

RESEARCH ARTICLE

Mowing Reduces Exotic Annual Grasses but Increases Exotic Forbs in a Semiarid Grassland

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Abstract

Cheatgrass (*Bromus tectorum*) and other exotic winter-active plants can be persistent invaders in native grasslands, growing earlier in the spring than native plants and pre-empting soil resources. Effective management strategies are needed to reduce their abundance while encouraging the reestablishment of desirable native plants. In this 4-year study, we investigated whether mowing and seeding with native perennial grasses could limit growth of exotic winter-actives, and benefit growth of native plants in an invaded grassland in Colorado, United States. We established a split-plot experiment in October 2008 with 3 mowing treatments: control, spring-mowed, and spring/summer-mowed (late spring, mid-summer, and late summer), and 3 within-plot seeding treatments: control, added *B. tectorum* seeds, and added native grass seeds. Cover of plant species and aboveground biomass were measured for 3 years. In March and June of 2010, 2011, and

March of 2012, *B. tectorum* and other winter-annual grasses were half as abundant in both mowing treatments as in control plots; however, cover of non-native winter-active forbs increased 2-fold in spring-mowed plots and almost 3-fold in spring/summer-mowed plots relative to controls. These patterns remained consistent 1 year after termination of treatments. Native cool-season grasses were most abundant in spring-mowed plots, and least abundant in control plots. There was higher cover of native warm-season grasses in spring/summer-mowed plots than in control plots in July 2011 and 2012. The timing of management can have strong effects on plant community dynamics in grasslands, and this experiment indicates that adaptive management can target the temporal niche of undesirable invasive species.

Key words: *Bromus tectorum*, invasive species, mowing, phenological niche, semiarid grassland, time-sensitive management.

Introduction

Grasslands have historically been impacted by humans, but more recently, human-caused disturbance and the introduction of non-native species have increasingly led to the loss of native grassland ecosystems (Sala & Paruelo 1997; Zhou et al. 2002; Suttie et al. 2005). In some extreme cases, native plant communities have shifted to less desirable stable states dominated by exotic species (Kulmatiski 2006; Seastedt & Pysek 2011). Grasslands provide a host of important ecosystem services such as carbon sequestration, forage and habitat for wildlife, and soil conservation, among others (Sala & Paruelo 1997). Thus, it is of vital importance to understand how and when to intervene (Hobbs et al. 2011) in grasslands in order to maintain important ecosystem services in the future (Choi et al. 2008; Seastedt et al. 2008).

Many of the exotic species invading grasslands around the world grow at different times of year than native species

(Wolkovitch & Cleland 2011). Some of the most successful invaders are winter-active species that germinate in the late fall or early spring and grow earlier in the season than native species. One particularly invasive plant that grows earlier in the year than most natives is *Bromus tectorum*, a species that has successfully invaded rangelands throughout the Great and Colombia Basins in the western United States. (Mack 1981; Pyšek & Hulme 2005). In regions where this species has become dominant, *B. tectorum* can alter fire frequencies (D'Antonio & Vitousek 1992; Baker 2013), alter soil resources (Melgoza et al. 1990; Sperry et al. 2006; Schaeffer et al. 2012), and reduce diversity and abundance of native plants (Prevéy et al. 2010; Concilio et al. 2013).

Effective management techniques are needed to reduce undesirable invasive species and maintain ecosystem services in grasslands. Management strategies that take advantage of phenological differences between invaders and desirable natives (Wolkovitch & Cleland 2011) can damage early-growing exotics and reduce or eliminate their seed production. Exotic plants can produce many seeds, and continued propagule supply can allow ecosystems to remain in invaded states dominated by exotic species (Fensham et al. 2013). In many cases, management of an annual species that is invading a historically perennial system can be addressed by reducing seed production. Even if such treatments temporarily harm perennial species,

