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When landscapes are heavily impacted by biological invasion, local populations of native plant species may no longer be adapted to altered environmental conditions. In these cases, it is useful to investigate alternative sources of germplasm, such as cultivars, for planting at restoration sites. This study compared cultivated and wild (local) varieties of the native perennial bunchgrass, *Poa secunda* J. Presl, grown with and without exotic, invasive *Bromus tectorum* L. in both a greenhouse and field setting. While cultivars emerged and grew more rapidly than wild seed sources, this advantage declined in the presence of *B. tectorum*. Given the novel genetic background of cultivars and their potential to alter patterns of dominance in native plant communities, we recommend the use of local or regional wild seed sources when possible to conserve regional patterns of genetic diversity and adaptation.

AN INVESTIGATION OF THE IMPACTS OF SEED ORIGIN ON GRASSLAND RESTORATION SUCCESS

By

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TABLE OF CONTENTS

LIST OF TABLES/FIGURES

CHAPTER ONE: INTRODUCTION

Indigenous plant communities consist of taxonomically and genetically diverse species, each having an important role in community structure and processes (SER 2004; Polley et al. 2005). Recently, anthropogenic activities have accelerated biodiversity loss by degrading and homogenizing the planet's biota (Olden 2004; Rooney et al. 2004). When land is disturbed, humans can accelerate the rate of recovery by implementing ecological restoration practices. An important goal and measure of success for every restoration plan is recovery of biodiversity at both taxonomic and genetic levels (SER 2004; Reynolds et al. 2012). For a restored plant community to sustain itself, resident populations must be well adapted and resilient to local environmental conditions and stressors. To ensure a site's vegetative adaptation and resilience, it is important for practitioners to consider the origin of seed selected for revegetation (Jones 2013).

Ecological restoration commonly requires reintroduction of plants to degraded sites, and long-term vegetation establishment is a critical component of restoration success. Guidelines for seed sourcing recommend using of local germplasm to increase the likelihood that seeds are adapted to site conditions, maintain site biodiversity, and improve long-term sustainability of restored plant populations (McKay et al. 2005; Bischoff et al. 2008). However, native seeds are scarce and practitioners often purchase cultivated varieties of seeds to meet native vegetation goals and to reduce costs. Through selection and production, cultivated varieties, or cultivars, of native species are genetically modified for selective traits to improve germination, establishment, vigor, and competition (Lesica & Allendorf 1999; Burton & Burton 2002). Use of cultivated varieties of native plant species for conservation and restoration purposes illustrates fundamental differences in views of plant and animal biodiversity. Introductions of native plant species are often based on a foundation of cultivation and agricultural increase, while animal introductions focus on genetic rescue with corresponding guidelines for the maintenance of subspecies, varieties and genetic integrity (IUCN 1998).

Cultivars of native plants are desirable because they are readily available and cost efficient compared to wild seed collections. Cultivated seed sources, however, generally represent novel genotypes derived from a limited number of sources across a species' growing range. Non-local genotypes may not be suited to site conditions due to adaptive divergence among populations within a plant species (Hufford & Mazer 2003; Fig. 1). There is considerable evidence for adaptation to local environments among plant populations (Turesson 1922; Turesson 1925; Clausen et al. 1941; Antonovics & Bradshaw 1970), and these data support using of local genotypes in restoration (Linhart & Grant 1996). Non-local seed sources can potentially swamp local genotypes and threaten biodiversity, or fail to establish by succumbing to novel environmental stressors. As a result, the geographic origin and genetic composition of seed stock can have significant consequences for restoration outcomes, and poor establishment of introduced plants represents high costs for both ecosystem function and economic investment.

While using local plant genotypes conserves biodiversity and adaptation to historical site conditions, widespread biological invasion represents a significant complicating factor for ecological restoration. Recommendations to use locally adapted seed sources are based on the assumption that environmental conditions to which plants are adapted remain relatively unchanged. However, some environments are so radically altered by exotic, invasive weeds that original environmental conditions may no longer exist (D'Antonio & Vitousek 1992). *Bromus tectorum* L. (cheatgrass or downy brome) is an example of an aggressive exotic invasive species threatening biodiversity in the Intermountain West by homogenizing plant communities and indirectly altering natural plant succession through increased fire frequency (Davies et al. 2011).

Despite eradication efforts, invasive species persist and interactions among them are unpredictable. Under these circumstances, vigorous non-local cultivars of native species may have an advantage at highly disturbed sites, and the assumption that local genotypes are better adapted to site conditions than cultivars may no longer hold (Lesica & Allendorf 1999; O'Brien & Krauss 2010; Wilkinson 2010). Both the advantages and drawbacks of using native cultivars and local genotypes for restoration require further investigation in the field.

To compare and contrast performance of local populations and cultivars, we investigated the outcome of multiple *Poa secunda* J. Presl (Sandberg bluegrass) introductions at MPG Ranch, a historically grazed site in western Montana undergoing active restoration. *Poa secunda* is an important component of sagebrush-grassland vegetation in the western United States (Peterson 2002). It is one of the first plants to start growing in early spring and its seeds mature in early summer. Because of its early seedling vigor, *P. secunda* acts as a primary source of forage for both wildlife and livestock at the beginning of the growing season. Due to its early growth period and extensive root system, *P. secunda* may be able to establish and compete for resources at sites invaded by exotic species (Perry et al. 2009).

Poa secunda is commonly targeted for restoration because of its vast distribution (Majerus et al. 2009). In North America, it occurs from southeastern Alaska across southern Canada as far as Quebec, and then south through the Intermountain West and Great Plains states to northwest Mexico (Stubbendieck et al. 2011; Fig. 2). Widely disjunct populations have been found in Chile and Argentina, but occur less frequently there. Because of its broad distribution and high demand by restoration practitioners, several seed accessions of *P. secunda* are available for purchase from private and public native plant producers. The United States Department of Agriculture (USDA) Natural Resource Conservation Service (NRCS) Plant Materials Program lists five available conservation plant releases: "Canbar", "High Plains Germplasm", "Opportunity Germplasm", "Sherman", and "Service" (Majerus et al. 2009). "Canbar" originates from southeast Washington and is used in stabilizing soils subject to wind erosion and restoration of natural areas. "High Plains Germplasm" originates from the high plains region of Wyoming and is a composite of three accessions collected from northeast, central, and southwest regions of the state. Its intended use is for native seed mixes, wildlife habitat plantings, and native plant community restoration. "Opportunity Germplasm" originates from southwest Montana and is intended for use in heavy metal contaminated mineland reclamation, post-fire reclamation, native range restoration, wildlife habitat and logging road revegetation. "Sherman" originates from north-central Oregon and is intended for use in stabilization of dry land soils, dry land pasture, and restoration of natural areas. "Service" originates from Whitehorse, Yukon Territory, Canada. It is intended for use in reclamation, native habitat restoration and erosion control throughout most of Alaska

The USDA Agriculture Research Service (ARS) released the accession, "Reliable", which is a multi-origin germplasm stemming from 28 collections representing seven USDA-NRCS ecological sites. This accession was developed for its high genetic diversity and suitability for planting over a broad ecological range. L&H Seeds in Connell, Washington supply "Hanford Source", originating from Hanford, Washington. It is adapted to drought and/or locations with well drained sandy soils. Benson Farms Inc. in Moses Lake, Washington carries "Duffy Creek" and "Wallowa" releases. Both are intended for use in arid sites throughout the western states. "UP Colorado Plateau" was collected on the Uncompahgre Plateau in western

Colorado by the Uncompahgre Partnership's Colorado Plateau Native Plant Initiative (Uncompahgre Partnership Project 2009). It is intended for use as a site-adapted native plant material for the Colorado Plateau region and interestingly, it was rated superior to 12 other accessions, including two known commercially available cultivars, "Canbar" and "High Plains", over a three year study. Lastly, Seeds of Success lists multiple wild, non-cultivated accessions collected from California, Oregon, Idaho, Wyoming, Colorado, Utah, and Nevada (SOS 2012).

This study focused on comparisons of six accessions: three cultivars and three local populations collected from MPG Ranch. Cultivars "High Plains", "Mountain Home", and "Reliable" were included in all aspects of the project based on their recommended use at the study site. Collections of wild *P. secunda* have been made from 16 different source populations at MPG Ranch. From those populations, three populations were selected for the study based on sufficient seed quantity.

To investigate impacts of seed source on grassland restoration success, this thesis addressed the following research questions: 1) does plant performance differ between and among local and cultivated varieties? and 2) are cultivars better competitors in the presence of exotic invasive species than wild accessions? We tested multiple wild and cultivated accessions of the native cool-season *P. secunda* both with and without completion from the exotic invasive *B. tectorum* in both a greenhouse and field setting.

Results of this project contribute to development of new and improved ways to restore disturbed lands, and conserve plant community diversity. Consequences of multiple cultivar revegetation projects on the genetic diversity of a species are unknown. This study determines the degree of genetic and adaptive divergence among cultivated and local seed sources, and contributes to our understanding of how seed provenance affects competitive interactions of native flora with a widespread invasive species. Use of local genotypes is important for preserving species biodiversity at the genetic level, and may be important for restoration success if they are better adapted to site conditions and more likely to establish than cultivars. However, the growing impact of invasive species and high levels of site degradation may require innovative methods for reintroduction of native species, such as planting potentially vigorous cultivars. It is critical that we examine the different impacts of cultivated seed sources versus local genotypes to determine best practice for their use.

References

Antonovics J. and A. D. Bradshaw. 1970. Evolution in closely adjacent plant populations. VIII. Clinal patterns at a mine boundary. Heredity **25**:349–362.

BFI Native Seeds, Grasses. URL: http://www.bfinativeseeds.com/grasses.aspx [accessed on 1 April 2012]

Bischoff, A., Steinger, T. and H. Müller-Schärer. 2008. The importance of plant provenance and genotypic diversity of seed material used for ecological restoration. Restoration Ecology **18:**338–348.

Burton, P. J. and C. M. Burton. 2002. Promoting Genetic Diversity in the Production of Large Quantities of Native Plant Seed. Restoration Ecology **20**:117–123.

Clausen J., Keck, W. M. and H. W. Hiesey. 1941. Regional differentiation in plant species. American Naturalist **75**:231–250.

Davies, K. W., Boyd, C. S., Beck, J. L., Bates, J. D., Svejcar, T. J. and M. A. Gregg. 2011. Saving the sagebrush sea: An ecosystem conservation plan for big sagebrush plant communities. Biological Conservation **144**:2573–2584.

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.

Hufford, K. M. and S. J. Mazer. 2003. Plant ecotypes: genetic differentiation in the age of ecological restoration. Trends in Ecology and Evolution **18**:147–155.

International Union for Conservation of Nature (IUCN). 1998. IUCN guidelines for re-introductions. Prepared by the IUCN/SSC Re-introduction Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK. URL www.iucn.org/themes/ssc/pubs/policy [accessed on 10 April 2012]

Jones, T. A. 2013. Ecologically appropriate plant materials for restoration applications. BioScience **63**:211–219.

Lesica, P. and F. W. Allendorf. 1999. Ecological genetics and the restoration of plant communities: mix or match? Restoration Ecology **7**:42–50.

Linhart, Y. B. and M. C. Grant. 1996. Evolutionary significance of local genetic differentiation in plants. Annual Review of Ecology and Systematics **27**:237–277.

Majerus, M., Holzworth, L., Tilley, D., Ogle, D. and M. Stannard. 2009. Plant guide for Sandberg bluegrass (*Poa secunda* J. Presl). US Natural Resources Conservation Service, Idaho Plant Materials Center, Aberdeen, Idaho.

McKay, J. K., Christian, C. E., Harrison, S. P. and K. J. Rice. 2005. "How local is local?"—a review of practical and conceptual issues in the genetics of restoration. Restoration Ecology **13**:432–440.

O'Brien, E. K. and S. L. Krauss. 2010. Testing the home-site advantage in forest trees on disturbed and undisturbed sites. Restoration Ecology **18**:359–372.

Olden, J. D., LeRoy, N., Douglas, M. R., Douglas, M. E. and K. D. Fausch. 2004. Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology and Evolution **19**:18–24.

Perry, L.G., Cronin, S.A. and M. W. Paschke. 2009. Native cover crops suppress exotic annuals and release native perennials in a greenhouse competition experiment. Plant Ecology **204**:247–259.

Peterson, J. S. 2002. Plant fact sheet: Sandberg bluegrass (*Poa secunda* J. Presl). US Natural Resource Conservation Service, Plant Materials Program, Washington, DC.

Polley, H. W., Derner, J. D. and B. J. Wilsey. 2005. Patterns of plant species diversity in remnant and restored tallgrass prairies. Restoration Ecology **13**:480–487.

Reynolds, L. K., McGlathery, K. J. and M. Waycott. 2012. Genetic diversity enhances restoration success by augmenting ecosystem services. PLoS ONE **7**:e38397.

Rooney, T. P., Wiegmann, S. M., Rogers, D. A. and D. M. Waller. 2004. Biotic impoverishment and homogenization in unfragmented forest understory communities. Conservation Biology. **18**:787–798.

Rowe, C. L. and E. A. Leger. 2011. Competitive seedlings and inherited traits: a test of rapid evolution of *Elymus multisetus* (big squirreltail) in response to cheatgrass invasion. Evolutionary Applications. **4**:485–498.

Seeds of Success, Species. URL http://www.nps.gov/plants/sos/species/index.htm [accessed on 1 April 2012]

Society for Ecological Restoration International Science & Policy Working Group. 2004. The SER international primer on ecological restoration. Tucson: Society for Ecological Restoration International (available from www.ser.org).

Stubbendieck, J., Hatch, S. L. and N. M. Bryan. 2011. North American wildland plants: a field guide. 2nd edition. University of Nebraska Press.

Turesson, G. 1922. The genotypical response of plant species to the habitat. Hereditas **3**:211–350.

Turesson, G. 1925. The plant species in relation to habitat and climate. Contributions to the knowledge of genecological units. Hereditas **6**:147–236.

Uncompahgre Partnership Project. 2009. Sandberg bluegrass (*Poa secunda*). (available from http://www.upproject.org/up_project/assests_folder/POSE%20flyer.pdf).

Wilkinson, D. M. 2001. Is local provenance important in habitat creation? Journal of Applied Ecology. **38**:1371–1373.

Figures

Figure 1. Hypothetical ordination plot representing genetic or morphological divergence among local ecotypes and cultivars of the same species; both used for restoration in the same location. In nonmetric multidimensional scaling analysis, proximity of points implies similarity. Each point represents an individual plant, and colors represent different seed origins.

