RESEARCH ARTICLE

Site-Specific Effects of Exotic Annual Grass Control Integrated with Revegetation

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ABSTRACT

Invasion by exotic annual grass species such as downy brome and Japanese brome has been implicated in ecosystem degradation in much of the western United States and strategies to restore lands dominated by these species are needed. We evaluated integration of herbicide and revegetation to restore old-field and rangeland sites dominated by annual brome species. In split-plot field studies, we compared three imazapic herbicide rates and eight seeding treatments at an old-field and a rangeland site. We evaluated brome, seeded species, and existing vegetation response to our treatments. Herbicide controlled annual brome at both sites, with > 95% decreases in brome biomass in plots treated with the high rate compared to non-sprayed controls. Control of annual brome persisted for two growing seasons at the old-field site and one season at the rangeland site. Annual brome abundance in non-treated control plots at both sites decreased by 80% between the first and second growing season. No seeded individuals established at the old-field site, but they persisted through two growing seasons at the rangeland site. Seeded species establishment at the rangeland site was impacted by both herbicide rate and seed mix, but no clear patterns emerged. Finally, while we controlled brome at both sites, existing desired vegetation increased only at the old-field site, where perennial grass biomass increased by about 30% in plots sprayed with both rates of herbicide. The differing responses of the existing and seeded plant communities across the two sites highlight the importance of integrating site-specific knowledge into restoration plans.

Keywords: *Bromus arvensis*, *Bromus tectorum*, Conservation reserve program, downy brome, Japanese brome, land use history

Exotic annual grass invasion has been implicated in ecological damage and change around the globe (D'Antonio and Vitousek 1992). In the western United States, downy brome (*Bromus tectorum*) invasion in particular has been associated with decreased recruitment of desired species, altered fire regimes, and degradation of wildlife habitat (Mack 2011, Balch et al. 2013). This species has also been identified as a barrier to restoration efforts in degraded lands (Allen 1995, Di Tomaso 2000). Japanese brome (*Bromus arvensis*) is another exotic annual grass closely related to downy brome (Baskin and Baskin 1981). Although Japanese brome does not have the invasive potential of downy brome, these two species often grow together in the western United States, particularly in the Northern Great Plains, and are a concern in both cropland and rangeland settings (Ogle et al. 2003, Gasch et al. 2013).

Simply controlling exotic annual grasses does not necessarily restore a desired perennial plant community on a given site. In some cases, desired perennial vegetation increases in abundance following removal of annual grasses (Davies and Sheley 2011, Elseroad and Rudd 2011). In other cases, long-term dominance by exotic annual grasses leads to the loss of desired perennial species from plant communities through decreased recruitment and seed bank impoverishment, hindering the long-term success of control programs (Humphrey and Schupp 2001, 2004). These differences in plant community responses to management are driven by site-specific factors such as perennial plant community composition, land use history, and abiotic characteristics such as episodic events of episodic precipitation for a given year (Radosevich et al. 2007).

In some cases, weed control and revegetation should be integrated as a long-term strategy to suppress exotic annual grasses and provide habitat for livestock and wildlife (Elseroad and Rudd 2011, Hirsch-Shantz et al. 2014). However, re-establishing desired species is often difficult on lands dominated by invasive annual grasses (Allen 1995, Di Tomaso 2000). Though many factors can influence establishment of seeded perennial species, competition from exotic annual grasses in particular can decrease establishment of perennial grasses and contribute to failure of seeding efforts (Hull and Stewart 1948, Romo and Eddleman 1987, Davies et al. 2010, but see James and Svejcar 2010). Suppression of annual grasses may help perennial species to establish during revegetation (Morris et al 2009, Davies and Sheley 2011).

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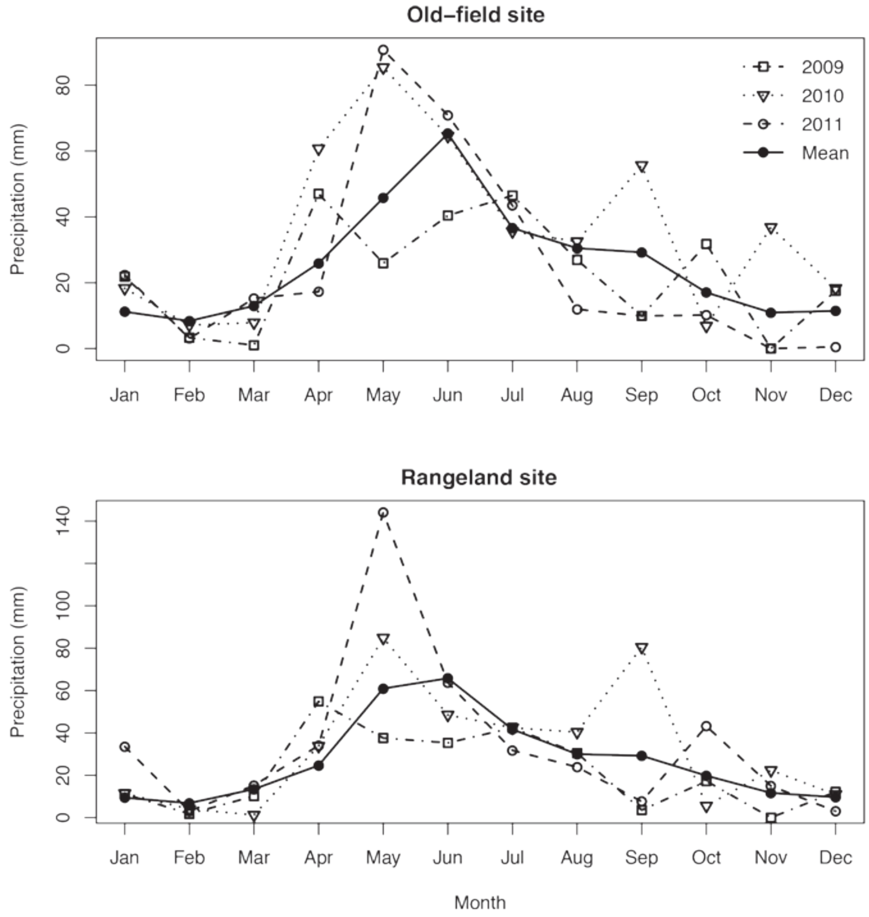