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the regrowth and persistence of these has the potential to generate propagule limitation for the invader and should favor the perennials in the subsequent composition of the system. Hence, seasonally timed fire, mowing, or grazing are suggested as likely management activities (Kelley et al. 2013). Here, in order to expedite a replicated experimental design within a relatively small area, mowing was chosen as the treatment to target key phenological periods of undesirable invaders. In California, mowing of invaded grasslands in early spring has allowed for the suppression of exotics because it occurs when they are physiologically active (Maron & Jefferies 2001). In a relic patch of tallgrass prairie in Colorado, intensive spring grazing by cattle allowed for maintenance of native tallgrass species that usually require fire to maintain dominance (Seastedt et al. 2008). Although over-grazing of rangelands has been associated with ecosystem degradation, especially in arid grasslands (Zhou et al. 2002; Reisner et al. 2013), short-duration grazing or mowing applications may increase diversity and production of some grassland ecosystems (Collins et al. 1998; Jackson 1999; Zhou et al. 2002; Fensham et al. 2014). Moreover, the ecosystem function of grasslands with an evolutionary history of grazing may benefit from mowing or grazing applications (Mack & Thompson 1982; Milchunas et al. 1988; Milchunas & Lauenroth 1993). In addition, seeding with native species may help suppress future growth of exotic species in disturbed grassland ecosystems (Cleland et al. 2013), and native seed addition can help compensate for native seed predation and limitation in degraded grasslands (Seabloom et al. 2003). Time-sensitive management applications, in conjunction with seeding of native species, could allow for successful restoration of desirable grassland communities.

In this study, we investigated effects of seasonal mowing and seeding with native perennial grasses on growth of non-native winter-active species and native plants in an invaded grassland in Colorado. We also seeded with *B. tectorum*, to observe how mowing treatments would interact with increased invasion pressure to affect community composition. The study site has a mix of native and non-native species in distinct functional groups that grow at different times of year, so it is an ideal location to

test effects of management strategies targeted at phenological timing. We focused on five functional groups of plants in this study: winter-active exotic grasses, winter-active exotic forbs, early-growing native grasses, later-growing native grasses, and later-growing native forbs. In June 2009, we established an experiment with three levels of mowing and seeding: control, spring-mowing, and spring/summer-mowing (late spring, mid-summer, and late summer), and three within-plot seeding treatments: control, added *B. tectorum* seeds, and added native grass seeds. We then examined effects on plant community composition and ecosystem processes. We hypothesized that: (1) Native grasses would increase in plots that received early spring-mowing and added native grass seed, because mowing would impact early-growing exotic grasses and forbs while they were active without harming the later-growing native perennials and allow for establishment of more desirable native species. (2) Primary production would be greatest in spring-mowed plots because early mowing would reduce cover of exotic species, and this reduction in growth would allow for increased growth and production of perennials through the growing season. (3) Ongoing removal of vegetation in spring/summer-mowed plots would reduce primary productivity of all species.

Methods

Site Characteristics

This experiment was established in a foothills mixed-grass prairie located approximately 15 km northwest of Boulder, Colorado, United States (40°07'N, 105°18'W). Elevation at the site is 1,798 m, with an average precipitation of 475 mm/year, and an average temperature of 10.5°C (NOAA, 2009–2013). Climate over the study period is shown in Figure S1, Supporting Information. Vegetation at the site is representative of plant communities in foothills and montane meadow ecosystems across the Front Range of Colorado. The community is characterized by a mix of exotic winter-annual species, exotic perennial species, and native grasses and forbs (Knoche & Seastedt 2010, Table 1). A complete site description is found in Prev  y (2014).

Table 1. Mean values for absolute percent cover of functional groups, litter, bare ground, aboveground biomass, and nitrogen extracted from resin bags over all analyzed sample dates, \pm standard error.

