

RESEARCH ARTICLE

Attempting to Restore Herbaceous Understories in Wyoming Big Sagebrush Communities with Mowing and Seeding

Kirk W. Davies^{1,2} and Jon D. Bates¹

Abstract

Shrub steppe communities with depleted perennial herbaceous understories often need to be restored to increase resilience and resistance. Mowing has been applied to Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) steppe plant communities to reduce sagebrush dominance and restore native herbaceous vegetation, but success has been limited and hampered by increases in exotic annuals. Seeding native bunchgrasses after mowing may accelerate recovery and limit exotics. We compared mowing followed by drill-seeding native bunchgrasses to mowing and an untreated control at five sites in southeastern Oregon over a 4-year period. Mowing and seeding bunchgrasses increased bunchgrass density; however, bunchgrass cover did not differ among treatments. Exotic annuals increased with mowing whether or not post-mowing seeding occurred. Mowing,

whether or not seeding occurred, also reduced biological soil crusts. Longer term evaluation is needed to determine if seeded bunchgrasses will increase enough to suppress exotic annuals. Seeded bunchgrasses may have been limited by increases in exotic annuals. Though restoration of sagebrush communities with degraded understories is needed, we do not recommend mowing and seeding native bunchgrasses because this treatment produced mixed results that may lower the resilience and resistance of these communities. Before this method is applied, research is needed to increase our understanding of how to improve establishment of seeded native bunchgrasses. Alternatively, restoration practitioners may need to apply treatments to control exotic annuals and repeatedly seed native bunchgrasses.

Key words: brush management, drill seeding, exotic annual grass, invasion, resilience, resistance, understory restoration.

Introduction

Restoring resilience and resistance in degraded native plant communities is often needed to prevent crossing generally irreversible thresholds to undesirable states (Brooks & Chambers 2011). In degraded Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young) communities, restoration of resilience to fire and resistance to invasion is critical to preventing conversion to an exotic annual grass-dominated state. Overuse by livestock can negatively impact the perennial bunchgrass component of sagebrush communities (Anderson & Inouye 2001; Reisner et al. 2013). This has resulted in a large portion of the sagebrush ecosystem

of western North America having a depleted native understory and an increased dominance by sagebrush (West 2000). In contrast, relatively intact Wyoming big sagebrush plant communities, which have experienced limited grazing pressure, generally have nearly equal cover of large native bunchgrasses and sagebrush (Davies et al. 2006). Degraded sagebrush communities are likely to convert to exotic annual grasslands because resilience and resistance are greatly decreased with the loss of perennial herbaceous species (Chambers et al. 2007). Restoration of resilience and resistance in degraded sagebrush communities to prevent additional losses of sagebrush habitat is critical because millions of hectares of the sagebrush ecosystem have already been converted to exotic annual grasslands, introduced grasslands (*Agropyron cristatum* [L.] Gaertn. and *A. desertorum* [Fisch. Ex Link] Schult.), or conifer woodlands (Davies et al. 2011a), resulting in a substantial loss of habitat for sagebrush-associated wildlife. This has resulted in more than 350 sagebrush-associated animals and plants being considered species of conservation concern (Suring et al. 2005; Wisdom et al. 2005).

Wyoming big sagebrush communities with depleted understories are less resilient to disturbances and are at an elevated risk of conversion to exotic annual grasslands. Davies

¹USDA-Agricultural Research Service, Eastern Oregon Agricultural Research Center, Burns, OR, U.S.A.

²Address correspondence to K. W. Davies, email kirk.davies@oregonstate.edu

Mention of a proprietary product does not constitute a guarantee or warranty of the product by USDA, Oregon State University, or the authors and does not imply its approval to the exclusion of other products. USDA is an equal opportunity provider and employer.

Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

doi: 10.1111/rec.12110

et al. (2012b) found that mowing Wyoming big sagebrush communities with a depleted understory increased exotic annual grasses and forbs. Burning Wyoming big sagebrush communities with a depleted understory have also fostered exotic annual grass invasion and dominance (Stewart & Hull 1949; Young & Allen 1997). Both burning and mowing sagebrush communities increase soil nutrients (Davies et al. 2007; Davies et al. 2011b). Increases in soil nutrients, especially with a depleted native understory, favor exotic annual grasses (Young & Allen 1997; Vasquez et al. 2008). The limited abundance of large perennial bunchgrasses in these communities is probably the major reason they are susceptible to exotic annual grass invasion when sagebrush is significantly reduced. Resource acquisition by large perennial bunchgrasses overlaps greatly with exotic annual grasses (James et al. 2008). Therefore, large perennial bunchgrasses are the most important plant functional group for limiting exotic annual grass invasion and for resilience in sagebrush steppe plant communities (Davies 2008; James et al. 2008).

Not disturbing Wyoming big sagebrush plant communities with depleted native understories may intuitively seem a prudent management action owing to the risk of exotic annual grass invasion. However, these plant communities will at some point probably burn in a wildfire and, thus, it is critical to restore their resilience prior to a wildfire event (Davies et al. 2012b). Restoration of the large perennial bunchgrass component is also critical to improving resistance to invasion (Reisner et al. 2013), because they are the dominant herbaceous plant functional group in relatively intact Wyoming sagebrush steppe communities comprising approximately 40–80% of the total herbaceous cover (Davies et al. 2006; Davies & Bates 2010).

Long-term exclusion of livestock has been attempted to restore depleted understories in sagebrush communities, but increases in perennial bunchgrasses have been minimal (Sneva et al. 1980; West et al. 1984). Increases in perennial bunchgrasses are probably limited by dense sagebrush overstories and thus, sagebrush may need to be reduced to encourage perennial bunchgrass recovery (Sneva et al. 1980; Boyd & Svejcar 2011). However, reducing sagebrush in these plant communities has not necessarily increased the native herbaceous understory (Beck et al. 2012; Davies et al. 2012b), possibly owing to a depleted seed bank. Perennial grass seed is often limited in the seed bank in degraded sagebrush communities (Young & Evans 1975; Chambers 2000). Mowing, to reduce sagebrush dominance, followed by seeding native perennial bunchgrasses may restore the native perennial bunchgrass component by overcoming a depleted seed bank. Information, however, on the effects of mowing and seeding native bunchgrasses in Wyoming big sagebrush communities is lacking.

