatments in 2009, and subsequently in 2010 and 2011 within each sampling plot. Within each sampling plot, variables were measured at four fixed locations within the center 2 m² of each sampling plot by placing a 20 cm × 50 cm Daubenmire frame on the soil surface and estimating percentage cover for each species encountered in the frame. Data from the four locations within a sampling plot were averaged. Soils were collected adjacent to the four Daubenmire frame locations using a 10 cm diameter × 20 cm length corer. The four soil samples from each sampling plot were combined, mixed, and kept in a chilled cooler during transport to the laboratory. Soil water infiltration was measured only once in late April 2009 adjacent to the soil

sampling locations using a mini-disk infiltrometer (Decagon Devices, Pullman, WA, USA). Infiltrometers were filled with water, placed on bare soil, and the loss of water was measured every 30 s for 2 min to determine the infiltration rate (cm · s⁻¹). Soil accumulation of mineral ions was measured in 2009, 2010, and 2011 using sets of ion exchange membrane probes (PRS probes; Western Ag Innovations, Saskatoon, SK, Canada). A probe set consisted of anion and cation resin stakes (four each), which were inserted into the moist soil in late April where infiltration measurements were taken. Probes were retrieved after 60 d. In brief, because ion accumulation is highly dependent on soil water availability, the 10 cm² resins capture ions that move through the soil solution. We did not measure or account for variability between years in soil water availability at the sampling plot level; however, probes were placed in the ground during a 60-d period of the year when the ground is no longer frozen and soil water availability has not yet become limiting to plant growth in this region (Booth et al. 2003). After retrieval from the field, probes were washed in deionized water and sent back to the manufacturer for analysis of the following ions: nitrate, ammonium, calcium, magnesium, potassium, and phosphate. In 2010 and 2011, probes were analyzed only for nitrate because results from the previous year indicated that this soluble form of nitrogen was most responsive to the treatments. Soil ammonium for the sampling periods was undetectable in most sampling plots, which was likely due to its lack of bioavailability in the soil solution, and was thus not analyzed.

Field-collected soil was used to determine gravimetric water content (2009 and 2010) by taking a 30-g sample from each plot and drying it in a convective oven at 100°C and reweighing. The field-collected soil samples were air-dried for 14 d and passed through a 2-mm sieve to further remove debris and gravel. Soil texture was determined with a hydrometer to quantify percentage sand, silt, and clay. A 40-g sample was mixed with 100 mL of a sodium hexametaphosphate-water solution and 250 mL of deionized water, shaken at 150 rpm for 1 h, placed into a cylinder, and the cylinder was filled with deionized water to attain 1 L. A custom plunger was used to mix the slurry before measuring its temperature and density (g · L⁻¹) after 30 s and 1440 min with a Bouyoucos hydrometer (14-331-5C; Thermo Scientific, Beverly, MA, USA). Soil pH was measured by mixing a 15-g soil sample with 30 mL of deionized water, shaking at 100 rpm for 30 min, then measuring the slurry with a pH meter (Orion 3 Star bench-top pH meter; Thermo Scientific). Electrical conductivity was determined by mixing a 50-g soil sample with 50 mL of deionized water, shaking at 200 rpm for 2 h, and filtering through a filter paper (Grade 4; Whatman International, Maidstone, England) using a vacuum system. Electrical conductivity was measured on the filtered solution with an ionic probe (Orion 3 Star bench-top conductivity meter; Thermo Scientific).

Statistical Analyses

Data collected within sampling plots were assessed for normality and homogeneity of variances with Shapiro-Wilk and Levene tests, respectively. Data transformations to improve normality included the following: log(water infiltration,

electrical conductivity, and soil nitrate) and log(brome cover) in 2009; square root(downy brome cover) in 2010 and 2011; and log(soil nitrate) in 2009 and 2010.

To characterize the relationships among soil properties and the abundance of downy brome, we used only data collected in 2009 prior to applying treatments. These data were standardized with a transformation so that the mean equals 0 and the variance equals 1. Because all variables were unimodally distributed, principal components analysis (PCA) and common factor analysis were used to evaluate the relationships among variables using JMP 8.02 (SAS Institute, Cary, NC, USA).

PCA seeks to identify the importance and relationships among chosen variables by reducing the multiple response variables down to a few best predictor variables (McCune and Grace 2002). To identify the best predictor variables, a cross-products matrix of the correlations among variables (i.e., downy brome and nine soil variables) was calculated. Eigenanalysis is then used to quantify variables into eigenvectors. Eigenvectors describe the amount of total variation among plots captured in two-dimensional axes and variables that account for the highest amount of variation in the model have the longest eigenvector length. We also conducted factor analysis to illustrate the correlation of the two-dimension axes and the PCA loading variables (i.e., downy brome and nine soil variables).

For simplicity of interpretation, we extracted only the first two principal components to explain the variation of this ecosystem using two-axis biplots. Subjecting the two extracted PCA axes to a Varimax rotation generated uncorrelated, orthogonal, high factor loadings for the most important variables. Factor loadings were graphed as *x,y* plots, which illustrate the correlation between each variable and the two extracted PCA axes. In addition, the relationship between downy brome cover and the other independent variables was determined with Pearson product-moment pairwise correlation. Significance was set at $P < 0.05$ and indicated on graphs.

