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Eugene W. Schupp, *Utah State University*



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Soil Resources Influence Vegetation and Response to Fire and Fire-Surrogate Treatments in Sagebrush-Steppe Ecosystems

Benjamin M. Rau,¹ Jeanne C. Chambers,² David A. Pyke,³ Bruce A. Roundy,⁴ Eugene W. Schupp,⁵ Paul Doescher,⁶ and Todd G. Caldwell⁷

Authors are ¹Research Ecologist, USDA Forest Service, Southern Research Station, Aiken, SC 29803, USA; ²Research Ecologist, USDA Forest Service, Rocky Mountain Research Station, Reno, NV 89512, USA; ³Supervisory Research Ecologist, US Geological Survey, Forest and Rangeland Ecosystem Science Center, Corvallis, OR 97331, USA; ⁴Professor and Range Ecologist, Brigham Young University, Department of Plant and Wildlife Sciences, Provo, UT 84602, USA; ⁵Professor and Plant Ecologist, Utah State University, Wildland Resources Department, Logan, UT 84322, USA; ⁶Professor and Plant Ecologist, Oregon State University, Department of Forest Resources, Corvallis, OR 97331, USA; and ⁷Research Associate, University of Texas at Austin, Bureau of Economic Geology, Austin, TX 78713, USA.

Abstract

Current paradigm suggests that spatial and temporal competition for resources limit an exotic invader, cheatgrass (*Bromus tectorum* L.), which once established, alters fire regimes and can result in annual grass dominance in sagebrush steppe. Prescribed fire and fire surrogate treatments (mowing, tebuthiuron, and imazapic) are used to reduce woody fuels and increase resistance to exotic annuals, but may alter resource availability and inadvertently favor invasive species. We used four study sites within the Sagebrush Steppe Treatment Evaluation Project (SageSTEP) to evaluate 1) how vegetation and soil resources were affected by treatment, and 2) how soil resources influenced native herbaceous perennial and exotic annual grass cover before and following treatment. Treatments increased resin exchangeable NH_4^+ , NO_3^- , H_2PO_4^- , and K^+ , with the largest increases caused by prescribed fire and prolonged by application of imazapic. Burning with imazapic application also increased the number of wet growing degree days. Tebuthiuron and imazapic reduced exotic annual grass cover, but imazapic also reduced herbaceous perennial cover when used with prescribed fire. Native perennial herbaceous species cover was higher where mean annual precipitation and soil water resources were relatively high. Exotic annual grass cover was higher where resin exchangeable H_2PO_4^- was high and gaps between perennial plants were large. Prescribed fire, mowing, and tebuthiuron were successful at increasing perennial herbaceous cover, but the results were often ephemeral and inconsistent among sites. Locations with sandy soil, low mean annual precipitation, or low soil water holding capacity were more likely to experience increased exotic annual grass cover after treatment, and treatments that result in slow release of resources are needed on these sites. This is one of few studies that correlate abiotic variables to native and exotic species cover across a broad geographic setting, and that demonstrates how soil resources potentially influence the outcome of management treatments.

Key Words: exotic annual grass, herbicide, mowing, prescribed fire, soil nutrients, soil water

INTRODUCTION

Current paradigm suggests that resistance to exotic plant invasions is largely a function of resource limitation and biological resource partitioning. Ecosystems are believed to be relatively resistant to invasion if most available resources are utilized by the existing native vegetation through time and space (Veresoglou and Fitter 1984; Tilman et al. 1997; Duke and Caldwell 2001; Booth et al. 2003; James et al. 2008). Resistance to invasion decreases if increases in resource availability occur due to disturbance or other factors (Davis et al. 2000). Much less is known about the influence of inherent

resource levels and resource fluctuations in ecosystems with persistent populations of invaders. Because vegetation management treatments designed to reduce invaders typically cause increases or pulses in resource availability, understanding the interactions of invasive species with the abiotic environment and native species in the vegetation community is essential for predicting outcomes.

Semi-arid shrub-steppe systems are often limited by one or more soil resources, typically water, nitrogen (N), or phosphorus (P) due to lack of consistent precipitation, poor soil development, low N-fixation and deposition, lack of organic matter, high carbonate content, or alkaline soil pH. Native species are well adapted to these conditions, and shrub-steppe ecosystems with intact native perennial woody and herbaceous species often have tightly coupled water and nutrient cycles that can increase resistance to invasion (James et al. 2008; Prevey et al. 2010; McGlone et al. 2011; Roundy et al. 2014). However, disturbance of semi-arid sagebrush (*Artemisia* L.) ecosystems in the intermountain United States due to inappropriate land uses or management practices can result in dominance of exotic annual grasses (e.g., cheatgrass; Knapp 1996).

Invasion of semi-arid sagebrush ecosystems is closely linked to changes in disturbance regimes and community composition

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Correspondence: Benjamin M. Rau, USDA, Forest Service, Southern Research Station, 241 Gateway Dr, Aiken, SC 29803, USA. Email: benjaminmrau@fs.fed.us

At the time of the research, Rau was a Postdoctoral Researcher, Dept of Natural Resources and Environmental Science, University of Nevada, Reno, 1000 Valley Rd, Reno, NV 89512, USA.

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that result in increased resource availability for growth and reproduction of exotic annuals (D'Antonio and Vitousek 1992; Pellant 1996). Introduction of domestic ungulate grazers to the Great Basin in the 1860s decreased native perennial herbaceous species cover, and likely altered soil resource availability throughout much of the region (Mack and Thompson 1982; Young et al. 1987; Melgoza et al. 1990). Native herbaceous perennials in the Great Basin are largely caespitose grasses that did not evolve with and are not tolerant of repeated intensive grazing (Branson 1953; Hickey 1961; Jewiss 1972; Mack and Thompson 1982). Removal of these grasses can increase soil nutrient and water availability in shrublands, which, in turn, can facilitate dense sagebrush stands with low resistance to exotic annual species (Dodd et al. 1998; Blank et al. 2007). Dense sagebrush stands are prone to high intensity fires that increase availability of soil nutrients and soil moisture, and because sagebrush are killed by fire, simultaneously decrease competition for soil resources (Blank et al. 2007; Leffler and Ryel 2012). Temporary pulses of soil N, P, K, micronutrients, and water in the absence of native perennial herbaceous species significantly reduce resistance to invasion (Blank et al. 2007; Chambers et al. 2007). Increases in resources following fire can persist for several years, prolonging the invasion window (Stubbs and Pyke 2005; Rau et al. 2007; Roundy et al. 2014).

Success of exotic annual grasses like cheatgrass (*Bromus tectorum* L.) is largely a function of high growth and reproductive rates and the capacity to take advantage of increases in resource availability. Cheatgrass can germinate from autumn to spring depending on soil water availability (Mack and Pyke 1983; Roundy et al. 2007); is capable of root elongation and growth at relatively cold temperatures (Melgoza and Nowak 1990; Aguirre and Johnson 1991); and exhibits a high growth rate allowing it to complete its lifecycle early in the growing season. Early growth and high rates of resource uptake make it competitive for available resources, which decrease resources for native perennial herbaceous species (Melgoza et al. 1990; Booth et al. 2003). Mature native species are capable of effectively competing with cheatgrass (Booth et al. 2003; Chambers et al. 2007; Blank and Morgan 2012), but seedlings of native species are not (Booth et al. 2003; Monaco et al. 2003; James et al. 2011). Therefore, mature native herbaceous perennial species represent the best defense against invasion (McGlone et al. 2011).

Managers are seeking effective methods for reducing fuels, increasing abundance of perennial native herbaceous species, and decreasing annual grass dominance in sagebrush-steppe ecosystems to protect biological diversity and maintain ecosystem function. Restoration of sagebrush-steppe has focused on reducing competition from woody species and increasing perennial herbaceous species abundance through prescribed fire, mechanical and chemical treatments, and seeding of perennials. To date, these treatments have met with variable success, and exotic annual grasses continue to expand their range (Pyke et al. 2013). Many of these treatments tend to increase soil resources and may actually be facilitating exotic annual grass invasion (Prevey et al. 2010). Much of the research surrounding annual grass invasion and sagebrush-steppe restoration has focused on soil water and N with significantly less attention being given to other nutrients and the interacting effects of abiotic factors (Kay and Evans 1965;

Wilson et al. 1966; Melgoza et al. 1990; Booth et al. 2003; Lowe et al. 2003; Monaco et al. 2003; Vasquez et al. 2008). The purpose of this research is to examine the set of vegetation, soil, and abiotic factors likely to influence resilience to management treatments (recovery potential) and resistance to cheatgrass in Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) ecosystems. We use fuel reduction treatments across a large geographic area in the interior western United States to ask how inherent abiotic factors, vegetation composition, and soil resources influence relative abundance of native perennial herbaceous species and cheatgrass in sagebrush ecosystems before and after treatment. We address specific questions: (1) How are vegetation cover and soil resources (N, P, K, soil water) influenced by vegetation management treatments? And (2) How are native perennial herbaceous species and cheatgrass cover related to soil resources before and after treatment? The experiment is part of the Sagebrush Steppe Treatment Evaluation Project (www.sagestep.org), which was established to examine effectiveness of fuel reduction treatments for maintaining resilient sagebrush-steppe ecosystems that can resist cheatgrass invasion. Several other articles describing the SageSTEP study deal more extensively with initial vegetation response to treatment and cover a larger number of sampled sites (Chambers et al. 2014; Pyke et al. 2014). However, annual soil nutrient availability, moisture, and temperature data are only available for a subset of sites within the larger study. Vegetation data included in this study describes the general vegetation response to treatment on this subset of sites, and sets the context for our evaluation of interactions between soil resources, vegetation, and management treatments. This study represents one of the few observational studies to correlate abiotic factors with vegetation cover across a broad region, and is one of even fewer studies that attempt to determine the factors that relate treatment success to a broad range of biotic and abiotic variables.