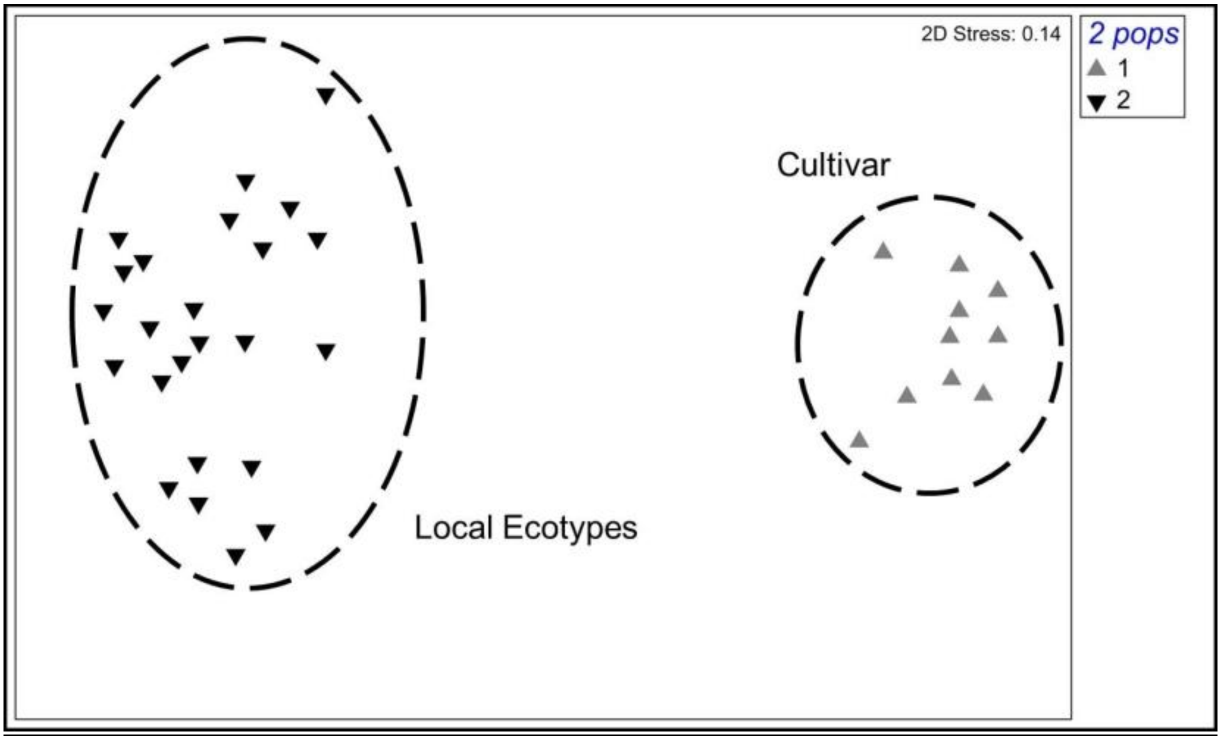
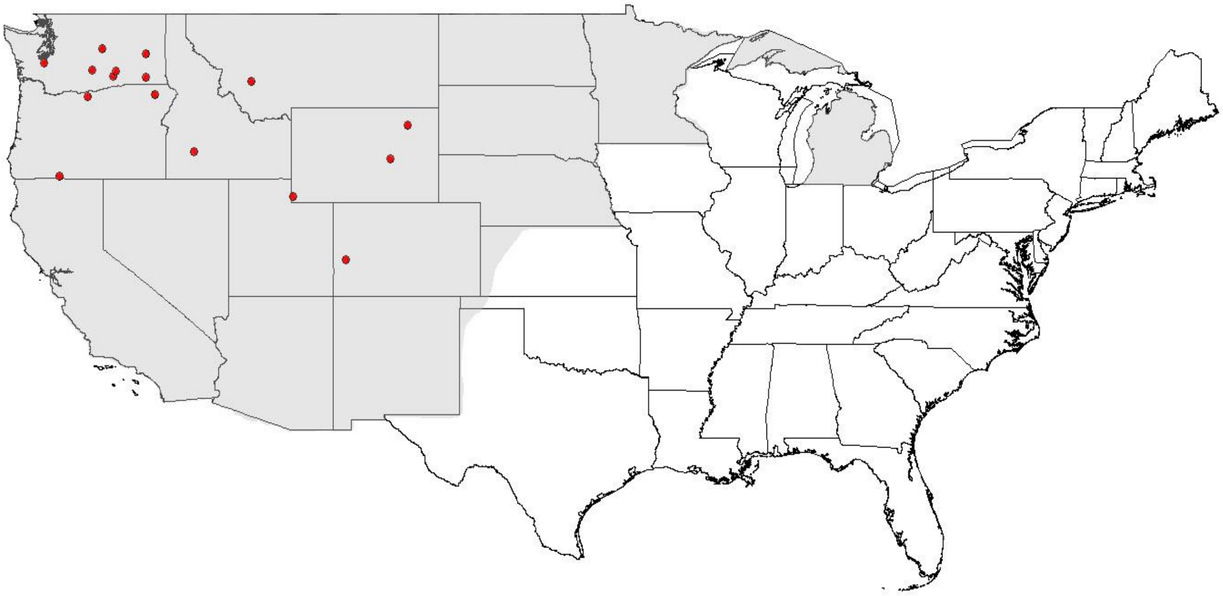


Figure 2. Grey shaded area indicates the recommended planting range of *P. secunda* cultivars in the United States. Dots on the map represent approximate origins of cultivars available for purchase at present, minus "Service" from Alaska (Majerus et al. 2009; BFI Native Seeds 2012; Uncompahgre Partnership Project 2009).



CHAPTER TWO: EFFECTS OF SEED SOURCE AND COMPETITION WITH *BROMUS TECTORUM* ON EARLY ESTABLISHMENT OF *POA SECUNDA*: CAN SEED SOURCE IMPACT RESTORATION SUCCESS?

Abstract

When landscapes are heavily impacted by biological invasion, local populations of native plant species may no longer be adapted to altered environmental conditions. In these cases, it is useful to investigate alternative sources of germplasm, such as cultivated varieties, for planting at restoration sites. This study compared cultivated and wild (local) varieties of the native perennial bunchgrass, *Poa secunda* J. Presl (Sandberg bluegrass), grown with and without *Bromus tectorum* L. While cultivated varieties emerged and grew more rapidly than wild seed sources, this advantage declined in the presence of *B. tectorum* and cultivated germplasm did not outperform wild accessions in the presence of an invasive species. Given the novel genetic background of cultivars and the potential for cultivated varieties to alter patterns of dominance in native plant communities, we recommend the use of local or regional wild seed sources when possible to conserve regional patterns of genetic diversity and adaptation. In cases where sites are heavily impacted by exotic, invasive species, use of multiple wild or cultivated seed sources may improve the potential for capturing vigorous genotypes that, in conjunction with other control measures, may improve establishment of native species in grassland restoration programs.

Introduction

Invasive exotic species represent one of the single greatest obstacles to grassland restoration in North America (Bakker et al. 2003; Stromberg et al. 2007). A well documented example is the introduction of the annual grass *Bromus tectorum* L. (cheatgrass or downy brome) in the late 19th century, which resulted in widespread conversion of native perennial grasslands in the western United States (Mack 1981; Stubbendieck et al. 2011). Introduced species such as *B. tectorum* spread rapidly with land disturbance, and are highly competitive due to their pioneer growth habit, early germination period relative to native species, and abundant seed production (Sakai et al. 2001). Moreover, increased fire frequency associated with higher fuel loads in *B. tectorum* dominated grasslands promotes continued dominance despite ongoing efforts to restore native plant communities (D'Antonio & Vitousek 1992). When exotic species alter ecosystem properties, and landscapes are no longer dominated by historical plant communities, restoration may require new strategies for reestablishment of native plants (Vitousek 1990; Brooks et al. 2004). A novel approach is the study of intraspecific diversity, which may play an important role in susceptibility and tolerance of plant communities to invasion (Hooper et al. 2005; Crutsinger et al. 2008)

Guidelines for restoration of native species commonly recommend useing local germplasm to maintain biodiversity, to increase the likelihood that plants are adapted to site conditions, and to improve long-term sustainability of reintroduced populations (Hufford and Mazer 2003; McKay et al. 2005; Jones 2013). When landscapes are heavily impacted by biological invasion, however, local genotypes may no longer be adapted to altered environments. In these cases, it may be useful to investigate alternative sources of germplasm, such as cultivated varieties of native species. Cultivated varieties, or cultivars, represent novel germplasm selected for improved vigor, seed germination, and biomass production (Lesica & Allendorf 1999). Many cultivars are offered for commercial sale and are commonly used in restoration and reclamation due to their increased availability and lower cost (Burton & Burton

2002). Vigorous, cultivated genotypes may have the ability to outperform their wild counterparts in the presence of invasive species, but evidence also suggests cultivars can alter patterns of dominance among species in native plant communities (Gustafson et al. 2004; Klopf & Baer 2011). Further research is needed to compare cultivated seed sources to wild populations and to determine whether cultivars are more likely to establish at sites impacted by biological invasion.

This study compared cultivated and wild (local) varieties of the native perennial bunchgrass, *Poa secunda* J. Presl (Sandberg bluegrass), grown with and without *B. tectorum*. *Poa secunda* is an important native perennial bunchgrass of the sagebrush ecosystem in the western United States, and is commonly targeted in grassland restoration (Peterson 2002; Majerus et al 2009). We selected *P. secunda* due to its early growth period, extensive root system, and potential for establishment in the presence of invasive, exotic species such as *B. tectorum* (Perry et al. 2009). Our objectives were to: (1) study differences in fitness related traits between cultivars and wild seed sources of *P. secunda*, and (2) test the hypothesis that vigorous cultivars are more likely to tolerate the presence of invasive species relative to wild seed sources. We also examined *B. tectorum* performance when grown with *P. secunda* to characterize effects of competition for the invasive species, ultimately with the goal to understand consequences of intraspecific variation for restoration of native plant communities in sites heavily impacted by *B. tectorum*.

Methods

Study species

Poa secunda occurs from central Alaska through the Intermountain West and Great Plains states to northwestern Mexico (Stubbendieck et al. 2011). A perennial bunchgrass, *P. secunda* emerges in early spring and serves as a primary source of forage for both wildlife and livestock at the start of the growing season. Because of its broad distribution and soil conservation value, several cultivated accessions of *P. secunda* are available for purchase from commercial seed growers. We made comparisons of three wild accessions and three commercially available cultivars recommended for use in our study region. Cultivars included "High Plains" sourced from Wyoming, "Mountain Home" originating from Idaho, and "Reliable" with origins in Washington (USDA 2013). Wild accessions were sourced from MPG Ranch, a 10,000 acre conservation property in the Bitterroot Valley of western Montana. Both wild *P. secunda* and *B. tectorum* seeds were collected at MPG Ranch during the summer of 2012 and subsequently stored at room temperature (15–25°C) until planting in the greenhouse. Wild seed sources represented an elevation (1,000–1,300 m) and distance (3–6 km) transect within the ranch.

Experimental design

We conducted our experimental study at the Research and Extension Center greenhouses in Laramie, Wyoming (elev. 2,184 m). Seeds were sown into 164 ml Ray Leach "Cone-tainer" pots (Stuewe & Sons, Inc., Corvallis, Oregon, U.S.A.) to limit available growing space for plants in competition. Six hundred pots were sown with combinations of *P. secunda* and *B. tectorum* to evaluate the overall vigor and competitive response of cultivated and wild *Poa* seed sources.

Control pots included 40 replicates of each of the six *Poa* accessions and competition pots included another 40 replicates of each *Poa* accession sown with *B. tectorum*. An additional 120 pots were sown solely with seeds of *B. tectorum* to allow comparisons of *B. tectorum* growth between control and competition treatments. This experimental design resulted in 360 controls planted with either *Poa* or *B. tectorum*, and 240 competition pots. Each pot was lined with cheesecloth to prevent the loss of planting medium, while simultaneously allowing drainage. Pots were filled with a medium consisting of 1:1 finely sieved sand and peat moss; this medium was chosen to facilitate root harvest at the end of the study. Initially, four seeds of each species were sown into designated control or competition pots to ensure that at least one plant established per replication. Experimental pots were placed under a bank of misting nozzles for two weeks to promote germination at the start of the study.

Pots were monitored daily to record seedling emergence. Emergence was recorded as the number of days after planting (day 0) until a new seedling was observed. After two weeks, emerged seedlings were thinned to one plant per control pot, and one *Poa* and one *B. tectorum* plant per competition pot. Trays containing up to 49 pots were then transferred to a standard greenhouse bench for the duration of the study. Thereafter, pots were randomized within trays and trays were rotated weekly to limit differences in light and temperature gradients within the greenhouse. Plants were watered twice daily and daylight was supplemented with artificial lights to provide a 12-hour photoperiod from December through March for an experimental duration of four months.

Measurements of leaf count, plant height, and plant width were taken every five weeks beginning one week after seeds were sown, for a total of four consecutive surveys. Leaf count was recorded as the number of live and senesced leaves per plant. Plant height was recorded as the length of the tallest leaf to the nearest millimeter. Plant width was recorded at the widest point (mm) of the base of each plant. After four months, a final survey of survival was recorded for each plant, and above- and belowground biomass were harvested separately, washed (belowground biomass only), and dried in an oven at 60°C for three days. Dry weights were measured to 0.0001 g using an analytical balance (Mettler Toledo). Roots could not be separated by species in competition pots and belowground weights were recorded as the combined root mass of *Poa* and *B. tectorum*.

Differences in seedling performance among *Poa* accessions may be a consequence of adaptive variation or maternal effects (Roach and Wulff 1987). Cultivated seed sources likely experienced different maternal environments as a result of commercial production. As a last step, we examined seed weight differences among seed sources. Ten groups of 50 seeds from original seed collections were weighed to 0.0001 g using an analytical balance (Mettler Toledo) for all *Poa* accessions.

Statistical Analyses

Data for analysis included measured variables for each *Poa* and *Bromus* individual grown in control and competition pots. Emergence data were square-root transformed prior to analyses to meet assumptions of normality (Gotelli & Ellison 2004). We used two-factor analysis of variance (ANOVA) to analyze the mean number of days until emergence for each species, accession (*P. secunda*) and competition treatment (Proc GLM; SAS version 9.3; SAS Institute Inc., Cary, NC, U.S.A.). Subsequent analyses incorporated measured variables for emerged seedlings only.

Survival data were analyzed using a logistic model with a logit function assuming a binomial distribution (Proc GENMOD, SAS). We compared the effects of accession, competition treatment and their interaction using a two-factor ANOVA for survival of each species. In this and all other analyses, we compared differences among accessions using least square means with the Tukey-Kramer adjustment for multiple comparisons. We also conducted contrasts in SAS between pooled wild and cultivated seed sources to test the hypothesis that seed sources differed in each competition treatment, and to test the hypothesis that competition treatments differed for each seed source.

We used simple linear regression to evaluate the correlation of plant size variables with aboveground dry weight, and determined plant width was highly correlated with biomass ($R^2 = 0.84$). Plant width measurements were used as a proxy for plant growth over time, and these data were $\log_{10}$ transformed prior to analyses to meet assumptions of statistical tests (Zar 2010). Repeated-measures analysis was performed to determine how plant width (hereafter, plant growth) varied over time using a mixed model three-factor ANOVA in SAS. The model incorporated an autoregressive covariance structure and accession and treatment were fixed effects, while trays were modeled as random effects (Kincaid 2005).

We used a mixed model two-factor ANOVA to test for differences in aboveground biomass among *Poa* accessions within and between competition pots. Accession and competition treatment were analyzed as fixed effects and trays were modeled as random effects. Biomass data were $\log_{10}$ transformed prior to analyses. Aboveground biomass of *Bromus* was also tested with a single-factor ANOVA to determine if *B. tectorum* biomass differed between competition and control pots.

We subsequently examined differences in belowground biomass using two-factor ANOVA to examine the three categories of *Poa* root biomass, *Bromus* root biomass, and the combined root biomass of competition pots. Since we were unable to differentiate between roots of the two species in competition pots, we tested the hypothesis that belowground biomass was significantly different in competition pots relative to control pots of either species.

Separate from our greenhouse study analyses, we examined seed weight differences among seed sources by performing a single-factor ANOVA. A general linear model was used to analyze the mean seed weight for all *Poa* accessions. Seed weight was not included as a covariate in all other analyses to examine potential maternal effects because average seed weight directly corresponded to accession.

Results

Emergence

Ninety percent of experimental pots had an emerged plant and were monitored over the duration of the study. One wild accession, MPG-5, was removed from the study due to low emergence (< 8%) in both the control and competition treatment and this was likely the result of poor seed viability at the time of collection. Ultimately, 98% of experimental pots had an emerged plant and were included in the competition study. Only MPG-10 had less than 100% emergence (89%). This outcome may reflect differences in either seed quality or germination and establishment of seeds among accessions.

Seedling emergence varied by accession (Table 1). Cultivars as a group emerged more quickly than wild accessions (8 days versus 12 days; $p < 0.0001$). Among accessions, High Plains seedlings were the first to appear, while MPG-10 seedlings emerged last (Fig. 1). *Bromus* *tectorum* took an average of 6 days to emerge. Post-hoc tests revealed that *B. tectorum* had a significantly faster emergence rate when compared to pooled *Poa* accessions (6 days versus 9 days; $p < 0.0001$), but did not differ from the individual *Poa* accession, High Plains (6.0 days versus 6.3 days; $p = 0.4636$).

Plant Growth

Poa secunda plant growth was influenced by the interaction of accession, competition treatment, and survey (Table 2). Cultivars had more rapid growth than wild plants ($p < 0.0001$). All experimental accessions grew larger over time for both competition treatments (Fig. 2); the only exceptions to this were competing plants of the accessions MPG-10 and Reliable between the last two surveys. The effect of competition was apparent by the second survey – all accessions were significantly larger when grown alone relative to competition pots for the final three surveys. Overall, cultivars High Plains and Mountain Home grew larger than all other accessions, and this effect was consistent between control and competition treatments. *Bromus tectorum* plant growth increased over time ($p < 0.0001$) but did not differ between control and competition treatments ($p = 0.1993$).

Survival

At the end of the study, Sandberg bluegrass survival was impacted by the main effects of accession and competition treatment (Table 3). Wild and cultivated varieties of *P. secunda* had similar rates of survival ($p = 0.8907$) and both groups had lower survival when in competition with *B. tectorum* (wild $p = 0.0030$; cultivar $p = 0.0148$). Among accessions, High Plains had the highest average survival rate, but was only significantly greater than Reliable, which had the lowest number of survivors ($p = 0.0433$; Fig. 3). Plants in competition pots had lower survival than plants in control pots. There was no effect of competition on *B. tectorum* survival ($p = 0.1695$).