We used a mixed-model ANOVA to evaluate the independent and combined treatments of prescribed burning, pre-emergence herbicide application, and targeted biomass removal on downy brome abundance and soil resource availability data for 2009, 2010, and 2011 at each research site (SAS Institute). This study was analyzed as a factorial experiment; treatment and year were considered fixed effects, and replication was considered a random effect. Sites were analyzed separately because they differed in downy brome cover, disturbance and management history, soil texture, and elevation. Preliminary analysis testing for the significance of replication revealed that this effect was never significant for any of the variables. Thus, replication and the replication by burn error terms were combined resulting in two degrees of freedom to test the effects of burning. For significant effects, differences between interaction means were determined using the slice option in SAS, which partitioned the analysis of least square-means (i.e., simple effects analysis). Data for percentage crested wheatgrass cover did not meet the assumptions of normality and were thus analyzed with nonparametric Kruskal-Wallis tests using JMP 8.02. This analysis independently compared cover among 2009, 2010, and 2011 within the eight treatment combinations using the χ^2 statistic (χ^2 test, $df=2$; $n=14$, with pooled sampling plots).

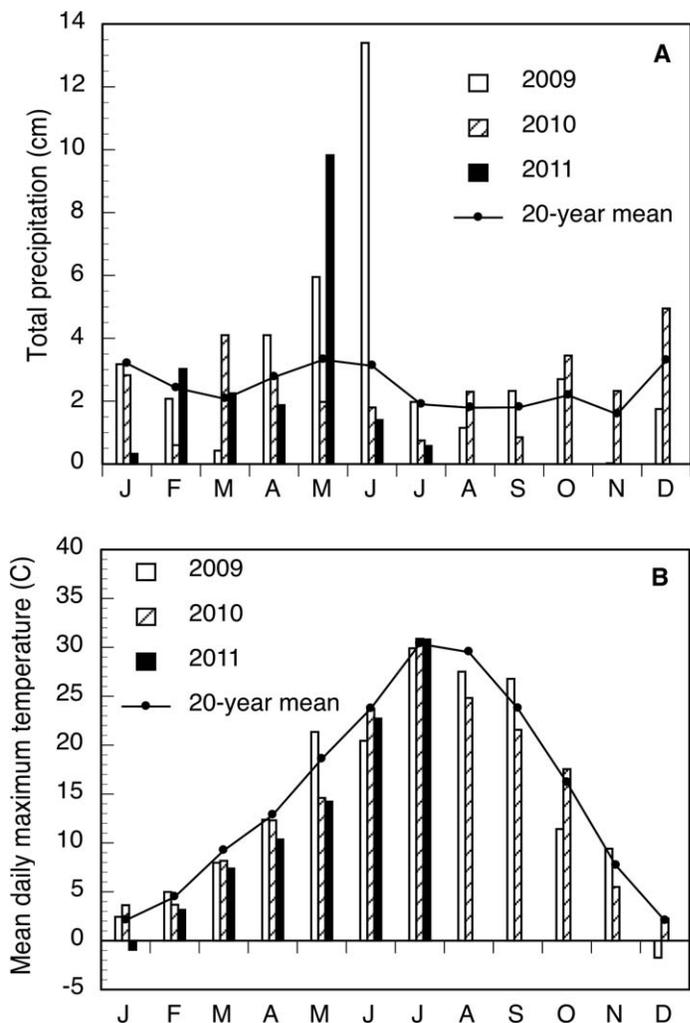


Figure 1. Total monthly precipitation, **A**, and mean daily maximum air temperature, **B**, for Park Valley, Utah, USA, in 2009, 2010, and 2011. Twenty-year monthly means for precipitation and temperature are indicated with overlay lines. Data compiled from NRCS (2011b) and USU-CS (2011).

RESULTS

Precipitation and General Growth Conditions: 2009–2011

Precipitation was higher than the 20-yr mean during spring (April–June) in 2009 and for May and July in 2011 (Fig. 1A). In addition, precipitation in early spring and late autumn of 2010 exceeded the 20-yr mean. In general, low maximum air temperature during May 2010 and 2011 (Fig. 1B) facilitated the growth of downy brome much later than would typically be observed during a typical year.

Interrelationships Among Soil Properties and Downy Brome Abundance

Principal component axes 1 and 2 explained 31.6% and 45.8% of the total variation among sampling plots at the upper site and 30.6% and 46.3% of the total variation at the lower research site, respectively. Factors that accounted for the highest amount of variation at the upper research site included magnesium, potassium, nitrate, soil water content, and sand. At the lower site, factors that accounted for the highest amount