Figure 1. Annual and long term precipitation data for the closest weather station to each study site (Ft. Assiniboine, Montana, US for the old-field site [~30 km from site]; Malta 7 E, Montana, US for the rangeland site [~ 8 km from site]). All years in the period of record were used to calculate means (94 and 39 years for Ft. Assiniboine and Malta 7 E, respectively) (WRCC 2014).

Imazapic is an herbicide that can be used to control winter annual grasses in rangelands and old-field sites (Morris et al. 2009, Mangold et al. 2013) and help revegetation efforts. Integrating imazapic with seeding can favor seeded species, but it could also result in non-target effects. For example, research suggests that high rates of imazapic reduce seeded species establishment and damage beneficial plants, though these effects are species-specific and depend on timing of herbicide application relative to seeding (Shinn and Thill 2004, Sheley et al. 2007, Sbatella et al. 2011). Thus, evaluation of perennial species that are competitive with annual grasses and tolerant of imazapic rates recommended for annual grass control is needed to improve revegetation practices. To achieve this goal, we evaluated the integration of herbicide (imazapic) and seeding to restore sites in the Northern Great Plains that are dominated by annual brome species. At two contrasting sites, we compared two herbicide application rates that would facilitate the emergence and survival of seeded species by decreasing annual brome species abundance. Further, we tested the performance of three species in monoculture and mixes commonly used in revegetation settings. We hypothesized that controlling annual brome species would increase seeded species emergence and establishment and increase existing perennial plant abundance. Second, we hypothesized that the responses of brome and the existing perennial plant community to our treatments would be site-specific.

Methods

We conducted this study over three years (2009–2011) at an old-field and a rangeland site in north-central Montana, U.S.A. Sites differed in land use history, existing plant community composition, and annual brome species composition. During the course of this study, both sites experienced normal to above average annual precipitation compared to historical means (old-field, 1917–2011; rangeland, 1972–2011) (Western Regional Climate Center 2014; Figure 1).

Old-field Study Site

The old-field site (48°26′55.40″ N, 109°51′57.45″ W) was located at an elevation of 800 m, with fine loam soils and mean annual precipitation of 307 mm (Soil Survey Staff 2013, Western Regional Climate Center 2014). The site was located in a former agricultural field which was plowed and seeded to a perennial grass mix in 2003 as part of the Conservation Reserve Program (CRP). We initiated our study in 2009 and by then a mix of downy brome and Japanese brome, hereafter referred to as brome, dominated the site, with an associated substantial litter layer. When we started our study, the existing non-brome plant community was comprised of remnant perennial grasses seeded by the private landowner in 2003 (western wheatgrass [*Pascopyrum smithii*], green needlegrass [*Stipa viridula*], and crested wheatgrass [*Agropyron cristatum*]) and weedy perennial and annual forbs (dandelion [*Taraxacum officinale*], field bindweed [*Calystegia hederacea*], yellow sweetclover [*Melilotus officinalis*], prickly lettuce [*Lactuca serriola]*, and kochia [*Bassia scoparia*]).

Rangeland Study Site

The rangeland site (48°08′23.59″ N, 107°52′15.58″ W) was located at an elevation of 725 m, with clay loam soils and mean annual precipitation of 329 mm (Soil Survey Staff 2013, Western Regional Climate Center 2014). This site was on private land used primarily for cattle production and had no history of plowing or cultivation. Japanese brome dominated the site, with an associated sparse litter layer. The remaining plant community was comprised largely of native species including perennial grasses (Sandberg bluegrass [*Poa secunda*], blue grama [*Bouteloua gracilis*] and western wheatgrass), perennial forbs (prairie coneflower [*Ratibida columnifera*], scarlet globemallow [*Sphaeralcea coccinea*], and common yarrow [*Achillea millefolium*]), and shrubs (plains pricklypear [*Opuntia polyacantha*] and yellow rabbitbrush [*Chrysothamnus vicidifloris*]). Clubmoss (*Selaginella densa*) was also prevalent at this site.

Experimental Design

At each site, we implemented a randomized split-plot design with four replications arranged as blocks. Eight seeding treatments were randomly assigned to 11.0 m × 2.4 m main plots, and three herbicide rates were randomly assigned to 3.0 m × 2.4 m subplots. There were 1.2 m buffers between main plots, and 1 m buffers between subplots.