Biomass

Poa secunda aboveground biomass was influenced by accession and competition treatment (Table 4). Cultivars produced greater aboveground biomass than wild plants in controls (p <0 .0001). Aboveground biomass did not differ, however, among seed sources when grown in competition ($p = 0.2661$). Biomass of both cultivated and wild seed sources was reduced by competition with *B. tectorum*, and all five experimental accessions produced greater aboveground biomass in control pots compared to competition pots ($p < 0.0001$; Fig. 4). For control pots, biomass differed among *Poa* accessions. High Plains had the greatest average aboveground biomass compared to all other accessions. *Bromus tectorum* aboveground biomass was also influenced by competition ($p = 0.0152$). However, *B. tectorum* produced significantly greater biomass in competition pots relative to control pots (335 mg versus 315 mg between competition and control pots, respectively). Post-hoc analyses indicated this effect was primarily due to one *Poa* accession, MPG-15. *Bromus tectorum* biomass was no longer significantly greater in competition pots when MPG-15 was removed from analyses ($p = 0.0738$).

Root biomass in *Poa* control pots was influenced by accession ($p = 0.0002$). Cultivars had greater root biomass than wild plants ($p = 0.0277$). Among accessions, MPG-15 root biomass did not differ from cultivars High Plains and Mountain Home (Fig. 5). As anticipated, there was less *Poa* root biomass in control pots relative to combined root biomass in competition pots ($p < 0.0001$). However, average root biomass in competition pots did not differ from *B.*

tectorum root biomass in control pots ($p = 0.9009$), indicating that the majority of belowground biomass in competition pots could potentially be attributed to *B. tectorum*.

Seed Weight

Seed weight differed among *Poa* accessions ($p < 0.0001$). Seeds from wild populations were smaller than cultivated seeds ($p < 0.0001$). High Plains had the largest seed mass compared to all other accessions, followed by Reliable, Mountain Home, MPG-15, and MPG-10 (Fig. 6). All pair-wise comparisons among accessions were significantly different.

Discussion

Similar to other studies of cultivated and non-cultivated grassland species, *Poa secunda* cultivars were more vigorous relative to wild accessions (Klopf & Baer 2011; Lambert et al. 2011a; Schröder & Prasse 2013b). We identified significant differences between cultivated and wild accessions in control pots for all measured variables except survival, where differences were likely minimized due to the relatively benign greenhouse environment. Intraspecific variation was apparent among accessions as well, and the average trait values for High Plains were consistently greater than measures for other cultivated and wild seed sources. Traits measured in the remaining cultivars were generally similar to, or greater than, the wild accessions.

Observed differences in emergence and growth were likely due, in part, to maternal effects resulting from differences in initial seed weight (Roach & Wulff 1987). Seeds of the High Plains cultivar weighed more than seeds of other accessions, and average seed weight among cultivars was greater than seeds of wild populations. However, seed weight did not correlate with traits such as biomass, and the accession with the smallest seeds (MPG-10) produced aboveground biomass similar to three other accessions, including two of the three cultivars. Consequently, it is likely both maternal effects and heritable differences influenced plant performance in this species (Roach & Wulff 1987; Knapp & Rice 1994), and the lack of correspondence between seed weight and other measured variables indicated differences among accessions are due to multiple traits, rather than seed mass alone.

Contrary to our expectations, cultivars were on average no more tolerant of *B. tectorum* than wild accessions when grown in competition. Among measured variables for competition pots, only plant growth was greater in cultivars than wild accessions, and this effect was limited to two out of the three cultivar accessions (High Plains and Mountain Home). In this case, both cultivars presented some evidence of greater tolerance, and Mountain Home is noted for its use in reseeding in post-fire restoration of *B. tectorum* dominated landscapes (Lambert et al. 2011b). For all other traits, cultivars and wild accessions had similar rates of survival and aboveground biomass production. Both cultivars and wild plants had significantly fewer survivors, less growth, and smaller aboveground biomass when in competition compared to when grown alone. This effect is notable given the overall advantage of cultivars when grown without competition, as trait values for cultivated seed sources experienced a greater decline than values for wild accessions when grown with *B. tectorum*. Our results support prior findings indicating competition with an exotic species significantly impacts the overall performance of native perennial grasses, and may reduce phenotypic variability among native accessions during the first growing season (Corbin & D'Antonio 2004; Crutsinger et al. 2008; Mangla et al. 2011; Phillips 2012). Our study is unique, however, in that we compared and contrasted plant performance among different cultivated and wild accessions grown with and without an invasive species.

To determine the long-term effects of accession and competition on *P. secunda* fitness, this research would benefit from further study in the field and over multiple growing seasons. It is possible that traits which differ significantly early in the study will no longer be significant when plants are fully established. Alternatively, early advantages in growth may lead to increased long-term population viability over time (Knapp & Rice 2004). For example, reduced biomass of wild accessions may correspond to increased allocation to inflorescence production over the long-term, and therefore improved overall fitness. Goergen et al. (2011) demonstrated that local collections of *P. secunda* increased flower production when in competition with *B. tectorum*, but only by allocating less energy to leaf production relative to non-competing plants.

Bromus tectorum survival and growth did not differ between competition treatments, however it produced greater aboveground biomass when in competition relative to controls. These results differ from studies that have shown a reduction in *B. tectorum* performance when competing with *P. secunda* (Goergen et al. 2011; Mangla et al. 2011). An increase in *B. tectorum* biomass production in competition may indicate that the experimental accessions chosen for this study have not yet evolved to respond to invasion by *B. tectorum* at their location of origin (Rowe & Leger 2011). Alternatively, other studies have also reported an increase in *B. tectorum* biomass in competition with native perennial grasses, and they hypothesized that as *B. tectorum* takes advantage of available resources, its rapid growth rate contributes to increased biomass, thus creating a positive feedback mechanism between size and resource uptake (Lowe et al. 2003; Vasquez et al. 2008). This feedback is especially evident with increasing available nitrogen. Hence, field research is needed to evaluate the competitive response of different seed sources of *P. secunda* when grown in the presence of *B. tectorum*.

To conclude, evidence indicates that the source of seeds selected for restoration can influence seedling establishment and performance in ecological restoration (Hufford & Mazer 2003; McKay et al. 2005). When grown alone, native *P. secunda* cultivars were more vigorous than wild populations, and yet select wild accessions performed as well as select cultivar accessions. Despite consistent evidence for increased vigor, cultivars did not perform better than wild populations when grown with exotic, invasive *B. tectorum*. Small differences noted among *P. secunda* accessions suggest that knowledge of competitive ability of different cultivated or wild seed sources may improve seed source selection when sites are affected by invasive species. Additionally, the use of multiple wild or cultivated accessions may increase the odds that a more vigorous genotype such as High Plains is included in the seed mix (Lesica & Allendorf 1999). Given that intraspecific variation in performance among seed sources may alter patterns of dominance in restored populations and native plant communities, we recommend the use of representative local or regional seed sources when possible (Gustafson et al. 2004; Klopf & Baer 2011). If restoration sites are heavily impacted by exotic species such as *B. tectorum*, additional control measures such as the use of herbicides will remain necessary before reseeding with native perennial grasses.

References

Bakker, J. D., S. D. Wilson, J. M. Christian, X. Li, L. G. Ambrose, and J. Waddington. 2003. Contingency of grassland restoration on year, site, and competition from introduced grasses. Ecological Applications **13**:137–153.

Brooks, M. L., D'Antonio, C. M., Richardson, D. M., Grace, J. B., Keeley, J. E., DiTomaso, J. M., Hobbs, R. J., Pellant, M. and D. Pyke. 2004. Effects of Invasive Alien Plants on Fire Regimes. BioScience **54**:677–688.

Burton, P. J. and C. M. Burton. 2002. Promoting genetic diversity in the production of large quantities of native plant seed. Restoration Ecology **20**:117–123.

Corbin, J. D. and C. M. D’Antonio. 2004. Competition between native perennial and exotic annual grasses: implications for an historical invasion. Ecology **85**:1273–1283.

Crutsinger, G. M., Souza, L. and N. J. Sanders. 2008. Intraspecific diversity and dominant genotypes resist plant invasions. Ecology Letters **11**:16–23.

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

Goergen, E. M., Leger, E. A. and E. K. Espeland. 2011. Native perennial grasses show evolutionary response to *Bromus tectorum* (cheatgrass) invasion. PLoS ONE **6**:e18145.

Gotelli, N. J. and A. M. Ellison. 2004. A primer of ecological statistics. Sinauer Associates, Inc. Sunderland, MA.

Gustafson, D. J., Gibson, D. J. and L. Nickrent. 2004. Competitive relationships of *Andropogon gerardii* (Big Bluestem) from remnant and restored native populations and select cultivated varieties. Functional Ecology **18**:451–457.

Hooper, D. U., Chapin III, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J. and D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. Ecological Monographs **75**:3–35.

Hufford, K. M. and S. J. Mazer. 2012. Local adaptation and the effects of grazing on the performance of *Nassella pulchra*: implications for seed sourcing in restoration. Restoration Ecology **20**:688–695.

Jones, T. A. 2013. Ecologically appropriate plant materials for restoration applications. BioScience **63**:211–219.

Kincaid, C. 2005. Guidelines for selecting the covariance structure in mixed model analysis, paper 198-30. In SAS Institute, Inc. [ED.], Proceedings of the thirtieth annual SAS users' group international conference. SAS Institute, Inc., Cary, NC.

Klopf, R. P. and S. G. Baer. 2011. Root dynamics of cultivar and non-cultivar population sources of two dominant grasses during initial establishment of tallgrass prairie. Restoration Ecology **19:**112–117.

Knapp, E. E. and K. J. Rice. 1994. Starting from seed: genetic issues in using native grasses for restoration. Restoration and Management Notes **12**:40–45

Lambert, A. M., Baer, S. G. and D. J. Gibson. 2011a. Intraspecific variation in ecophysiology of three dominant prairie grasses used in restoration: cultivar versus non-cultivar population sources. Restoration Ecology **19:**43–52.

Lambert, S. M., Monsen, S. B. and N. Shaw. 2011b. Notice of release of Mountain Home Germplasm Sandberg bluegrass (selected germplasm, natural track). US Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Lesica, P. and F. W. Allendorf. 1999. Ecological genetics and the restoration of plant communities: mix or match? Restoration Ecology **7**:42–50.

Lowe, P. N., Lauenroth, W. K. and I. C. Burke. 2003. Effects of nitrogen availability on competition between *Bromus tectorum* and *Bouteloua gracilis*. Plant Ecology **167**:247–254.

Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into western North America: An ecological chronicle. Agro-Ecosystems **7**:145–165.

Majerus, M., Holzworth, L., Tilley, D., Ogle, D. and M. Stannard. 2009. Plant guide for Sandberg bluegrass (*Poa secunda* J. Presl). US Natural Resources Conservation Service, Idaho Plant Materials Center, Aberdeen, Idaho.

Mangla, S. Sheley, R. L., James, J. J. and S. R. Radosevich. 2011. Intra and interspecific competition among invasive and native species during early stages of plant growth. Plant Ecology **212**:531–542.

McKay, J. K., Christian, C. E., Harrison, S. P. and K. J. Rice. 2005. “How local is local?”—a review of practical and conceptual issues in the genetics of restoration. Restoration Ecology **13**:432–440.

Perry, L. G., Cronin, S. A. and M. W. Paschke. 2009. Native cover crops suppress exotic annuals and release native perennials in a greenhouse competition experiment. Plant Ecology **204**:247–259.

Peterson, J. S. 2002. Plant fact sheet: Sandberg bluegrass (*Poa secunda* J. Presl). United States Department of Agriculture, Natural Resource Conservation Service, Plant Materials Program.

Phillips, A. J. 2012. Phenotypic plasticity within the native perennial grass, *Poa secunda* (Sandberg bluegrass), an important component of the western United States sagebrush grassland vegetation. Thesis. University of Nevada, Reno.

Roach, D. A. and R. D. Wulff. 1987. Maternal effects in plants. Annual Review of Ecology and Systematics **18**: 209–235.

Rowe, C. L. and E. A. Leger. 2011. Competitive seedlings and inherited traits: a test of rapid evolution of *Elymus multisetus* (big squirreltail) in response to cheatgrass invasion. Evolutionary Applications **4**:485–498.

Sakai, A. K., Allendorf, F. W., Holt, J. S., Lodge, D. M., Molofsky, J., With, K. A., Baughman, S., Cabin, R. J., Cohen, J. E., Ellstrand, N. C., McCauley, D. E., O'Neil, P., Parker, I. M., Thompson, J. N. and S. G. Weller. 2001. The population biology of invasive species. Annual Review of Ecology, Evolution, and Systematics **32**:305–32.

Schröder, R. and R. Prasse. 2013. From nursery into nature: A study on performance of cultivated varieties of native plants used in re-vegetation, their wild relatives and evolving wild × cultivar hybrids. Ecological Engineering **60**:428–437.

Stromberg, M. R., D'Antonio, C. M., Young, T. P., Wirka, J. and P. R. Kephart. 2007. California grassland restoration. Pages 254-280 in M. R. Stromberg, J. Corbin, and C. M. D'Antonio, editors. California grasslands. University of California Press.

Stubbendieck, J., Hatch, S. L. and N. M. Bryan. 2011. North American wildland plants: a field guide. 2nd edition. University of Nebraska Press.

USDA, NRCS. 2013. Sandberg bluegrass (*Poa secunda* ssp. *secunda*): a native grass for conservation use in Montana and Wyoming. In Plant materials technical note No. MT-94, Bridger, MT.

Vasquez, E., Sheley, R. 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.

Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. Oikos **57**:7–13.

Zar, J. H. 1999. Biostatistical Analysis, fourth edition. Prentice-Hall, New Jersey.

Tables

Table 1. ANOVA of *Poa secunda* average emergence (transformed data).

Effect	*DF*	*Type III SS*	*Mean Square*	*F Value*	*Prob > F*
accession	4	38.89	9.72	33.23	<0.0001
competition	1	0.76	0.76	2.60	0.1078
accession × competition	4	1.06	0.27	0.91	0.4588

Table 2. Repeated measures analysis of seed source and competition treatment effects on *Poa secunda* plant growth (transformed data) for surveys 1-4.

Effect	*Numerator DF*	*Denominator DF*	*F Value*	*Prob > F*
accession	4	1492	21.29	<0.0001
competition	1	1492	468.04	<0.0001
accession × competition	4	1492	1.22	0.2985
survey	3	1492	2549.23	<0.0001
accession × survey	12	1492	2.16	0.0117
competition × survey	3	1492	285.40	<0.0001
accession × competition × survey	12	1492	2.64	0.0017

Table 3. ANOVA of *Poa secunda* survival at the end of the 16 week growing period.

Effect	*DF*	*Chi-Square*	*Prob > Chi-Square*
accession	4	10.23	0.0367
competition	1	12.39	0.0004
accession × competition	4	2.31	0.6780

Table 4. ANOVA of *Poa secunda* average aboveground biomass ($\log_{10}$ transformed).

Effect	*Numerator DF*	*Denominator DF*	*F Value*	*Prob > F*
accession	4	364	12.93	<0.0001
competition	1	364	1551.71	<0.0001
accession × competition	4	364	5.30	0.0004

Figures

Figure 1. Mean number of days until seedling emergence among *Poa secunda* accession (+ 1SE).