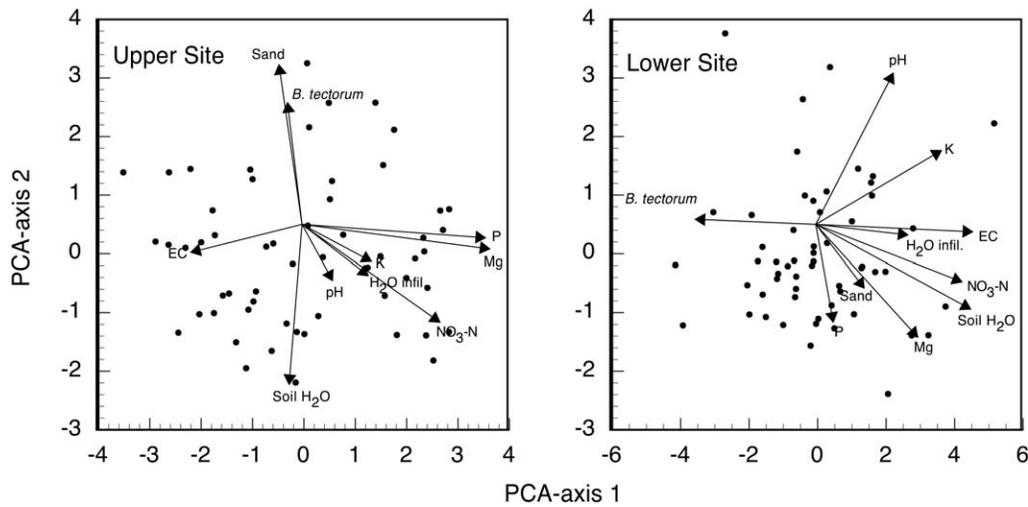


Figure 2. Principal Components Analysis (PCA) of sampling plots (dots) based on 9 factors (arrows) measured in 2009 at the upper and lower salt desert shrub research sites in Park Valley, Utah, USA. Direction and length of arrows indicate correlations with PCA axes 1 and 2.

of variation included soil water content, pH, nitrate, electrical conductivity, and magnesium. At the upper site, factor loadings for downy brome cover and sand were similarly correlated in a positive fashion with axis 2 (Fig. 2A). Alternatively, soil water was negatively correlated with axis 2, and polar to downy brome cover. Soil pH, water infiltration, potassium, and nitrate were also negatively correlated with axis 2, yet were generally correlated with axis 1, in a direction opposite to soil electrical conductivity. At the lower site, downy brome cover was negatively correlated with axis 1, while the other nine soil factors were positively correlated with this axis—most notably soil water, nitrate, electrical conductivity, potassium, and water infiltration (Fig. 2B). Variation along axis 2 was primarily demonstrated by positive correlations with pH, and negative correlations with magnesium, sand, and phosphate.

Pairwise correlations corroborated principal components/factor analyses, illustrating the negative association between downy brome cover and both soil water and nitrate at both research sites (Fig. 3). The negative pairwise correlations between downy brome cover and both electrical conductivity

and magnesium also agree with how these variables were primarily polar with principal components axis 1 at the lower site.

Treatment Effects on Downy Brome Cover: Upper Site

Cover of downy brome depended on year by burn by herbicide interactions (Table 1). Within the no burn treatment, downy brome cover more than doubled between 2009 and 2010 regardless of herbicide treatment, yet this increase did not occur in the burn treatment (Fig. 4A). By 2011 downy brome increased between 3- and 10-fold in the no burn–no herbicide and the burn–herbicide treatments, respectively. The increase in downy brome during the 3-yr evaluation was highly significant ($P < 0.0001$) for all burn-by-herbicide combinations at the upper site ($F_{2,16} = 209.04$ for no burn–no herbicide, 173.60 for no burn–herbicide, 158.95 for burn–no herbicide, and 70.21 for burn–herbicide). In the absence of burning, the herbicide treatment resulted in lower downy brome in 2011 than the no herbicide treatment ($F_{1,16} = 5.18$; $P = 0.037$). Within the burning treatment, however, the herbicide reduced downy

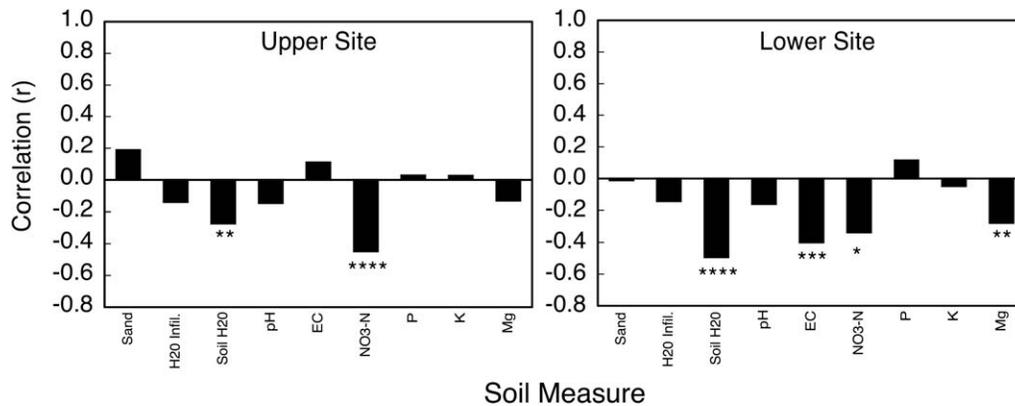


Figure 3. Pairwise correlations between downy brome cover and nine soil variables (see Methods for details) measured in 2009 at the upper and lower salt desert shrub sites in Park Valley, Utah, USA.

Table 1. Results of mixed-model ANOVA evaluating the effects of burning, herbicide, and mowing on downy brome cover, soil nitrate, and soil water over 3 yr at two research sites. Significant *P* values are in boldface; NS indicates nonsignificant effects. Degrees of freedom (*F*_{df}) are indicated for each *F* test; soil water numerator df=1 for the effect of year and associated interaction terms.