Herbicide treatments were applied before brome species emergence in fall 2009 with a CO_2–pressurized backpack sprayer (August 31, 2009 at rangeland site; September 1, 2009 at old-field site). Herbicide (Plateau®; BASF Corporation, Research Triangle Park, NC, U.S.A) application rates were control (no herbicide), low (66 g ai imazapic/ha; 296 ml Plateau®/ha), and high (105 g ai imazapic/ha; 473 ml Plateau®/ha).

Seeding treatments were applied the spring following the herbicide application (April 19, 2010 at the rangeland site; April 20, 2010 at the old-field sites). We used a 120 cm wide hoe seeder to sow eight rows in each main plot at 30 cm spacing and two cm depth. We chose three species for each location based on site characteristics (e.g., precipitation and soil type), fall-applied imazapic tolerance according to the product label, and observations of local plant communities (Anonymous 2008, Sheley et al. 2008). Species consisted of two grasses and a forb at each site, and seeding rates for single species plots followed Sheley et al. (2008). Seeded species and rates at the old-field site were thickspike wheatgrass (*Elymus lanceolatus* 'Bannock') at 12 kg pure live seed (PLS)/ha, pubescent wheatgrass (*Thinopyrum intermedium* 'Luna') at 16 kg PLS/ha, and purple prairieclover (*Dalea purpurea* 'Bismark') at 9 kg PLS/ha. At the rangeland site, we sowed western wheatgrass ('Rosana') at 18 kg PLS/ha, and pubescent wheatgrass and purple prairieclover at the same rates as above. Each species was sown singly, and in all combinations of two and three species for a total of eight seeding treatments including a non-seeded control. For mixtures, we adjusted seeding rates so the total number of seeds/m^2 remained constant and species were seeded in equal proportions.

Sampling was conducted in 2010 and 2011 to quantify brome and plant community response to herbicide treatments, and seeded species emergence (2010) and establishment (2011). For all measurements, three 20 cm × 50 cm (0.1 m^2) sampling frames were randomly placed in each subplot, each centered lengthwise on a seeded row. Frame locations were permanently marked for repeated sampling. For all sampling dates listed below, aboveground biomass samples were collected after canopy cover and density were recorded. At the old-field site, we measured annual brome canopy cover and seeded species density on June 22, 2010; annual brome biomass was sampled on June 30, 2010. We measured annual brome canopy cover and biomass again on June 29, 2011, as well as perennial grass cover and biomass, seeded species density, and cover of forbs, litter, and bare ground. At the rangeland site, we sampled Japanese brome canopy cover and biomass and seeded species density on July 7, 2010. On June 27, 2011 we measured Japanese brome canopy cover and biomass, seeded species density, and canopy cover of perennial grasses, forbs, club moss, and bare ground. All biomass was dried to constant mass and weighed.

We sampled brome biomass slightly differently in 2010. In that year, we did not destructively sample brome biomass within permanently marked frames, and we did not sample all seeding treatments because we assumed the effect of seeded species on brome biomass would be negligible two months after seeding. Thus, we randomly selected four subplots per replication of each spray treatment and sampled biomass from two randomly located frames in each.

Table 1. Means ± standard errors for plant community attributes of an old-field and a rangeland site in north-central Montana, US. Each site was sampled in 2010 and 2011. Cover is the percent cover for each group. Seeded species were sown in April 2010. Herbicide rates were control (no herbicide), low (66 g ai imazapic/ha), and high (105 g ai imazapic/ha). Brome refers to a mix of annual brome species (downy and Japanese brome), and BRJA refers to Japanese brome. Values in each row within a year which do not share the same letter are different (α = 0.05, ANOVA followed by Wald post hoc test). NA (not applicable) means we did not sample a variable in the year indicated.

Year Sampled	2010			2011		
Herbicide Rate	Control	Low	High	Control	Low	High
Old-field site						
Seeded species plants m^{-2}	31 ± 6^a	56 ± 13^{ab}	53 ± 8^b	0	0	0
Brome g/m^2	180 ± 34^a	17 ± 3^b	7 ± 2^c	38 ± 9^a	8 ± 2^b	4 ± 1^c
Brome cover	48 ± 6^a	19 ± 3^b	11 ± 2^c	5 ± 2^a	1 ± 0.4^b	1 ± 0.2^c
Perennial grass g/m^2	N/A	N/A	N/A	252 ± 20^a	339 ± 27^b	322 ± 19^b
Perennial grass cover	N/A	N/A	N/A	18 ± 2^a	24 ± 2^b	25 ± 2^b
Litter cover	N/A	N/A	N/A	75 ± 2	72 ± 2	72 ± 2
Rangeland site						
Seeded species plants/ m^2	48 ± 7	38 ± 8	61 ± 11	20 ± 4	15 ± 3	18 ± 4
BRJA g/m^2	31 ± 3^a	4 ± 3^b	1 ± 0.3^c	6 ± 1	7 ± 1	5 ± 1
BRJA cover	4 ± 1^a	1 ± 0.2^b	0.2 ± 0.1^c	2 ± 0.4	2 ± 0.3	2 ± 0.2
Perennial grass cover	N/A	N/A	N/A	32 ± 3	34 ± 3	32 ± 3
Forb cover	N/A	N/A	N/A	17 ± 1^a	12 ± 1^b	14 ± 1^{ab}
Club moss cover	N/A	N/A	N/A	25 ± 3	27 ± 3	28 ± 3
Litter cover	N/A	N/A	N/A	13 ± 2	13 ± 3	12 ± 3
Bare ground cover	N/A	N/A	N/A	11 ± 1	11 ± 2	11 ± 1