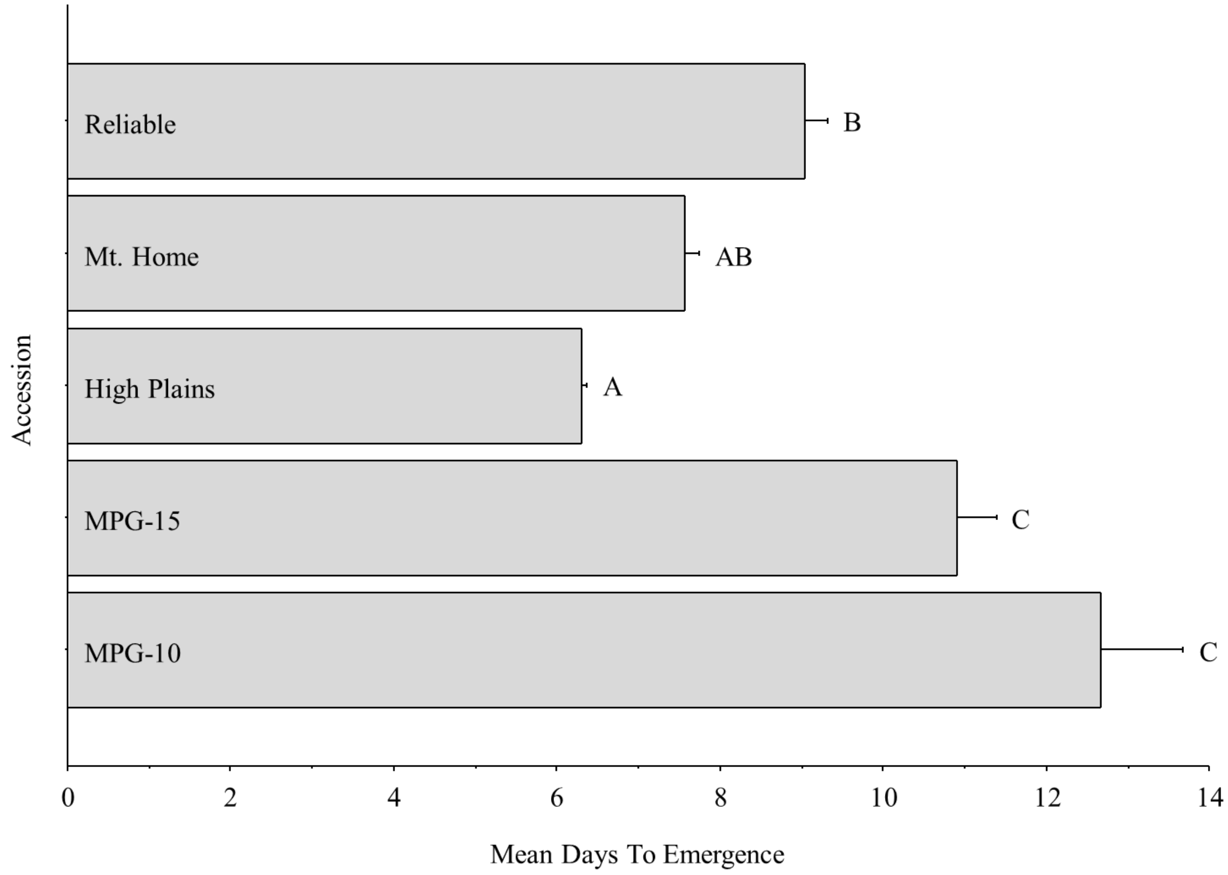


Figure 2. Average plant growth per *Poa secunda* accession between non-competing (solid line) and competing plants (dashed line) measured at four surveys over a 16 week growth period (± 1SE).

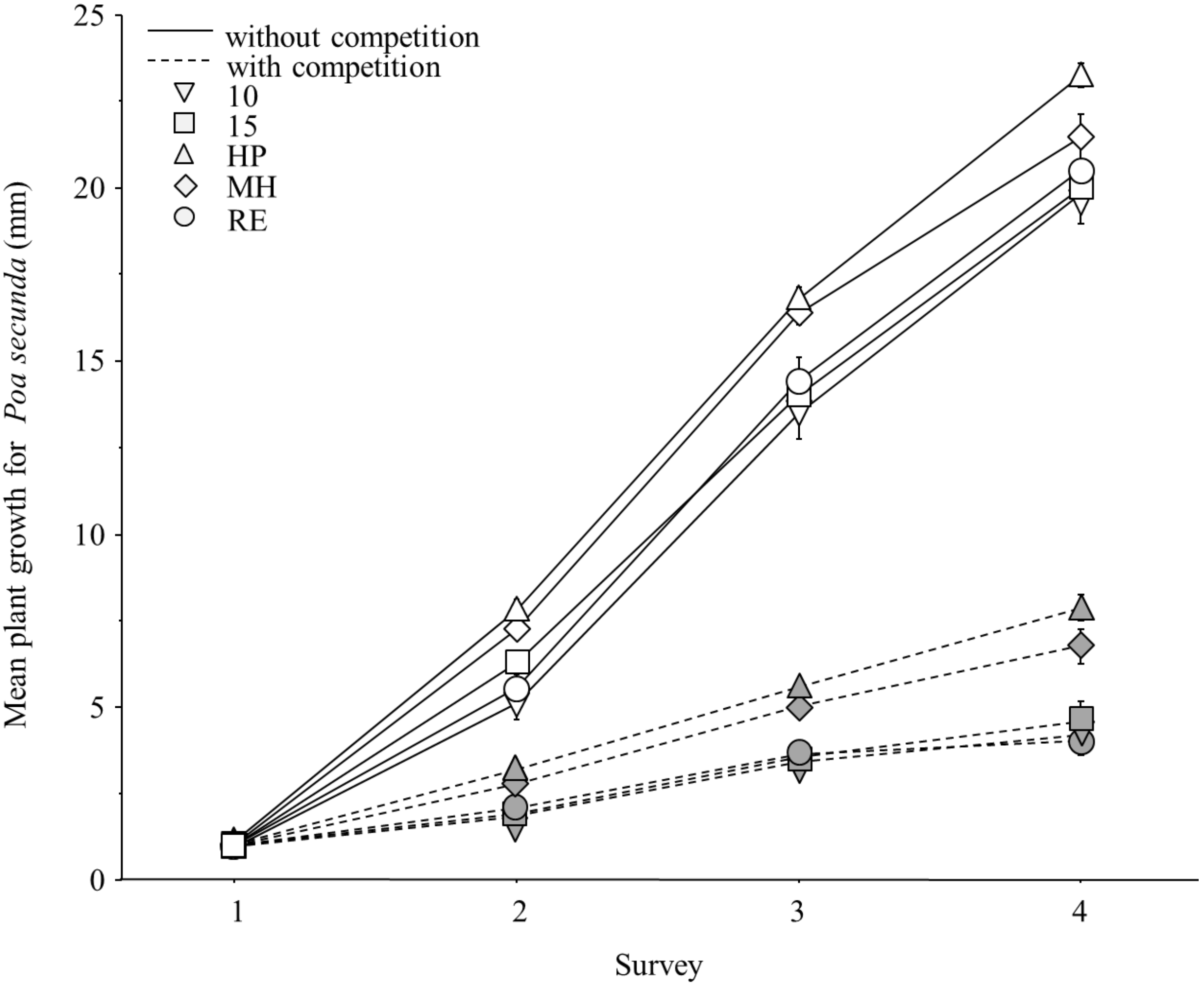


Figure 3. Average proportion survival per *Poa secunda* accession between non-competing and competing plants at the end of the 16 week growth period (+ 1SE).

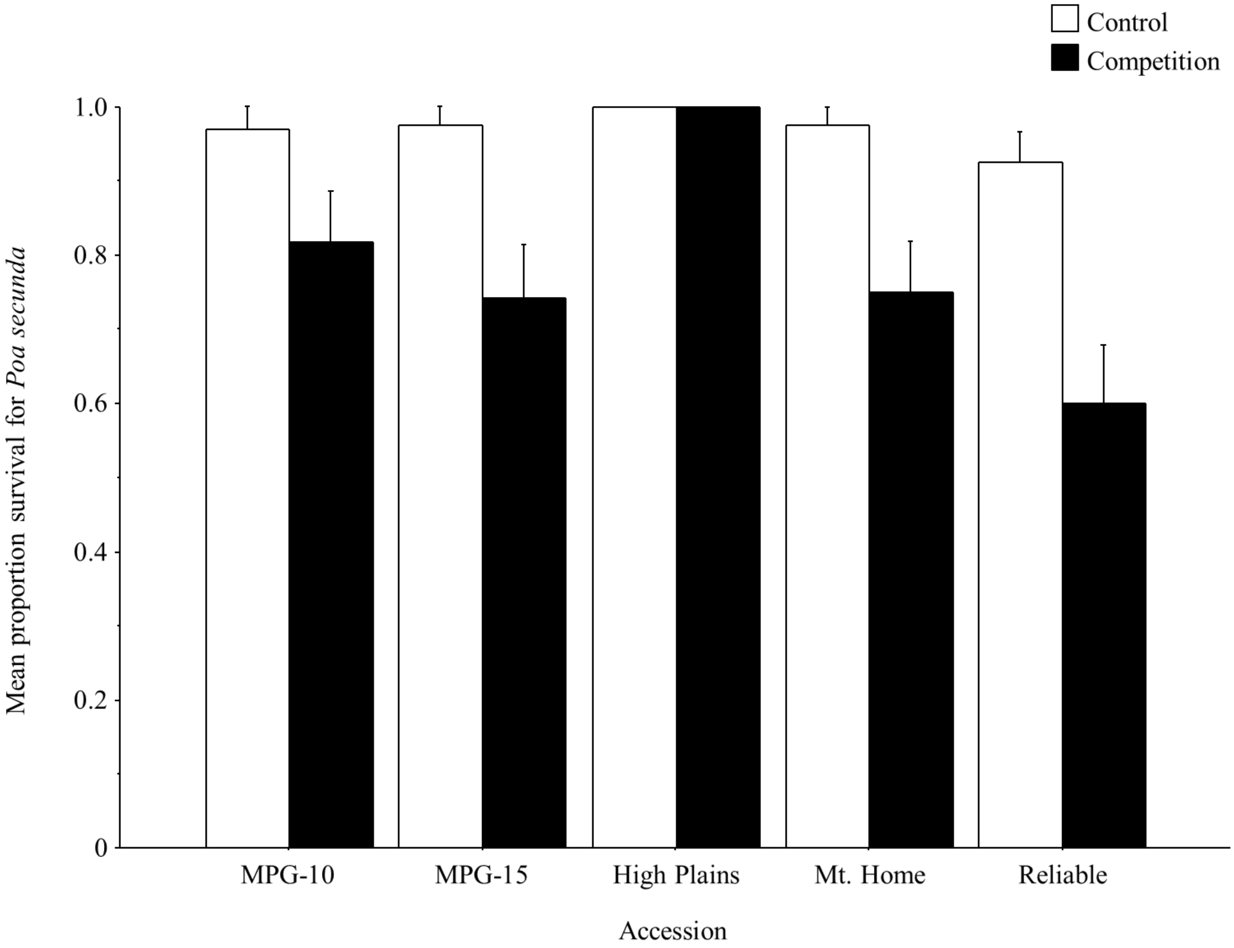


Figure 4. Average aboveground biomass of *Poa secunda* per accession between control (white) and competing plants (black) (+ 1SE). Different uppercase letters denote significance differences among non-competing accessions ($p \leq 0.05$). Different lowercase letters denote significance differences among competing accessions ($p \leq 0.05$). All accessions differed between competition treatments ($p \leq 0.05$).

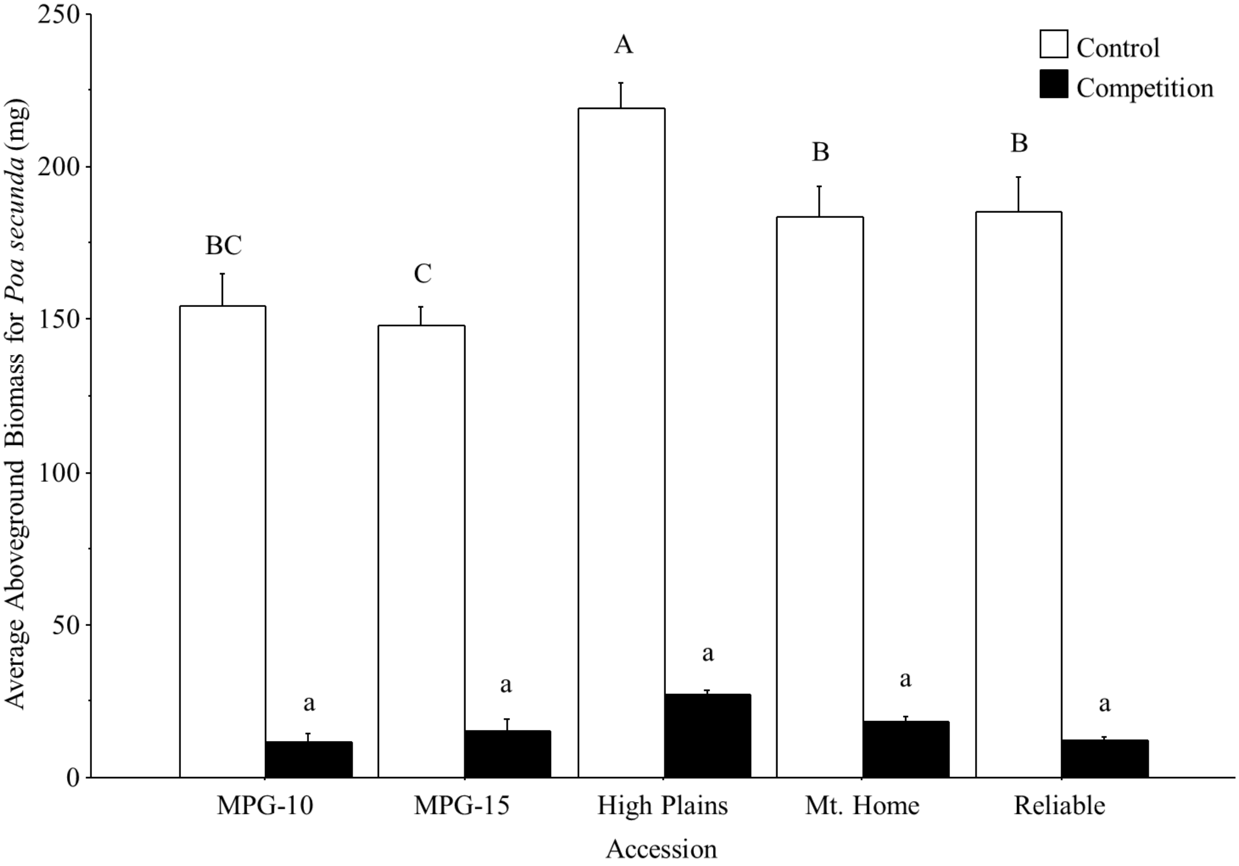


Figure 5. Average root biomass for non-competing *Poa secunda* plants per accession (+ 1SE). Different letters denote significance differences among accessions ($p \leq 0.05$).