METHODS

Experimental Area and Design

We focused on four of the seven arid Wyoming big sagebrush sites (McIver and Brunson 2014; [Onaqui, Utah; Roberts, Idaho; Rock Creek, Oregon; Saddle Mountain, Washington]) that encompassed a range of soil and weather patterns (Table 1). These are the only four Wyoming big sagebrush sites within the study where annual soil nutrient, soil moisture, and soil temperature data were collected in conjunction with vegetation data. The experiment was a randomized complete block split-plot design with repeated measures. Each of the four sites was a replicate block that contained four core treatment plots (20–80 ha). Core treatment plots were on similar soils and supported vegetation that was dominated by perennial grass and shrub cover with variable amounts of cheatgrass cover (0–50% areal cover). This mix of vegetation represents sites that may currently be stable, but are at risk of becoming dominated by annual grasses. At each site, four treatments were implemented, one per treatment plot: 1) prescribed fire, 2) mowing sagebrush at a blade height selected to reduce sagebrush cover \approx 50%, 3) tebuthiuron herbicide applied at a rate selected to thin

Table 1. Name, location and select soil and vegetation properties for the four sites in the study. Vegetation abbreviations follow USDA plants database nomenclature (<http://www.plants.usds.gov>).

	Onaqui	Rock Creek	Roberts	Saddle Mountain
Latitude	40.19914166	42.71718456	43.76891468	46.74985749
Longitude	−112.46043876	−119.49088703	−112.28263537	−119.35260281
Year treated	2006	2007	2007	2008
Soil classification	Loamy-skeletal, mixed, active, mesic Xeric Haplocalcids	Loamy, mixed, superactive, frigid, shallow Xeric Haplodurids	Loamy, mixed, superactive, frigid Lithic Xeric Haplocalcids	Coarse-silty, mixed, superactive, mesic Xeric Haplocambids
Geology	Limestone alluvium	Basalt/Tuff	Loess over Basalt	Loess over Lacustrine
Elevation (m)	1 660	1 462	1 483	303
Mean annual temperature (°C)	9	8	6	11
Mean annual precipitation (mm)	300	275	263	215
Soil depth (cm)	70 to > 90	26 to > 90	9 to > 90	48 to > 90
% Coarse fragments	12	17	9	1
% Sand	27	30	35	32
% Silt	52	49	49	57
% Clay	21	19	17	9
Soil available water (cm)	14	8	7	14
Surface pH (0–15 cm)	8.1	7.4	7.7	7.7
Total soil organic C (mg · ha ^{−1})	38.2	27.9	35.0	25.0
Total soil N (mg · ha ^{−1})	3.7	3.0	3.0	3.5
Total extractable soil H ₂ PO ₄ [−] (mg · ha ^{−1})	71.2	87.9	120.0	89.0
Common herbaceous vegetation ¹	POSE, ELEM5, ACHY, PSSP6, LECI4, ACTH7	POSE, ELEM5, ACHY, PSSP6, ACTH7	POSE, ACHY, PSSP6	ELEM5, ACHY, PSSP6

¹POSE indicates *Poa secunda*; ELEM5, *Elymus elymoides*; ACHY, *Achnatherum hymenoides*; PSSP6, *Pseudoroegneria spicata*; LECI4, *Leymus cinereus*; and ACTH7, *Achnatherum thurberianum*.

sagebrush by $\approx 50\%$, and 4) untreated “control.” Burn plots that did not have complete mortality were spot burned to blacken all shrubs within a subplot. Mowing was done at a height of 35.6–38.1 cm with a rotary mower, and tebuthiuron was applied as 1.68 kg · ha^{−1} of Spike 20P. The pre-emergent herbicide imazapic was applied immediately post treatment, to half of the (30 × 33 m) split-plots (from here on referred to as measurement subplots) that were randomly selected from within each treatment plot, including the control. Imazapic was applied as Plateau at rate of 438 mL · ha^{−1}, 511 mL · ha^{−1}, and 584 mL · ha^{−1} for fire, tebuthiuron and control, and mow, respectively. For this study we chose to monitor effects of imazapic only on untreated “control” and prescribed fire woody fuel treatments, due to funding constraints. We collected data before and after treatment implementation (from 2006–2010) on all sites. All fuel reduction treatments were conducted during the same year within a site. However, all sites were not treated in the same year (McIver and Brunson 2014). For this reason, measurements taken in the growing season immediately before treatment are considered year 0, and the first three growing seasons following treatment are considered years 1, 2, and 3. The exception was Saddle Mountain, which was treated in 2008 and has only 2 yr of posttreatment data.

Sample Collection and Processing

All measurements were taken within subplots. Five permanent transects were established within each subplot to determine vegetation cover by species and distance between perennial plants (gaps) using the line point intercept method (Herrick et al. 2005; see Pyke et al. 2014 for details). Cover by species was

reclassified posthoc into plant functional groups (shrubs, exotic annual grass, annual forbs, deep rooted perennial grasses, shallow rooted perennial grasses, and lichens and moss). Plant available soil nutrients (NH₄⁺, NO₃[−], H₂PO₄[−], and K⁺) were measured within each subplot at four “microsites”: under shrub canopies, under the shallow-rooted perennial bunchgrass *Poa secunda* J. Presl, under a deep-rooted perennial bunchgrass (typically *Elymus elymoides* [Raf.] Swezey ssp.), and in bare ground or “interspace.” Soil nutrients were measured using Plant Root Simulator (PRS) probes (Western Ag Innovations Inc, Saskatoon, Saskatchewan, Canada). PRS probes measure ions in soil solution that are able to diffuse to the resin surface, much like a plant root. Probes consist of a plastic frame (3 × 15 cm) with an ion exchange resin sheet. Probes were inserted vertically into the ground to a depth of 10 cm, so that the resin sheet was completely below the soil surface and only the probe handle was exposed. Probes were inserted in pairs to measure both cations and anions. One set of probes was inserted at each microsite in each subplot. Probes under shrub canopies were placed halfway between the shrub bole and the drip line, while those under perennial grasses were placed immediately adjacent to the plant base. Probes were deployed twice per year: spring (inserted March–retrieved June) and summer (inserted June–retrieved September). No sampling was done over winter. Probes were retrieved at the end of each sample period, washed with deionized water, placed in a polyethylene lock type bag, and returned to the manufacture where the probes were extracted with 17.5 mL of 0.5 N HCl for 1 h. The extract was analyzed for NH₄⁺ and NO₃[−] colorimetrically using a Technicon Autoanalyzer II (Seal Analytical, Mequon, WI). The remaining ions (K⁺ and H₂PO₄[−]) were analyzed with the use of

inductively coupled plasma emission spectroscopy (Perkin Elmer Optima 3000-DV ICP; Perkin Elmer Inc, Shelton, CT). Values reported for probes are $\mu\text{mol} \cdot \text{cm}^{-2}$ of resin surface.

A single soil core also was collected from each subplot to determine soil physical and chemical properties (particle size distribution, coarse fragment content, soil water holding capacity, total soil organic C, and total soil N) to a depth of 90 cm or an impenetrable obstruction (see Rau et al. 2011 for full methodology). Coarse fragment % was determined by sieving soil cores to < 2 mm, rinsing the > 2-mm fraction with DI water to remove fines, drying at 102°C, and weighing. Sand % was determined by treating the < 2-mm fraction with 30% H_2O_2 , then sieving the < 2-mm fraction to 63 μm , drying at 102°C, and weighing. Silt and Clay % were determined by laser diffraction (Micromeritics Saturn DigiSizer 5200, Norcross, GA; Gee and Or 2002). Soil hydraulic properties were estimated using the pedotransfer function described by Schaap et al. (2004). The < 2-mm soil textural components and soil matrix density (assuming a coarse fragment particle density of $2.65 \text{ g} \cdot \text{cm}^{-3}$) were determined as described in Young et al. (2009). Water holding capacity was determined as the difference in water content at -0.33 MPa and -1.5 MPa integrated over the sampling depth and corrected for coarse fragment content. Soil organic C and total N were determined by dry combustion using a LECO Truspec CN analyzer (LECO Corp, St. Joseph, MI).

Soil temperature and matric potential were measured using thermocouples and gypsum blocks (Delmhorst, Inc, Towaco, NJ) that were buried at 1–3, 13–15, 18–20, and 28–30 cm, and located in one under shrub canopy microsite at the east-side drip line and in three interspaces between shrubs in each subplot where resin exchangeable nutrient measurements and soil cores occurred. Data loggers were programmed to read sensors every 60 s and to store hourly averages. Gypsum block resistance was converted to water potential using standard calibration curves (Campbell Scientific, Inc, 1983, Logan, UT). Derived variables were calculated for the seasons corresponding with PRS deployments: spring (March–June) and summer (June–September). Derived variables included total number of wet days (total hours $\cdot 24 \text{ h}^{-1}$ when hourly average soil water matric potential $> -1.5 \text{ MPa}$), degree days (summation of hourly average soil temperatures for each hour that average soil temperature was $> 0^\circ\text{C} \cdot 24 \text{ h}^{-1}$), wet degree days (degree days when soil water matric potential $> -1.5 \text{ MPa}$), and hourly average soil temperatures (Roundy et al. 2014).

Statistical Analyses

To compare vegetation and soil variables at the annual time step, vegetation and soil variables were summarized at the subplot level and compared across all four sites. For this analysis, resin exchangeable nutrients were averaged across all microsites and the two measurement periods within a subplot for each year. Degree days, wet days, and wet degree days were averaged across all microsites and depths within a subplot, and then summed over the two measurement periods for each year. Average soil temperature was calculated as the mean of all microsites, depths, and measurement periods for each year.

Soil nutrient (N, P, K), moisture (wet days), temperature (degree days, wet degree days, mean soil temperature), and

vegetation cover (shrub, native perennial herbaceous, exotic annual grass) response were analyzed for treatment effects using SAS 9.2 generalized linear mixed models (Proc GLIMMIX). We used a staggered start framework and repeated measures where sites were blocks and calendar year was considered random (Loughin 2006). Means comparisons were made using Tukey's test ($\alpha=0.05$).

Sites were analyzed for pretreatment biotic and abiotic similarities and differences using SAS IML Studio 3.3 canonical discriminant analysis (Proc DISCRIM). The analysis of pretreatment abiotic variables utilized all of the soil physical and chemical variables obtained from soil cores and PRS resin probes (Appendix 1). The analyses of pre- and posttreatment vegetation communities utilized the posthoc functional groups and metrics derived from the line point transects (Appendix 1). Univariate ANOVA was used to test that group means were different, and Wilks' lambda was used to determine linear relationships between predictor and group variables (Rencher 1992). Predictor variables were considered collinear if the pooled within-group correlation was greater than 0.8 (Rencher 1992).