Data Analysis

Sites were analyzed separately due to differences in plant community composition and land use history. Split-plot analysis of variance (ANOVA) with repeated measures through time was used to determine the effects of herbicide rate and seeding treatment on annual brome cover and biomass. Additionally, split-plot ANOVA was used to investigate the effects of herbicide rate and seeding treatment on existing plant community functional group cover at both sites, and perennial grass biomass at the old-field site. For the rangeland site, split-plot ANOVA with repeated measures through time was used to determine the effects of herbicide rate and seeding treatment on seeded species emergence and establishment (density two months and 14 months after planting, respectively). Seeded species did not persist through the first growing season at the old-field site, so only seeded species emergence was considered for analysis for that site. There were few existing forbs and very little bare ground (mean cover of 1 ± 0.2% and 1 ± 0.4%, respectively) at the old-field site, so these variables were also excluded from further analysis.

Response variables were natural log transformed as needed to achieve normal distributions and homogeneity of variance. Mean separations were accomplished using post hoc Wald tests, and differences were considered significant at $p \leq 0.05$. Non-transformed means for all variables are presented in the results. Analyses were conducted using R software including the nlme, lme4, gmodels, and LMERConvenienceFunction packages (Pinheiro et al. 2013, Tremblay and Ransijn 2013, Warnes et al. 2013).

Results

Old-field Site

The effect of herbicide on the brome population persisted over two growing seasons as shown by a lack of herbicide rate by year interaction for both brome cover (ANOVA; $F_{2,112} = 0.97$, $p = 0.3297$) and biomass ($F_{2,65} = 1.22$, $p = 0.303$) estimates. Annual brome biomass and cover decreased with increasing herbicide rate in both years (Table 1). For example, in 2010, untreated brome biomass was 180 ± 34 g/m^2 (mean ± standard error), while plots treated with low and high herbicide rates had brome biomass values of 17 ± 3 g/m^2 and 7 ± 2 g/m^2, respectively (Table 1). The pattern of decreasing brome abundance with increasing herbicide rate persisted in 2011, when control biomass was 38 ± 9 g/m^2 and low and high plots had biomass of 8 ± 2 g/m^2 and 4 ± 1 g/m^2, respectively (Table 1). It is important to note that brome biomass in non-sprayed control plots was 180 ± 34 g/m^2 in 2010, and decreased to 38 ± 9 g/m^2 in 2011, a decrease of about 79%.

Herbicide rate positively impacted existing perennial grass cover and biomass (ANOVA; $F_{2,62} = 6.83$ and 4.27, $p = 0.002$ and 0.018, respectively). In 2011, non-sprayed control plots had the lowest existing perennial grass biomass with 252 ± 20 g/m^2 (Table 1). We failed to detect a difference between plots treated with low (339 ± 27 g/m^2) and high (322 ± 19 g/m^2) rates of herbicide, where perennial grass biomass increased by 35% and 28%, respectively compared to the non-sprayed control. We failed to detect a response of litter cover to our herbicide treatments

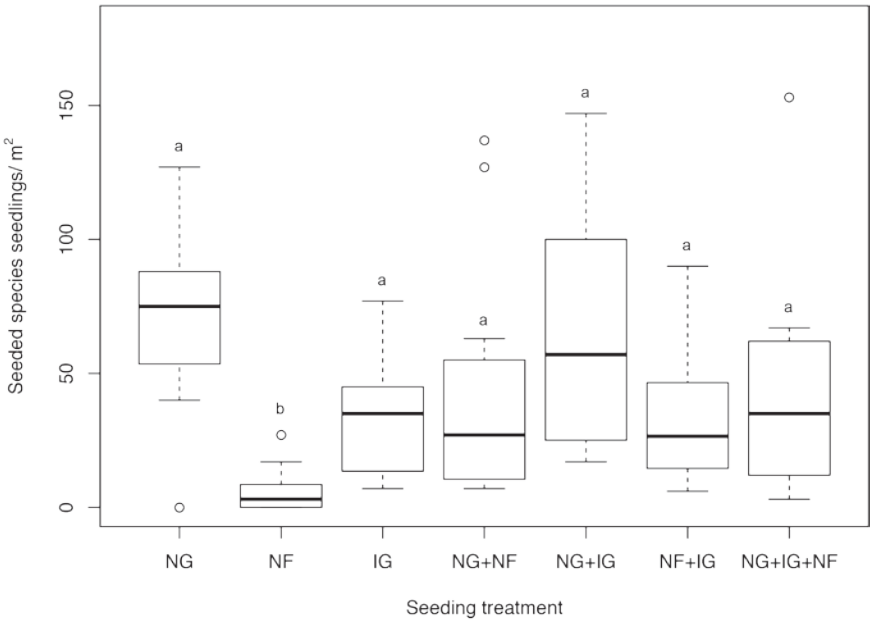

Figure 2. Effects of seeding treatment on seeded species density two months after seeding an old-field site located in Montana, US. Seedlings did not persist to the second season after sowing at this site. NG is native grass thickspike wheatgrass, IG is introduced grass pubescent wheatgrass, and NF is native forb purple prairie clover. Letters separate means that differed according to post hoc Wald tests ($\alpha = 0.05$).

(ANOVA; $F_{2,62} = 1.33$, $p = 0.272$), and it had an overall mean value of 73 ± 2%.