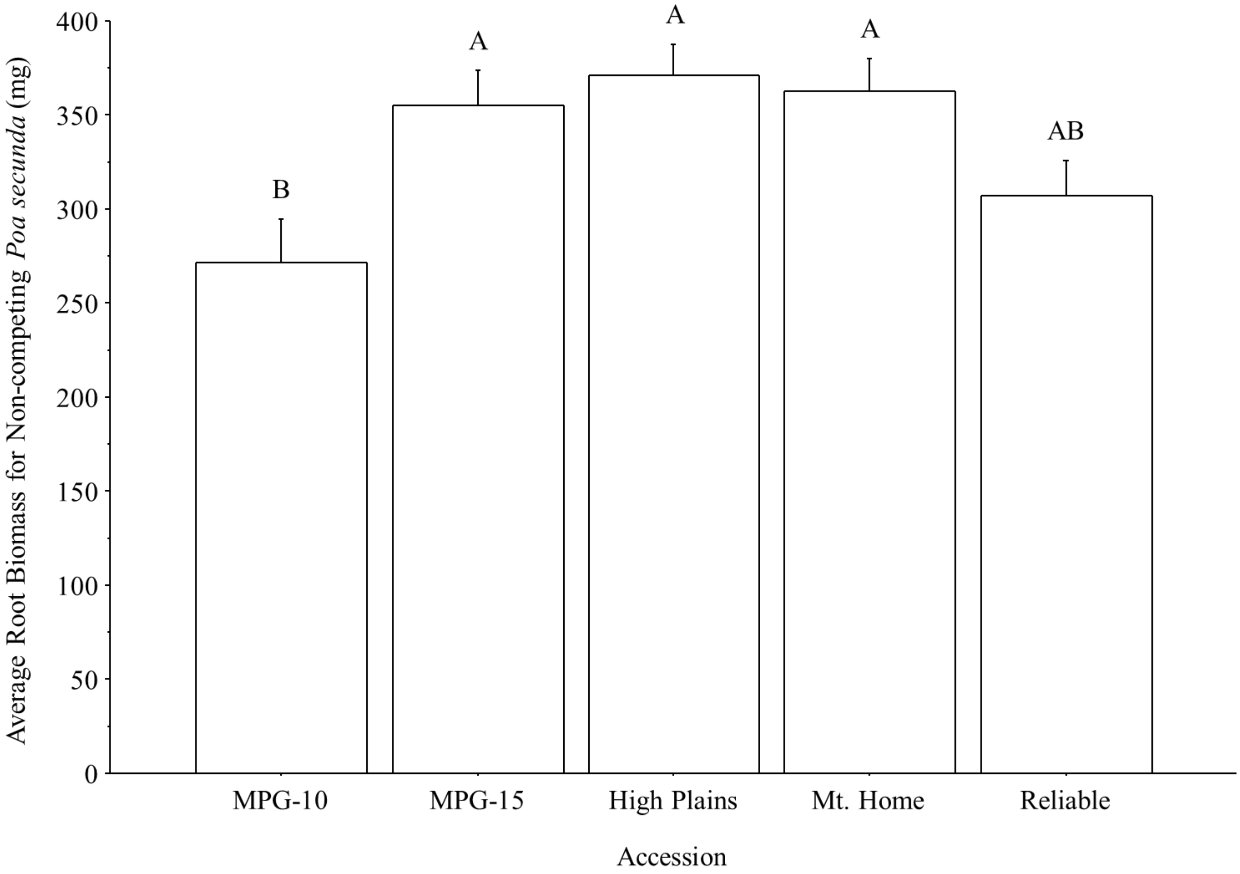
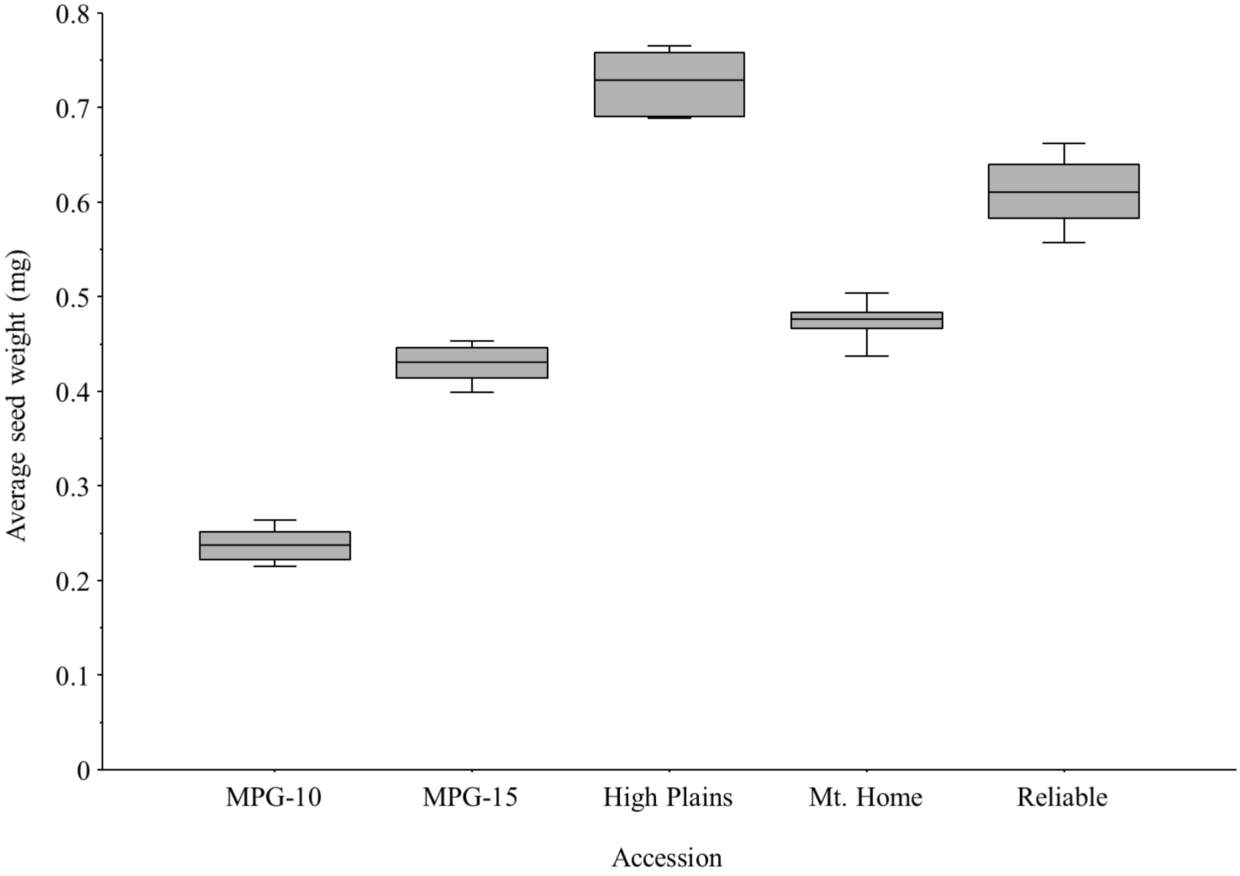


Figure 6. Box-Whisker plots of *Poa secunda* seed weight among accessions. The median value is indicated by the central horizontal line, and the lower and upper quartiles by the corresponding horizontal ends of the box. The whiskers indicate the range of the data. All accessions are significantly different from one another ($p \leq 0.05$).



CHAPTER THREE: CONSEQUENCES OF SEED ORIGIN AND BIOLOGICAL INVASION FOR RESTORATION OF A NORTH AMERICAN GRASS SPECIES

Abstract

Locally, wild-collected seeds of native plants are recommended for use in ecological restoration to maintain patterns of adaptive variation. However, some environments are so drastically altered by exotic, invasive weeds that original environments to which plants were adapted may no longer exist. Under these circumstances, cultivated varieties may have an advantage at highly disturbed sites. Cultivars are selected for improved germination and vigor, and represent novel genotypes relative to wild populations.

This study investigated differences in seedling performance between wild and cultivated seed sources of the native grass, *Poa secunda*, grown with and without the invasive grass, *Bromus tectorum*. We measured seedling survival and aboveground biomass for one growing season at two experimental sites in western Montana.

We found that the source of seeds selected for restoration can influence establishment at the restoration site. Cultivars had an overall advantage when compared with local genotypes, supporting evidence of greater vigor among cultivated varieties of native species. This advantage, however, declined rapidly in the presence of *B. tectorum* and most accessions were not significantly different for growth and survival in competition plots. Only one cultivar had a consistent advantage despite a strong decline in its performance when grown with *B. tectorum*. As a result, cultivated varieties did not meet expectations for greater establishment and persistence relative to local genotypes in the presence of invasive, exotic species.

Given that intraspecific variation in performance among seed sources may alter patterns of dominance in restored plant communities, we recommend using representative local or

regional seed sources grown to minimize commercial selection. If competition with exotic species is severe and control is ineffective, a mix of cultivars may capture vigorous genotypes and increase chances that native species will reestablish at restoration sites.

Introduction

There is considerable evidence for adaptation to local environments among populations within plant species (Turesson 1922; Turesson 1925; Clausen et al. 1941; Antonovics & Bradshaw 1970). Reciprocal transplant studies often detect a home-site advantage, in which the local seed source has higher fitness when planted at local sites relative to geographically or environmentally distant sites (Kawecki & Ebert 2004). Intraspecific variation for adaptive traits can have significant impacts on population establishment and resilience, and may also drive community level variation (Hughes & Stachowicz 2004; Gibson et al. 2012). As a result, guidelines for ecological restoration recommend using local seed sources to increase the likelihood that plants are adapted to site conditions, maintain genetic diversity and improve long-term sustainability of restored plant populations (McKay et al. 2005; Bischoff et al. 2008).

While local, wild-collected seed is recommended for ecological restoration, its availability is scarce and restoration practitioners frequently purchase commercially produced seed sources to meet native vegetation goals and reduce costs (Burton & Burton 2002; Smith et al. 2007). Commercial seeds are often derived from cultivated plant varieties—or cultivars—and represent a limited number of native species suitable for agricultural production. Cultivars are selected for improved germination, vigor and competitive ability, and are likely to represent novel genotypes and low levels of genetic diversity relative to wild populations (Lesica & Allendorf 1999). Few data are available for the short-and long-term consequences of the use of cultivars in restoration, but evidence suggests cultivated varieties differ from local genotypes in morphological and physiological traits, and may alter patterns of dominance within plant communities (Gustafson et al. 2004; Klopf & Baer 2011; Schröder & Prasse 2013). Large scale introductions of novel genotypes may therefore have unintended consequences, such as the swamping of local genotypes, and altered community structure and function (Hufford & Mazer 2003; Lambert et al. 2011).

Recommendations to use locally adapted seed sources are based on the assumption that environmental conditions to which plants are adapted remain relatively unchanged. However, some areas are so drastically altered by exotic, invasive weeds that original environmental conditions may no longer exist (D'Antonio & Vitousek 1992; Gasch et al. 2013). Because of their increased vigor, cultivars may have an advantage at highly invaded restoration sites and the assumption that local genotypes are better adapted to site conditions than cultivars may no longer hold (Lesica & Allendorf 1999; Wilkinson 2001; Jones 2013). In light of widespread biological invasion, geographic origin and genetic composition of seed stock can have significant consequences for restoration outcomes (Hufford & Mazer 2003; Gustafson et al. 2005). Both the advantages and drawbacks of using cultivars and local genotypes for restoration require further investigation in the field.

Spread of *Bromus tectorum* L. (cheatgrass or downy brome) in North America is a well documented example of land conversion as a result of biological invasion (Mack 1981). *Bromus tectorum* currently dominates millions of acres in the Intermountain West and represents a significant challenge for restoration of native plant species (Brown et al. 2008). *Bromus tectorum* is a winter annual and has a competitive advantage over native plants germinating later during the growing season (Aguirre & Johnson 1991). Stands of *B. tectorum* are also responsible for increased fire frequency, which can significantly alter both abiotic and biotic environmental conditions at restoration sites (D'Antonio & Vitousek 1992). Thus, the choice of appropriate seed sources for restoration may benefit from investigations of intraspecific variation and performance of native plants in environments altered by biological invasion (Leger 2008).

This study investigated performance of wild and cultivated seed sources of *Poa secunda* J. Presl (Sandberg bluegrass) by measuring biomass and survival over one growing season at sites impacted by *B. tectorum*. *Poa secunda* is a native, cool-season perennial grass commonly targeted for restoration because of its vast distribution (Majerus et al. 2009) and potential ability to establish and compete for resources at sites invaded by exotic species (Monsen et al. 2004). We asked two questions relevant for grassland restoration: 1) Does performance of wild seed sources differ from cultivated seed sources? 2) Are cultivars more likely than their wild relatives to establish and persist in the presence of invasive, exotic weeds? If seed origin affects plant performance, the choice of seeds for reintroduction may represent an important consideration in restoration planning. At the same time, if evidence suggests cultivars are more likely to persist in the presence of *B. tectorum*, the selection of suitable seed sources may change with the level of invasion at the restoration site.

Materials and Methods

Study Area

We conducted this study at MPG Ranch, a conservation property consisting of 9,500 acres in western Montana. The ranch is located on the west-facing slope of the Bitterroot Valley in the Northern Rocky Mountains. Dominant native species present in MPG grasslands are *Pseudoroegneria spicata* (Pursh) Á. Löve, *Festuca idahoensis* Elmer, *Koeleria macrantha*

(Ledeb.) Schultes, and *Poa secunda*, while dominant exotic species present are *B. tectorum* and *Poa bulbosa* L. (D. Mummey & L.N. Shreading, unpublished data). Prior to its transition to a conservation property in 2009, MPG Ranch had been used for agricultural production and livestock grazing for more than a century. The ranch is no longer grazed by livestock and the majority of crop fields are out of production.

Our experiment was conducted at two sites on MPG Ranch to evaluate interactions of local environmental conditions and competition by exotic invasive plants with wild and cultivated accessions of *P. secunda*. The first (Lower) site was located at an elevation of 998 m and consisted of sandy loam soil and an average soil pH of 6.3. Prior to establishment of experimental plots, the area had been used for soybean production. The second (Upper) site was located 1,023 m further upslope, at an elevation of 1,076 m. This site consisted of loam soil with an average pH of 6.6. Prior to recent efforts to remove introduced species, the Upper Site was dominated by *Agropyron cristatum* (L.) Gaertn, (crested wheatgrass) with a *Poa bulbosa* understory and used as a grazing lot for cattle. Historical climate data taken from the PRISM Climate Group (http://prism.oregonstate.edu) indicates that the average annual precipitation for the area is approximately 35 cm and mean annual temperature is 7°C (range of -9–30°C). For the duration of this study, annual precipitation recorded at the nearest MPG Ranch weather station was approximately 20 cm and mean temperature was 9°C (-17–37°C).

Study Species

Poa secunda is an important component of sagebrush steppe and temperate grassland vegetation in the western United States (Peterson 2002). A native perennial bunchgrass, *P. secunda* serves as a primary source of forage for both wildlife and livestock at the beginning of the growing season (Stubbendieck et al. 2011). *Poa secunda* occurs from Alaska through the Intermountain West and Great Plains states. *P. secunda* germinates early in the spring, and reproduces by tillering and by seed maturation in early summer. Seed production is commonly the result of apomixis, but outcrossed pollination and subsequent self-fertilization contributes to distinct genetic lines (Kellogg 1985).

Three U.S. Department of Agriculture cultivars were selected for inclusion in the study because of their recommended use in the study region and similar, early maturing attributes within the *P. secunda* complex (Majerus et al. 2009). These cultivars included "High Plains Germplasm" with origins in Wyoming, "Mountain Home Germplasm" with origins in Idaho, and "Reliable" from Washington State (Table 1; Fig. 1). Cultivars were compared with three wild populations (MPG-5, MPG-10, MPG-15) derived from sites differing in elevation, aspect, and surrounding plant community. Wild populations with sufficient seed quantity were selected to capture an elevation and distance gradient. Both wild *P. secunda* and *B. tectorum* seeds were collected at MPG Ranch during the summer of 2012 and subsequently stored at room temperature (15–25°C) until planting.

Experimental Design

We established and planted our study sites in early fall 2012. Both sites were initially disked, chain harrowed, and raked to remove existing vegetation and litter to ensure a smooth and even seedbed. Fencing was installed around the perimeter of each experimental site to prevent herbivory by large ungulates.

The experiment was organized as a randomized complete block design with five paired-plot replicates at both study sites, resulting in ten plots per site (Fig. 2). One plot of each pair was either weed-free or planted with *Bromus tectorum* (hereafter, *Bromus*). *Bromus* seeds were broadcast into experimental plots at a rate of 7,600 pure live seed m^{-2} based on previous density findings by Griffith (2010) and Humphrey & Schupp (2011), and incorporated into the soil by raking before planting *P. secunda*. Subsequently, each plot replicate was established with 50 *Poa secunda* (hereafter, *Poa*) individuals per accession, and planted at random order in 30 cm × 30 cm cells to avoid intraspecific competition. To account for viability differences among seed sources, four seeds of the same accession were planted per cell to ensure at least one *Poa* plant established in the spring (Hironaka & Tisdale 1972). A color-coded toothpick was then placed in the center of the four planted seeds to aid in locating the plants and to identify which accession had been planted. When plants emerged in early spring, the four seedlings were thinned to one plant per cell. Due to the effects of drought, plots were watered during the first week of May; each plant received a one time application of approximately 30 ml of water via a sprinkler system.

Each plot had dimensions of 1.8 x 15 m and each pair of weed-free and competition plots was separated by 1 m. All plots contained a 45 cm wide buffer around the edge; buffer zones were cleared for weed-free plots, and planted with *Bromus* for competition plots to avoid edge effects. This experimental design resulted in 300 *Poa* plants (50 for each of the 6 accessions) per plot.

Sampling Method

Experimental plots were surveyed for emergence during spring 2013 after seeds had overwintered. A survey of survival was subsequently conducted once every 3 weeks during the spring/summer growing season, resulting in four surveys for all experimental plots. A plot-wide survey of *B. tectorum* canopy cover was taken at its maximum production period in July to determine if levels of competition were even between study sites. *Bromus* cover was estimated using Daubenmire's six cover classes (Daubenmire 1959). Sites were cleared of all non-experimental vegetation between surveys to minimize competition in the weed-free plots, and to ensure competition was due to the presence of *Bromus* in the weed plots. At the same time, we noted the presence or absence of herbivory for each plant surveyed. At the end of the growing season, aboveground biomass for all *Poa* plants was clipped and dried in an oven at 60°C for three days. Dry weights for aboveground biomass were measured to 0.0001 g using an analytical balance (Mettler Toledo, Columbus, OH, U.S.A.).

Statistical Analyses

Data for analyses comprised experimental plot means for each accession with respect to the proportion of survivors and mean biomass. We calculated the proportion of survivors as the number of surviving seedlings divided by the original number of cells per plot (50 per accession). Average aboveground biomass was calculated for the number of survivors per accession per plot ($n \leq 50$). Prior to analyses, survival data were arcsine square-root transformed and biomass data were log transformed to satisfy assumptions of statistical tests (Zar 1999).

Repeated-measures data for survival were analyzed using a split-plot analysis of variance (ANOVA) where block was nested within site. Block was considered a random factor and accession, site, and competition treatment were analyzed as fixed factors. The repeated measures model incorporated compound symmetry covariance structure which resulted in the smallest Akaike's Information Criterion (Littell et al. 2006).