The objective of this research project was to determine if mowing and seeding large native perennial bunchgrasses (native bunchgrasses excluding Sandberg bluegrass [*Poa secunda* J. Presl]) in Wyoming big sagebrush plant communities with a depleted understory foster native bunchgrass recovery without significantly increasing exotic annuals. We hypothesized that: (1) mowing with seeding would increase native bunchgrasses; (2) mowing without seeding would favor exotic annuals; and

(3) exotic annuals would initially increase with mowing and seeding, but decrease as bunchgrasses become a dominant component of the understory.

Methods

Study Area

The study was conducted at five Wyoming big sagebrush-dominated sites in southeastern Oregon 5–15 km south of Riley, Oregon, U.S.A. The herbaceous understory was considered depleted at all sites because native large perennial bunchgrass and native perennial forb density and cover were low. Averaged across study sites, sagebrush, Sandberg bluegrass, large perennial bunchgrass, and perennial forb foliar cover were 14.9, 1.7, 1.5, and 0.5% prior to treatment, respectively. The cover of native perennial herbaceous plant functional groups was lower in our study sites than in relatively intact Wyoming big sagebrush communities (Davies et al. 2006; Davies & Bates 2010). The most pronounced difference was that large perennial bunchgrass cover was 5.9- to 6.7-fold less at our study sites than in relatively intact Wyoming big sagebrush communities (Davies et al. 2006; Davies & Bates 2010). Higher than average sagebrush cover also suggests sagebrush may be limiting herbaceous vegetation. Sagebrush cover was 1.2- to 1.5-fold greater at our study sites than the average reported for relatively intact Wyoming big sagebrush steppe (Davies et al. 2006; Davies & Bates 2010). Bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] A. Löve), Thurber's needlegrass (*Achnatherum thurberianum* [Piper] Barkworth), squirreltail (*Elymus elymoides* [Raf.] Swezey), and Sandberg bluegrass were found at study sites. Bluebunch wheatgrass and Thurber's needlegrass would have been dominant perennial bunchgrasses if these plant communities were not degraded (NRCS 2013). Cheatgrass (*Bromus tectorum* L.) and the exotic annual forb desert madwort (*Alyssum desertorum* Stapf) were common at study sites, but their cover was <1% the year prior to treatment. Climate across the study area is characteristic of the northern Great Basin: hot dry summers with most of the precipitation occurring during the cool, wet winter, and spring months. Annual precipitation averages between 250 and 275 mm across the study area (Oregon Climatic Service 2009). Crop-year (1 October to 30 September) precipitation was 87, 101, 118, and 62% of this long-term average in 2009, 2010, 2011, and 2012, respectively (EOARC 2012). Study sites were on the Loamy 10–12PZ (PZ = inch precipitation zone; 254–305 mm) (R023XY212OR) ecological site. Study sites were 1,263–1,350 m above sea level and slopes were relatively flat (0–4%). Soils are loamy, well drained, and 50–100 cm deep to a duripan. Soil surfaces had a physical crust with vesicular pores. Historic livestock use of this area was heavy and often season-long (Davies et al. 2012b). Current management rotates the season of livestock use and grazing pressure is moderate (~40% use of available forage). In general, one year grazing is early (mid-April to June or July) and then the next year late (July or August to late September). Treatment plots were fenced to exclude livestock during the experiment.

Experimental Design and Measurements

We used a randomized complete block (site) design to determine the response of Wyoming big sagebrush plant communities with degraded understories to mowing and mowing followed by seeding native perennial bunchgrasses (Table S1, Supporting Information). Treatments were (1) mowed (MOW); (2) mowed and then seeded with native perennial bunchgrasses (SEED + MOW); and (3) untreated control (CONTROL). Treatments were randomly applied to one of three 30 × 60-m plots at each of the five sites. These five sites occurred in different grazing pastures and were on average separated by 10 km with a minimum of 2 km and a maximum of 12 km between sites. Mowing was applied in September of 2008 with a Schulte XH 1500 rotary cutter (Schulte Equipment, Co., Englefield, Saskatchewan, Canada) set to mow at 20 cm height. The SEED + MOW treatment was drill seeded with a Laird Rangeland Drill (Laird Welding & Manufacturing Works, Merced, CA, U.S.A.) after mowing. Drill rows were 30 cm apart and 5-cm diameter pipes were dragged behind the drill to cover the seeds. The seed mix was composed of bluebunch wheatgrass, basin wildrye (*Leymus cinereus* [Scribn. & Merr.] Á. Löve), and bottlebrush squirreltail with each species seeded at 5.6 kg/ha pure live seed (PLS). Soil characteristics and elevation varied among sites.

Vegetation, bare ground, and biological soil crust were measured each June for 4 years post-treatment (2009–2012). Each treatment plot was sampled with four 50-m transects spaced 5 m apart. Herbaceous canopy cover and density, bare ground, litter, and biological soil crust cover were estimated using 40 × 50-cm quadrats located at 3-m intervals along the 50-m transects (15 quadrats per transect, 60 quadrats per plot). Ground cover was visually estimated based on markings that divided the quadrats into 1, 5, 10, 25, and 50% segments. Density was measured by counting all herbaceous plants rooted in the 40 × 50-cm quadrats. Shrub canopy cover was measured using the line intercept method (Canfield 1941) on each of the 50-m transects. Shrub density was measured by counting all shrubs rooted in four, 2 × 50-m belt transects positioned over the four 50-m transects.