Effect	<i>F</i> _{df}	Downy brome cover	Soil nitrate	Soil water
Upper site				
Burn	1,2	NS	NS	NS
Herbicide	1,2	0.0422	NS	NS
Mow	1,4	0.0902	NS	NS
Burn × herb	1,2	NS	NS	NS
Burn × mow	1,4	NS	NS	NS
Herb × mow	1,4	NS	NS	NS
Burn × herb × mow	1,4	NS	NS	NS
Year	2,16	< 0.0001	< 0.0001	< 0.0001
Burn × year	2,16	0.0003	0.0021	NS
Herbicide × year	2,16	0.0024	0.0025	0.0105
Mowing × year	2,16	NS	NS	NS
Burn × herb × year	2,16	0.0691	NS	NS
Burn × mow × year	2,16	NS	NS	NS
Mow × herb × year	2,16	NS	NS	NS
Burn × herb × mow × year	2,16	NS	NS	NS
Lower site				
Burn	1,2	NS	NS	NS
Herbicide	1,2	NS	0.0858	NS
Mow	1,4	NS	NS	NS
Burn × herb	1,2	NS	NS	NS
Burn × mow	1,4	NS	NS	NS
Herb × mow	1,4	NS	NS	NS
Burn × herb × mow	1,4	NS	NS	NS
Year	2,16	< 0.0001	< 0.0001	< 0.0001
Burn × year	2,16	0.0224	NS	NS
Herbicide × year	2,16	0.0036	0.0306	0.0131
Mowing × year	2,16	NS	NS	NS
Burn × herb × year	2,16	0.0147	NS	NS
Burn × mow × year	2,16	NS	NS	NS
Mow × herb × year	2,16	NS	NS	NS
Burn × herb × mow × year	2,16	NS	NS	NS

brome cover relative to the no herbicide treatment in both 2010 ($F_{1,16}=5.59$; $P=0.031$) and 2011 ($F_{1,16}=39.860$; $P<0.0001$). Without herbicide, burning did not significantly impact downy brome cover in either 2010 or 2011. However, within the herbicide treatment, downy brome cover was significantly lower in the burn treatment than the no burn treatment in both 2010 ($F_{1,16}=3.11$; $P=0.097$) and 2011 ($F_{1,16}=29.56$; $P<0.0001$). Mowing did not interact with any other factor but did have a significant effect on mean percentage downy brome cover, which was lower in the mow treatment (20.60 ± 1.84) than the no mow treatment (22.75 ± 1.96).

Treatment Effects on Downy Brome Cover: Lower Site

Cover of downy brome was more than threefold greater on the lower site than the upper site prior to applying treatments in

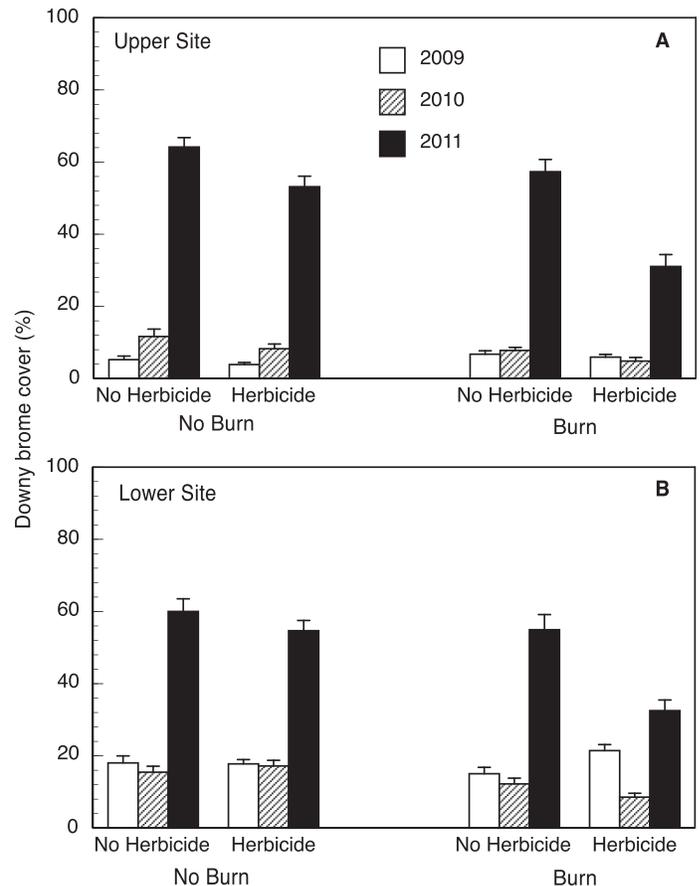


Figure 4. Mean (± 1 SE; $n=2$) percentage downy brome cover for the significant interactions between year, burning, and herbicide application at the upper, **A**, and lower, **B**, salt desert shrub sites in Park Valley, Utah, USA.