A split-plot mixed model ANOVA (block nested within site) was used to calculate the significance of main and interaction effects for aboveground biomass of each cultivated and wild seed source between weed-free and competition plots. Block was treated as a random factor and accession, site, and competition treatment were analyzed as fixed factors. All calculations for survival and biomass data were made using the MIXED procedure in SAS version 9.3.1, using an alpha of 0.05 (SAS Institute Inc., Cary, NC, U.S.A.). Presence or absence of herbivory was added to the models as a covariate. Degrees of freedom were estimated using Satterwaite's method (Littell et al. 2006) and paired comparisons were made using least-squares means. We tested assumptions of higher vigor among cultivars relative to wild populations with contrasts of pooled seed sources (i.e. wild versus cultivar) and also examined performance of individual cultivar and wild accessions.

As a last step, we assessed *Bromus* cover to ensure the level of competition was consistent among all treatment plots in the study. The midpoint of the Daubenmire cover class range was averaged across each treatment plot. Average *Bromus* cover values were compared to determine if cover class differed among competition plots.

Results

A total of 2,627 *Poa* seeds germinated and established, and 1,773 were monitored after thinning to one plant per cell. One of the wild seed sources (MPG-5) had near-zero rates of establishment and as a result, this seed source was removed from analyses. Despite efforts to account for differences in seed viability, cultivated seeds had higher rates of seedling establishment when compared with the two wild seed sources (0.48 vs. 0.15, $p < 0.001$). This outcome may reflect differences in the viability or germination and establishment of seeds among accessions. Herbivory, likely caused by small rodents, was noted during the final two surveys. Approximately 21% of experimental *Poa* plants were impacted by herbivory at the time of the third survey, and this number increased to 28% by the final survey. Average *Bromus* canopy cover for competition plots ranged from 46–69%. Plot cover differences were not significant and we included competition effects in analyses measured as the presence or absence of *Bromus*.

Survival

Patterns of *Poa* survival were influenced by accession, competition, site, and survey, resulting in a significant four-way interaction in analysis of the full dataset (Table 2). Due to the difficulty of testing and interpreting these results, we conducted exploratory data analysis guided by field observations of survival among survey periods. As a result, we report repeated measures analyses of survival data for the first three surveys separate from analysis of the final survey at the end of the growing season. Patterns of survival differed among accessions at the end of the summer relative to data collected earlier in the growing season.

Results of the repeated measures analysis for surveys 1–3 revealed significant differences in seedling survival for the interactive effects of accession, site, survey, and competition treatment (Table 3). Survival differed among each *Poa* accession ($p < 0.001$), and in all cases, survival declined over time (Fig. 3). We did not detect an effect of competition with *Bromus* for *Poa* survival early in the growing season (Fig. 4). Overall, cultivars were more likely to survive than wild accessions ($p < 0.001$) and survival of High Plains seedlings was greater than all other cultivated and wild accessions ($p < 0.001$).

At the end of the growing season, survival was impacted by the interaction of *Poa* accession, competition treatment and differences between experimental sites (Table 4). Of note was the significant competition effect in weed plots (Fig. 5). Survival rates were lower for *Poa* seedlings grown with *Bromus* later in the season when plants of both species were larger and competition for resources was greater. Survival rates were higher for all seed sources in weed-free plots at the Lower Site relative to competition plots. However, no differences were detected for any of the five seed sources at the Upper Site when survival in weed-free plots was compared with competition plots. Herbivory was greater at the Upper Site, although this effect was not significant for survival at the final survey.

Cultivars were more likely to survive than wild plants by the time of the last survey ($p < 0.001$), although that effect was solely the result of greater survival of the High Plains cultivar (cultivar vs. wild when High Plains removed, $p = 0.207$). Among accessions, the High Plains cultivar had the greatest number of survivors regardless of site or competition treatment ($p < 0.001$). We also noted that survival of MPG-15 seedlings did not differ significantly from Mountain Home and Reliable seedlings, suggesting that some wild populations may perform as well as some cultivated accessions. Only MPG-10 and Mountain Home had a similar proportion of survivors in competition and weed-free plots. However, the number of survivors was low for these accessions and we were unable to determine if this effect was due to the ability of these accessions to tolerate *Bromus*, or the result of a lack of statistical power.

To sum, we noted significant differences in survival among accessions for both experimental sites, and survival differences between weed-free and competition plots for the Lower Site, at the fourth survey. The significant 3-way interaction at the final survey between site, accession and competition effects may be the result of greater herbivory rates at the Upper

Site later in the growing season. The Upper Site was in a more remote location than the Lower Site, and it is likely that *Poa* seedlings were exposed to greater rates of herbivory in weeded plots, resulting in similar numbers of surviving seedlings between weed-free and competition plots over time.

Biomass

Poa biomass was influenced by the accession and interactions between the accession, the experimental site, and the competition treatments (Table 5). Cultivars had greater biomass relative to wild plants ($p = 0.025$), although that effect was no longer significant when the High Plains cultivar was removed from the contrast ($p = 0.482$). High Plains produced the greatest average biomass compared to all other accessions ($p = 0.0004$). On average, the five accessions produced more biomass at the Lower Site than the Upper Site, but this difference was only significant for MPG-15. At the Lower Site, wild accessions performed as well as a subset of cultivars (MPG-15 performed as well as High Plains and Mountain Home, and MPG-10 was similar to Mountain Home and Reliable), while MPG-15 was similar to cultivars Mountain Home and Reliable at the Upper Site. Regardless of accession, competition with *Bromus* negatively affected *Poa* biomass at the Lower Site ($p = 0.003$). However, there was no effect of competition at the Upper Site ($p = 0.237$), and this was likely the result of high levels of herbivory that reduced biomass of *Poa* in weed-free plots by the final survey. Biomass did not differ between sites in competition plots.

Regardless of site, High Plains yielded the greatest biomass compared to all other accessions when in competition with *Bromus* ($p < 0.001$; Fig. 6). Cultivars, overall, produced significantly more biomass compared to wild plants when in competition ($p = 0.007$), and this effect was due to the performance of High Plains (cultivar vs. wild when High Plains removed, $p = 0.232$). Wild accessions did not differ from cultivars in weed-free plots ($p = 0.372$). Both wild accessions performed as well as at least two cultivars in weed-free plots (MPG-15 was similar to all three cultivars, while MPG-10 was similar to Mountain Home and Reliable), and they performed as well at least one cultivar in competition plots (MPG-15 was similar to Mountain Home and Reliable, while MPG-10 matched Reliable). Three accessions (High Plains, Mountain Home and MPG-15) produced similar amounts of biomass between weed-free and competition plots, while two accessions (MPG-10 and Reliable) produced significantly lower biomass in competition plots relative to weed-free plots.

Discussion

In the present study, we investigated seedling establishment and growth among local and cultivated genotypes of *Poa secunda* at sites planted with *B. tectorum*. We noted differences in performance among seed sources for measured variables in nearly all cases, suggesting that the source of seeds can have a significant impact on plant performance and, as a result, restoration outcomes (Mijnsbrugge et al. 2010). Mean biomass and survival of cultivars was greater than wild plants on average, and these results reflect the increased vigor documented for cultivars relative to wild populations (e.g. Gustafson et al. 2004; Klopf & Baer 2011). Differences in vigor were also apparent between local accessions, and MPG-15 had higher fitness and increased seed viability relative to MPG-10. Among the five local and cultivated seed sources, performance of the High Plains cultivar was distinctive. High Plains seedlings maintained their overall performance advantage among seed sources in both weed-free and competition plots. The High Plains cultivar was originally derived from high elevation sites with a semi-arid climate, which may have been an advantage when the plants were grown at exposed sites in this study (Weißhuhn et al. 2011). Experimental plots imitated seedbeds for ecological restoration and likely represented relatively low soil moisture and extremes in temperature range, which negatively impact seedling establishment (Banerjee et al. 2006).

Competition effects in *Bromus* plots were only apparent late in the growing season and were significant at the final survey. This indicated a window of opportunity to minimize competition with weeds when restoration sites are cleared prior to seeding, and improve establishment of desired species with continued management of exotics (Bakker et al. 2003; Sher et al. 2008). Despite the overall advantage of cultivars as a group, in each test, one or more wild accessions performed similar to when compared to one or more cultivated accessions, particularly in competition plots. In addition, seedling performance also varied among cultivars and between the two wild seed sources. While High Plains seedlings had the greatest vigor among accessions in competition plots, the performance of Mountain Home seedlings exhibited the smallest decline in the presence of *Bromus* for all measured variables, indicating its potential for tolerance of invasive species. One of Mountain Home's reported uses is in post-fire restoration of *Bromus* dominated landscapes (Lambert et al. 2011), and the competitive ability of this cultivar warrants further investigation in the field.

Our study did not test local adaptation because we were unable to reciprocally transplant seed sources, the resident plant community was removed prior to site establishment, and sites were weeded throughout the duration of the experiment (Bischoff et al. 2006). Evidence for adaptive variation may only be apparent in competition with surrounding vegetation (Rice & Knapp 2008). However, restoration commonly includes site preparation and weed control prior to seeding. In that regard, our results provide key information for planting success of cool season grasses early in restoration and in the presence of one of North America's most destructive invasive species. Early establishment is likely to improve the success of native species and minimize competition effects in the presence of exotics (Stevens & Fehmi 2011). A next step for evaluation of different seed sources of *P. secunda* would be to determine the replicability of these results when plants are grown in a matrix of the resident (native and non-native) plant community.

Environmental conditions such as soil, slope, precipitation, and elevation may have influenced differences in seedling performance between experimental sites. Low emergence rates across accessions could be explained by the drier than normal conditions during the spring. Early in the field season, survival of experimental plants was greater at the Upper Site where loam soils had more potential for moisture retention relative to sandy loam soil at the Lower Site (Gupta & Larson 1979). During the second half of the growing season, plant performance at the Upper Site declined rapidly when compared to the Lower Site, and this was likely a result of differences in slope and rates of herbivory. Herbivory obscured variation among seed sources at the Upper Site, suggesting that grazing may reduce the advantage of dominant genotypes in the short term (Hufford et al. 2008).

In summary, we found that cultivars had an overall advantage over local genotypes, supporting evidence of greater vigor among cultivated varieties of native species. This advantage, however, declined rapidly in the presence of *Bromus* and most accessions were not significantly different for growth and survival in competition treatments. As a result, cultivated varieties as a group did not meet our expectations for greater establishment and persistence relative to local plants in the presence of invasive, exotic species. Other control measures would be needed to reduce competition with invasive plants, and promote the establishment of desirable, native vegetation (e.g. herbicide; Rafferty & Young 2002). Additionally, numerous studies suggest that the differences in vigor between cultivated and non-cultivated varieties can impact community-level interactions and population dynamics (Booth & Grime 2003; Gibson et al. 2012). Non-cultivated wild populations therefore remain the best choice to maintain population genetic diversity and avoid risks of large-scale introductions of non-local genotypes (Hufford & Mazer 2003). Measures should be taken to ensure high viability of local seed stock before planting to improve establishment.

In cases where sites are heavily impacted by invasive species and other control measures are not feasible or are ineffective, cultivars may provide some advantage for establishment of natives. However, the ability to discern among cultivars is difficult unless data are available for competitive ability, dominance, and overall vigor (such as in the case of High Plains). If no data are available, the use of multiple cultivars might increase the odds of including highly competitive genotypes in the restoration seed mix. This strategy, however, is not without risks and may be most useful in highly invaded settings. Given the concerns for large-scale introductions of cultivated plants, and the variability in their performance relative to wild populations, we recommend the use of a composite mixture of seed sources representing appropriate local or regional variation either via wild collections or limited field production of region-specific varieties to avoid directional selection and altered patterns of genetic variation. This approach would maintain intraspecific patterns of genetic diversity, and may improve plant community diversity as well as resistance to biological invasion (Hughes & Stachowicz 2004; Crutsinger et al. 2006; Gibson et al. 2012).

References

Aguirre, L. and D. A. Johnson .1991. Influence of temperature and cheatgrass competition on seedling development of two bunchgrasses. Journal of Range Management **44**, :347–354.

Antonovics J. and A. D. Bradshaw. 1970. Evolution in closely adjacent plant populations. VIII. Clinal patterns at a mine boundary. Heredity **25**:349–362.

Bakker, J. D., Wilson, S. D., Christian, J. M., Li, X., Ambrose, L. G. and J. Waddington. 2003. Contingency of grassland restoration on year, site, and competition from introduced grasses. Ecological Applications **13**:137–153.

Banerjee, M. J., Gerhart, V. J. and E. P. Glenn. 2006. Native plant regeneration on abandoned desert farmland: effects of irrigation, soil preparation, and amendments on seedling establishment. Restoration Ecology **14**:339–348.

Bischoff, A., Cremieux, L., Smilauerova, M., Lawson, C. S., Mortimer, S. R., Dolezal, J., Vojtech, L., Edwards, A. R., Brook, A. J., Macel, M., Leps, J., Steinger, T. and H. Müller-Schärer. 2006. Detecting local adaptation in widespread grassland species–the importance of scale and local plant community. Journal of Ecology **94**:1130–1142.

Bischoff, A., Steinger, T. and H. Müller-Schärer. 2008. The importance of plant provenance and genotypic diversity of seed material used for ecological restoration. Restoration Ecology **18**:338–348.

Brown, C. S., Anderson, V. J., Claassen, V. P., Stannard, M. E., Wilson, L. M., Atkinson, S. Y., Bromber, J. E., Grant III, T. A. and M. D. Munis. 2008. Restoration ecology and invasive plants in the semiarid West. Invasive Plant Science and Management **1**:399–413.

Booth, R. E. and J. P. Grime. 2003. Effects of genetic impoverishment on plant community diversity. Journal of Ecology **91**:721–730.

Burton, P. J. and C. M. Burton. 2002. Adaptive genotype strategy promoted and tested in nursery field plots studies and plantings in British Columbia. Ecological Restoration **20**:117–123.

Clausen J., Keck, W. M. and W. M. Hiesey. 1941. Regional differentiation in plant species. American Naturalist **75**:231–250.

Crutsinger, G. M., Collins, M. D., Fordyce, J. A., Gompert, Z., Nice, C. C. and N. J. Sanders. 2006. Plant genotypic diversity predicts community structure and governs an ecosystem process. Science **313**:966–968.

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

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science **33**:43–64.

Gasch, C. K., Enloe, S. F., Stahl, P. D. 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.

Gibson, D. J., Allstadt, A. J., Baer, S. G. and M. Geisler. 2012. Effects of foundation species genotypic diversity on subordinate species richness in an assembling community. Oikos **121**:496–507.

Griffith, A. B. 2010. Positive effects of native shrubs on *Bromus tectorum* demography. Ecology **91**:141–154.

Gupta, S. C. and W. E. Larson. 1979. Estimating soil water retention characteristics from particle size distribution, organic matter percent, and bulk density. Water Resources Research **15**:1633–1635.

Gustafson, D. J., Gibson, D. J. and D. L. Nickrent. 2004. Competitive relationships of *Andropogon gerardii* (Big Bluestem) from remnant and restored native populations and select cultivated varieties. Functional Ecology **18**:451–457.

Gustafson, D. J., Gibson, D. J. and D. L. Nickrent. 2005. Using local seeds in prairie restoration–data support the paradigm. Native Plants Journal **6**:25–28.

Hironaka, M. and E. W. Tisdale. 1972. Growth and development of *Sitanion hystrix* and *Poa sandbergii.* US/IBP Desert Biome Research Memorandum 72–24. Utah State University, Logan, UT.

Hufford, K. M. and S. J. Mazer. 2003. Plant ecotypes: genetic differentiation in the age of ecological restoration. Trends in Ecology and Evolution **18**:147–155.

Hufford, K. M., Mazer, S. J. and M. D. Camara. 2008. Local adaptation and effects of grazing among seedlings of two native California bunchgrass species: implications for restoration. Restoration Ecology **16**:59–69.

Hughes, A. R. and J. J. Stachowicz. 2004. Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. Proceedings of the National Academy of Sciences of the United States of America **101**:8998–9002.

Humphrey, L. D. and E. W. Schupp. 2011. 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.

Jones, T. A. 2013. When local isn't best. Evolutionary Applications **6**:1109–1118.

Kawecki, T. J. and D. Ebert. 2004. Conceptual issues in local adaptation. Ecology Letters **7**:1225–1241.

Kellogg, E. A. 1985. A biosystematics study of the *Poa secunda* complex. Journal of the Arnold Arboretum **66**:201–242.

Klopf, R. P. and S. G. Baer. 2011. Root dynamics of cultivar and non-cultivar population sources of two dominant grasses during initial establishment of tallgrass prairie. Restoration Ecology **19**:112–117.

Lambert, A. M., Baer, S. G. and D. J. Gibson. 2011 Intraspecific variation in ecophysiology of three dominant prairie grasses used in restoration: cultivar versus non-cultivar population sources. Restoration Ecology **19**:43–52.