Statistical Analyses

We used repeated measures analysis of variance (ANOVA) using the mixed models procedure (Proc Mixed) in SAS version 9.2 (SAS Institute, Inc., Cary, NC, U.S.A.) with years as the repeated factor to compare response variables among treatments. Block (site) and block by treatment interactions were treated as random variables in the analyses. The appropriate covariance structure (compound symmetry, autoregressive, or unstructure) was selected for each model using the Akaike's Information Criterion (Littell et al. 1996) in SAS version 9.2. When there was a significant year by treatment interaction data were separated by year to determine treatment effect in individual years. For analyses, herbaceous cover and density were grouped into five plant functional groups: large perennial bunchgrasses, Sandberg bluegrass, perennial forbs, exotic annual grasses, and annual forbs. Sandberg bluegrass was

analyzed as a separate plant functional group from the other perennial grasses because it is smaller in stature and its phenological development occurs earlier than other native bunchgrasses (James et al. 2008). Cheatgrass was the most common exotic annual grass at the study sites. Desert madwort, an exotic annual forb, comprised 83 and 84% of the total annual forb cover and density, respectively. The perennial forb and perennial bunchgrass functional groups were composed of native species. Shrub cover and density were separated into two groups: Wyoming big sagebrush and other shrubs. Wyoming big sagebrush was treated as a separate group because it was the dominant shrub and all other shrubs were resprouters. Data that violated assumptions of normality were log transformed. Original data (i.e. non-transformed) were presented in figures and text. Treatment means were separated using Fisher's protected least significant difference ($p \leq 0.05$). Means were reported with standard errors (mean + SE).

Results

Cover

Herbaceous plant functional groups varied in their response to treatments (Fig. 1). Large perennial bunchgrass cover did not differ among the treatments (Fig. 1a; $p = 0.29$). Sandberg bluegrass and perennial forb cover also did not differ among treatments (data not presented; $p = 0.72$ and 0.37 , respectively). Annual grass, annual forb, and total herbaceous cover were greater in the SEED + MOW and MOW treatments compared with the CONTROL treatment (Fig. 1; $p < 0.01$), but did not differ between the SEED + MOW and MOW treatments ($p > 0.05$). In 2012, annual grass cover was 6- and 9-fold greater in the SEED + MOW and MOW treatments than in the CONTROL.

Bare ground was lower in the SEED + MOW and MOW treatments compared with the CONTROL (Fig. 2a; $p < 0.01$), but did not differ between the SEED + MOW and MOW treatments ($p = 0.48$). Litter cover varied by the interaction between treatment and year (Fig. 2b; $p < 0.01$). Litter was generally greater in the SEED + MOW and MOW treatments compared with the CONTROL ($p < 0.01$), but in 2010 there was no difference among treatments ($p = 0.09$). Biological soil crust cover was lower in the SEED + MOW and MOW treatments compared with the CONTROL ($p < 0.01$), but did not differ between the SEED + MOW and MOW treatments ($p = 0.16$). In 2012, biological soils crust cover was 3.8- and 2.9-fold less in the SEED + MOW and MOW treatments, respectively, compared with the CONTROL treatment (Fig. 2c). Sagebrush cover was less in the SEED + MOW and MOW treatments compared with the CONTROL treatment (Fig. 2d; $p < 0.01$), but did not differ between the SEED + MOW and MOW treatments ($p = 0.10$). Averaged across all years, sagebrush cover was 4.8- and 3.3-fold less in the SEED + MOW and MOW treatments, respectively, compared with the CONTROL treatment. Other shrub cover did not differ among treatments (data not presented; $p = 0.25$).