2009 (Fig. 4B). Similar to the upper site, the interaction between year, burning, and herbicide application was significant (Table 1), and by 2011, all treatment combinations except burn and herbicide experienced many-fold increases in cover. The increase in cover during this 3-yr period was highly significant ($P<0.0001$) for all burn by herbicide combinations at the lower site ($F_{2,16}=65.74$ for no burn–no herbicide, 52.57 for no burn–herbicide, 74.45 for burn–no herbicide, and 30.42 for burn–herbicide). Unlike the upper site, cover did not increase between 2009 and 2010 within the no burn treatment combinations, or it was reduced by more than half when burning and herbicide were combined. In the absence of burning, herbicide application did not significantly influence cover; however, similar to the upper site, herbicide significantly reduced cover relative to the no herbicide treatment in burned areas in 2011 ($F_{1,16}=16.58$; $P=0.0009$). As at the upper site, burning did not impact cover when herbicide was not applied; however, within the herbicide treatment, cover was significantly lower in the burn treatment than the no burn treatment in both 2010 ($F_{1,16}=5.40$; $P=0.034$) and 2011 ($F_{1,16}=11.79$; $P<0.0034$).

Treatment Effects on Crested Wheatgrass Cover: Upper Site

Cover for the minor exotic annual forb species was very low, i.e., $<5\%$ cover, and varied during the course of the study

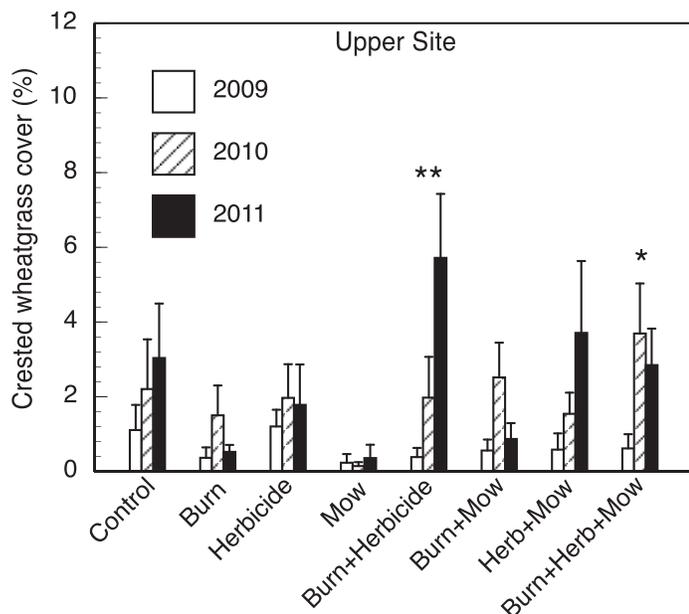


Figure 5. Mean (± 1 SE; $n=14$) percentage crested wheatgrass cover in 2009, 2010, and 2011 at the upper salt desert shrub site in Park Valley, Utah, USA. Asterisks indicate significant differences among median values within a treatment based on Kruskal-Wallis tests (χ^2_{2df} ; ** $P < 0.05$, *** $P < 0.01$).

within independent treatments, which often appeared spurious (data not shown). However, percentage cover of the perennial grass crested wheatgrass, which occurred only at the upper site, was significantly greater in 2010–2011 than 2009 for the two treatments that included both burning and herbicide application (Fig. 5).

Treatment Effects on Soil Nitrate and Water

Simultaneous to the sharp increase in downy brome cover during the study, the accumulation of soil nitrate over a 60-d period in spring of each year significantly changed at both sites (Table 1). At the upper site, a significant year-by-burning interaction occurred due to large differences in nitrate between the no burn and burn treatments in 2009 ($F_{1,16}=11.28$; $P < 0.004$) and 2010 ($F_{1,16}=7.36$; $P < 0.015$), but not in 2011 (Fig. 6). The effect of year also interacted with herbicide at the upper site as a result of soil nitrate being significantly different between the no herbicide and herbicide treatments in 2009 ($F_{1,16}=3.54$; $P=0.0781$) and 2010 ($F_{1,16}=16.36$; $P=0.0009$), but not 2011 (Fig. 7A). In contrast to the upper site, at the lower site, where downy brome cover was initially twofold higher, soil nitrate was relatively lower and burning did not have a significant effect on soil nitrate. However, similar to the upper site, soil nitrate was significantly greater in the herbicide treatment relative to the no herbicide treatment in 2010 ($F_{1,16}=19.76$; $P=0.0004$; Fig. 7B).

Soil water content at both research sites was significantly impacted by the year-by-herbicide interaction, which was only measured pretreatment in 2009 and 1-yr posttreatment in 2010 (Table 1). While large differences in soil water were observed between 2009 and 2010, the relatively small increase with herbicide relative to the no-herbicide treatment in 2010 was also significant for both sites (Figs. 7C–7D).

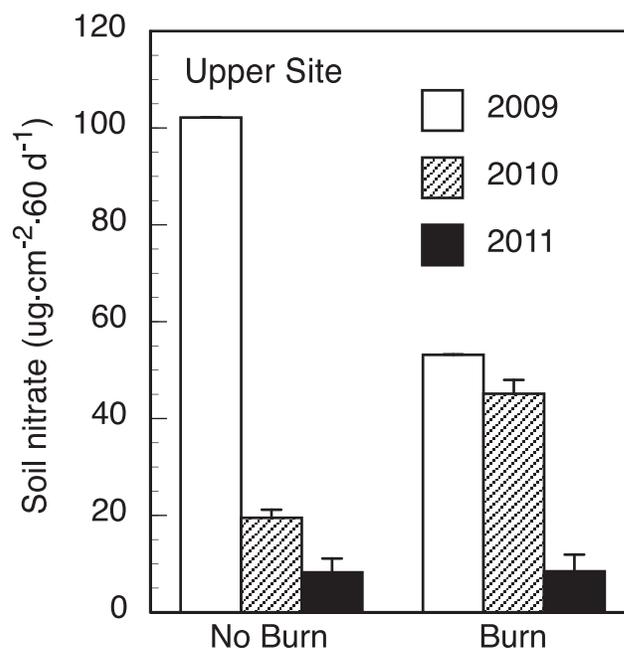


Figure 6. Mean (± 1 SE; $n=4$) soil nitrate for the interaction between year and burning at the upper salt desert shrub site in Park Valley, Utah, USA.