Lambert, S. M., Monsen, S. B. and N. Shaw. 2011 Notice of release of Mountain Home Germplasm Sandberg bluegrass (selected germplasm, natural track). US Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Leger, E. A. 2008. The adaptive value of remnant native plants in invaded communities: an example from the Great Basin. Ecological Applications **18**:1226–1235.

Lesica, P. and F. W. Allendorf. 1999. Ecological genetics and the restoration of plant communities: mix or match? Restoration Ecology **7**:42–50.

Littell, R. C., Milliken, G. A., Stroup, W. W., Wolfinger, R. O. Schabenberger. 2006. SAS for mixed models. SAS Institute, Inc., Cary, NC.

Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into Western North America: an ecological chronicle. Agro–Ecosystems **7**:145–165.

Majerus, M., Holzworth, L., Tilley, D., Ogle, D. and M. Stannard. 2009. Plant Guide for Sandberg bluegrass (*Poa secunda* J. Presl). US Natural Resources Conservation Service, Idaho Plant Materials Center, Aberdeen, Idaho.

McKay, J., Christian, C. E., Harrison, S. and K. J. Rice. 2005. "How local is local?" – A review of practical and conceptual issues in the genetics of restoration. Restoration Ecology **13**:432–440.

Mijnsbrugge, K. V., Bischoff, A. and B. Smith. 2010. A question of origin: where and how to collect seed for ecological restoration. Basic and Applied Ecology **11**:300–311.

Monsen, S. B., Stevens, R. and N. Shaw. 2004. Grasses. In: Restoring western ranges and wildlands. General Technical Report GTR-136-vol. 2. US Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Peterson, J. S. 2002. Plant Fact Sheet: Sandberg bluegrass (*Poa secunda* J. Presl). US Natural Resource Conservation Service, Plant Materials Program, Washington, DC.

Rafferty, D. L. and J. A. Young. 2002. Cheatgrass competition and establishment of desert needlegrass seedlings. Journal of Range Management **55**:70–72.

Rice, K. J. and E. E. Knapp. 2008. Effects of competition and life history stage on the expression of local adaptation in two native bunchgrasses. Restoration Ecology **16**:12–23.

Schröder, R. and R. Prasse. 2013. Do cultivated varieties of native plants have the ability to outperform their wild relatives? PloS ONE **8**:e71066.

Sher, A. A., Gieck, S., Brown, C. S. and S. J. Nissen. 2008. First-year responses of cheatgrass following *Tamarix* spp. control and restoration-related disturbances. Restoration Ecology **16**:129–135.

Smith, S. L., Sher, A. A. and T. A. Grant III. 2007. Genetic diversity in restoration materials and the impacts of seed collection in Colorado’s restoration plant production industry. Restoration Ecology **15**:369–374.

Stevens, J. M. and J. S. Fehmi. 2011. Early establishment of a native grass reduces the competitive effect of a non-native grass. Restoration Ecology **19**:399–406.

Stubbendieck, J., Hatch, S. L. and N. M. Bryan. 2011. North American Wildland Plants: A Field Guide, 2nd edn. University of Nebraska Press.

Turesson, G. 1922. The genotypical response of plant species to the habitat. Hereditas **3**:211–350.

Turesson, G. 1925. The plant species in relation to habitat and climate. Contributions to the knowledge of genecological units. Hereditas **6**:147–236.

Weißhuhn, K., Auge, H. and D. Prati. 2011. Geographic variation in the response to drought in nine grassland species. Basic and Applied Ecology **12**:21–28.

Wilkinson, D. M. 2001. Is local provenance important in habitat creation? Journal of Applied Ecology **38**:1371–1373.

Zar, J. H. 1999. Biostatistical Analysis, 4th edn. Prentice-Hall, New Jersey.

Tables

Table 1. Site characteristics at the origin of each *Poa secunda* accession.

Accession	*Approximate Location*	*Latitude, Longitude*	*Elevation (m)*	*Plant Community*	*Annual Temp. (°C)*	*Annual Precip. (cm)*
MPG-5 (5)	Florence, MT	46° 41' 35" N, 114° 1' 5" W	1,144	*Bromus tectorum,* *Hesperostipa comata,* *Aristida purpurea*	7.0	35.0
MPG-10 (10)	Florence, MT	46° 40' 18" N, 114° 1' 43" W	1,026	*Pseudoroegneria spicata,* *Bromus tectorum,* *Poa bulbosa*	"	"
MPG-15 (15)	Florence, MT	46° 42' 50" N, 113° 59' 49" W	1,333	*Thinopyrum intermedium,* *Bromus tectorum* *Pseudoroegneria spicata*	"	"
High Plains (HP)	Casper, WY, Granger, WY, Gillette, WY	42° 47′ 37″ N, 107° 35′ 54″ W	1,647	*Hesperostipa comata,* *Pascopyrum smithii,* *Bouteloua gracilis*	8.3	26.7
Mountain Home (MH)	Mountain Home, ID	42° 52′ 4″ N, 115° 34′ 57″ W	900	*Elymus elymoides,* *Bromus tectorum,* *Sisymbrium altissimum*	9.5	20.0
Reliable (RE)	Yakima, WY	46° 45′ 40″ N, 120° 11′ 29″ W	639	*Pseudoroegneria spicata,* *Artemisia tridentate wyomingensis,* *Achillea millefolium occidentalis*	11.6	21.0

Table 2. Repeated measures analysis of seed source, competition treatment, and planting location effects on *Poa secunda* proportion survival for surveys 1-4.

Effect	*Numerator DF*	*Denominator DF*	*F Value*	*Prob > F*
accession	4	34.7	210.42	<0.001
competition	1	8.2	3.38	0.102
site	1	8.84	0.02	0.888
survey	3	248	276.46	<0.001
accession × competition	4	31.7	0.99	0.428
accession × site	4	33.7	4.11	0.008
accession × survey	12	239	16.93	<0.001
competition × site	1	8.04	1.12	0.320
competition × survey	3	244	11.69	<0.001
site × survey	3	247	13.82	<0.001
accession × competition × site	4	31.3	0.82	0.522
accession × competition × survey	12	238	1.66	0.077
accession × site × survey	12	238	0.91	0.534
competition × site × survey	3	240	18.9	<0.001
accession × competition × site × survey	12	237	1.87	0.039
herbivory	1	278	2.33	0.128

Table 3. Repeated measures analysis of seed source, competition treatment, and planting location effects on *Poa secunda* proportion survival for surveys 1-3.

Effect	*Numerator DF*	*Denominator DF*	*F Value*	*Prob > F*
accession	4	64.7	227.22	<0.001
competition	1	16.1	1.33	0.265
site	1	16.8	0.07	0.800
survey	2	162	107.75	<0.001
accession × competition	4	63.7	0.18	0.948
accession × site	4	64.7	3.65	0.010
accession × survey	8	159	5.47	<0.001
competition × site	1	16.1	0.25	0.621
competition × survey	2	160	5.99	0.003
site × survey	2	162	17.22	<0.001
accession × competition × site	4	63.7	0.53	0.717
accession × competition × survey	8	159	1.73	0.096
accession × site × survey	8	159	1.36	0.220
competition × site × survey	2	160	0.73	0.484
accession × competition × site × survey	8	159	0.72	0.674
herbivory	1	167	6.93	0.009

Table 4. ANOVA of *Poa secunda* proportion survival for survey 4.

Effect	*Numerator DF*	*Denominator DF*	*F Value*	*Prob > F*
accession	4	37.8	33	<0.001
competition	1	14.7	8.08	0.013
site	1	13.4	2.71	0.123
accession × competition	4	34.2	2.87	0.037
accession × site	4	35.4	1.16	0.343
competition × site	1	8.14	8.14	0.021
accession × competition × site	4	33.1	4.12	0.008
herbivory	1	66.7	1.6	0.210

Table 5. ANOVA of *Poa secunda* average biomass.

Effect	*Numerator DF*	*Denominator DF*	*F Value*	*Prob > F*
accession	4	16.8	6.61	0.002
competition	1	7.47	2.78	0.137
site	1	7.21	4.62	0.068
accession × competition	4	48	2.72	0.041
accession × site	4	49	4.72	0.003
competition × site	1	3.76	16.59	0.017
accession × competition × site	4	49	0.75	0.564
herbivory	1	50.4	36.05	<0.001

Figures

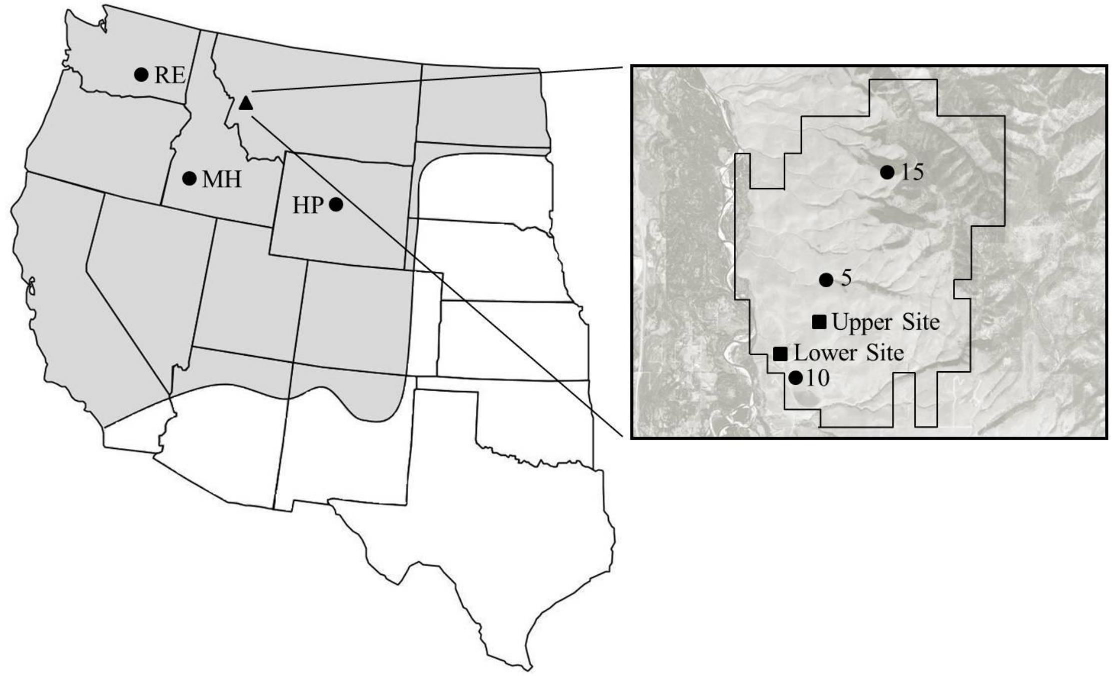


Figure 1. On the left is the distribution of *Poa secunda* in the contiguous western United States (shaded area; adapted from Stubbendieck, Hatch & Bryan 2011). The location of the MPG Ranch field site is indicated by the triangle. Circles indicate the origin locations of the cultivated accessions. To the right is an aerial image of MPG Ranch property lines. Circles mark the locations of the three wild seed source origins (MPG accessions 5, 10 and 15). The two experimental sites are indicated by squares.

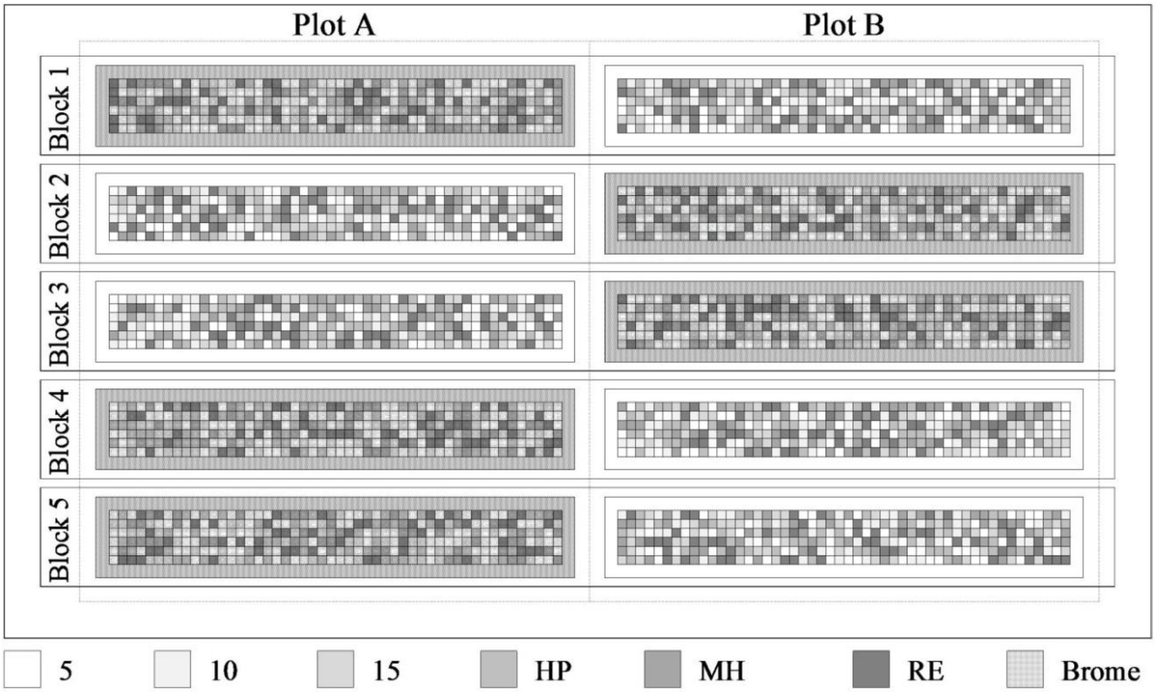


Figure 2. Experimental design of each study site. Each site contained five blocks, split between one weed-free plot (white border) and one paired *B. tectorum* plot (shaded border). Every plot contained 50 individuals of all six *Poa secunda* accessions, placed randomly within each plot (each small square cell within a plot corresponded to one individual *Poa*).

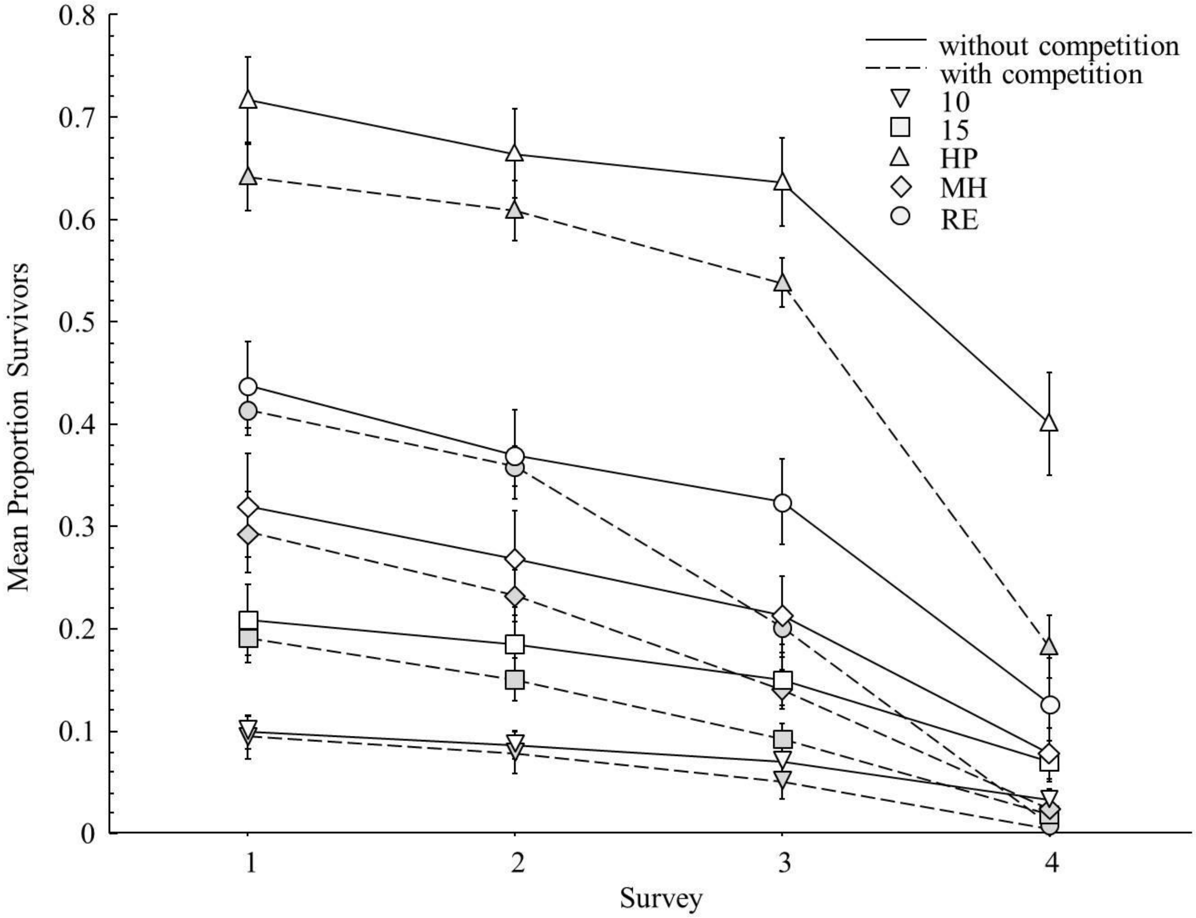


Figure 3. Average proportion survival per *Poa secunda* accession between non-competing and competing plants over time (± 1SE).