Relationships between native perennial herbaceous plant cover, exotic annual grass cover, and abiotic variables were determined using SAS Enterprise Guide 4.3 linear regression models (Proc REG). Stepwise linear regression was utilized; variables were allowed to enter the model if they were significant at the 95% confidence limit and remain in the model as long as they remain significant. The best overall models were selected using the Akaike Information Criteria and Mallows' $C(p)$. The analysis of pre- and third year posttreatment exotic annual grass cover and native perennial herbaceous species cover utilized mean annual temperature and precipitation, and all of the soil physical and chemical variables obtained from soil cores and PRS resin probes along with plant functional groups and metrics derived from the line point transects (Appendix 1). Variables within each model were deemed collinear and removed from the model if the variance inflation factor for a parameter was greater than 10 (SAS Institute Inc, Cary, NC).

RESULTS

Vegetation Response to Treatments

All of the vegetation variables in our analysis exhibited a significant response to treatment, and there were significant treatment method \times time interactions for shrub and exotic annual grass cover (Table 2). Prior to treatment, shrub cover was similar across treatments and control plots (Table 3). Shrub cover decreased in the first year after treatment by 78%, 88%, and 45% in fire, fire+imazapic, and mow treatments, respectively, when compared to control plots (Table 3). Shrub cover remained lower in the second year posttreatment in fire, fire+imazapic, and mow plots compared to controls (Table 3). Three years after treatment, shrub cover was lower on fire plots by 67% and lower on fire+imazapic plots by 76% than on control plots (Table 3). Shrub cover had largely recovered on mow plots in the third year posttreatment and was no longer significantly different than control plots (Table 3). Though not statistically significant, shrub cover in tebuthiuron plots

Table 2. Results from the generalized linear mixed effects model for resin extractable soil nutrients, soil moisture, and vegetation cover as affected by treatment method and time.

	df	NH ₄ ⁺			NO ₃ ⁻			H ₂ PO ₄ ⁻			K ⁺			Wet days ¹			Degree days			Wet degree days			Average soil temperature			Shrub			Native perennial herb			Exotic annual grass		
		F	P		F	P		F	P		F	P		F	P		F	P		F	P		F	P		F	P		F	P		F	P	
Treatment method	5,15	5.33	0.0052	36.47	<0.0001	6.05	0.0029	12.33	<0.0001	5,15	0.98	0.4634	0.35	0.876	5,1	0.0063	0.55	0.7374	5,15	23.06	<0.0001	5.79	0.0036	10.63	0.0002									
Time	3,8	25.43	0.0002	9.18	0.0057	122.56	<0.0001	6.62	0.0147	2,4	26	0.0016	0.65	0.6164	16.72	0.0021	1.76	0.2709	3,8	21.47	0.0003	3.28	0.0796	4.82	0.0334									
Treatment method × time	15,40	3.73	0.0004	8.13	<0.0001	1.25	0.2805	2.05	0.0356	10,17	0.65	0.7772	0.74	0.7026	0.54	0.8774	1.28	0.3044	15,40	3.36	0.0011	1.64	0.1066	2.26	0.0204									

¹Wet days indicates total hours · 24 h⁻¹ when hourly average soil water matric potential > -1.5 MPa; degree days, summation of hourly average soil temperatures for each hour that average soil temperature was > 0°C · 24 h⁻¹; and wet degree days, degree days when soil water matric potential > -1.5 MPa.

trended to be lower than control plots by 27% in the third year posttreatment, but the results were variable across sites (Table 3).

Prior to treatment, native herbaceous perennial cover was similar among all plots (Table 3). Herbaceous perennial cover increased posttreatment by 27% on mow plots and 21% on tebuthiuron plots relative to controls, and mean comparisons indicate that by the third year following treatment herbaceous perennial cover increased on fire plots relative to control plots (Table 3). Perennial herbaceous cover was 27% lower on fire+imazapic plots after treatment compared to controls (Table 3).

Exotic annual grass cover was largely similar among treatment and control plots prior to treatment, although the fire+imazapic treatment tended to have higher cover and the tebuthiuron treatment tended to have lower cover (Table 3). In the first year posttreatment, exotic annual grass cover was 84% lower, compared to controls, on plots where imazapic was applied alone, and exotic annual grass cover was 79% lower, compared to controls, where imazapic was applied following fire treatments (Table 3). In the second year posttreatment, exotic annual grass was 93% lower on the imazapic treatment and 79% lower on the fire+imazapic treatments compared to controls (Table 3). Exotic annual grass on the tebuthiuron plots was 60% lower in the second year posttreatment relative to control plots (Table 3). By the third year posttreatment, exotic annual grass cover was still > 80% lower on imazapic and fire+imazapic plots when compared to control plots (Table 3).

Soil Resource Response to Treatments

All of the resin exchangeable soil variables in our analyses exhibited significant responses to treatment, and there were treatment method × time interactions for all of these variables except H₂PO₄⁻ (Table 2). Wet degree days also had a significant response to treatment (Table 2). In the first year following treatment, NH₄⁺ increased 56% in fire plots, 95% in fire+imazapic plots, 87% in mow plots, and 98% in tebuthiuron plots relative to control plots (Table 4). By the second and third year posttreatment, there were no differences in NH₄⁺ between any treatment and control plots. Resin exchangeable NO₃⁻ increased by 167% and 168% in fire and fire+imazapic plots in the first year following treatment relative to control plots (Table 4). NO₃⁻ remained elevated in the second year following treatment on fire plots (211%), and on tebuthiuron plots (124%) relative to control plots (Table 4). NO₃⁻ on fire+imazapic plots was > 500% higher than on control plots in the second year posttreatment (Table 4). In the third year following treatment, fire+imazapic plots still had higher (> 400%) resin exchangeable NO₃⁻ when compared to controls, but no differences existed for any other treatment (Table 4). Resin exchangeable H₂PO₄⁻ was elevated by 21%, 33%, and 44% relative to control plots on imazapic, fire+imazapic, and fire plots, respectively. Resin exchangeable K⁺ increased 67% on fire plots and 49% on fire+imazapic plots in the first year following treatment relative to controls. Although K⁺ increased on tebuthiuron plots relative to control plots, there were pretreatment differences in the same direction between tebuthiuron and control plots (Table 4). In the second year posttreatment, it appeared that all treatments had

Table 3. Means and standard errors for vegetation cover (%) before treatment (time 0) and for 3 yr posttreatment (time 1, 2, 3) across the four research sites. Means not represented by a common letter are not statistically similar across treatment and time for each variable (Tukey's test $P < 0.05$).

Treatment method	Time	Shrub		Native perennial herb		Exotic annual grass	
Control	0	20.9 ± 3.3	AB	20.0 ± 2.7	BCDEFG	9.3 ± 2.2	DEF
Imazapic	0	19.3 ± 2.7	AB	21.8 ± 2.6	BCDEFG	7.3 ± 2.4	DEF
Fire	0	22.9 ± 2.7	A	16.6 ± 2.6	DEFG	7.2 ± 2.8	DEF
Fire + Imazapic	0	19.2 ± 2.5	AB	15.7 ± 2.8	EFG	13.0 ± 2.8	CD
Mow	0	22.5 ± 2.3	A	21.1 ± 3.1	BCDEF	8.0 ± 2.5	DEF
Tebuthiuron	0	20.5 ± 2.4	AB	20.9 ± 2.1	BCDEF	3.6 ± 1.1	EF
Control	1	20.2 ± 2.8	AB	21.7 ± 3.9	BCDEF	11.8 ± 2.7	CDE
Imazapic	1	17.8 ± 1.9	AB	18.2 ± 3.3	CDEFG	1.2 ± 0.4	F
Fire	1	4.5 ± 1.5	G	15.2 ± 2.8	FG	9.1 ± 3.3	DEF
Fire + Imazapic	1	3.3 ± 1.6	G	10.0 ± 3.0	G	2.4 ± 1.0	F
Mow	1	11.1 ± 2.3	DEF	26.2 ± 3.9	ABCD	11.4 ± 4.2	CDE
Tebuthiuron	1	17.9 ± 1.5	AB	26.7 ± 2.4	ABC	3.8 ± 1.1	EF
Control	2	19.4 ± 2.4	AB	21.8 ± 4.8	BCDEF	19.7 ± 7.6	ABC
Imazapic	2	18.9 ± 1.9	AB	20.2 ± 3.8	BCDEF	1.1 ± 0.4	F
Fire	2	4.8 ± 1.6	G	19.8 ± 2.3	BCDEFG	23.0 ± 5.9	AB
Fire + Imazapic	2	4.1 ± 2.2	G	13.3 ± 3.6	FG	4.1 ± 1.5	EF
Mow	2	11.9 ± 2.6	CDE	31.8 ± 6.8	A	25.0 ± 8.1	A
Tebuthiuron	2	16.9 ± 1.8	ABC	28.1 ± 4.2	AB	6.5 ± 2.4	DEF
Control	3	21.3 ± 3.7	AB	18.0 ± 4.6	BCDEFG	12.5 ± 3.8	CDE
Imazapic	3	21.8 ± 2.7	AB	19.3 ± 4.7	BCDEF	0.9 ± 0.4	F
Fire	3	6.9 ± 2.3	EFG	33.7 ± 3.0	A	15.0 ± 5.1	BCD
Fire + Imazapic	3	5.8 ± 3.0	FG	18.7 ± 4.7	BCDEF	2.6 ± 1.3	F
Mow	3	16.3 ± 3.7	ABCD	24.5 ± 5.7	ABCDEF	16.4 ± 6.9	ABCD
Tebuthiuron	3	15.2 ± 2.4	BCD	23.2 ± 2.4	ABCDE	6.5 ± 2.7	DEF

Table 4. Means and standard errors for resin exchangeable soil nutrients ($\mu\text{g} \cdot \text{cm}^{-2}$) before treatment (time 0) and for 3 yr posttreatment (time 1, 2, 3) across the four research sites. Means not represented by a common letter are not statistically similar across treatment and time for each variable (Tukey's test $P < 0.05$).