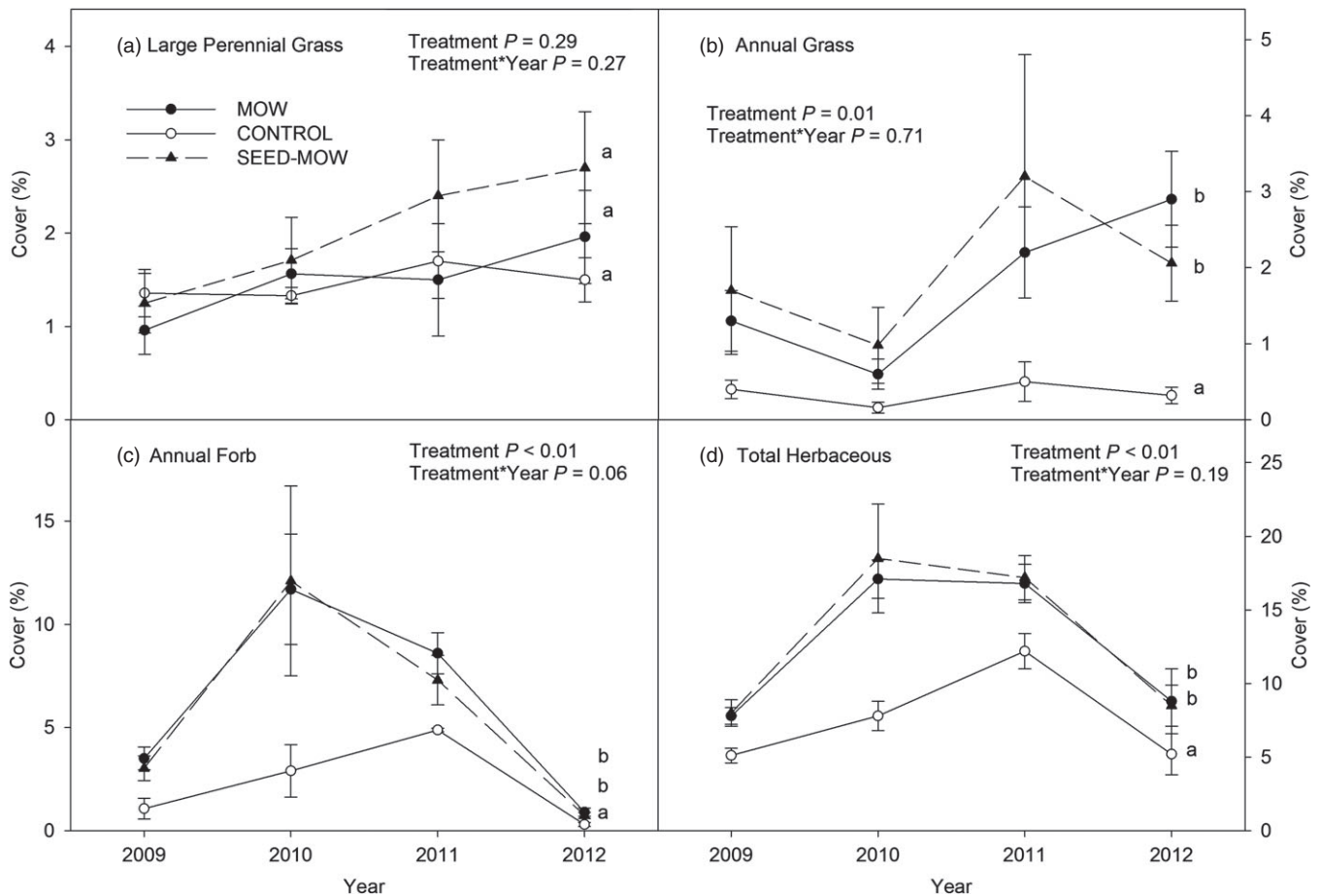


Figure 1. Plant functional group cover (mean \pm SE) in Wyoming big sagebrush plant communities that were mowed (MOW), mowed and seeded with native bunchgrasses (SEED + MOW), and an untreated control (CONTROL). Treatments were applied in the fall of 2008 and vegetation response was measured in June of the following 4 years. Different lower case letters indicate significant differences among treatments.

Density

Large perennial grass density varied by treatment (Fig. 3a; $p \leq 0.01$). When averaged across all years, large perennial bunchgrass density was 2.1- and 1.8-fold greater in the SEED + MOW treatment compared with the MOW and CONTROL treatments, respectively. Perennial bunchgrass density did not differ between the MOW and CONTROL treatments (Fig. 3a; $p = 0.51$). Sandberg bluegrass and perennial forb density did not differ among treatments (data not presented; $p = 0.65$ and 0.16 , respectively). Annual grass density was greater in the SEED + MOW and MOW treatments compared with the CONTROL treatment (Fig. 3b; $p = 0.01$). In 2012, annual grass density was 7- and 5-fold greater in the MOW and SEED + MOW treatments than the CONTROL, respectively. Annual forb density varied by the interaction between treatment and year (Fig. 3c; $p = 0.02$). Annual forb density did not differ among treatments in 2009 and 2012 ($p = 0.20$ and 0.21 , respectively), but in 2010 and 2011 annual forb density was greater in the SEED + MOW and MOW treatments compared with the CONTROL treatment ($p < 0.01$). Sagebrush density was approximately 1.5-fold greater in the CONTROL

treatment compared with the SEED + MOW and MOW treatments (Fig. 3d; $p < 0.01$). Other shrub density did not differ among treatments (data not presented; $p = 0.29$).

Discussion

Our hypothesis that mowing sagebrush followed by seeding native perennial bunchgrasses would increase bunchgrasses was partially supported by the density data. However, cover of large perennial bunchgrasses in mowed and seeded plots was still low and not statistically different from unseeded areas. Thus, it is doubtful that resilience and resistance has increased in the 4 years post-treatment. Less than 3% large perennial bunchgrass cover is considerably less than found in relatively intact Wyoming big sagebrush/bluebunch wheatgrass–Thurber's needlegrass and Wyoming big sagebrush/bluebunch wheatgrass plant communities where perennial bunchgrass cover averages 9–12% (Davies et al. 2006). More than doubling the perennial grass density with mowing and seeding is a positive indicator and further suggests the value in longer term evaluation of the treatment. Most of the perennial bunchgrasses were relatively