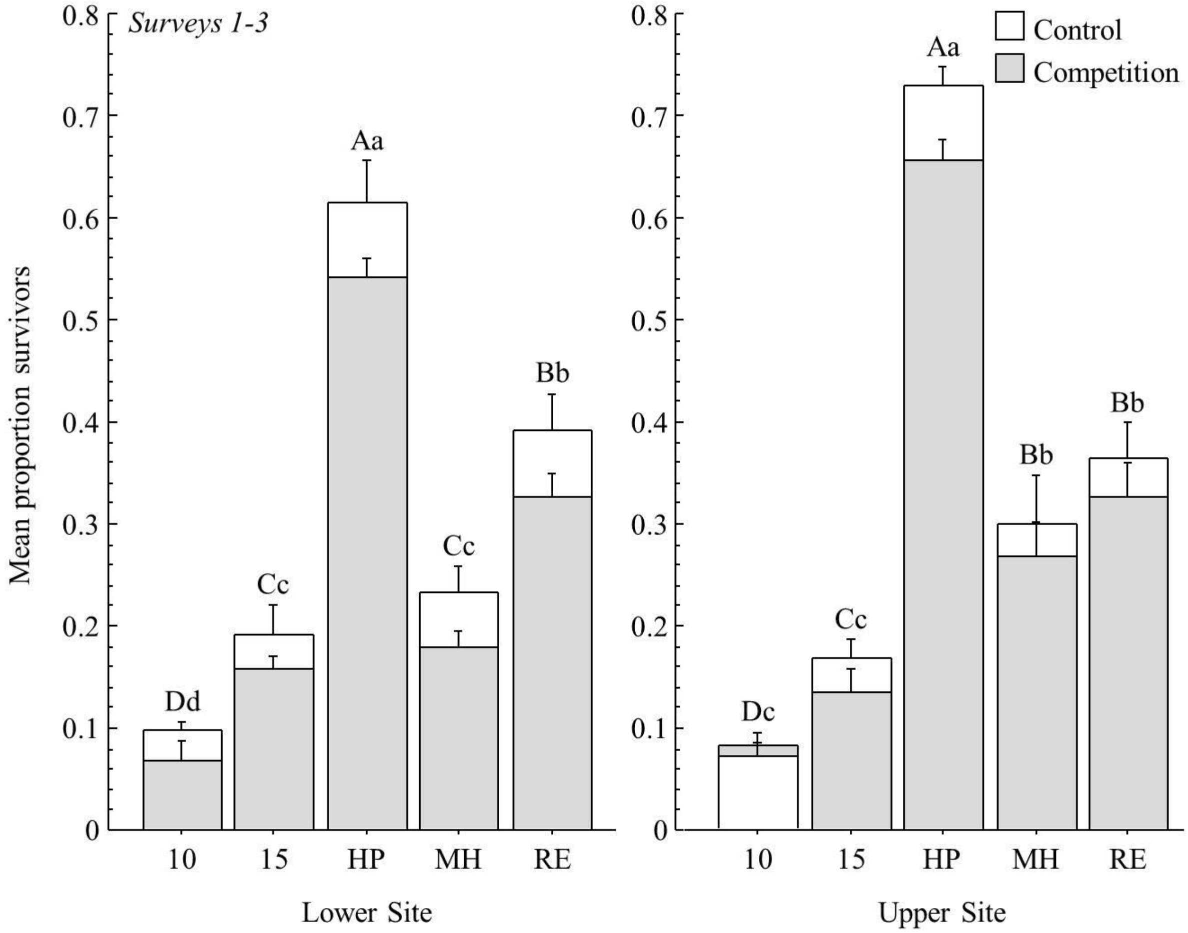


Figure 4. Average proportion survival per accession for Surveys 1–3 between non-competing and competing plants (+ 1SE). Different uppercase letters denote significant differences among non-competing accessions and lowercase letters denote differences among competing accessions.

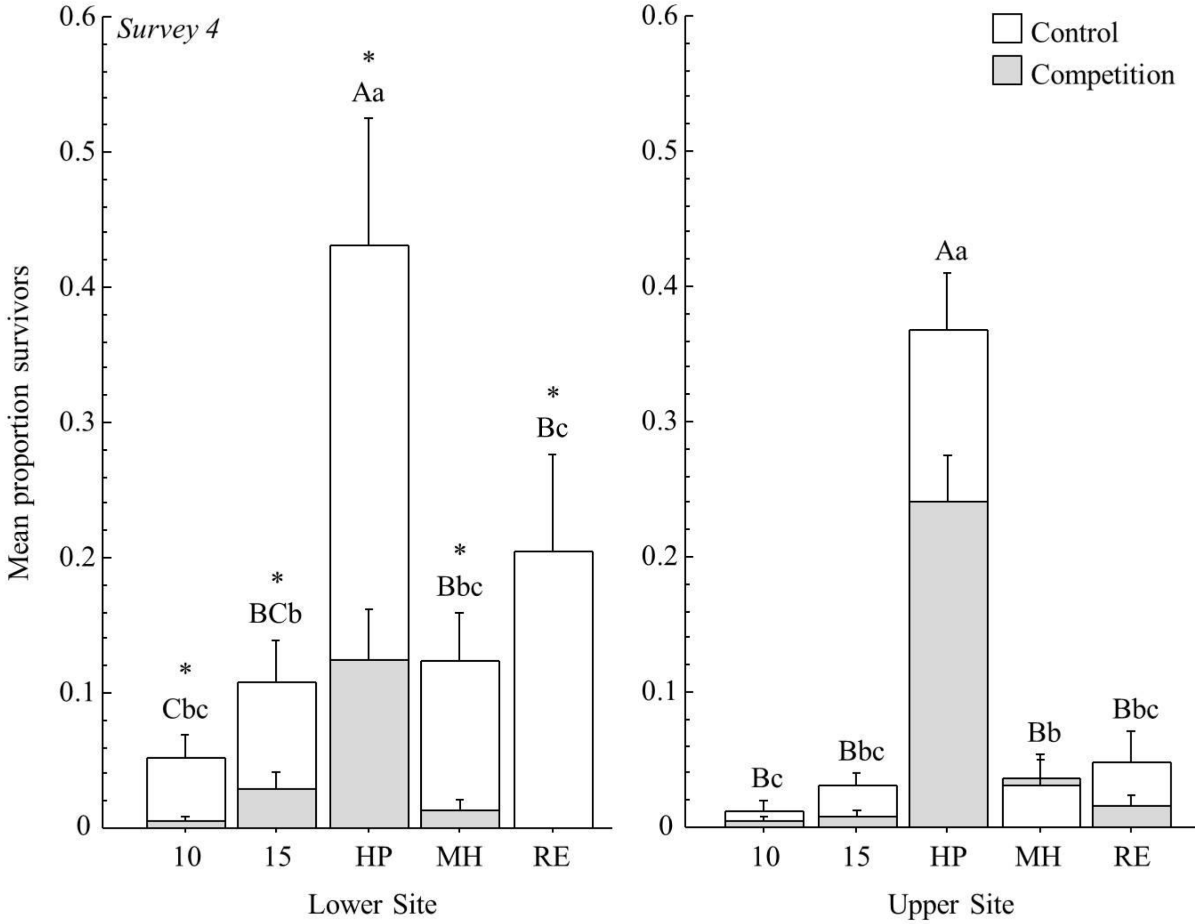


Figure 5. Average proportion survival per accession at Survey 4 between non-competing and competing plants (+ 1SE). Asterisks denote significances within accessions between competition treatments. Different uppercase letters denote significant differences among non-competing accessions and lowercase letters denote differences among competing accessions.

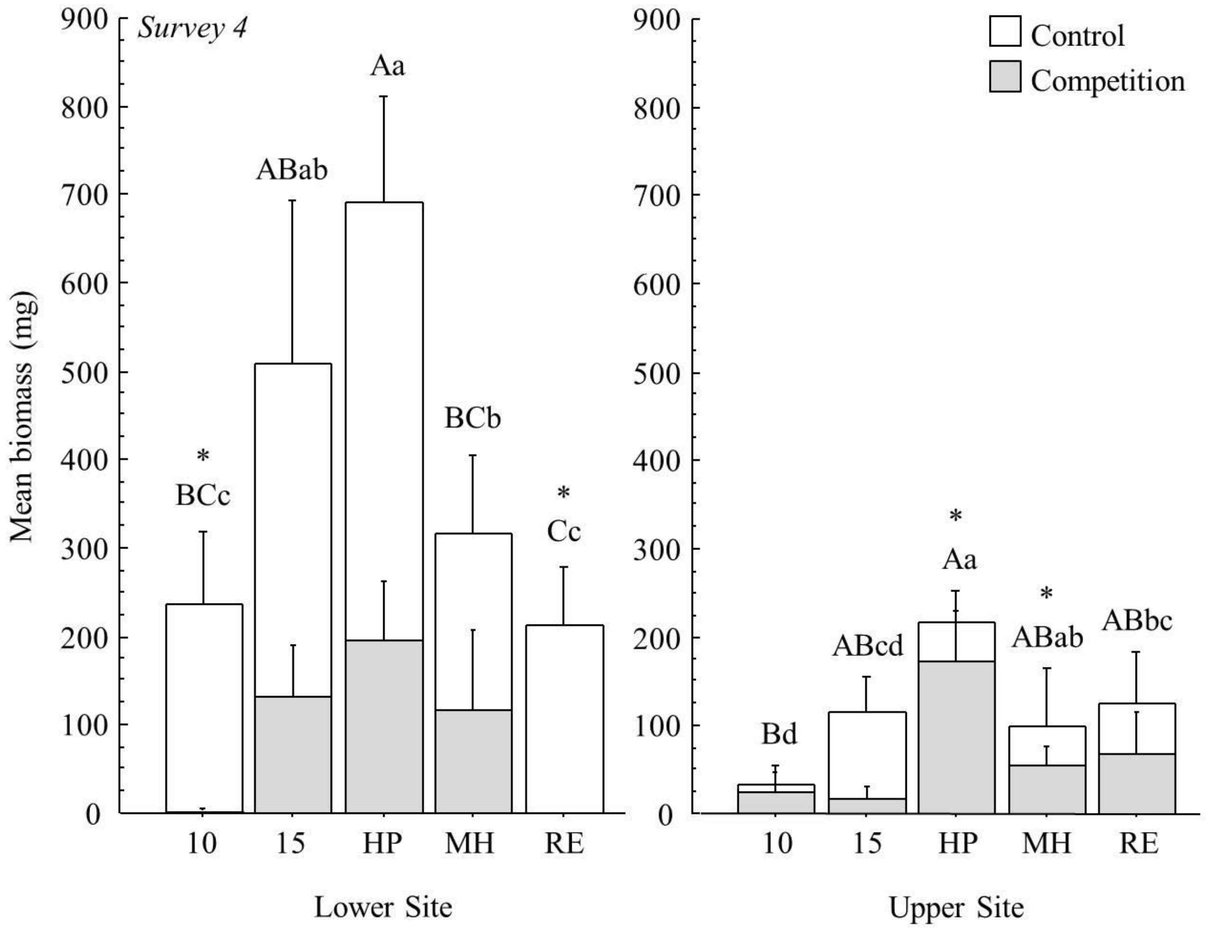


Figure 6. Average aboveground biomass of surviving plants at Survey 4 per accession between non-competing and competing plants (+ 1SE). Asterisks denote significance within accessions between competition treatments. Different uppercase letters denote significant differences among non-competing accessions, and lowercase letters denote differences among competing accessions.

CHAPTER FOUR: CONCLUSION

These two studies provide information for selecting appropriate native seed sources for restoration of a highly invaded site. Both the greenhouse and field studies demonstrated that *Poa secunda* J. Presl (Sandberg bluegrass) plants traits differ between seed sources, and among all experimental accessions. On average, cultivars had greater emergence, biomass, and survival compared to wild accessions in control pots and plots. However, this was mostly due to the highly vigorous cultivar, High Plains, which consistently had the greatest values for all measured variables. Traits measured in the remaining cultivars were generally equal to or greater than the wild accessions.

Results from the *Bromus tectorum* L. competition studies varied slightly between the greenhouse and field settings. *Poa secunda* plants grown in the greenhouse resulted in similar vegetative traits between seed sources at the end of the growing season, while the field study resulted in a greater amount of variation among accessions. At MPG Ranch, cultivars performed better than wild plants on average when grown with *B. tectorum*, but similar to the greenhouse results, and this was primarily due to the overall success of the Wyoming-sourced cultivar High Plains. Differences in results between the greenhouse and field study could be the result of stochastic patchiness of environmental variables, weed distribution, or herbivory in the field, the relatively benign greenhouse environment, or adaptation to local environmental variables by some accessions (Joshi et al. 200; Miner et al. 2005).

Knowledge of the competitive ability of different cultivated or wild seed sources may improve seed source selection in the presence of exotic species. Given that intraspecific variation in performance among seed sources may alter patterns of dominance in restored populations and plant communities, we recommend the use of representative local or regional seed sources. Cultivated varieties of native species were on average more vigorous than wild populations in both the greenhouse and field settings, and yet wild collections performed as well as several select cultivars. Despite evidence for increased vigor in control settings, cultivated varieties of native species did not outperform wild populations when grown with *B. tectorum*. The use of multiple wild or cultivated accessions may increase the odds that a more vigorous genotype such as High Plains is included in the seed mix (Lesica & Allendorf 1999). If restoration sites are heavily impacted by invasive exotic species, additional control measures, such as the use of herbicides or prescribed burning, would be necessary before reseeding with native perennial grasses. If competition with exotics species is severe, exotic control is ineffective, and higher native species vigor is desired, a mix of seed sources may improve the odds that natives will reestablish at the restoration site (SER 2004).

A common garden study is a classic approach to investigate heritable genetic variation within species (Hufford & Mazer 2003). However, our findings do not reveal whether intraspecific variation among seed sources is important for long-term population sustainability (Miner et al. 2005). It is clear that competition between exotic and native species influence structure, pattern and dynamics of plant communities (Crawley 1997), but the relative role of competition may vary dramatically among different ecosystems and over time (Mangla et al. 2011). Future work is needed with these and other species to examine the generality of these findings, and this project would be complemented by new greenhouse and field trials to test the competitive response of native bunchgrass species, such as *P. secunda*, to exotic invasive species, such as *B. tectorum*, for multiple generations.

References

Crawley, M. J. 1997. Plant Ecology, Second Edition. Blackwell Science, Oxford.

Hufford, K. M. and S. J. Mazer. 2003. Plant ecotypes: genetic differentiation in the age of ecological restoration. Trends in Ecology and Evolution **18**:147–155.

Joshi, J., Schmid, B., Caldeira, M. C., Dimitrakopoulos, P. G., Good, J., Harris, R., Hector, A., Huss-Danell, K., Jumpponen, A., Minns, A., Mulder, C. P. H., Pereira, J. S., Prinz, A., Scherer-Lorenzen, M., Siamantziouras, A.S., Terry, A. C., Troumbis, A. Y. and J. H. Lawton. 2001. Local adaptation enhances performance of common plant species. Ecology Letters **4**:536–544.

Lesica, P. and Allendorf, F. W. 1999. Ecological genetics and the restoration of plant communities: mix or match? Restoration Ecology **7**:42–50.

Mangla, S. Sheley, R. L., James, J. J. and S. R. Radosevich. 2011. Intra and interspecific competition among invasive and native species during early stages of plant growth. Plant Ecology **212**:531–542.

Miner, B. G., Sultan, S. E., Morgan, S. G., Padilla, D. K. and R. A. Relyea. 2005. Ecological consequences of phenotypic plasticity. Trends in Ecology and Evolution **20**:685–692.

Society for Ecological Restoration International Science & Policy Working Group. 2004. The SER international primer on ecological restoration. Tucson: Society for Ecological Restoration International (available from www.ser.org).