Response Variable	Control	Spring-Mowed	Spring/Summer-Mowed	Degrees of Freedom	Wald Statistic χ^2	<i>p</i>
Exotic grass (%)	40.99 \pm 3.76 ^a	19.12 \pm 2.48 ^b	7.92 \pm 1.08 ^c	2	102	<0.0001
Exotic forb (%)	17.95 \pm 2.34 ^a	28.59 \pm 2.48 ^b	42.01 \pm 3.44 ^c	2	40.3	<0.0001
Native cool-season grass (%)	6.52 \pm 1.02 ^a	12.07 \pm 1.16 ^b	6.32 \pm 0.81 ^a	2	9.93	0.007
Native warm-season grass (%)	25.10 \pm 3.63 ^a	29.24 \pm 3.84 ^a	36.54 \pm 3.71 ^a	2	2.68	0.26
Native forb (%)	14.25 \pm 1.47 ^a	13.52 \pm 1.38 ^{ab}	8.65 \pm 1.02 ^b	2	8.28	0.016
Litter (%)	34.2 \pm 8.73 ^a	28.4 \pm 7.24 ^{ab}	26.9 \pm 7.00 ^b	2	0.04	0.04
Bare ground (%)	0.56 \pm 0.63 ^a	1.67 \pm 2.53 ^a	6.40 \pm 2.49 ^b	2	113	<0.0001
Aboveground biomass (g/m ²)	222.4 \pm 19.44 ^a	192.3 \pm 15.27 ^a	158.7 \pm 15.72 ^b	2	23.5	<0.0001
NH ₄ (��g/g)	49.10 \pm 17.77 ^a	60.91 \pm 37.99 ^a	58.30 \pm 32.33 ^a	2	0.31	0.86
NO ₃ (��g/g)	258.2 \pm 95.76 ^a	236.1 \pm 104.9 ^a	238.3 \pm 89.75 ^a	2	0.16	0.92
Total nitrogen (��g/g)	307.3 \pm 110.9 ^a	297.1 \pm 128.9 ^a	296.6 \pm 116.3 ^a	2	0.94	0.12

Post-treatment measurements on June 2013 were not included in mean values. Wald statistics are shown for individual GEEs, and *p* values are shown for ANOVAs comparing GEE models for each functional group with and without the whole-plot treatment effect. Treatments with different letters across the row are significantly different (pairwise contrasts adjusted with Bonferroni corrections).

Experimental Design

Plots were established in October 2008, and manipulations were conducted for the following 4 years, from 2009 to 2012. Twenty-four $4 \times 4 \text{ m}^2$ plots were established at the study site in October 2008. Experimental plots had a split-split plot design, with mowing as the whole-plot treatment and seeding as the within-plot treatment. Each plot was randomly assigned to one of three whole-plot treatments: control, spring-mowed, or spring/summer-mowed. The whole-plot mowing treatments were conducted using a mower that left cut vegetation in the plots to reduce nutrient removal caused by the treatment. Plots were mowed at a height of approximately 5 cm above ground. Each plot was then divided into three within-plot treatments: no added seed, added *B. tectorum* seed, and added native grass (*Pascopyrum smithii* and *Elymus trachycaulus*) seed. The within-plot treatments were $1 \times 4 \text{ m}^2$ long strips, separated by 0.25M buffers. Seeding treatments were applied in the same locations within each plot. Seeds were broadcast along strips at rates of over 2,000 seeds/ m^2 . Seeds were added on 25 March 2009, 18 October 2009, 3 November 2010, and 20 April 2011. Mowing treatments began on 5 June 2009. Spring-mowed plots were treated only once yearly, in late May or early June during 2009–2012. In the foothills of northern Colorado, *B. tectorum* begins flowering from May through early June. Spring mowing was timed to damage flowering stalks of *B. tectorum* before seeds had fully developed. Spring/summer-mowed plots were treated three times per year in late spring, mid-summer, and late summer during 2009–2012.

Measurements

We measured cover of plant species using the point-intercept procedure with a 1 m^2 quadrat in each within-plot treatment. The number of points intercepting a living plant species was divided by the total number of points sampled in the quadrat (75) to calculate absolute percent cover. Pre-treatment cover was measured in early June 2009 and was measured again in September 2009, and March, June, late July, and September of 2010–2012. To observe how vegetation was responding 1 year after treatments had stopped, cover was measured again in June 2013. To assess how mowing treatments affected net primary production, we measured aboveground biomass on all plots in late July or early August 2009–2013 during peak biomass. Yearly production of aboveground biomass was collected from ground level in 0.1 m^2 subplots from each within-plot treatment. In addition, clipped biomass was collected within a 0.1 m^2 subplot at 5 cm height from all mowed plots at each mowing event. Clipped biomass was added to August clippings to determine total aboveground biomass production of mowed plots.