Seeded species emergence at the old-field site was positively affected by both herbicide rate (ANOVA; $F_{2,42} = 3.42$, $p = 0.042$) and seeding treatment (ANOVA; $F_{6,18} = 9.34$, $p < 0.001$). According to post hoc tests, only the high herbicide rate increased seeded species emergence compared to control plots (Table 1). Control plots had seeded species emergence of 31 ± 6 seedlings/m^2, while those treated with the low and high herbicide rate had emergence of 56 ± 13 and 53 ± 8 seedlings/m^2, respectively. Plots sown with only the native forb had the lowest mean emergence at 6 ± 8 seedlings/m^2, and we failed to detect a difference in emergence between the other six seed mix treatments, which had overall mean emergence of 53 ± 46 seedlings/m^2 (Figure 2).

Rangeland Site

At the rangeland site, the effect of herbicide on Japanese brome biomass and cover differed by year as shown by the rate by year interactions for both variables (ANOVA; $F_{2,68} = 66.58$ and $F_{2,112} = 32.91$, $p < 0.001$ for both variables). Increasing herbicide rate led to decreased Japanese brome biomass and cover one year after treatment, but the effect of herbicide did not persist to the second year after treatment (Table 1). For example, Japanese brome biomass in control plots one year after treatment was 31 ± 3 g/m^2, and it decreased to 4 ± 3 g/m^2 and 1 ± 0.3 g/m^2 in the low and high herbicide rate plots, respectively (Table 1). However, there was no difference in Japanese brome biomass between herbicide rates two years after treatment (Table 1). Interestingly, Japanese brome biomass in non-sprayed control plots was 31.2 ± 3 g/m^2 in 2010, and decreased to 6 ± 1 g/m^2 in 2011, a decrease of about 82%.

At the rangeland site, we found no evidence to support our hypothesis that controlling annual Japanese brome would increase abundance of the remnant plant community. Only existing forb cover responded to herbicide treatments (ANOVA; $F_{2,62} = 5.02$, $p = 0.010$). Forb cover was highest in control plots at 17 ± 1%, and we failed to detect a difference between the low and high rates, which had forb cover values of 12 ± 1% and 14 ± 1%, respectively (Table 1). Overall mean existing perennial grass cover was 33 ± 17%, and did not change with herbicide application (ANOVA; $F_{2,62} = 1.71$, $p = 0.190$). Similarly, cover of club moss, litter, and bare ground were not impacted by herbicide rate (ANOVA; $F_{2,62} = 0.791, 0.058$ and 0.092, $p = 0.458$, 0.944 and 0.912, respectively) with overall mean values of 27 ± 15%, 13 ± 14%, and 11 ± 8%, respectively (Table 1).

Seeded species density at the rangeland site differed by year (ANOVA; $F_{1,80} = 9.52$, $p = 0.002$). Mean seeded species density was 49 ± 5 plants/m^2 in 2010 and 17 ± 2 plants/m^2 in 2011. Seeded species were also impacted by an interaction between herbicide rate and seed mix (ANOVA, $F_{12,80} = 2.88$, $p = 0.001$). Herbicide rate affected seeded species density in four of the seven seeding treatments, but we did not observe a clear pattern in this relationship (Figure 3). For example, the native grass alone had the

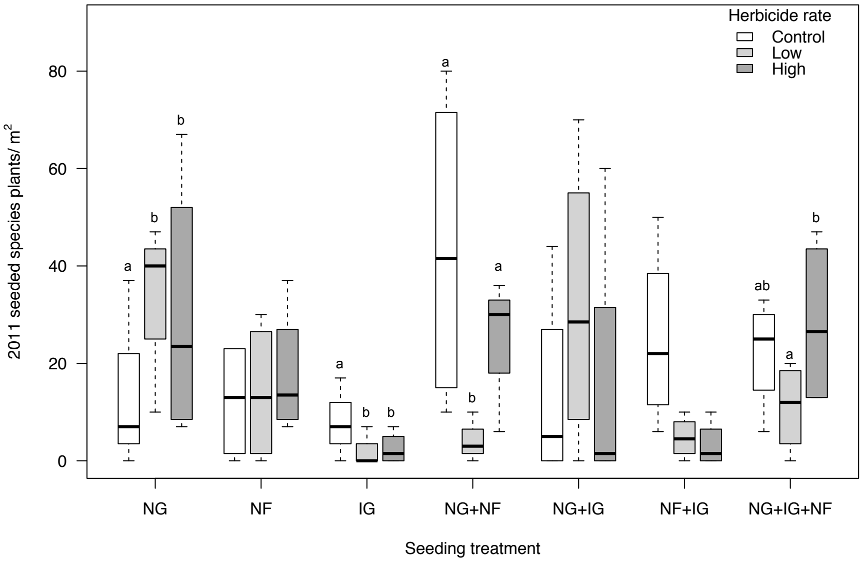

Figure 3. Effects of seeding treatment and herbicide rate on seeded species density 14 months after sowing at a rangeland site located in Montana, US. Herbicide treatments were control (no herbicide), low (66 g ai imazapic/ha), and high (105 g ai imazapic/ha). NG is native grass western wheatgrass, IG is introduced grass pubescent wheatgrass, and NF is native forb purple prairie clover. Letters separate means for herbicide rates that differed within seeding treatments according to post hoc Wald tests ($\alpha = 0.05$).

lowest establishment in non-sprayed control plots, while the introduced grass sown alone had the highest establishment in non-sprayed control plots (Figure 3). In contrast, we failed to detect a difference in establishment between the control and high rates of herbicide in the native grass + native forb and native grass + introduced grass + native forb seed mixes, while the low rate of herbicide yielded the lowest density of established seedlings (Figure 3). For the remaining three seed mixes, we failed to detect an effect of herbicide rate on seedling establishment.