Treatment method	Time	Ammonium (NH_4^+)		Nitrate (NO_3^-)		Phosphate (H_2PO_4^-)		Potassium (K^+)	
Control	0	0.44 ± 0.06	BCD	5.0 ± 0.8	CD	0.61 ± 0.06	GH	11.2 ± 1.1	E
Imazapic	0	0.36 ± 0.05	CDEF	4.5 ± 0.6	DE	0.58 ± 0.08	H	12.9 ± 1.0	DE
Fire	0	0.39 ± 0.05	CDEF	2.8 ± 0.5	DE	0.71 ± 0.12	GH	11.7 ± 1.2	DE
Fire + Imazapic	0	0.51 ± 0.07	BC	4.6 ± 1.1	CDE	0.77 ± 0.10	FGH	12.2 ± 1.0	DE
Mow	0	0.40 ± 0.06	CDEF	4.0 ± 0.8	ED	0.67 ± 0.10	GH	11.7 ± 1.0	DE
Tebuthiuron	0	0.33 ± 0.05	DEF	4.4 ± 0.7	ED	0.70 ± 0.08	GH	14.6 ± 1.1	BCD
Control	1	0.37 ± 0.04	DEF	3.2 ± 0.4	E	0.50 ± 0.06	H	11.8 ± 0.9	DE
Imazapic	1	0.40 ± 0.03	CDEF	4.7 ± 0.6	DE	0.64 ± 0.07	GH	12.2 ± 0.9	DE
Fire	1	0.57 ± 0.05	B	7.9 ± 0.9	B	0.83 ± 0.09	FG	19.6 ± 1.0	A
Fire + Imazapic	1	0.71 ± 0.06	A	8.0 ± 1.0	B	0.72 ± 0.08	GH	17.6 ± 1.1	ABC
Mow	1	0.68 ± 0.05	A	4.1 ± 0.5	DE	0.52 ± 0.07	GH	13.8 ± 1.0	DE
Tebuthiuron	1	0.72 ± 0.05	A	3.3 ± 0.3	DE	0.55 ± 0.05	H	16.6 ± 1.0	BC
Control	2	0.37 ± 0.03	CDEF	2.6 ± 0.3	E	1.26 ± 0.15	DE	10.2 ± 1.1	E
Imazapic	2	0.27 ± 0.03	F	4.8 ± 0.8	DE	1.44 ± 0.15	ABCD	11.8 ± 1.1	DE
Fire	2	0.31 ± 0.03	EF	7.7 ± 1.2	BC	1.59 ± 0.14	ABC	17.0 ± 1.2	ABC
Fire + Imazapic	2	0.35 ± 0.03	DEF	16.0 ± 1.5	A	1.24 ± 0.13	DE	14.7 ± 1.2	BCD
Mow	2	0.46 ± 0.05	BCD	5.1 ± 1.1	CDE	1.21 ± 0.15	DE	14.2 ± 1.2	CD
Tebuthiuron	2	0.43 ± 0.03	BCDE	5.6 ± 0.9	BCD	1.28 ± 0.15	DE	17.4 ± 1.2	AB
Control	3	0.47 ± 0.05	BCDE	3.2 ± 0.6	E	1.13 ± 0.14	EF	12.1 ± 1.4	DE
Imazapic	3	0.40 ± 0.03	CDEF	3.7 ± 0.5	DE	1.55 ± 0.19	ABCD	11.8 ± 1.4	DE
Fire	3	0.47 ± 0.05	BCDE	5.6 ± 0.8	CDE	1.85 ± 0.16	AB	17.9 ± 1.8	ABC
Fire + Imazapic	3	0.42 ± 0.06	CDEF	14.3 ± 1.9	A	1.92 ± 0.23	A	14.5 ± 1.5	CDE
Mow	3	0.46 ± 0.04	BCDEF	4.7 ± 0.7	DE	1.45 ± 0.18	CDE	15.6 ± 1.7	BCD
Tebuthiuron	3	0.43 ± 0.04	CDEF	5.6 ± 1.1	CDE	1.53 ± 0.18	BCD	15.6 ± 1.6	BCD

Table 5. Means and standard errors for derived soil moisture and temperature variables before treatment (time 0) and for 3 yr posttreatment (time 1, 2, 3) across the four research sites. Means not represented by a common letter are not statistically similar across treatment and time for each variable (Tukey's test $P < 0.05$).

Treatment method	Time	Wet days		Degree days		Wet degree days		Average soil temperature	
Control	0	29.94 ± 1.65	EF	2397.01 ± 143.53	AB	67.59 ± 16.87	F	12.44 ± 1.18	AB
Imazapic	0	28.13 ± 1.26	F	2424.26 ± 131.03	AB	60.84 ± 17.94	F	12.61 ± 1.18	ABC
Fire	0	—	—	—	—	—	—	—	—
Fire + Imazapic	0	—	—	—	—	—	—	—	—
Mow	0	—	—	—	—	—	—	—	—
Tebuthiuron	0	27.88 ± 1.50	F	2383.27 ± 144.52	AB	74.81 ± 15.23	EF	12.70 ± 1.25	ABC
Control	1	34.04 ± 6.43	CDEF	1937.09 ± 507.74	AB	74.01 ± 12.77	EF	11.40 ± 1.10	BC
Imazapic	1	29.49 ± 5.14	DEF	1618.58 ± 520.03	AB	53.37 ± 9.19	EF	10.14 ± 1.03	C
Fire	1	35.85 ± 6.75	BCDE	1917.75 ± 618.88	AB	100.48 ± 25.04	DEF	11.36 ± 1.29	BC
Fire + Imazapic	1	40.65 ± 4.21	ABCD	2581.48 ± 131.86	AB	246.79 ± 63.03	BCDEF	13.65 ± 1.23	AB
Mow	1	30.62 ± 10.98	CDEF	1913.09 ± 624.90	AB	61.84 ± 9.24	DEF	11.60 ± 1.27	BC
Tebuthiuron	1	34.75 ± 4.42	CDEF	1999.61 ± 420.89	AB	105.56 ± 26.57	DEF	11.66 ± 1.05	BC
Control	2	51.00 ± 7.30	A	2231.25 ± 118.90	AB	399.03 ± 85.82	ABC	12.01 ± 0.73	AB
Imazapic	2	44.09 ± 5.71	AB	1940.85 ± 293.84	AB	284.71 ± 64.03	BCDE	11.03 ± 0.75	ABC
Fire	2	50.30 ± 7.89	A	2012.32 ± 309.51	AB	532.12 ± 87.51	ABC	11.32 ± 0.79	ABC
Fire + Imazapic	2	51.18 ± 9.76	A	1741.29 ± 392.95	AB	597.05 ± 148.02	ABC	10.64 ± 0.81	BC
Mow	2	37.02 ± 9.90	ABC	1490.80 ± 443.28	AB	237.84 ± 84.72	CDEF	10.41 ± 0.89	BC
Tebuthiuron	2	41.50 ± 9.34	AB	2225.37 ± 121.80	AB	369.86 ± 64.07	ABC	13.78 ± 0.76	A
Control	3	42.02 ± 9.91	AB	2047.36 ± 38.49	AB	233.75 ± 39.54	CDEF	10.74 ± 0.82	AB
Imazapic	3	38.88 ± 11.98	AB	1999.48 ± 36.63	AB	192.98 ± 53.73	CDEF	10.53 ± 0.81	AB
Fire	3	41.92 ± 10.04	AB	1755.88 ± 342.87	AB	213.48 ± 49.17	CDEF	10.05 ± 0.86	ABC
Fire + Imazapic	3	40.53 ± 6.63	AB	1719.66 ± 332.67	AB	490.59 ± 189.47	AB	10.63 ± 0.98	AB
Mow	3	43.19 ± 10.33	AB	2078.21 ± 8.11	AB	239.01 ± 51.79	CDEF	11.17 ± 0.82	AB
Tebuthiuron	3	44.06 ± 11.83	A	2027.95 ± 32.48	AB	275.21 ± 65.34	BCD	10.18 ± 0.85	ABC

increased K^+ relative to control plots with the exception of the imazapic only treatment (Table 4). Increases were 64%, 42%, 38%, and 69% on fire, fire+imazapic, mow, and tebuthiuron plots, respectively (Table 4). In the third year following treatment resin, exchangeable K^+ was still 50% higher on fire plots compared to controls, but there were no other statistically significant differences (Table 4).

Due to logistical difficulties installing equipment and data logger failures, we did not have pretreatment soil moisture and temperature data for all treatments. However, the data we have indicate that wet degree days had a significant response to treatment (Table 2), and the number of wet degree days posttreatment was 48% higher on fire+imazapic treatments when compared to control plots (Table 5).

Vegetation Interactions With Soil Resources

Canonical discriminant analyses for pretreatment vegetation cover revealed two significant canonical axes. The first axis explained 90% of the variance and was positively correlated with shrub cover, shallow rooted perennial grass cover, and lichen and moss cover (Table 6). The second axis explained 7% of the variance and was negatively correlated with gap size (Table 6). The analysis indicates that prior to treatment, there were two relatively distinct vegetation associations: 1) relatively low shrub, lichen, moss, and shallow rooted perennial grass cover (Roberts and Rock Creek); 2) relatively high shrub, lichen, moss, and shallow rooted perennial grass cover (Onaqui and Saddle Mountain; Fig. 1). The canonical discriminant

analysis for site physical and chemical properties also indicated two significant canonical axes. The first axis explained 74% of the variance and was positively correlated with increasing resin exchangeable N, P, and K, and negatively correlated with increasing soil water holding capacity (WHC; Table 6). The second axis explained 18% of the variance and was positively correlated with soil clay content and negatively correlated with sand percentage (Table 6). The sites may be described as fitting into three relatively distinct abiotic groups: 1) relatively infertile soils with low clay content (Saddle Mountain); 2) moderately fertile soils with higher clay content (Onaqui and Rock Creek); and 3) relatively fertile soils with low clay content (Roberts; Fig. 1).

A regression model with three variables explained the cover of native perennial herbaceous plants before treatment ($n=47$; $R^2=0.92$; $P<0.0001$; Table 7). Native perennial herbaceous cover was positively correlated with mean annual precipitation, which explained 82% of the variance in the model (Table 7; Fig. 2). Cover of native herbaceous perennials was also positively correlated with lichen and moss cover and negatively correlated with distance between perennial plants (Table 7; Fig. 2). Following treatments, a four-variable regression model best described native perennial herbaceous cover ($n=63$; $R^2=0.82$; $P<0.0001$; Table 7). Native perennial herbaceous cover was positively correlated with increasing wet days, which explained 74% of the variance and positive correlations with resin exchangeable NH_4^+ and $H_2PO_4^-$ explained another 6%.

Table 6. Correlation coefficients for individual variables as they relate to derived canonical axes from the Canonical Discriminant Analysis for pretreatment vegetation and soil physical and chemical characteristics. Variables with correlation coefficients > 0.50 were considered influential.