After 1 year of treatment manipulation, we placed ion-exchange resin bags in plots to determine how different mowing regimes would affect plant-available inorganic nitrogen. Resin bags were constructed with Amberlite® mixed-bed ion-exchange resins (Sigma-Aldrich, St. Louis, MO, U.S.A.) following methods similar to Lajtha (1988). Two resin bags were placed in the center of each plot at 5 cm below

the soil surface. Resin bags were inserted horizontally in soil using a trowel so as not to disturb soil above resin bags. We placed separate sets of resin bags in plots over spring, summer, and winter 2011 and 2012 to examine seasonal fluctuations in available nitrogen. After collection from the field, resins were extracted with 2M KCl to leach inorganic nitrogen. The amount of NO_3^- and NO_2^- (hereafter NO_3^-), and NH_4^+ in KCl extractions was measured on a Lachat QuickChem 8500 Flow injection analyzer (Lachat Instruments, Loveland, CO, U.S.A.).

Statistical Analyses

Prior to analyses, plant species were grouped into five functional groups based on phenology, growth form, and native/non-native status. The five groups were: exotic grasses, exotic forbs, native cool-season grasses, native warm-season grasses, and native forbs.

To see if mowing treatments were significantly changing the composition of the plant community, we performed multivariate analyses (PERMANOVAs) using the vegan package in R (Oksanen et al. 2012; R Development Core Team 2012) on percent cover of the five functional groups and litter in June 2009 (pre-treatment), June 2010, June 2011, and June 2012. The *p* values from pairwise comparisons were adjusted with the Bonferroni method.

To specifically examine how treatments affected abundance of each functional group, we analyzed percent cover of individual groups over time with generalized estimating equations (GEEs) in R (Højsgaard et al. 2006). GEEs were used to account for nonindependence of cover measurements made in the same plots over multiple sampling dates. Whole-plot mowing treatment, within-plot seeding treatment, year, and sampling date were predictor variables in GEEs. Data that strongly violated assumptions of normality were square-root transformed before analysis. For each functional group, only dates that species were physiologically active were included in analyses. For instance, cover of exotic grasses declined sharply in all treatments after June sampling dates because the grasses senesce in mid-June, so only March and June dates were used in analysis of exotic grass cover.

To address effects of mowing treatments on net primary productivity and nutrient cycling, we also analyzed aboveground biomass and nitrogen extracted from resin bags with GEEs. Wald chi-square statistics (χ^2), *p* values from analyses of variance (ANOVAs) comparing models, and statistical contrasts were used to test for significant effects of predictor variables on cover, aboveground biomass, and nitrogen variables and are reported in results. In addition to examining effects of treatments on nitrogen availability, we evaluated whether plant community composition and aboveground biomass affected the amount of nitrogen collected in resin bags, a proxy for inorganic nitrogen availability. To examine the relationship between biomass production, plant species composition, and nitrogen availability, we used linear models to correlate percent cover of plant functional groups and aboveground biomass with total nitrogen per plot in spring and summer of 2011 and 2012.