Discussion

Overall, this study highlights the concept that efficacy of restoration practices depends on site-specific factors (Sheley et al. 2010). We investigated the utility of restoring an old-field and a rangeland site by integrating herbicide and revegetation. These two sites differed in land-use history, soil type, and annual brome species composition and abundance, which precluded a formal comparison between sites. However, we speculate that these differences led to the dissimilar responses to our treatments. While brome species were controlled with herbicide at both sites, duration of control differed between sites. Furthermore, sites differed in whether control actually translated into greater seeded species establishment and increased abundance of the existing plant community.

Annual brome abundance differed between our two sites and this difference was most likely driven by land use history. Downy brome was much more abundant at our old-field site compared to Japanese brome at the rangeland site; where mean pre-treatment cover in the non-sprayed control plots was ~ 48% and ~ 4%, respectively. Similarly, in a survey of CRP fields versus undisturbed rangeland sites in Colorado, Munson and Lauenroth (2012) found that annual grasses had an average canopy cover of 37% which peaked in seven-year-old CRP stands, while undisturbed rangeland had annual grass canopy cover of 1%. It is likely that the higher abundance and productivity of annual brome at the old-field site was a result of the history of cultivation disturbance inherent to CRP lands, and the resulting early- to mid-successional status of the plant community (Munson and Laurenroth 2012).

At both the old-field and rangeland sites, annual brome abundance declined by approximately 80% in non-treated control plots between 2010 and 2011, meaning that they declined due to factors other than the treatments we imposed. Because a comparable decline occurred in these two sites that had different land use history, different annual grass species composition, and were relatively far apart (160 km), we speculate that it was caused by climatic factors. Annual plant abundance can vary substantially with year to year variations in precipitation amount and seasonality, and the pattern often observed is that annual grasses increase in abundance in years with more spring or fall moisture than average (Mack and Pyke 1983, Haferkamp et al. 1993, Concilio et al. 2013). We observed an opposite pattern, with a marked decrease in annual grass abundance in the summer of 2011 after average to above average precipitation during fall and spring of 2009 through 2011.

The timing of precipitation and temperatures during key periods of annual grass growth are probable explanatory factors. For example, in November of 2010 the weather stations associated with both sites experienced 18 days of relatively warm temperatures ranging between 4° and 24°C followed by seven days with lows ranging from −22° to −28°C (NOAA 2014). It is possible that a cohort of annual brome emerged during the warm weeks and was killed off by the cold snap, leading to the annual grass reduction we observed in the 2011 growing season.

Annual brome abundance decreased as a result of applying herbicide before annual brome emerged in the fall, with a higher rate (105 g ai imazapic) causing a greater reduction than a lower rate (66 g ai imazapic). However, control duration differed between sites; we detected an effect of herbicide throughout the two-year sampling period at the old-field site and for only one year at the rangeland site. It is possible that the previously discussed annual grass decline may have affected our results. However, our results correspond to previous studies that observed that duration of annual brome control with imazapic is site-specific, with reductions in abundance lasting between one and four years (i.e., Morris et al. 2009, Elseroad and Rudd 2011).

Despite controlling annual brome, herbicide rate had weak effects on seeded species emergence at the old-field site, and there was no clear pattern in the effect of herbicide rate on seeded species emergence or establishment at the rangeland site. Previous research has shown that applying 105 g ai/ha imazapic at least 120 days before seeding perennial grasses caused little or no injury to seeded species (Sbatella et al 2011), and that imazapic rates up to 105 g ai/ha can increase establishment of seeded perennial species in annual grass dominated sites (Morris et al. 2009). For these reasons, it is unlikely that herbicide injury confounded the effects of herbicide on establishment in our study. Instead, we suspect that the relatively low abundance of annual grasses at the rangeland site made it difficult to detect a response from the applied management practices. In a similar study, James and Svejcar (2010) found that hand-weeding a low density of annual grasses had no detectable effect on sown seedling establishment. These results suggest that at low levels of invasion, removing invasive annual grasses may not increase seeded species establishment. However, our result should be interpreted cautiously: we implemented our restoration project during a time of annual grass decline, but populations of these annual species can re-expand fairly rapidly (Smith et al. 2008).

Seeded species persisted through two growing seasons at the rangeland site, but no seeded individuals established at the old-field site, despite comparable emergence rates two months after sowing. Among the many possible factors that may have contributed to the old-field seeding failure are site history and the more resilient existing vegetation at that site. This site had a history of agricultural production and cultivation which may have had residual effects on soil fertility, leading to a productive remnant plant community. It was also sown with a relatively competitive perennial grass mix in 2003, and these species markedly increased after brome management. Compared to non-sprayed control plots, existing perennial grass productivity was ~ 30% greater when annual brome was removed with herbicide, increasing from 2,520 kg/ha to 3,220 kg/ha two years after herbicide treatment. This relatively vigorous perennial plant community may have been too competitive for sown seedlings to persist in treated plots, while the dense annual brome species stands in the non-sprayed control plots may have had a similar effect. These plant communities were likely limited in the number of safe sites available for sown seedling establishment. James and Svejcar (2010) reported similar findings in post-fire sagebrush steppe revegetation, where they concluded that a robust remnant native plant community caused sown seedling density to decrease over time. Taken together, these results are consistent with a review of seed addition experiments conducted by Turnbull et al. (2000), who illustrated that safe sites tend to be more limited in plant communities with high vegetation cover. These responses highlight the importance of assessing a plant community before undertaking an extensive restoration effort that includes seeding, and perhaps implementing an invasive species control program before seeding to assess the existing plant community's resilience.