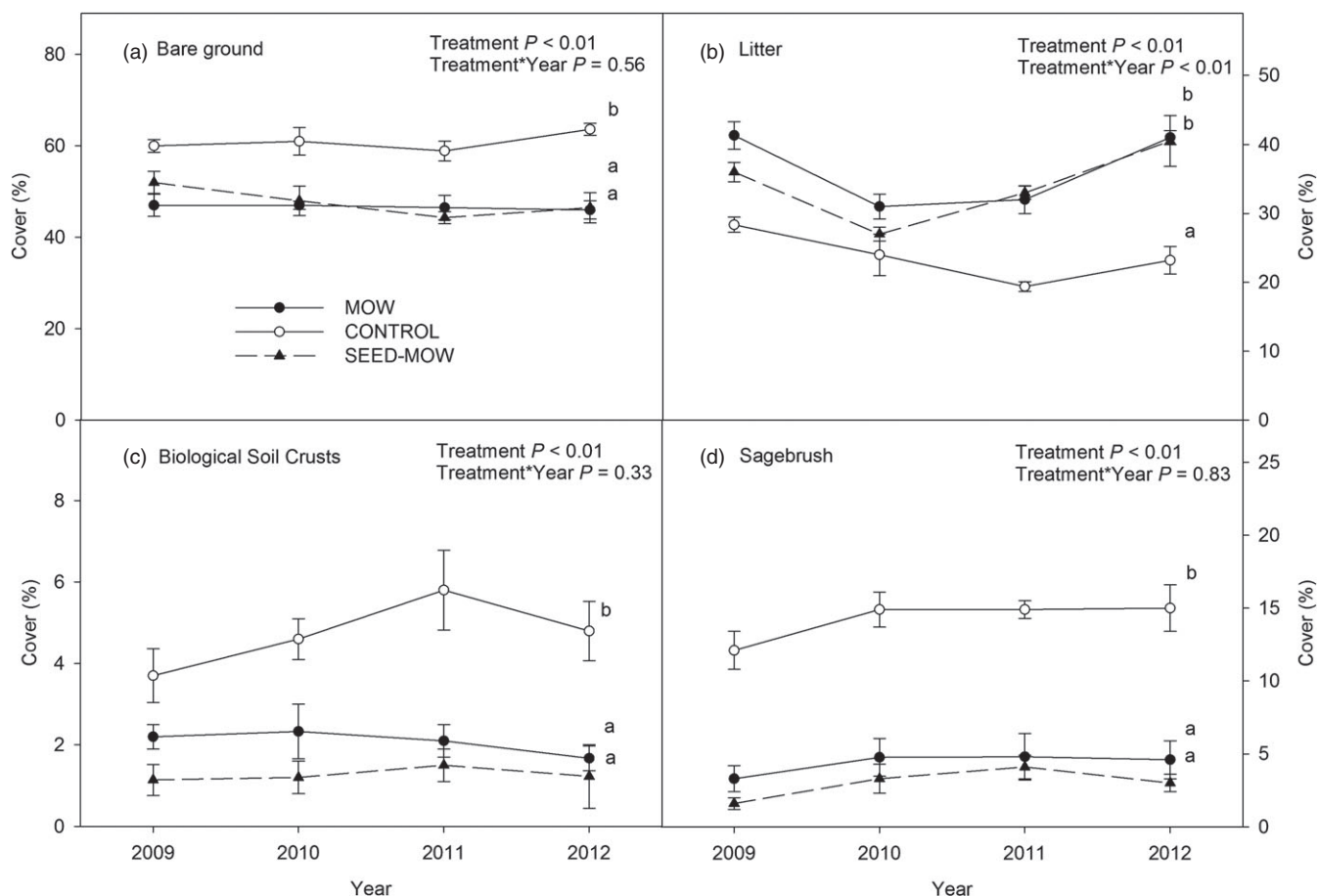


Figure 2. Cover (mean \pm SE) in Wyoming big sagebrush plant communities that were mowed (MOW), mowed and seeded with native bunchgrasses (SEED + MOW), and an untreated control (CONTROL). Treatments were applied in the fall of 2008 and responses were measured in June of the following 4 years. Different lower case letters indicate significant differences among treatments.

small and may eventually grow and become a more important component of the herbaceous understory. Native perennial bunchgrass in arid and semiarid communities can be relatively slow growing (Holmes & Rice 1996; James et al. 2009).

Our data supported our hypothesis that mowing without seeding would increase exotic annuals, but not native perennial bunchgrasses. This suggests that native bunchgrass seed bank is probably limited in these communities; however, there may have been some native bunchgrass in the seed bank that failed to establish because of adverse conditions. Young and Evans (1975) found no perennial grass seed in the seed bank in a degraded big sagebrush community. Thus, simply removing the overstory vegetation is not going to result in recovery of the understory. Similarly, Beck et al. (2012) suggested that applying treatments to reduce Wyoming big sagebrush to restore native herbaceous understory was often unsuccessful.

Our third hypothesis that exotic annuals would initially increase in mowed and seeded plots and then decrease as native perennial grasses increased was not supported by our results as cover and density of exotic annuals were similar for both of the mowed treatments. Both annual forbs, largely composed of exotics, and exotic annual grasses increased with mowing

whether or not native perennial bunchgrasses were seeded after mowing. Annual forb cover and density peaked in 2011 and then declined in 2012. This was probably a precipitation effect as 2011 and 2012 received 118 and 62% of average crop-year precipitation, respectively. Annual forbs in the sagebrush steppe are very responsive to variation in climate, especially precipitation (Bates et al. 2006). Of concern is that exotic annual grasses did not follow a similar trajectory. Exotic annual grasses cover and density were relatively similar in 2011 and 2012, suggesting that exotic annual grasses may be well situated to take advantage of more favorable precipitation years in the future. Exotic annual grasses usually fluctuate with precipitation (Hull 1949; Stewart & Hull 1949); thus, their limited response suggests that they may have been initially seed limited in 2011 and that they may continue to increase. Alternatively, if native perennial bunchgrasses that established in the mowed and seeded plots increase in size, they might limit exotic annuals in the future. Our data, however, do not provide evidence that perennial bunchgrasses will recover enough to suppress exotic annuals.

The increase in resources and litter with mowing probably favored exotic annuals. Mowing sagebrush increases soil nutrient concentrations (Davies et al. 2011b), which often favors