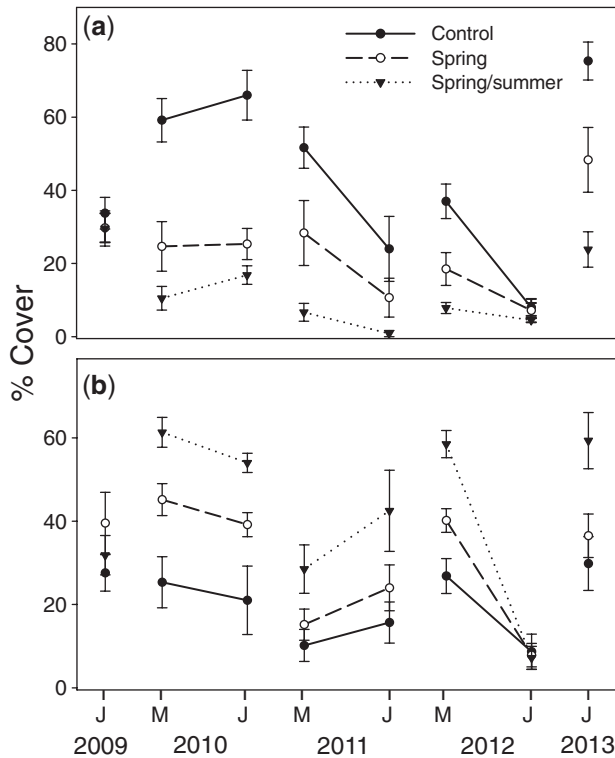


Figure 1. Percent cover of exotic grasses (a) and exotic forbs (b), \pm standard error. Cover measurements taken 5 June 2009 (pre-treatment), 31 March 2010, 15 June 2010, 31 March 2011, 20 June 2011, 1 April 2012, 11 June 2012, and 13 June 2013 (post-treatment).

Results

Community Composition

The within-plot seeding treatment had no effect on cover of functional groups or aboveground biomass over sampling dates (all $p > 0.1$); thus, the within-plot treatment was removed from PERMANOVA and GEE models and response variables were averaged over whole-plots.

Pre-treatment cover of functional groups did not differ between experimental plots (PERMANOVA, $p > 0.85$). In June 2010, composition of functional groups differed significantly between all whole-plot treatments ($p < 0.04$). In June 2011 and 2012, composition of functional groups differed between control and spring/summer treatments ($p < 0.05$), but not the spring-mowed treatment ($p > 0.3$).

Exotic grass cover significantly differed between each whole-plot treatment (Table 1; Fig. 1). Exotic grasses were over four times more abundant in control plots than in spring/summer-mowed plots over all sampling dates, except June 2012 (Fig. 1). The most abundant exotic grass species in plots was *Bromus tectorum* (Table S1). Cover of exotic forbs was diametrically opposite, with the highest cover in spring/summer-mowed plots and the lowest cover in control plots (Table 1; Fig. 1). *Erodium cicutarium* and *Convolvulus arvensis* were the most abundant exotic forbs in plots (Table S1).

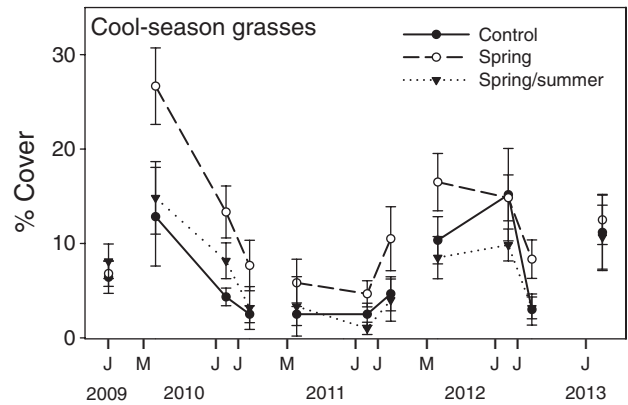


Figure 2. Percent cover of native cool-season grasses \pm standard error. Cover measurements taken 5 June 2009 (pre-treatment), 31 March 2010, 15 June 2010, 27 July 2010, 31 March 2011, 20 June 2011, 26 July 2011, 1 April 2012, 11 June 2012, 26 July 2012, and 13 June 2013 (post-treatment).

Cover of native cool-season grasses was almost two times greater in the spring-mowed treatment than in the spring/summer-mowed and control treatments over all analyzed dates (Fig. 2). *Pascopyrum smithii* was the most abundant cool-season grass in plots (Table S1). Cover of native warm-season grasses did not differ between treatments overall, although there was a trend for higher cover of warm-season grasses in the spring/summer-mowed plots, particularly in July 2010 and July 2011 (Fig. 3). Native forbs were most abundant in control plots, and least abundant in spring/summer-mowed plots (Fig. 3). Over all sampling dates, spring/summer-mowed plots had significantly more bare soil and less litter than control plots ($p < 0.0001$, 0.04, Table 1). Cover of all functional groups significantly differed between sampling months and years (all $p < 0.0001$, Figs. 1–3).