While we controlled annual brome species at both sites, existing desired vegetation increased only at the old-field site and only in the perennial grass functional group. These results mirror recent literature where, in some cases, removing annual grasses caused increased existing perennial grass and forb growth (Davies and Sheley 2011, Kyser et al. 2013), and in others it did not (Elseroad and Rudd 2011). In our study, the discrepancy in existing plant community response may be explained by differing brome species abundance. Controlling annual brome at the old-field site made relatively more space available for existing plants to spread into compared to the rangeland site. This process was recognized by Ortega and Pearson (2010) in spotted knapweed (*Centaurea stoebe*) invaded rangeland, where the effects of herbicide on plant community release depended on initial spotted knapweed abundance.

Differences in existing perennial grass community composition may have also impacted their responses to brome control. The old field site was dominated by western wheatgrass (*Pascopyrum smithii*), a colonizing rhizomatous grass, while the rangeland site was dominated by Sandberg bluegrass (*Poa secunda*) and blue grama (*Bouteloua gracilis*), two relatively small-statured bunchgrasses. In previous studies, western wheatgrass has been shown to increase in abundance following annual grass control. For example, Haferkamp and Heitschmidt (1999) found that hand-pulling Japanese brome led to a ~ 23% increase in western wheatgrass biomass production. In the same plant community, the remaining vegetation dominated, in part, by Sandberg bluegrass and blue grama, was not affected by removal of Japanese brome. These results support the idea that simply controlling annual grasses may or may not be sufficient to restore desired perennial plant communities (Elseroad and Rudd 2011), and that the composition of these communities is an important factor to consider when planning restoration efforts.

The differing responses of the existing and seeded plant communities to our herbicide and seeding treatments across the two sites highlight the importance of integrating site-specific knowledge into restoration plans. Conducting research such as what is presented here can help us better understand how major factors such as land use history, remnant plant community composition and invasive species abundance might help us refine application of treatments and predict subsequent outcomes of that management on a site-specific basis.

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References

Allen, E.B. 1995. Restoration ecology: Limits and possibilities in arid and semiarid lands. Pages 7–15 in *Proceedings of the Wildland Shrub and Arid Land Restoration Symposium*. Las Vegas, NV: Intermountain Research Station.

Anonymous. 2008. Plateau® herbicide product label. BASF Publication No. NVA 2011-04-126-0007. Research Triangle Park, NC: BASF.

Balch, J.K., B.A. Bradley, C.M. D'Antonio and J. Gómez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). *Global Change Biology* 19: 173–83.

Baskin, J.M. and C.C. Baskin. 1981. Ecology of germination and flowering in the weedy winter annual grass *Bromus arvensis*. *Journal of Range Management* 34:369–372.

Concilio, A.L., M.E. Loik and J. Belnap. 2013. Global change effects on *Bromus tectorum* L. (*Poaceae*) at its high-elevation range margin. *Global Change Biology* 19:161–72.

Davies, K.W., A.M. Nafus and R.L. Sheley. 2010. Non-native competitive perennial grass impedes the spread of an invasive annual grass. *Biological Invasions* 12:3187–3194.

Davies, K.W. and R.L. Sheley. 2011. Promoting native vegetation and diversity in exotic annual grass infestations. *Restoration Ecology* 19:159–165.

D'Antonio, C.M. and P.M Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63–87.

Di Tomaso, J.M. 2000. Invasive weeds in rangelands: Species, impacts, and management. *Weed Science* 48:255–265.

Elseroad, A.C. and N.T. Rudd. 2011. Can imazapic increase native species abundance in cheatgrass (*Bromus tectorum*) invaded native plant communities? *Rangeland Ecology and Management* 64:641–648.

Gasch, C.K., S.F. Enloe, P.D. Stahl and S.E. Williams. 2013. An aboveground-belowground assessment of ecosystem properties associated with exotic annual brome invasion. *Biology and Fertility of Soils* 49:919–928.

Haferkamp, M. and R. Heitschmidt. 1999. Japanese brome impacts on western wheatgrass in Northern Great Plains rangelands: An update. *Great Plains Resesarch* 9:315–327.

Haferkamp, M., J. Volesky, M. Borman, R. Heitschmidt and P. Currie. 1993. Effects of mechanical treatments and climatic factors on the productivity of Northern Great Plains rangelands. *Journal of Range Management* 46:346–350.

Hirsch-Shantz, M.C., T.A. Monaco, C.A. Call and R.L. Sheley. 2014. Large-scale downy brome treatments alter plant-soil relationships and promote perennial grasses in salt desert shrublands. *Rangeland Ecology and Management* 67:255–265.

Hull, A.C. and G. Stewart. 1948. Replacing cheatgrass by reseeding with perennial grass on southern Idaho ranges. *Journal of the American Society of Agronomy* 40:694–703.

Humphrey, L.D. and E.W. Schupp. 2001. Seed banks of *Bromus tectorum*-dominated communities in the Great Basin. *Western North American Naturalist* 61:85–92.