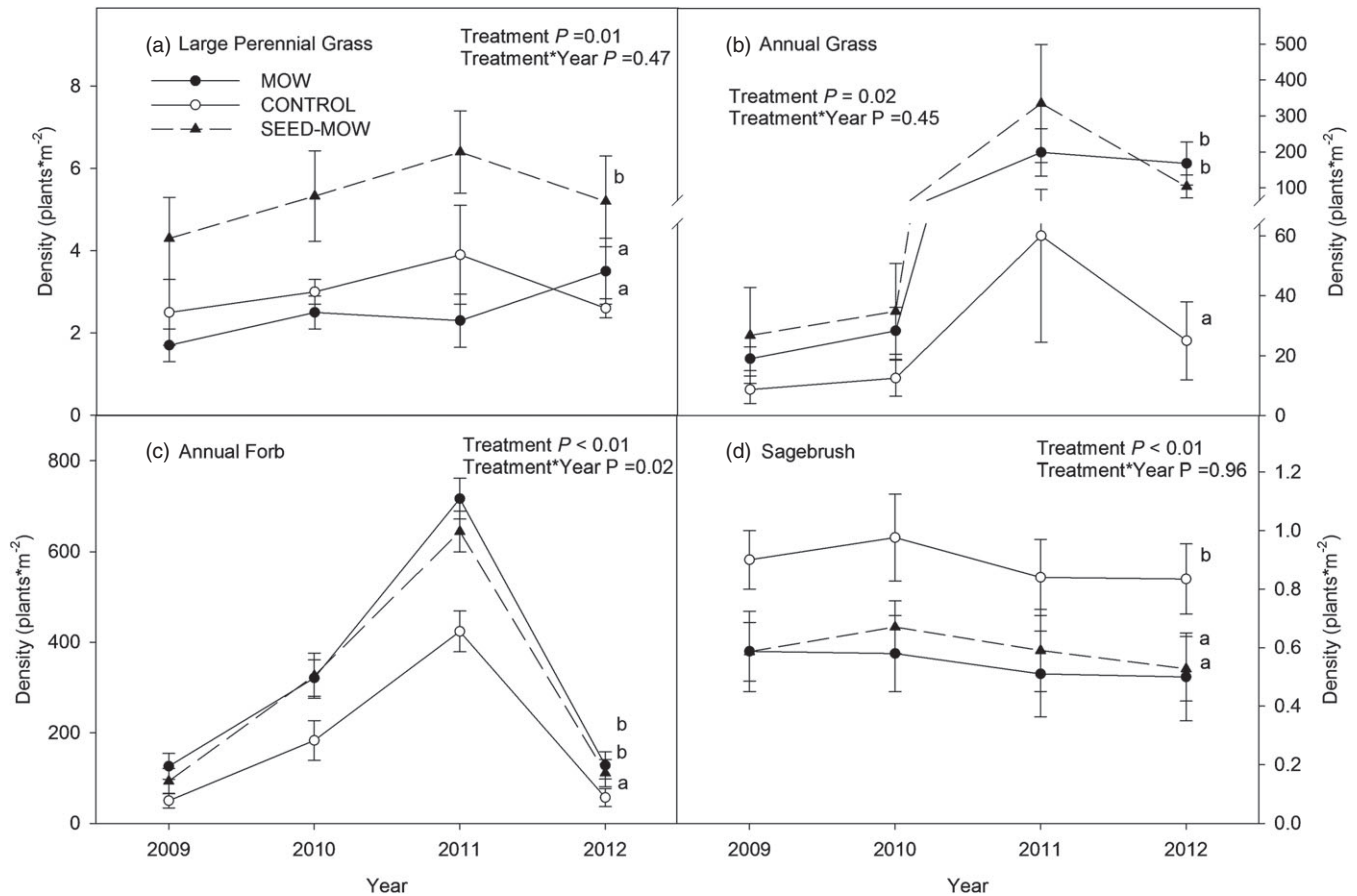


Figure 3. Plant functional group and sagebrush density (mean \pm SE) in Wyoming big sagebrush plant communities that were mowed (MOW), mowed and seeded with native bunchgrasses (SEED + MOW), and an untreated control (CONTROL). Treatments were applied in the fall of 2008 and vegetation response was measured in June of the following 4 years. Different lower case letters indicate significant differences among treatments.

exotic annuals. Exotic annual grasses are better able to take advantage of elevated soil resources than native plants (Young & Allen 1997; Vasquez et al. 2008). The success of exotic plant invasion generally increases with greater water and soil nutrient availability (Huenneke et al. 1990; Burke & Grime 1996; Davis et al. 2000). Similarly, greater litter with mowing probably favored exotic annuals, at least exotic annual grasses. Litter creates a favorable seedbed by mediating temperature and maintaining soil surface moisture longer for the establishment of exotic annual grasses (Evans & Young 1970, 1972). The presence of litter may have been especially important to exotic annual grasses in the last year of the study when it was unusually dry. Whisenant (1990) found that the importance of litter to Japanese brome (*Bromus japonicus* Thunb.), an exotic annual grass, increased as precipitation decreased, though Japanese brome density was greater when litter covered the soil surface regardless of precipitation.

The increase in exotic annuals probably suppressed the establishment and growth of seeded native bunchgrasses. Exotic annuals are competitive with plants native to Wyoming big sagebrush communities and may severely reduce their recruitment (Melgoza et al. 1990; Young & Mangold 2008). Exotic

annual grasses competitive advantage is greatest when native plants are in the seedling stage (Clausnitzer et al. 1999; Young & Mangold 2008); subsequently, successfully establishing native bunchgrasses from seed when exotic annual competition is high is unlikely. Controlling exotic annuals may improve the success of seeding native vegetation after mowing Wyoming big sagebrush; however, an additional treatment will further increase the cost. Davies (2010) found that successfully controlling an exotic annual grass with a pre-emergent herbicide prior to seeding perennial bunchgrasses resulted in a 10-fold increase in perennial grass cover compared to no control treatment prior to seeding.

Similar to other studies (e.g. Davies et al. 2011b, 2012a) we found that biological soil crusts were reduced with mowing treatments in sagebrush plant communities. Declines in biological soil crusts with mowing are probably due to soil surface disturbance (Davies et al. 2011b). Though not statistically significant, it appears that drill seeding after mowing may further decrease biological soil crusts probably because it is an additional soil surface disturbance. Others have linked soil surface disturbances in sagebrush communities to reductions in biological soil crusts (e.g. Ponzetti &

McCune 2001; Ponzetti et al. 2007; Root & McCune 2012; Dettweiler-Robinson et al. 2013b). The increase in exotic annuals in our study may have also negatively influenced biological soil crusts as increases in exotic annual grasses are correlated with declines in biological soil crusts (Dettweiler-Robinson et al. 2013a). Declines in biological soil crusts are concerning because they capture resources, prevent soil erosion, and reduce invasibility in arid and semi-arid plant communities (Belnap et al. 2001; Harper & Belnap 2001; Belnap 2006) and are slow to recover after disturbance (Hilty et al. 2004). However, the magnitude of their importance in sagebrush steppe communities is relatively unknown.

The general negative response of plant communities to mowing in our study implies that advances in technologies to reduce the disturbance needed to seed native bunchgrasses may be especially valuable. This research suggests that when restoration efforts entail substantial disturbances (i.e. mowing and drill seeding) there is significant risk of causing as much or more damage than good to the ecosystem. The decline in biological soil crust and increase in exotic annuals with mowing followed by drill seeding suggest that native plant communities' resilience to fire and resistance to invasion have been decreased. This suggests that these plant communities may now be on a trajectory toward an exotic annual-dominated state. Thus, caution is advised when restoration efforts in any ecosystem disturb vegetation and soil. This research also suggests that in areas where recruitment of native vegetation may be episodic (Crawley 1990) a one-time introduction of native seeds may not be enough to restore native vegetation. Therefore, restoration efforts should be carefully monitored to determine if additional treatments (reseeding, control of exotics, etc.) are needed to achieve desired outcomes. Subsequently, restoration projects, especially those with a high probability of failure, should probably include funds for additional treatments if initial efforts fail or, alternatively, not be implemented until technology improves the likelihood of success.