Biomass and Nitrogen

Aboveground biomass was higher in control and spring-mowed plots than in spring/summer-mowed plots over all sampling dates (Table 1; Fig. 4). Available nitrogen varied greatly between individual plots and over seasons. There was no significant effect of whole-plot treatments on NO_3^- , NH_4^+ , or total inorganic nitrogen over the study period (Table 1; Fig. S2). There was no relationship between the amount of aboveground biomass and total nitrogen in spring or summer ($p > 0.1$). However, cover of warm-season grasses in July and September 2011 and 2012 was negatively correlated to total nitrogen in summer 2011 ($p = 0.008$) and 2012 ($p \leq 0.0001$, Fig. 5).

Discussion

The mowing treatments greatly altered species composition in study plots; however, the within-plot seeding treatment did not influence species composition. As hypothesized, non-native grasses were less abundant in spring-mowed and spring/summer-mowed treatments. However, contrary to our

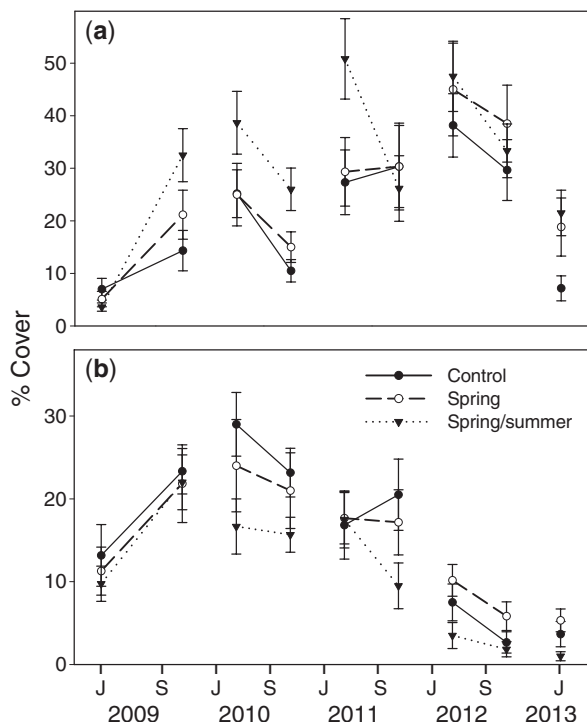


Figure 3. Percent cover of native warm-season grasses (a) and native forbs (b) \pm standard error. Cover measurements 5 June 2009 (pre-treatment), 16 September 2009, 27 July 2010, 13 September 2010, 26 July 2011, 14 September 2011, 26 July 2012, 10 September 2012, and 13 June 2013 (post-treatment).

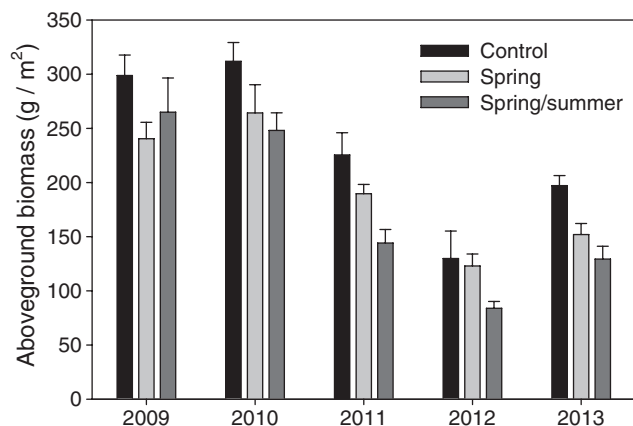


Figure 4. Aboveground biomass from control, spring-mowed, and spring/summer-mowed plots collected on 1 August 2009 (pre-treatment), 27 July 2010, 20 August 2011, 20 August 2012, and 20 August 2013, \pm standard error.

hypotheses, non-native forbs were more abundant in mowed treatments than in the control treatment. Overall, native species were most abundant in spring-mowed plots, suggesting that the reduction of non-native winter-active grasses may benefit natives. Contrary to our hypothesis, primary production was not highest in spring-mowed plots, and was significantly lower in spring/summer-mowed plots than in controls.