Variable	Axis 1	Axis 2	Axis 3
Pretreatment vegetation			
Shrub cover	0.81	0.21	—
Deep rooted perennial grass cover	-0.34	0.34	—
Shallow rooted perennial grass cover	0.68	0.37	—
Perennial forb cover	-0.23	0.33	—
Perennial gap size	-0.04	-0.65	—
Exotic annual grass cover	-0.27	-0.20	—
Lichen and moss cover	0.91	-0.13	—
Pretreatment physical and chemical characteristics			
Resin exchangeable NO ₃ ⁻	0.84	-0.27	—
Resin exchangeable NH ₄ ⁺	0.71	0.35	—
Resin exchangeable K ⁺	0.75	-0.28	—
Resin exchangeable H ₂ PO ₄ ⁻	0.66	0.22	—
Total soil N	-0.17	0.01	—
Total soil OC	0.20	0.13	—
Soil pH	-0.24	-0.28	—
Water holding capacity	-0.57	-0.07	—
% Coarse fragments	0.44	0.17	—
% Sand	0.27	-0.50	—
% Silt	-0.29	0.16	—
% Clay	0.10	0.86	—
Posttreatment vegetation			
Shrub cover	-0.02	0.37	-0.43
Deep rooted perennial grass cover	-0.30	0.06	0.21
Shallow rooted perennial grass cover	0.71	-0.32	0.45
Perennial forb cover	-0.37	-0.67	0.42
Perennial gap size	0.03	0.51	-0.06
Exotic annual grass cover	0.11	0.78	0.38
Lichen and moss cover	0.56	-0.05	-0.68
Simplified posttreatment vegetation			
Shrub cover	0.66	0.68	—
Native herbaceous perennial cover	-0.19	0.85	—
Exotic annual grass cover	0.50	-0.81	—

Native herbaceous perennial cover was negatively correlated with gap size (Table 7; Fig. 3).

Exotic annual grass cover before treatment was explained by a four-variable regression ($n=47$, $R^2=0.74$; $P<0.0001$; Table 7). Exotic annual grass cover was positively correlated with resin exchangeable H₂PO₄⁻, which explained 57% of the variance in the model (Table 7; Fig. 4). Exotic annual grass cover was also positively correlated with shrub cover and distance between perennial plants, but negatively correlated with increasing soil water holding capacity (Table 7; Fig. 4). After treatments, a five-variable regression model best described the cover of exotic annual grass ($n=63$; $R^2=0.75$; $P<0.0001$; Table 7). Exotic annual grass cover was positively correlated with increasing gap size (47% of variance), the number of wet growing degree days, and soil sand % (Table 7; Fig. 5). Exotic annual grass cover was negatively correlated with increasing soil water holding capacity (12% of variance) and total soil N content (Table 7; Fig. 5).

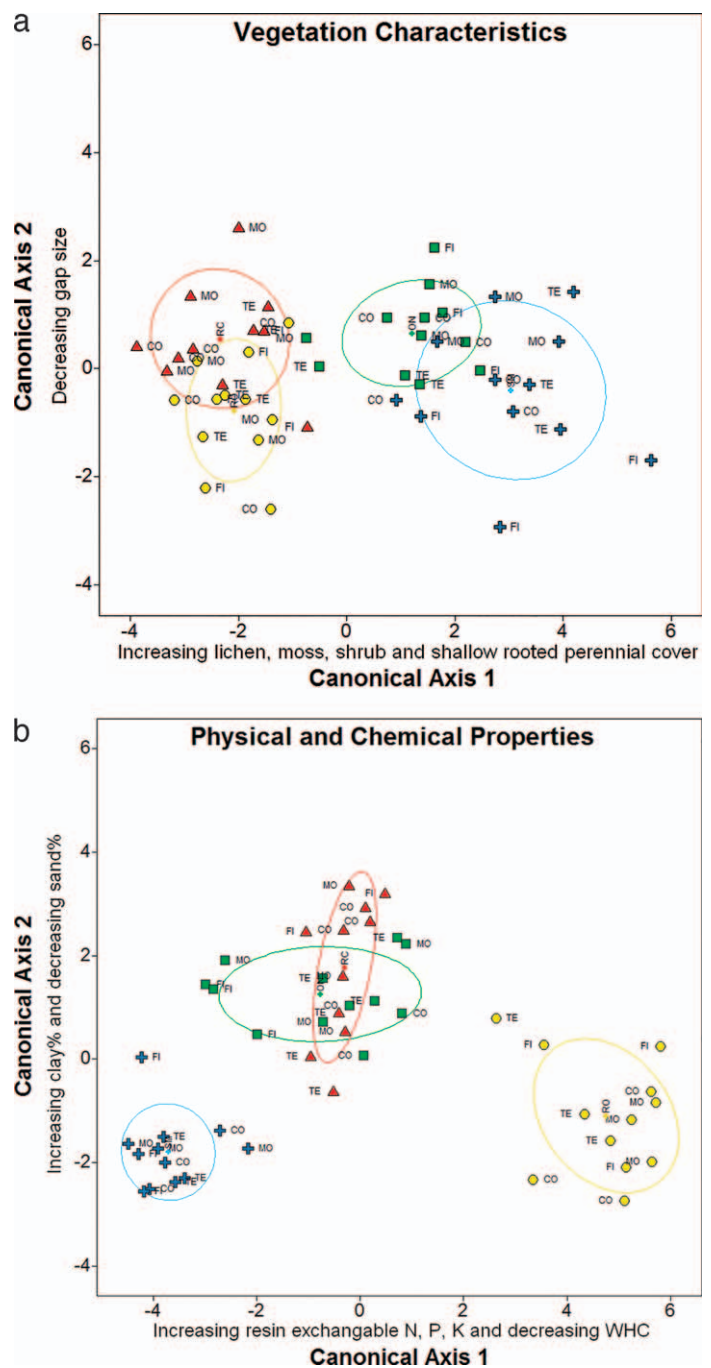


Figure 1. Biplots depicting the pretreatment plant functional groups (a) and soil physical characteristics (b) across the four sites (Onaqui = ■, Rock Creek = ▲, Roberts = ●, and Saddle Mountain = +). MO indicates Mow; FI, Fire; TE, Tebuthiuron; and CO, Control.

Following treatments, canonical discriminant analysis indicated there were three significant canonical axes explaining vegetation cover (Table 6). The first axis explained 47% of the variance, and was positively correlated with perennial shallow rooted grass cover and lichen and moss cover, and negatively correlated with perennial forb cover (Table 6). The second canonical axis explained 29% of the variance and was positively correlated with exotic annual grass cover and negatively correlated with perennial forb cover (Table 6). The

Table 7. Results from the stepwise regression model describing variables related to pre- and posttreatment native perennial herbaceous plant species and exotic annual grass cover.

Variable	Parameter	Partial Model Adjusted			F	P > F
		R ²	R ²	R ²		
Pretreatment native perennial herbaceous plants						
Mean annual precipitation	0.085	0.82	0.82	0.82	215.30	< 0.0001
Perennial gap size	−0.060	0.05	0.88	0.87	18.94	< 0.0001
Lichen and moss cover %	0.221	0.05	0.92	0.92	27.76	< 0.0001
Pretreatment exotic annual grass						
Resin exchangeable H ₂ PO ₄ [−]	0.863	0.57	0.57	0.57	61.05	< 0.0001
Perennial gap size	0.018	0.05	0.62	0.62	6.00	0.0183
Water holding capacity	−0.430	0.03	0.65	0.65	3.50	0.0479
Shrub cover %	0.526	0.09	0.74	0.72	14.27	0.0005
Posttreatment native perennial herbaceous plants						
Wet days	0.234	0.74	0.74	0.73	175.06	< 0.0001
Resin exchangeable NH ₄ ⁺	2.320	0.04	0.77	0.77	9.60	0.0029
Perennial gap size	−0.051	0.03	0.80	0.79	8.07	0.0061
Resin exchangeable H ₂ PO ₄ [−]	0.696	0.02	0.82	0.81	5.41	0.0235
Posttreatment exotic annual grass						
Perennial gap size	0.050	0.47	0.47	0.46	55.05	< 0.0001
Wet degree days	0.024	0.08	0.55	0.53	10.46	0.0020
Soil water holding capacity	−0.948	0.12	0.66	0.65	20.87	< 0.0001
Soil sand %	0.417	0.05	0.72	0.70	10.75	0.0018
Total soil nitrogen	−0.003	0.03	0.75	0.72	6.92	0.0109

third axis explained the remaining 23% of the variance and was negatively correlated with lichen and moss cover (Table 6). There was minimal overlap between sites following treatment, and they might be described as 1) moderate shallow rooted perennial grass cover, low exotic annual grass cover and high lichen and moss cover (Onaqui); 2) low shallow rooted perennial grass and exotic annual grass cover with low lichen and moss cover (Rock Creek); 3) high shallow rooted perennial grass cover and low to high exotic annual grass cover with high lichen and moss cover (Saddle Mountain); and 4) low shallow rooted perennial grass cover and intermediate to high exotic annual grass cover with intermediate lichen and moss cover (Roberts). In order to better understand the changes in plant community structure, we modified the posttreatment canonical discriminant analysis to only consider the relationships between native perennial herbaceous, exotic annual grass, and shrub cover. Results from this analysis indicate two significant canonical axes. The first axis explains 60% of the variance and is positively correlated with exotic annual grass cover (Table 6). The second axis explains 35% of the variance and is positively correlated with shrub cover and negatively correlated with native perennial herbaceous cover (Table 6). This analysis shows more overlap between sites, but more clearly shows how treatments influenced the ratio of exotic annual grass to natives within each site (Fig. 6). Tebuthiuron plots tended to plot closer to the lower left hand side of the diagram indicating lower exotic annual grass cover and higher perennial herbaceous species cover (Fig. 6).