Wyoming big sagebrush plant communities with degraded understories are a management conundrum. Without understory restoration (i.e. increasing large perennial bunchgrasses) they will probably burn in a wildfire and convert to exotic annual-dominated communities. However, restoration efforts are largely unsuccessful, costly, and, in general, increase exotic annuals. Seeding native perennial bunchgrasses after mowing increased perennial bunchgrass density, but cover was still low 4 years post-seeding and exotic annuals increased substantially. At this time, we do not consider this a successful restoration effort and it may have even decreased the resilience and resistance of these plant communities. Longer term evaluation is needed to determine if mowing and seeding will increase perennial bunchgrass cover and density enough to suppress exotic annuals and improve the resilience and resistance of these communities. Further advancements in science are needed to improve the success of restoring native herbaceous vegetation in degraded Wyoming big sagebrush plant communities before managers should attempt to restore these communities.

Implications for Practice

- Caution should be exercised when restoration efforts will entail substantial disturbance to vegetation and soils.
- Reducing Wyoming big sagebrush dominance in plant communities with depleted understories may do more harm than good if understories do not rapidly recover.
- We do not recommend mowing and seeding native perennial bunchgrasses in Wyoming big sagebrush communities with depleted understories as results were generally not favorable.
- If mowing sagebrush followed by seeding native bunchgrasses is attempted, we recommend that additional funds need to be available to control exotic annuals and potentially reseed bunchgrass if initial treatments are unsuccessful.
- Land managers should focus on limiting disturbances that greatly reduce sagebrush in Wyoming big sagebrush communities with depleted understories because of the risk of increasing exotic annuals.
- We recommend that preventing largely intact understories from shifting to depleted understories should be a high priority, because of the difficulty of restoring Wyoming big sagebrush plant communities.

Acknowledgments

We are grateful to the Burns-District Bureau of Land Management for allowing this research project to be conducted on lands they administer and for logistical support.

LITERATURE CITED

- Anderson, J. E., and R. S. Inouye. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. *Ecological Monographs* **71**:531–556.
- Bates, J. D., T. Svejcar, R. F. Miller, and R. A. Angell. 2006. The effects of precipitation timing on sagebrush steppe vegetation. *Journal of Arid Environments* **64**:670–697.
- Beck, J. L., J. W. Connelly, and C. L. Wambolt. 2012. Consequences of treating Wyoming big sagebrush to enhance wildlife habitat. *Rangeland Ecology and Management* **65**:444–455.
- Belnap, J. 2006. The potential roles of biological soil crusts in dryland hydrologic cycles. *Hydrological Processes* **20**:3159–3178.
- Belnap, J., R. Prasse, and K. T. Harper. 2001. Influence of biological soil crusts on soil environments and vascular plants. *Ecological Studies* **150**:281–300.
- Boyd, C. S., and T. J. Svejcar. 2011. The influence of plant removal on succession in Wyoming big sagebrush. *Journal of Arid Environments* **75**:734–741.
- Brooks, M. L., and J. C. Chambers. 2011. Resistance to invasion and resilience to fire in desert shrublands of North America. *Rangeland Ecology and Management* **64**:431–438.
- Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. *Ecology* **77**:776–790.
- Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. *Journal of Forestry* **39**:388–394.
- Chambers, J. C. 2000. Seed movement and seedling fate in disturbed sagebrush steppe ecosystems: implications for restoration. *Ecological Applications* **10**:1400–1413.
- Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invisable by *Bromus tectorum*? *Ecological Monographs* **77**:117–145.