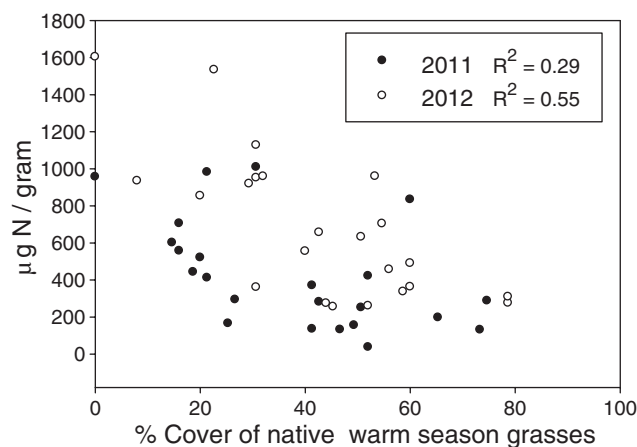


Figure 5. Correlation of total nitrogen extracted from resin bags in summers 2011 and 2012 to percent cover of native warm-season grasses in July 2011 ($p = 0.008$) and 2012 ($p < 0.0001$).

Our results showed that broadcast seeding into a relatively intact grassland with native cool-season wheatgrasses may not alter species abundances within grasslands. The amount of seeds added to plots was over five times greater than the seeding rate suggested for restoration projects (USDA NRCS, n.d.); however, we did not observe any germination of seeded species during the study period. The seeds germinated readily in the lab, so factors in the field determined the lack of germination in the experiment. Other studies have found that broadcast seeding is not very effective (Beyers 2004; Bernstein et al. 2013). This may result from seeds not being buried to a sufficient depth to germinate and survive, or seed predation by insects, rodents, and birds (Orrock et al. 2009; Defalco et al. 2012). Additionally, the timing of our seeding may not have coincided with favorable conditions for recruitment.

In contrast to seeding, the mowing treatments resulted in very different composition of plant species. Cover of non-native grasses, composed mostly of *B. tectorum*, declined rapidly in mowed plots after the first year of treatment applications. Mowing in late May and early June removed seed-heads of *B. tectorum* before they had after-ripened, so no new viable seed was added to plots. In June 2013, 1 year after termination of treatments, cover of exotic grasses was still significantly higher in control plots than mowed treatments (Fig. 3), indicating that reduction of *B. tectorum* and other exotic grasses continues beyond treatment applications. Several studies have shown that *B. tectorum* does not have a long-lived seedbank, as most seeds germinate readily after wet conditions in late fall through early spring (Hulbert 1955; Mack & Pyke 1983). In rangelands in western United States and Israel, grazing in late fall or early spring led to large reductions in the seedbanks of annual *Bromus* grasses (Sternberg et al. 2003; Diamond et al. 2012). Mowing or high intensity, short-duration grazing of invaded grasslands early in spring may be a very effective means to reduce abundance of undesirable winter-active grass species.

Although early spring and spring/summer-mowing decreased abundance of winter-active grasses, it also led to an increase

in exotic forbs. Although mowing and grazing are different in a variety of ways, the results of this mowing experiment were similar to grazing studies that differentially affected morphologically distinct groups of plant species (Hayes & Holl 2003; Stahlheber & D'Antonio 2013). Specifically, the two exotic forbs that benefited most from spring/summer-mowing, *Convolvulus arvensis* and *Erodium cicutarium*, have characteristics that benefit plant species in grazed areas worldwide (Diaz et al. 2007). These two low-statured species are prostrate, and either stoloniferous (*C. arvensis*) or rosette-forming (*E. cicutarium*). These traits give exotic forbs an advantage after disturbances that damage tall perennial species. Other studies have found *Erodium* spp. to increase after grazing in both Texas and California grasslands (Weigel et al. 1989; Kimball & Schiffman 2003). Thus, mowing or grazing may not be an adequate control to reduce abundance of low-growing exotic forbs.