Humphrey, L.D. and E.W. Schupp. 2004. Competition as a barrier to establishment of a native perennial grass (*Elymus elymoides*) in alien annual grass (*Bromus tectorum*) communities. *Journal of Arid Environments* 58:405–422.

James, J.J. and T. Svejcar. 2010. Limitations to postfire seedling establishment: The role of seeding technology, water availability, and invasive plant abundance. *Rangeland Ecology and Management* 63:491–495.

Kyser, G.B., R.G. Wilson, J. Zhang and J.M. DiTomaso. 2013. Herbicide-assisted restoration of Great Basin sagebrush steppe infested with medusahead and downy brome. *Rangeland Ecology and Management* 66:588–596.

Mack, R.N. 2011. Fifty years of 'waging war on cheatgrass', research advances, while meaningful control languishes. Pages 253–265 in D.M. Richardson (ed), *Fifty Years of Invasion Ecology: The Legacy of Charles Elton*. Oxford, UK: Wiley-Blackwell.

Mack, R.N. and D.A. Pyke. 1983. The demography of *Bromus tectorum*—Variation in time and space. *Journal of Ecology* 71:69–93.

Mangold, J., H. Parkinson, C. Duncan, P. Rice, E. Davis and F. Menalled. 2013. Downy brome (*Bromus tectorum*) control with imazapic on Montana grasslands. *Invasive Plant Science and Management* 6:554–558.

Morris, C., C.W. Rigby and T.A. Monaco. 2009. Variable impacts of imazapic rate on downy brome (*Bromus tectorum*) and seeded species in two rangeland communities. *Invasive Plant Science and Management* 2:110–119.

Munson, S. and W. Laurenroth. 2012. Plant community recovery following restoration in semiarid grasslands. *Restoration Ecology* 20:656–663.

NOAA. 1979–2014. Fort Assinniboine, MT, US, daily summary station details (accessed 27 June 2014). www.ncdc.noaa.gov/cdo-web/datasets/GHCND/stations/GHCND:USC00243110/detail

Ogle, S.M., W.A. Reiners and K.G. Gerow. 2003. Impacts of exotic annual brome grasses (*Bromus* spp.) on ecosystem properties of northen mixed grass prairie. *American Midland Naturalist* 149:46–58.

Ortega, Y.K. and D.E. Pearson. 2010. Effects of picloram application on community dominants vary with initial levels of spotted knapweed (*Centaurea stoebe*) invasion. *Invasive Plant Science and Management* 3:70–80.

Pinheiro, J., D. Bates, S. DebRoy , D. Sarkar and R Development Core Team. 2013. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1–113. Vienna, Austria: R development Core Team.

Radosevich, S.R., J.S. Holt and C.M. Ghersa. 2007. *Weed Ecology. Implications for Management*. 2nd ed. New York, NY: John Wiley and Sons, Inc.

Romo, J.T. and L.E. Eddleman. 1987. Effects of Japanese brome on growth of bluebunch wheatgrass, junegrass, and squirreltail seedlings. *Reclamation Revegetation Research* 6:207–218.

Sbatella, G.M., R.G. Wilson, S.F. Enloe and C. Hicks. 2011. Propoxycarbazone-sodium and imazapic effects of downy brome (*Bromus tectorum*) and newly seeded perennial grasses. Invasive Plant Science and Management 4:78–86.

Sheley, R.L., M.F. Carpinelli and K.J. Morghan. 2007. Effects of imazapic on target and nontarget vegetation during revegetation. *Weed Technology* 21:1071–1081.

Sheley, R.L., J. James, B. Smith and E. Vasquez. 2010. Applying ecologically based invasive plant management. *Rangeland Ecology and Management* 63:605–613.

Sheley, R.L., J. Mangold, K. Goodwin and G. Marks. 2008. Revegetation guidelines for the Great Basin: Considering invasive weeds. Washington, DC: US Department of Agriculture, Agricultural Research Service.

Shinn, S.L. and D.C. Thill. 2004. Tolerance of several perennial grasses to imazapic. *Weed Technology* 18:60–65.

Smith, D.C., S.E. Meyer and V.J. Anderson. 2008. Factors affecting *Bromus tectorum* seed bank carryover in Western Utah. *Rangeland Ecology and Management* 61:430–436.

Soil Survey Staff. 2013. United States Department of Agriculture. Natural Resouce Conservation Service. Web Soil Survey. websoilsurvey.nrcs.usda.gov/

Tremblay, A. and J. Ransijn. 2013. LMERConvenienceFunctions: A suite of functions to back-fit fixed effects and forward-fit random effects, as well as other miscellaneous functions. R package version 2.5. Vienna, Austria: R development Core Team.

Turnbull, L., Crawley, M. and M. Rees. 2000. Are plant populations seed-limited? A review of seed sowing experiments. *Oikos* 88:225–238.

Warnes, G.R., B. Bolker, T. Lumley and R.C. Johnson. 2013. gmodels: Various R programming tools for model fitting. R package version 2.15.4.1. Vienna, Austria: R development Core Team.

Western Regional Climate Center. 2014. Western U.S. Climate Historical Summaries. www.wrcc.dri.edu/summary/Climsmemt

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***Bouteloua gracilis*. USDA-NRCS PLANTS Database. Hitchcock, A.S. 1950. *Manual of the grasses of the United States.* Washington, DC: USDA Miscellaneous Publication No. 200.**