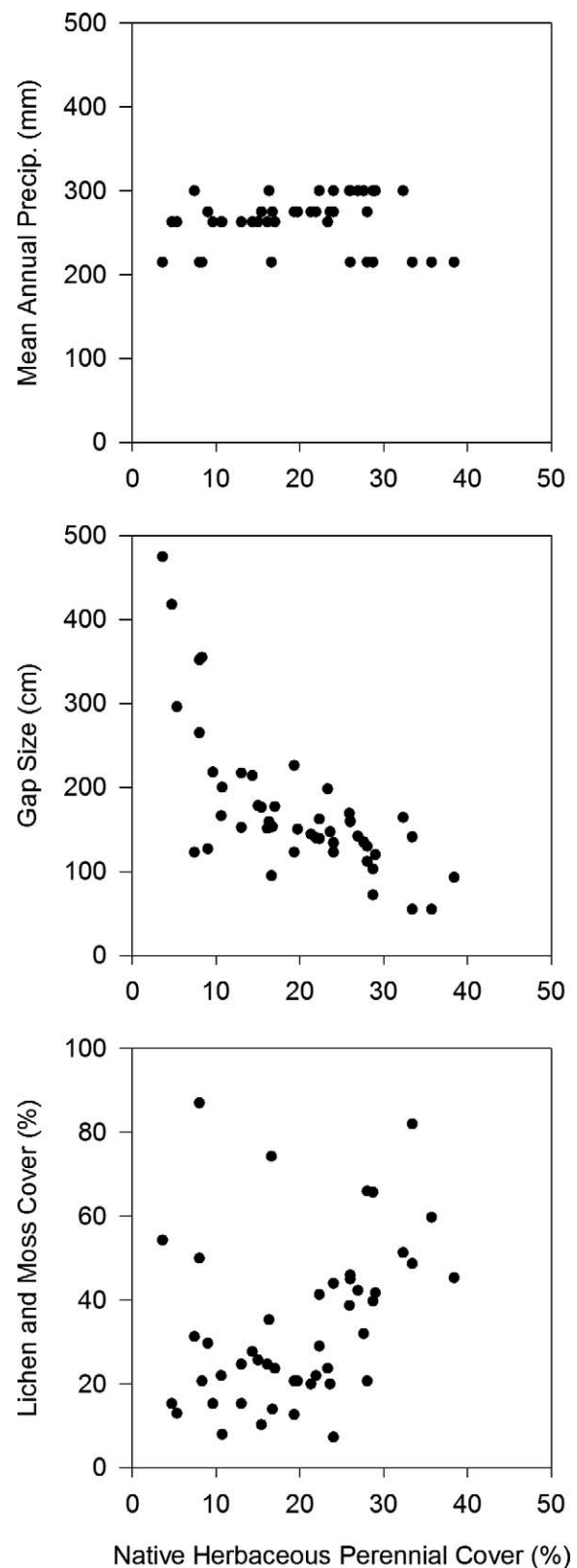


Figure 2. Scatter plots showing the relationships between pretreatment native perennial herbaceous cover and the individual variables determined to be significant from the pretreatment multiple regression for native perennial herbaceous cover.

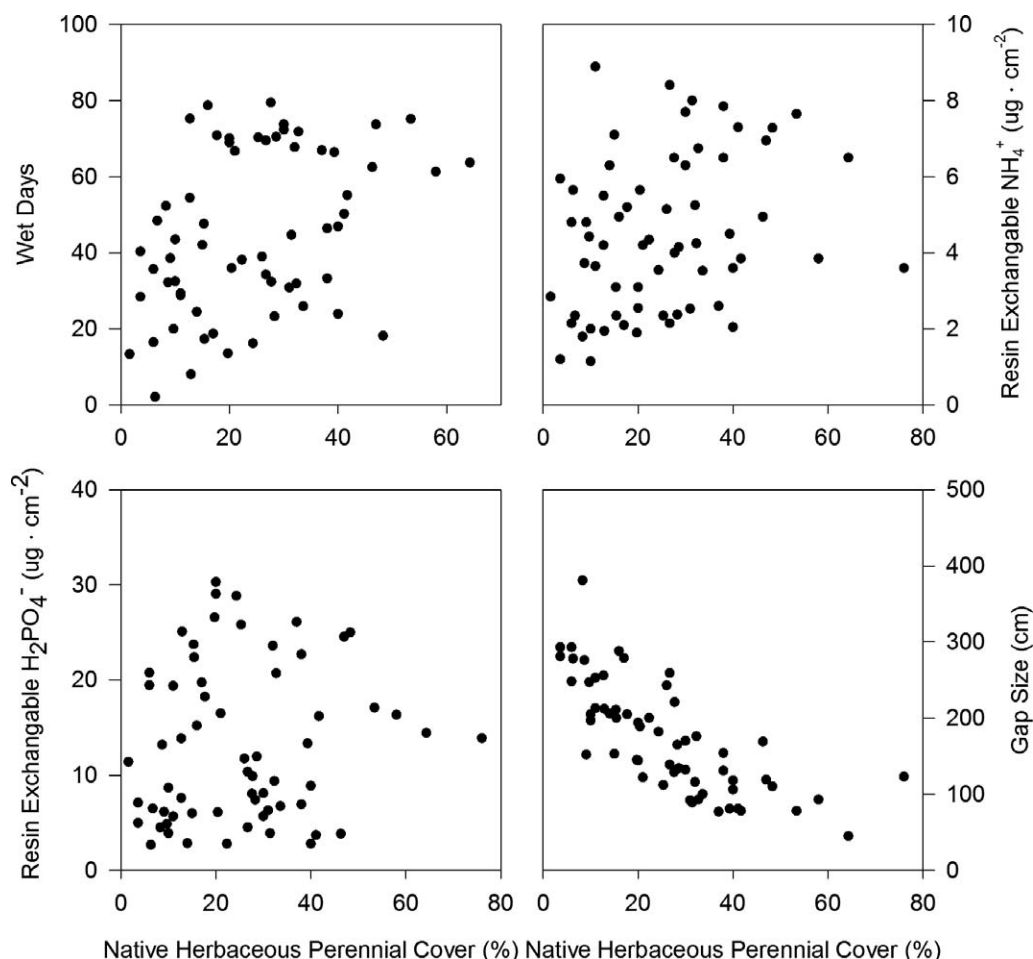


Figure 3. Scatter plots showing the relationships between posttreatment native perennial herbaceous cover and the individual variables determined to be significant from the posttreatment multiple regression for native perennial herbaceous cover.

DISCUSSION

Soil Resource Response to Treatments

Our results are consistent with previous studies showing that manipulation of woody and herbaceous vegetation by fire and mechanical methods alters soil water and nutrient availability (Neary et al. 1999; Roundy et al. 2014). We also document changes associated with herbicide methods. Burning increased NH_4^+ in the first year following treatments, but the increase disappeared by the second year as found elsewhere (Neary et al. 1999; Blank et al. 2007; Rau et al. 2007, 2008). Mowing and tebuthiuron application also increased NH_4^+ in the first year; mowing likely increased the amount of litter on the soil surface while both mowing and tebuthiuron likely decreased uptake of NH_4^+ by shrubs, by decreasing their vigor. Unlike NH_4^+ , only fire and fire+imazapic plots had a NO_3^- response. Increased NO_3^- following fire is well documented and is typically the result of microbial conversion of NH_4^+ (Blank et al. 1994, 2007; Neary et al. 1999; Rau et al. 2007, 2008). Nitrate was elevated on fire and fire+imazapic plots in the second year after treatment, but higher NO_3^- persisted into the third year posttreatment, only on fire+imazapic plots. The persistent increase in NO_3^- is likely related to synergistic effects of fire and suppression of vegetation following imazapic application. Imazapic suppressed exotic annual grasses and annual forbs

following treatment, but also suppressed native perennial herbaceous species, which likely influenced the rate of NO_3^- uptake following treatment. Posthoc regression analysis affirms that resin-exchangeable NO_3^- was inversely related to shrub, native perennial herbaceous, and exotic annual grass cover following treatments. Prescribed fire and fire+imazapic caused an increase in resin-extractable H_2PO_4^- posttreatment. Phosphorus chemistry is extremely complex, and the magnitude and direction of change following fire is dependent on several pedogenic variables including: pH, the concentration of other cations, and carbonates (Neary et al. 1999). Resin-exchangeable K^+ increased following fire, fire+imazapic, and tebuthiuron application in the first year after treatment. The increase in burned plots is expected as potassium in vegetation is oxidized and falls to the soil surface in ash (Neary et al. 1999). Potassium is also easily leached from leaves after senescence, so it is reasonable that tebuthiuron may also increase near surface soil K^+ . Similarly, the mow treatment resulted in elevated K^+ , but not until the second year posttreatment.

We found an increase in wet degree days following fire+imazapic (Table 5). Fire significantly decreased shrub cover on these plots, and the application of imazapic prohibited annual forbs and grasses from establishing. Similarly, native perennial herbaceous cover initially decreased on these plots. Thus, lower vegetation cover likely explained the increase in

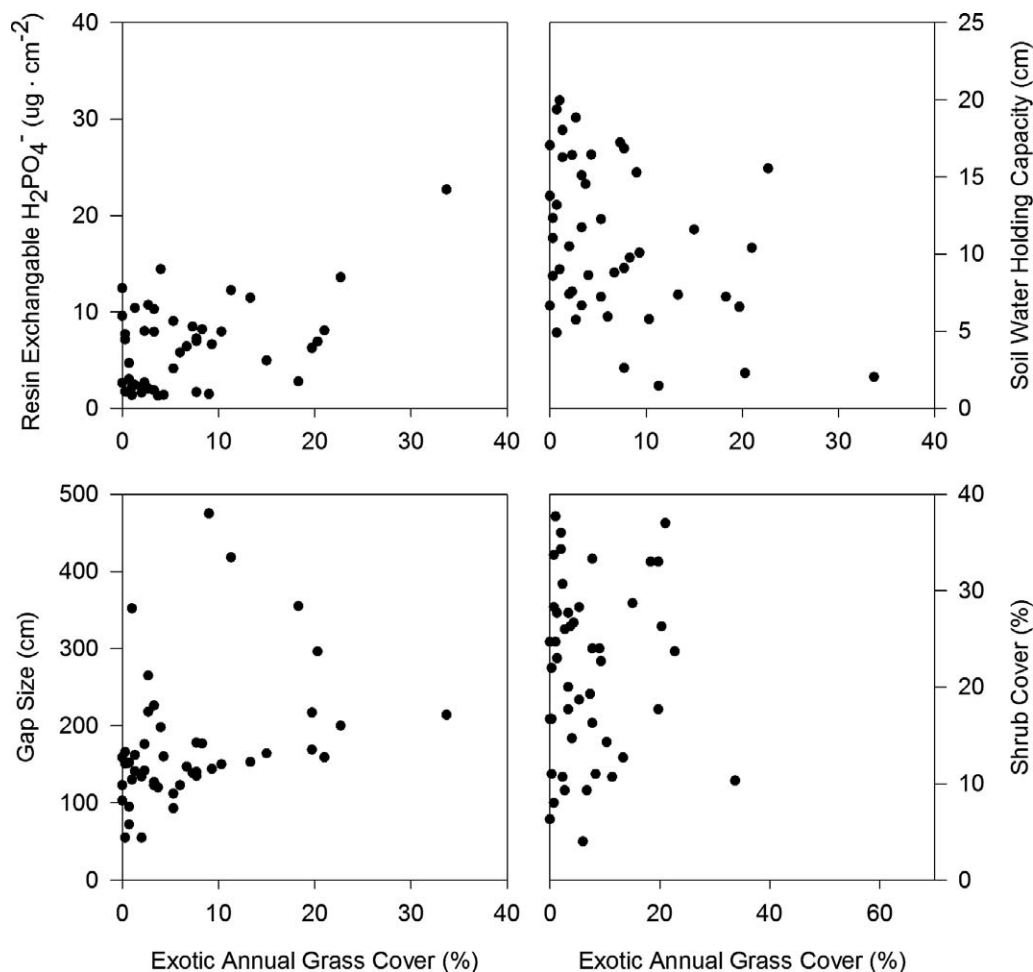


Figure 4. Scatter plots showing the relationships between pretreatment exotic annual grass cover and the individual variables determined to be significant from the posttreatment multiple regression for exotic annual grass cover.