DISCUSSION

Interpreting the relationships among soil properties and the abundance of downy brome was greatly enhanced by the pattern in which downy brome began at low abundance in the first year, doubled in the second year, and increased nearly 12-fold by the third year. The sharp increases in abundance was likely a consequence of the uncharacteristically high precipitation during the spring in both 2009 and 2011, which occurred during the period when downy brome is typically most productive and can yield very high seed production rates (Stewart and Hull 1949; Adair et al. 2008). Although high precipitation during this study increased vegetation growth, the treatment effects are likely similar to an average precipitation year, except magnified. While this pattern of interannual variation is typical of downy brome-dominated regions (Clinton et al. 2010), it is also common in many grassland and shrubland ecosystems (Cleland et al. 2004; Seastedt and Pysek 2011). Thus, our characterization of how downy brome abundance controls soil resources in salt desert shrublands of the Great Basin, and how these interrelationships are influenced by common management actions, will likely be useful for other regions impacted by annual grass invasion.

Relationships Among Soil Properties and Downy Brome Abundance

In this study we found that spatial variability in downy brome abundance is strongly related to soil resource availability. Because soil nitrate and water (both sites), and Mg (lower site only) were negatively correlated with downy brome cover during the primary growth period of this annual grass, our data support our first hypothesis that spatial and temporal variation in downy brome abundance and soil nitrate availability are inversely related for these two shrubland landscapes. This hypothesis is also supported by our observation that soil nitrate

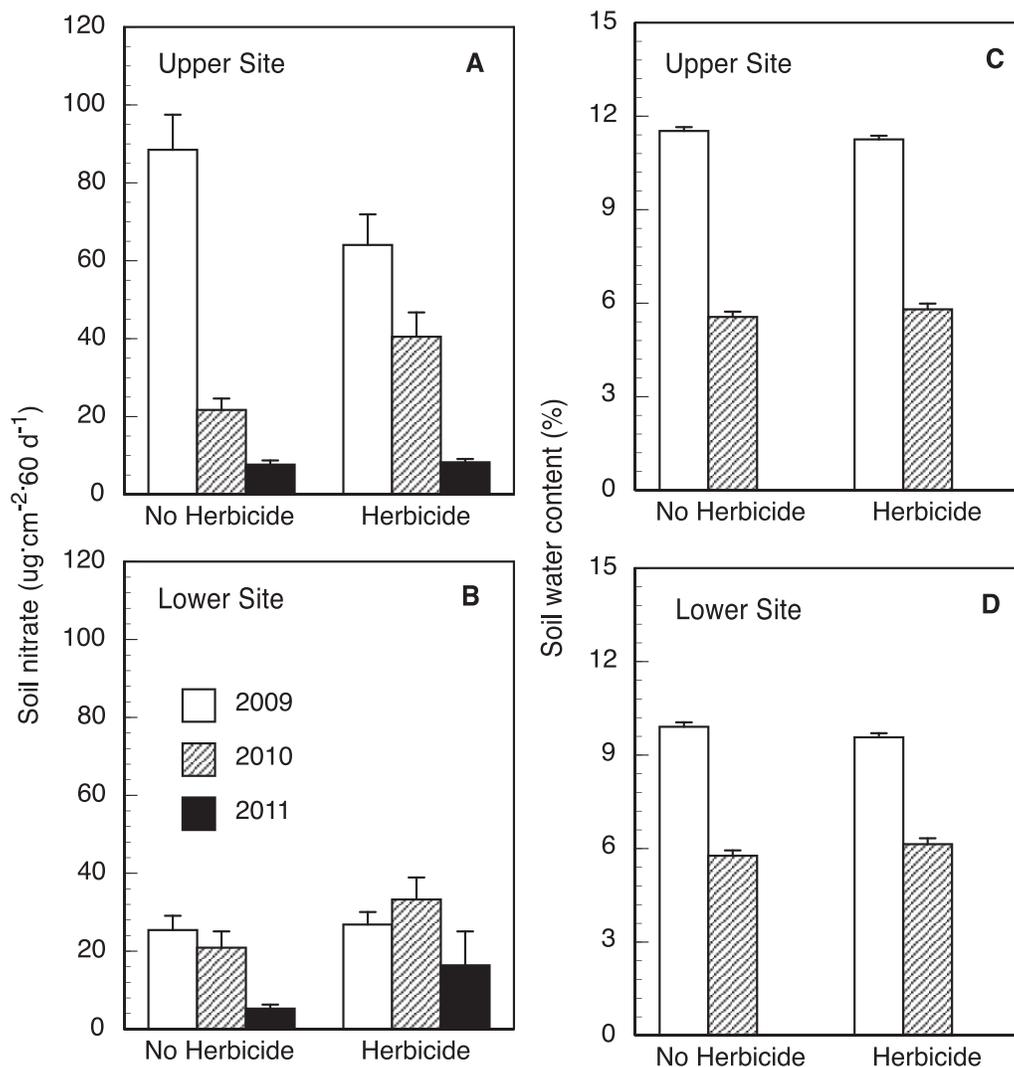


Figure 7. Mean (± 1 SE; $n=4$) soil nitrate and soil water content for the significant interactions between year and herbicide application at the upper, **A** and **C**, and lower, **B** and **D**, salt desert shrub sites in Park Valley, Utah, USA.