Native cool-season grasses were most abundant in spring-mowed plots, and *Pascopyrum smithii* was the most abundant cool-season grass. In mixed-grass prairie of Wyoming, *P. smithii* increased in areas receiving light grazing, but decreased in heavily grazed areas (Schuman et al. 1999). Unlike exotic annual grasses, this perennial grass can resprout from the base and may be stimulated by grazers. *P. smithii* performed especially well in spring-mowed plots in 2010 and 2012. *P. smithii* may have benefited from a lack of competition with non-native grasses in mowed treatments in those years. *P. smithii* could be an important species for restoration of disturbed grasslands. However, our study indicates that broadcast seeding may not be an effective way to establish this grass, so drill seeding or planting starters would be necessary.

Species of native warm-season grasses responded differentially to treatments. *Bouteloua gracilis* was most abundant in spring/summer-mowed plots (Table S1). Other studies have found *B. gracilis* to increase in areas that received light to heavy grazing (LeCain et al. 2002). *B. gracilis* may be a viable option for restoration of heavily grazed grasslands. In contrast, the warm-season grass *Sporobolus cryptandrus* had similar cover in all treatments, and had particularly high cover in September 2012 after a dry early summer and wet July. *S. cryptandrus* is extremely drought-tolerant (Weaver & Hansen 1939; Wan et al. 1993), and could be an important plant for restoration because of its drought tolerance and ability to grow in heavily invaded grasslands after non-native species senesce. Planting native species with differing phenologies and drought tolerances appears effective for restoring grasslands with highly variable precipitation patterns (Cherwin et al. 2009). In addition, the cover of warm-season grasses was negatively correlated to nitrogen availability in the soil, indicating that these grasses may help draw down soil nutrient availability, making nutrients less available for non-natives the following spring.

Our results indicate that grazing or mowing to target the temporal niche of winter-active grasses can be a successful management technique. Although mowing treatments did not reduce cover of all introduced species, the spring-mowed treatment did decrease cover of exotic grasses and increase the number of desirable native species. Mowing reduced biomass production in our plots, so intensive mowing or grazing applications may

reduce ecosystem function; however, short-duration mowing or grazing may increase native plant abundance without reducing primary productivity markedly. Similarly, in grasslands of northern China, heavy grazing reduced plant species richness and production, whereas light grazing led to higher species richness (Zhou et al. 2002). The use of mowing or grazing for ecological restoration has been successfully applied in invaded grasslands in other semiarid rangelands (Maron & Jefferies 2001; Diamond et al. 2012), and can be used for grasslands along the Front Range of Colorado. A meta-analysis of studies in California grasslands found grazing in early spring to be most effective in increasing cover of native species (Stahlheber & D'Antonio 2013), similar to results of this study. Strategically applied mowing or grazing treatments have positively maintained or enhanced diversity in a tallgrass prairie (Collins et al. 1998) and shortgrass steppe (Hart 2001). In an age of rapid environmental change, novel approaches to ecosystem management are becoming necessary to ensure continuation of important ecosystem services (Choi et al. 2008; Seastedt et al. 2008). This study shows that management strategies that exploit phenological differences in exotic and native species may allow for maintenance of resilient ecosystems that will continue to provide valuable services in the future (Wolkovitch & Cleland 2011).

Implications for Practice

- Management applications that are timed to limit seed production of exotic winter-annual grasses may decrease abundance of exotic grasses and increase abundance of native plants; however, exotic forbs may benefit as well.
- Broadcast seeding of native grasses may not be an effective method to enhance dominance of native species in moderately undisturbed grassland ecosystems.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Total monthly precipitation for Boulder, Colorado, over the 4-year duration of the study (solid line) compared to average monthly precipitation from 1948–2005 (dashed line). Precipitation data were collected from the Boulder weather station, located approximately 15 km from research site.

Figure S2. NH_4 and NO_3 extracted from ion-exchange resin bags in control, spring-grazed, and spring/summer grazed treatments + standard error.

Table S1. The average absolute percent cover of the two most common plant species of each functional group in control, spring-mowed, and spring/summer-mowed treatments, averaged over the sampling dates.