wet degree days due to reduced evapotranspiration, and higher temperatures resulted from reduced shading and reduced albedo of the blackened soil surface. Posthoc regression analysis confirms that the number of wet degree days was inversely related to shrub and annual forb cover. There were no other significant effects on soil water or temperature related variables as determined by mixed model analysis in this study.

Vegetation Interactions With Soil Resources

Prior to treatment, the four sites fell into two general floristic groups with the largest difference between the groups attributed to shrub, shallow rooted perennial grass, and lichen and moss cover. The remaining variance was explained by gap size. Exotic annual grass cover did not appear to be a major factor in separating the sites, and all sites typically averaged less than 20% exotic annual grass cover prior to treatments. However, sites with similar floristic structure were not necessarily similar in regards to abiotic factors (Table 6; Fig. 1).

Mean annual precipitation was the most important factor explaining pretreatment, native perennial herbaceous species cover (Table 7). This relationship was primarily driven by deep-rooted perennial grasses and perennial forbs. Both of these functional groups increased with increasing mean annual precipitation when analyzed independently (analyses not

shown). Soil moisture availability is closely linked to mean annual precipitation, is a primary determinant of native perennial plant establishment in sagebrush-steppe ecosystems (Chambers et al. 2000; Chambers and Linnerooth 2001; Humphrey and Schupp 2004), and also influences other factors including soil development and nutrient cycling. Unlike deep-rooted, perennial grass cover, we found that shallow-rooted, native perennial grass (i.e., *Poa secunda*) cover was best correlated with increasing mean annual temperature ($n=47$, partial $R^2=0.5802$; $P<0.0001$).

Prior to treatment, resin-exchangeable H₂PO₄⁻ best explained the variance in exotic annual grass cover (Table 7; Fig. 4). Research has typically focused on the relationship between annual grass cover and available N, because exotic annual grasses often respond favorably to increased N (Norton et al. 2004; Blank 2008; Vasquez et al. 2008; Blank and Morgan 2011; Johnson et al. 2011). Less attention has been devoted to the relationship between H₂PO₄⁻ and exotic annual grasses. Phosphorus may be more limiting to exotic annual grass than N on many semi-arid soils because of their high pH and carbonate content. It has been demonstrated that higher levels of K and P can increase cheatgrass emergence following germination (Howell 1998; Morrison 1999), and soils low in P may have lower susceptibility to invasion by exotic annual grass (Belnap

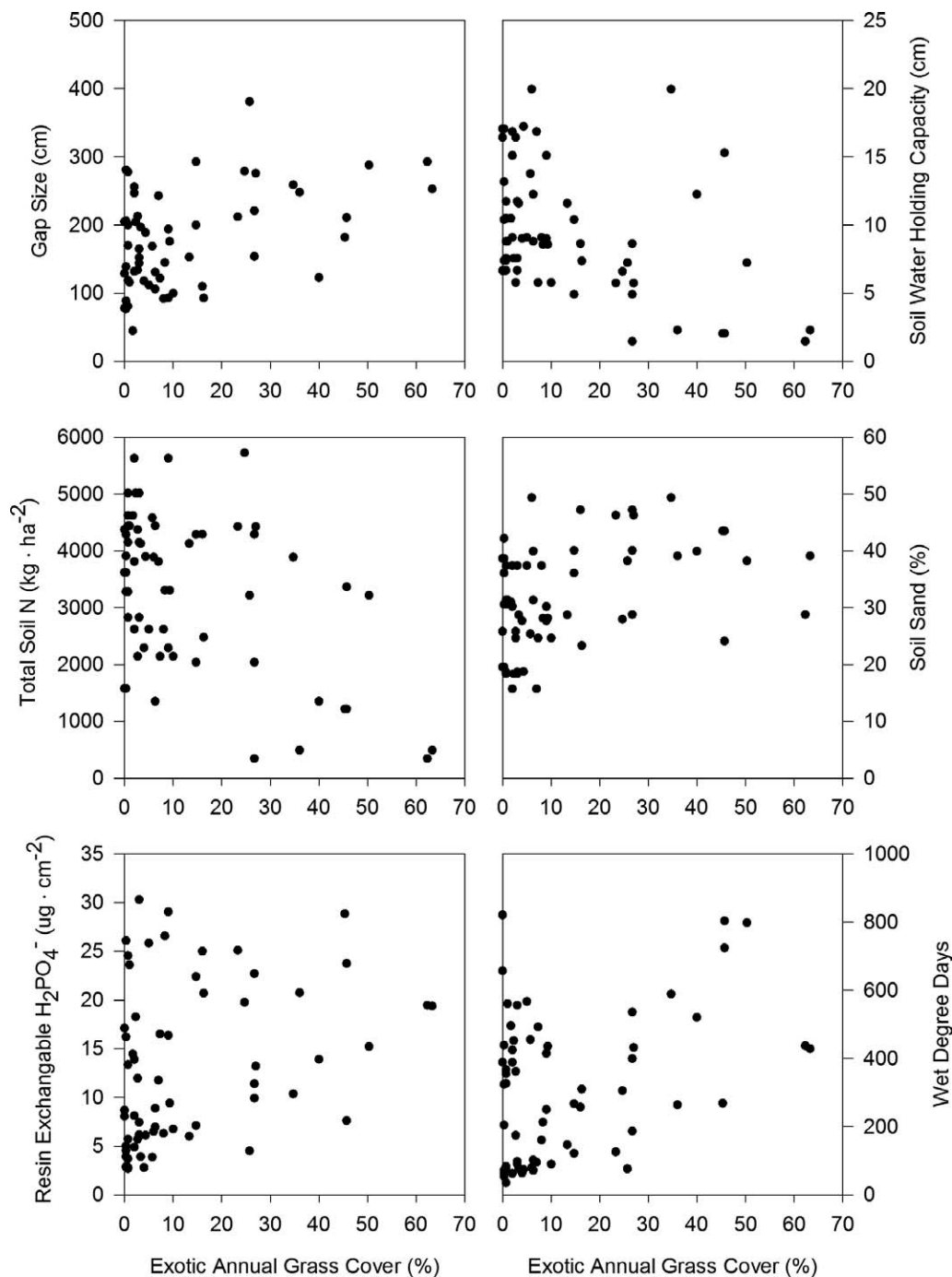


Figure 5. Scatter plots showing the relationships between posttreatment exotic annual grass cover and the individual variables determined to be significant from the posttreatment multiple regression for exotic annual grass cover. Resin exchangeable H_2PO_4^- is also displayed.

et al. 2003). More rigorous investigations will be needed across the region to determine where and how P might limit exotic annual grass invasion.

Our pretreatment model also showed that decreasing perennial herbaceous vegetation as indicated by increasing perennial gap size, and increasing woody plant dominance, as indicated by percentage shrub cover were associated with increasing annual grasses. Sagebrush and native herbaceous perennials have overlapping root systems, but sagebrush is able to draw a significant amount of resources from deeper in the soil profile, often exceeding 2 m, whereas many native

herbaceous perennials obtain a majority of resources from the top 50 cm of soil (Sturges et al. 1977; Dobrowski et al. 1990; Leffler and Ryel 2012). Chambers et al. (2007) reported that removal of native perennial herbaceous species from shrub interspaces resulted in increased soil available water and NO_3^- with or without fire, which in turn facilitated growth and reproduction of cheatgrass. Prior to treatments, gap size explained a relatively small amount of the variance in exotic annual grass cover (Table 7; Fig. 4). However, gap size was negatively correlated with total native, perennial herbaceous cover (Fig. 2), and gap size, rather than the cover of specific

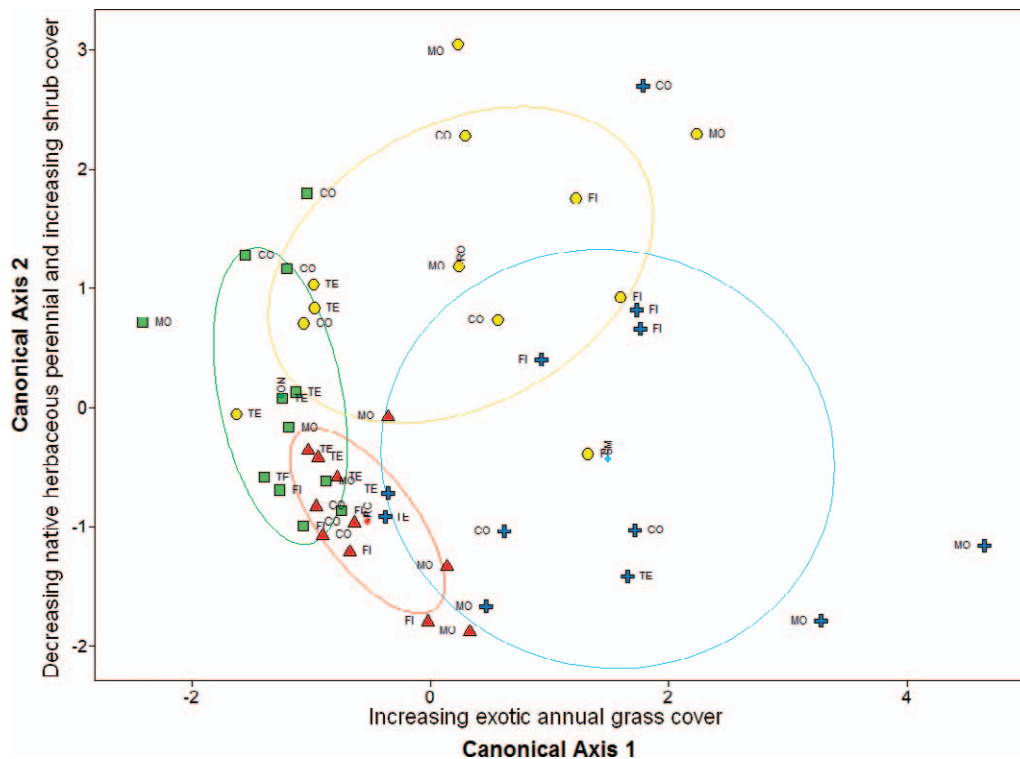


Figure 6. Biplot depicting the simplified third year posttreatment plant functional groups across the four sites (Onaqui = ■, Rock Creek = ▲, Roberts = ●, and Saddle Mountain = +). Observations that plot closer to the lower left corner have lower exotic annual grass cover, lower shrub cover, and higher native perennial herbaceous species cover. MO indicates Mow; FI, Fire; TE, Tebuthiuron; and CO, Control.