- Clausnitzer, D. W., M. M. Borman, and D. E. Johnson. 1999. Competition between *Elymus elymoides* and *Taeniatherum caput-medusae*. *Weed Science* **47**:720–728.
- Crawley, M. J. 1990. The population biology of plants. *Philosophical Transactions of the Royal Society of London Biological Sciences* **330**:125–140.
- Davies, K. W. 2008. Medusahead dispersal and establishment in sagebrush steppe plant communities. *Rangeland Ecology and Management* **61**:110–115.
- Davies, K. W. 2010. Revegetation of medusahead-invaded sagebrush steppe. *Rangeland Ecology and Management* **63**:564–571.
- Davies, K. W., and J. D. Bates. 2010. Vegetation characteristics of mountain and Wyoming big sagebrush plant communities in the northern Great Basin. *Rangeland Ecology and Management* **63**:461–466.
- Davies, K. W., J. D. Bates, and R. F. Miller. 2006. Vegetation characteristics across part of the Wyoming big sagebrush alliance. *Rangeland Ecology and Management* **59**:567–575.
- Davies, K. W., J. D. Bates, and R. F. Miller. 2007. Short-term effects of burning Wyoming big sagebrush steppe in southeastern Oregon. *Rangeland Ecology and Management* **60**:515–522.
- Davies, K. W., J. D. Bates, and A. M. Nafus. 2011a. Are there benefits to mowing intact Wyoming big sagebrush communities? An evaluation in southeastern Oregon. *Environmental Management* **48**:539–546.
- Davies, K. W., J. D. Bates, and A. M. Nafus. 2012a. Vegetation response to mowing dense mountain big sagebrush stands. *Rangeland Ecology and Management* **65**:268–276.
- Davies, K. W., J. D. Bates, and A. M. Nafus. 2012b. Mowing Wyoming big sagebrush communities with degraded herbaceous understories: has a threshold been crossed? *Rangeland Ecology and Management* **65**:498–505.
- Davies, K. W., C. S. Boyd, J. L. Beck, J. D. Bates, T. J. Svejcar, and M. A. Gregg. 2011b. Saving the sagebrush sea: an ecosystem conservation plan for big sagebrush plant communities. *Biological Conservation* **144**:2573–2584.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* **88**:528–534.
- Dettweiler-Robinson, E., J. D. Bakker, and J. B. Grace. 2013a. Controls of biological soil crust cover and composition shift with succession in sagebrush shrub-steppe. *Journal of Arid Environments* **94**:96–104.
- Dettweiler-Robinson, E., J. M. Ponzetti, and J. D. Bakker. 2013b. Long-term changes in biological soil crust cover and composition. *Ecological Processes* **2**:5–14.
- Eastern Oregon Agricultural Research Center (EOARC). 2012. Climatic dataset. Eastern Oregon Agricultural Research Center, Burns, Oregon.
- Evans, E. A., and J. A. Young. 1970. Plant litter and establishment of alien annual weed species in rangeland communities. *Weed Science* **18**:697–703.
- Evans, E. A., and J. A. Young. 1972. Microsite requirements for establishment of annual rangeland weeds. *Weed Science* **20**:350–356.
- Harper, K. T., and J. Belnap. 2001. The influence of biological soil crusts on mineral uptake by associated vascular plants. *Journal of Arid Environments* **47**:347–357.
- Hilty, J. H., D. J. Eldridge, R. Rosentreter, M. C. Wicklow-Howard, and M. Pellant. 2004. Recovery of biological soil crusts following wildfire in Idaho. *Journal of Range Management* **57**:89–96.
- Holmes, T. H., and K. J. Rice. 1996. Patterns of growth and soil-water utilization in some exotic annuals and native perennial bunchgrasses of California. *Annals of Botany* **78**:233–243.
- Huenneke, L. F., S. P. Hamburg, R. Koide, H. A. Mooney, and P. M. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* **71**:478–491.
- Hull, A. C. Jr. 1949. Growth periods and herbage production of cheatgrass and reseeded grasses in southwestern Idaho. *Journal of Range Management* **2**:183–186.
- James, J. J., K. W. Davies, R. L. Sheley, and Z. T. Aanderud. 2008. Linking nitrogen partitioning and species abundance to invasion resistance in the Great Basin. *Oecologia* **156**:637–648.
- James, J. J., J. M. Mangold, R. L. Sheley, and T. Svejcar. 2009. Root plasticity of native and invasive Great Basin species in response to soil nitrogen heterogeneity. *Plant Ecology* **202**:211–220.
- Littell, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS system for mixed models. SAS Institute Inc., Cary, North Carolina, 633 p.
- Melgoza, G., R. S. Nowak, and R. J. Tausch. 1990. Soil water exploitation after fire: competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* **83**:7–13.
- NRCS. 2013. Soil survey (available from <http://websoilsurvey.nrcs.usda.gov>) [accessed on 12 December 2013].
- Oregon Climatic Service. 2009 (available from <http://www.ocs.oregonstate.edu/index.html>) [accessed on 1 September 2009].
- Ponzetti, J. M., and B. McCune. 2001. Biotic soil crusts of Oregon's shrub steppe: community composition in relation to soil chemistry, climate, and livestock activity. *Bryologist* **104**:212–225.
- Ponzetti, J. M., B. McCune, and D. Pyke. 2007. Biotic soil crusts in relation to topography, cheatgrass and fire in the Columbia Basin, Washington. *Bryologist* **110**:706–722.
- Reisner, M. D., J. B. Grace, D. A. Pyke, and P. S. Doescher. 2013. Conditions favouring *Bromus tectorum* dominance of endangered sagebrush steppe ecosystems. *Journal of Applied Ecology* **50**:1039–1049.
- Root, H. T., and B. McCune. 2012. Regional patterns of biological soil crust lichen species composition related to vegetation, soils, and climate in Oregon, USA. *Journal of Arid Environments* **79**:93–100.
- Sneva, L. A., L. R. Rittenhouse, and P. T. Tueller. 1980. Forty years-inside and out. Pages 10–12 in Oregon Agricultural Experiment Station Special Report 586. Oregon State University, Corvallis.
- Stewart, G., and A. C. Hull. 1949. Cheatgrass (*Bromus tectorum* L.)—an ecological intruder in southern Idaho. *Ecology* **30**:58–74.
- Suring, L. H., M. M. Rowland, and M. J. Wisdom. 2005. Identifying species of conservation concern. Pages 150–162 in M. J. Wisdom, M. M. Rowland, and L. H. Suring, editors. *Habitat threats in the sagebrush ecosystem – methods of regional assessment and applications in the Great Basin*. Alliance Communications Group, Lawrence, Kansas.
- Vasquez, E., R. Sheley, and T. Svejcar. 2008. Nitrogen enhances the competitive ability of cheatgrass (*Bromus tectorum*) relative to native grasses. *Invasive Plant Science and Management* **1**:287–295.
- West, N. E. 2000. Synecology and disturbance regimes of sagebrush steppe ecosystems. Pages 15–26 in P. G. Entwistle, A. M. DeBolt, J. H. Kaltenecher, and K. Steenhof, editors. *Proceedings: sagebrush steppe ecosystem symposium*. USDI-Bureau of Land Management, Boise, Idaho.
- West, N. E., F. D. Provenza, P. S. Johnson, and M. K. Owens. 1984. Vegetation change after 13 years of livestock grazing exclusion on sagebrush semidesert in west central Utah. *Journal of Range Management* **37**:262–264.
- Whisenant, S. G. 1990. Postfire population dynamics of *Bromus japonicus*. *American Midland Naturalist* **123**:301–308.
- Wisdom, M. J., M. M. Rowland, L. H. Suring, L. Schueck, C. W. Meinke, and S. T. Knick. 2005. Evaluating species of conservation concern at regional scales. Pages 5–24 in M. J. Wisdom, M. M. Rowland, and L. H. Suring, editors. *Habitat threats in the sagebrush ecosystem – methods of regional assessment and applications in the Great Basin*. Alliance Communications Group, Lawrence, Kansas.
- Young, J. A., and F. L. Allen. 1997. Cheatgrass and range science: 1930–1950. *Journal of Range Management* **50**:530–535.
- Young, J. A., and R. A. Evans. 1975. Germinability of seed reserves in a big sagebrush community. *Weed Science* **23**:358–364.
- Young, K., and J. Mangold. 2008. Medusahead outperforms squirreltail through interference and growth rate. *Invasive Plant Science and Management* **1**:73–81.

Supporting Information

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

Table S1. Degrees of freedom for fixed effects in repeated measures ANOVAs in Proc Mixed in SAS version 9.2 (SAS Institute, Inc., Cary, NC, U.S.A.) using compound symmetry as the covariance structure.