declined by more than ninefold at the upper site, and by nearly fivefold at the lower site in control treatments as downy brome increased between 2009 and 2011. Our results corroborate with previous research illustrating high nitrate uptake rates in downy brome (James et al. 2008; Leonard et al. 2008) and reduced nitrate abundance during the growing season in soils that are currently invaded by downy brome (Booth et al. 2003). Consequently, we conclude that downy brome is indeed an ecosystem driver capable of directly controlling resource availability (Evans et al. 2001; Blank 2008), which suggests that plant species that germinate or begin growth after downy brome will thus experience unfavorable soil resource conditions for establishment and growth (Knapp 1992).

We also observed that spatial variation in brome abundance appears to be associated with certain soil physiochemical properties, but more so at the lower site. At the upper site, downy brome abundance was not limited by any inherent soil property and likely performed at its full biological potential in these well-drained soils (i.e., higher sand content). In contrast, the negative correlation between downy brome abundance and

soil electrical conductivity, and the importance of soil electrical conductivity and pH along the same principal components axis at the lower site, indicate that maximum downy brome abundance is limited by these inherent soil properties as opposed to the possibility that this annual species directly influencing EC and pH. Similarly, Belnap et al. (2003) found a positive relationship between downy brome abundance and pH when downy brome was grown in soils originally dominated by *Stipa* spp. While it has been shown that certain species can influence salinity and rhizosphere pH at root system scales, e.g., long-lived desert shrubs (Li et al. 2011), there is currently no reports of an annual grass doing such. This interpretation is supported by the fact that downy brome growth is readily stunted by high saline conditions, even for populations originating from saline-soil sites (Rasmuson and Anderson 2002). Accordingly, we attribute the greater association among downy brome and these soil physiochemical properties at the lower site to its closer proximity to the northern shoreline of the Great Salt Lake, where soils are known to have higher pH and high electrical conductivity (Jessop and Anderson 2007).

Treatment Effects on Downy Brome Cover

The nearly exponential increase in downy brome abundance during the 3 yr of this study, in spite of control treatments, showcase the extreme variability in productivity portrayed by this invasive grass and the difficulty in reducing its abundance. Consequently, although our treatments did not optimally reduce downy brome abundance, reduction was improved when treatments were applied in combination. The effectiveness of combined treatments is best illustrated by the fact that when applied alone, burning and herbicide application were generally not effective at reducing downy brome cover. Conversely, when herbicide was applied with burning, cover was significantly lower for both sites than when it was applied without burning. Improved downy brome reduction when these two treatments are applied together has been attributed to greater herbicide contact with soil in burned areas where litter has been consumed and the percentage of bare ground is increased (Monaco et al. 2005; Davies and Sheley 2011). Thus, without burning, litter may have obstructed the capacity for the herbicide imazapic to effectively bind with soils, which is a critical prerequisite to reduce germination and emergence of downy brome from the seed bank (Hirsch et al. 2012). On the other hand, poor downy brome reduction when burning was applied alone is likely associated with insufficient consumption of seed. For example, the ability of fire to reduce downy brome is strongly controlled by its prefire seed bank density and whether the fire is intense enough to consume seeds (Keeley and McGinnis 2007; Allen et al. 2008). High-intensity fires in the Great Basin typically occur in the hot summer months when fire is more effective at killing a much greater fraction of the seed bank. For example, Humphrey and Schupp (2001) found that high fire intensity reduced downy brome seed bank density by 97% in burned relative to unburned areas. The presence of woody fuels also may increase fire intensity, and when they are not present, grass fires are not severe enough to reduce downy brome seed banks (D'Antonio and Vitousek 1992; Young and Allen 1997; Pyke et al. 2010). In contrast to high-intensity summer wildfire, prescribed burns, as used in our study, are often applied when air temperature is lower and relative humidity is higher, which yields low intensity fires that may not be intense enough to consume seed distributed on the soil surface.

Although mowing had significant impacts on downy brome at the upper site, it resulted in minor reductions when compared to the large variation from year to year. Poor reduction in downy brome in response to mowing was likely a consequence of very favorable precipitation during the spring mowing period in 2009, which allowed high regrowth, including the production of additional inflorescences and seeds. Similarly, others have questioned the feasibility of reducing downy brome abundance and seed bank density with defoliation, because clipping needs to be conducted more than once to account for regrowth (Hempy-Mayer and Pyke 2008).