perennial herbaceous functional groups, appeared to serve as a strong indicator of resistance to exotic annual grass invasion. The distance between perennial plants serves as a surrogate measurement of both system degradation and available resources (Reisner et al. 2013). Larger gaps between perennial plants indicate a loss or lack of deep and/or shallow-rooted perennial grasses and forbs and an increase in resources available for exotic invaders such as cheatgrass. Gap size may be a better indicator of competition for resources than native perennial herbaceous species cover because it gives information on the spatial distribution of resource availability. In semi-arid environments, roots may extend far beyond the canopy of aboveground plant parts. However, it is likely that root density and, therefore, competition for resources decreases with increasing distance from the nearest aboveground plant (Hook and Lauenroth 1994; Reisner et al. 2013). The reduction in competition for resources, particularly water, has been shown to increase exotic annual grass seedling establishment in bunchgrass steppe (Hook and Lauenroth 1994).

Exotic annual grass cover decreased with increasing soil water holding capacity (Fig. 4), indicating that sites with deep or loamy soils are more resistant to invasion; perhaps because native perennial herbaceous vegetation experiences less stress from climatic anomalies given these soil conditions, and has the resources necessary to recover from repeated disturbance (Condon et al. 2011; Chambers et al. 2013).

After treatment, we found that differences in native perennial herbaceous cover were best associated with the number of wet days (Fig. 3). Our measurement of wet days was the number of days observed when soil matric potential exceeds -1.5 MPa.

Although some grasses and shrubs have very low cavitation resistance and can take up water at matric potentials below -1.5 MPa, growth is limited (Leffler and Ryel 2012). This is because soil water matric potential drastically decreases with small reductions in water content below this limit, and N diffusion to roots is limited because soil water only moves as vapor at matric potentials < -1.5 MPa (Leffler and Ryel 2012). Therefore, our measurement of wet days is a significant indicator of plant available water for growth, which is a function of precipitation, soil water holding capacity, and evapotranspiration.

Posttreatment cover of native herbaceous perennials was also positively correlated with increasing resin exchangeable NH_4^+ and H_2PO_4^- (Table 7; Fig. 3). Native perennial species can benefit from increasing nutrients following disturbance, particularly fire (Monaco et al. 2003; Rau et al. 2008).

Our posttreatment analyses indicated that exotic annual grass cover was again positively correlated with increasing gaps between perennial plants, but also increased with decreasing soil water holding capacity and increasing soil sand percentage (Fig. 5), which is similar to findings by Reisner et al. (2013). Decreasing soil water holding capacity and increasing soil sand % were not collinear as soil depth is also an important factor when considering total soil water holding capacity. Low soil water holding capacity and increased soil sand % are indicative of poorly developed soil profiles and variable resource availability. Sandy soils in particular are prone to highly variable moisture content due to greater infiltration, drainage, and initial evapotranspiration. Therefore, moisture availability and consequently nutrient availability are highly dependent on the timing

and magnitude of precipitation. Given highly variable resource availability, species that can respond quickly and compete for resources are benefitted (Davis et al. 2000). Cheatgrass has the ability to germinate and rapidly establish extensive root systems following disturbance (Mack and Pyke 1983). This allows rapid uptake of moisture in the soil profile and results in decreased available water for natives on drought prone sites (Melgoza et al. 1990). Our model also indicates that exotic annual grass cover increases with an increasing number of wet degree days (Table 5; Fig. 5). Therefore, it appears that sites with more persistent soil moisture are resistant to invasion, but that exotic annual grass does better on sites where temperatures are relatively warm when the soil has available moisture. This can be true of many low elevation sites that receive winter and spring precipitation and have relatively warm daytime temperatures, and is consistent with an analysis of all SageSTEP sites (Chambers et al. 2014). In the current study, this pattern was especially evident at the Saddle Mountain site.

Exotic annual grass cover also increased with decreasing total soil N content (Table 5; Fig. 5). The negative relationship between total soil N and exotic annual grass may seem to contradict research that suggests that cheatgrass is more competitive where N, particularly NO_3^- , is readily available (Kay and Evans 1965; Wilson et al. 1966; Lowe et al. 2003). However, sites with higher total N typically have finer texture soils and soil water holding capacity.

Ultimately, managers need to know what characteristics make a site more or less resistant to exotic annual grass dominance, and what type of management will be most effective in increasing resistance. In general, we found that low P availability may limit exotic annual grass invasion into some intact Wyoming sagebrush systems in the absence of disturbance, and that sites with higher mean annual precipitation support higher cover of native perennial herbaceous species. The sites most resilient to disturbance had more soil wet days and native perennial herbaceous species cover remained high after treatment, which in turn, kept the gaps between perennial plants small. There was a clear relationship between perennial herbaceous species cover and gap size, but gaps were consistently better predictors of resistance to invasion than perennial species cover. The sites least resistant to exotic annual grass invasion had larger gaps between perennial plants following management treatments, and also tended to have lower soil water holding capacity and higher soil sand %.

On sites with higher mean annual precipitation and soil clay %, for example Onaqui, the response to treatments was mostly neutral to positive (Table 1; Fig. 6). Three years following treatments, exotic annual grass cover remained low (<16%) after all treatments, but the response of native herbaceous perennials was variable. On sites with higher soil sand %, lower soil clay %, and lower mean annual precipitation, for example Saddle Mountain, the exotic annual grass cover after treatment was more variable (0–60%) and the response to treatment was potentially negative (Table 1; Fig. 6).

This is one of the few studies that links abiotic factors and vegetation response to management treatments over a broad range of soil and climatic conditions. However, considerable variation exists within the region, and is not completely addressed within our study. Furthermore, the data presented here represents only the first 3 yr following management

treatments. Several more years of observations will be necessary to determine the long-term trajectory of these sites, and further work should continue to determine which management options are best given the inherent site conditions.

MANAGEMENT IMPLICATIONS

In general, management treatments to reduce woody fuels can act much like an acute disturbance in that they cause decreased vigor and mortality of vegetation within the community. Fire and mowing treatments reduced shrub cover more than tebuthiuron immediately after treatment, and burning with imazapic application reduced perennial herbaceous species cover. The immediate reduction in vegetation cover caused by treatments tended to increase resource availability and reduce resistance to cheatgrass. Regardless of site type, tebuthiuron treatment appeared to have the lowest annual grass cover in our multivariate models (Fig. 6). Tebuthiuron works by inhibiting photosynthesis, which slowly starves sagebrush of carbohydrates leading to reduced vigor and/or death over several growing seasons. The result is a smaller pulse of available soil moisture (Prevey et al. 2010) and nutrients compared to prescribed fire, and less surface disturbance than mowing.

Our results indicate that mean annual precipitation and temperature, soil texture, and gaps between perennial plants may be good indicators for managers trying to identify Wyoming big sagebrush sites that will respond positively to management. These results are consistent with other work in sagebrush-steppe regarding the importance of precipitation and temperature regimes, perennial herbaceous species (Chambers et al. 2014; Chambers et al. 2014; Roundy et al. 2014), gap size, and soil texture in influencing resistance to cheatgrass (Reisner et al. 2013).

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Appendix 1. Variables utilized in the canonical discriminant and stepwise regression analyses.

Abiotic site descriptors	Pre- and posttreatment vegetation descriptors	Initial native perennial herbaceous species and exotic annual grass cover	Posttreatment perennial native herbaceous species and exotic annual grass cover
Resin exchangeable NO_3^-	Shrub cover	Shrub cover	Shrub cover
Resin exchangeable NH_4^+	Deep rooted perennial grass cover	Deep rooted perennial grass cover	Deep rooted perennial grass cover
Resin exchangeable H_2PO_4^-	Shallow rooted perennial grass cover	Shallow rooted perennial grass cover	Shallow rooted perennial grass cover
Resin exchangeable K^+	Perennial forb cover	Perennial forb cover	Perennial forb cover
Soil pH	Total native perennial herbaceous cover	Total native perennial herbaceous cover	Total native perennial herbaceous cover
Total soil N	Exotic annual grass cover	Lichen and moss cover	Lichen and moss cover
Total soil organic C	Distance between perennial plants (gaps)	Distance between perennial plants (gaps)	Distance between perennial plants (gaps)
Soil water holding capacity	Lichen and moss cover	Resin exchangeable NO_3^-	Resin exchangeable NO_3^-
Soil coarse fragment %		Resin exchangeable NH_4^+	Resin exchangeable NH_4^+
Soil sand %		Resin exchangeable H_2PO_4^-	Resin exchangeable H_2PO_4^-
Soil silt %		Resin exchangeable K^+	Resin exchangeable K^+
Soil clay %		Soil pH	Soil pH
		Total soil N	Total soil N
		Total soil organic C	Total soil organic C
		Soil water holding capacity	Soil water holding capacity
		Soil coarse fragment %	Soil coarse fragment %
		Soil sand %	Soil sand %
		Soil silt %	Soil silt %
		Soil clay %	Soil clay %
		Mean annual precipitation	Mean annual precipitation
		Mean annual temperature	Mean annual temperature
			Wet days
			Degree days
			Wet degree days
			Mean soil temperature