Treatment Effects on Soil Nitrate and Water

Despite the magnitude of interannual variability in soil resources, characterized by large declines in soil nitrate as downy brome proliferated, it is notable that significant increases in nitrate and soil water were observed in response

to both burning and herbicide treatments for both sites. In contrast, mowing did not significantly impact soil nitrate or water availability, suggesting that our one-time mowing to prevent seed dispersal of downy brome is not adequate to alter soil nutrient availability as it has in other systems (Maron and Jeffries 2001; Blank et al. 2007), especially when subsequent regrowth occurred during the favorable precipitation in 2009. Thus, our results for burning and herbicide support our second hypothesis, which postulated that reducing downy brome abundance by independent and combined treatments would increase soil nitrate availability. Although our results confirm that critical soil resources are strongly regulated by downy brome, whose uptake of nitrate and soil water are known to be very high in early spring (Leonard et al. 2008; Ryel et al. 2010), it is important to note that these significant reductions caused by burning and herbicide application were observed only for 2010, and by 2011 treatment effects on soil nitrogen and water were not detected.

Our observation of increased soil resources where downy brome was reduced indicates that resident species, which were primarily exotic annual species, did not compensate and acquire these resources or were not as effective at acquiring resources. This likely occurred because overall resident species abundance was low or resident species may have been negatively impacted by treatments. Although annual grass control treatments typically increase the abundance of resident plant species (Monaco et al. 2005; Davies and Sheley 2011), the only species that significantly increased was crested wheatgrass at the upper site when burning and herbicide application were combined. Davies and Sheley (2011) also found that reducing the invasive annual grass medusahead (*Taeniatherum caput-medusae* [L.] Nevski.) with burning and herbicide increased the abundance of perennial grasses in sagebrush (*Artemisia*)–bunchgrass steppe. Collectively, these findings suggest that reductions in downy brome are most likely positive for resident perennial species, because resource availability increases during a critical time period when other cool season species are rapidly growing. For example, Mazzola et al. (2011) found that when downy brome propagule abundance was reduced, native species cover and density increased. Based on this study, it is plausible that if resident perennial species propagules are abundant within a site, and they are not negatively impacted by treatments, they may be able to effectively take advantage of the increased resource availability within the first year following treatments. However, if resident species do not respond rapidly as illustrated by crested wheatgrass in our study, and downy brome recolonizes, the window of opportunity for species turnover is likely diminished.

MANAGEMENT IMPLICATIONS

Our results imply that high resiliency of the invasive annual grass-dominated ecosystem state cannot be overcome by merely reducing downy brome abundance to yield greater resource availability in the spring. While the combination of burning and herbicide led to 1) sustained reductions in downy brome at both sites relative to untreated controls, 2) increased soil resources for 1 yr posttreatment, and 3) increased crested

wheatgrass cover at the upper site, we suggest that additional tactics are clearly needed to alter demographic and plant-soil processes. First, our observation of high annual grass recolonization, which is often the case even in highly controlled smaller plot applications (Monaco et al. 2005; Morris et al. 2009), suggests that seed production, seed banks, and seedling emergence require greater reductions. Greater managerial influence on these processes may be possible by refining the precision and timing of burning and herbicide applications or through repeated applications to target annual grass demography at specific life stages (DiTomaso et al. 2006; Pyke et al. 2010). Second, improved tactics are needed to facilitate resource use following reductions in annual grass abundance. Because species functional diversity is characteristically diminished for annual-grass dominated ecological states, revegetation becomes crucial to increase overall resource use during the spring. The manner in which crested wheatgrass cover increased in our study, combined with numerous lines of evidence that established perennial grasses are effective at acquiring soil resources at the same time period in the spring as annual grasses, emphasizes the need to restore this functional group (James et al. 2008; Leonard et al. 2008) because ecosystems are theoretically less susceptible to invasion by exotic plant species when resource fluctuation is minimized (Davis et al. 2000; Chambers et al. 2007). Thus, when land treatments both adequately reduce annual grass abundance and successfully establish perennial grasses, the plant-soil interrelationships we discuss here may be altered such that the impoverished annual grass state can potentially transition into an ecological state characterized by greater species functional diversity and resistance to invasion.

Managing downy brome-invaded shrublands is extremely challenging due to the tremendous interannual variability in its abundance and the poor capacity of land treatments to effectively prevent recolonization. Identifying the effects of large-scale land management treatments is particularly important to practitioners because the effects of small-scale experiments may not always encompass the site trajectories at realistic operational scales. We illustrate the interrelationship between downy brome and soil nutrients in salt desert shrublands and demonstrate that the abundance of this invasive grass strongly influences soil nitrate availability. Furthermore, we clearly established that land treatments designed to reduce downy brome abundance simultaneously increase soil resource availability, which has been observed in other regions impaired by downy brome (Chambers et al. 2007; Adair et al. 2008). Because the plant-soil relationships of annual grass dominated systems are strongly driven by the abundance of downy brome, transitioning away from annual grass dominance may only be practical if a variety of tools and tactics are used to successfully establish greater species functional diversity within the first year following treatments.

ACKNOWLEDGMENTS

Research was funded by USDA, Agricultural Research Service, Area-Wide Project on Ecologically Based Invasive Plant Management EBIPM of Annual Grasses in the Great Basin. We thank Justin Williams, Beth Fowers, Robert Watson, Casey Snieder, Joe Lamb, Sarahi Felix, and Rui-Xiang Liu

for assistance with field and laboratory research. We also thank Bob Blank and Lora Perkins, whose insightful reviews improved this article.

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