

RESEARCH ARTICLE

# Effects of competition with *Bromus tectorum* on early establishment of *Poa secunda* accessions: can seed source impact restoration success?

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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 cultivated varieties, 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 the exotic, invasive *Bromus tectorum* L. in a greenhouse setting. While *P. secunda* cultivars 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 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. Use of multiple seed sources may increase the potential for capturing vigorous genotypes in the restoration seed mix. In cases where sites are heavily impacted by exotic, invasive species, other control measures will be necessary to improve establishment of native species in grassland restoration programs.

**Key words:** cheatgrass, cultivar, greenhouse, local genotype, Sandberg bluegrass, wild population

## Implications for Practice

- The source of seeds selected for restoration can influence seedling establishment and early performance at restoration sites.
- Cultivated varieties of native species are on average more vigorous than wild populations, and yet some wild accessions may perform as well as certain cultivars.
- Despite increased initial vigor, cultivars do not perform better on average than local plants when grown with *Bromus tectorum*.
- Given that intra-specific variation in performance among seed sources may alter patterns of dominance in restored plant communities, we recommend using representative local or regional seed sources when feasible.
- If competition with exotics is severe, a mix of seed sources encompassing more vigorous genotypes, as well as additional control measures, may enhance reestablishment of native plants at restoration sites.

## Introduction

Invasive exotic species are one of the greatest obstacles to rangeland 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 to annual-dominated systems (Mack 1981; Stubbendieck et al. 2011). Introduced species such as *B. tectorum* spread rapidly with land disturbance, and are highly competitive due to their rapid growth rate, early germination 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 invasion 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 (Brooks et al. 2004). A novel approach is the study of intraspecific diversity of native species used in reseeded restoration sites, which may play an important role in susceptibility and

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tolerance to biological invasion (Hooper et al. 2005; Crutsinger et al. 2008).

Guidelines for restoration of native species commonly recommend using local germplasm to maintain biodiversity, increase the likelihood that plants are adapted to site conditions, and improve long-term sustainability of reintroduced populations (Hufford & Mazer 2003; McKay et al. 2005; Jones 2013). However, local genotypes may no longer be adapted to altered environments in landscapes heavily impacted by biological invasion. In these cases, it is useful to investigate alternative sources of germplasm, such as cultivated, improved, or selected varieties of native species (hereafter 'cultivars'). Cultivars represent germplasm selected for improved vigor, seed germination, and biomass production (Lesica & Allendorf 1999; Johnson et al. 2010). Many cultivars are offered for commercial sale and are commonly used in restoration due to their increased availability and lower cost (Burton & Burton 2002). Vigorous, cultivated genotypes may be able 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. 2014). Further research is needed to compare cultivated seed sources to wild populations and to determine whether cultivars are more likely to establish in the presence of biological invasion.

This study compared cultivated and wild (local) accessions 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 and extensive root system, suggesting this species has the potential to compete with invasive, exotic species such as *B. tectorum* (Perry et al. 2009). Our objectives were to: (1) study differences in 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 on the invasive species, ultimately with the goal of understanding 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 early in the growing season. Because of its broad distribution and soil conservation value, several cultivars of *P. secunda* are available for purchase from commercial seed growers. We made comparisons of three wild accessions and three commercially available cultivar accessions recommended for use in our study region. At MPG

Ranch, a 10,000 acre conservation property in the Bitterroot Valley of western Montana, wild accessions were sourced from three distinct sites representing local populations and varying in elevation (1000–1300 m) and distance (3–6 km). Cultivated accessions included 'High Plains' sourced from Wyoming, 'Mountain Home' originating from Idaho, and 'Reliable' with origins in Washington (Majerus et al. 2009). During the summer of 2012, cultivar seeds were purchased from commercial seed growers, both wild *P. secunda* and *B. tectorum* seeds were collected at MPG Ranch, and all seeds were subsequently stored at room temperature (15–25°C) until planting in the greenhouse.

### Experimental Design

We conducted our experiment at the Research and Extension Center greenhouses in Laramie, Wyoming (elev. 2,184 m) in late 2012. Seeds were sown into 164 mL Ray Leach 'Cone-tainer' pots (Stuewe & Sons, Inc., Corvallis, Oregon, U.S.A.). 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 grown alone, 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 pooled control and competition treatments. This experimental design resulted in 360 controls planted with either *P. secunda* or *B. tectorum*, and 240 competition pots. Each pot was lined with cheesecloth to prevent the loss of planting medium while simultaneously allowing drainage, and pots were subsequently filled with 1:1 finely sieved sand and peat moss. 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 2 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 2 weeks, emerged seedlings were thinned to one plant per control pot, and one *Poa* and one *Bromus* 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 similar to the spring growing season. We monitored plants from December to March for an experimental duration of 4 months.

An initial survey determined that among variables of leaf count, plant height and width, plant width correlated strongly with aboveground biomass ( $r^2 = 0.84$ ;  $p < 0.001$ ) and we focused on this metric for analysis of plant growth. Data were recorded as the widest point of the base of each plant to the nearest millimeter. Measurements of plant width were taken every 5 weeks beginning 1 week after seeds were sown, for a total of

four consecutive surveys. After 4 months—a timeframe similar to that of *P. secunda*'s phenology in a field setting (Blaisdell 1958)—a final survey of survival was recorded for each plant, and aboveground biomass was harvested and dried in an oven at 60°C for 3 days. Dry weights were measured to 0.0001 g using an analytical balance (Mettler Toledo, Columbus, Ohio, U.S.A.).

Differences in seedling performance among *Poa* accessions may be a consequence of adaptive variation or maternal effects (Roach & Wulff 1987). Cultivated seed sources likely experience different maternal environments as a result of commercial production. To address maternal effects, we examined seed weight differences among sources. Ten groups of 50 seeds from original seed collections were weighed to 0.0001 g 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 *P. secunda* accession and competition treatment (Proc GLM; SAS version 9.3; SAS Institute Inc., Cary, NC, U.S.A.). 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 results of competition treatments differed for each seed source.

Plant width measurements were used as a proxy for plant growth and these data were  $\log_{10}$  transformed prior to analyses to meet assumptions of normality and homogeneity of variance (Zar 2010). A repeated-measures analysis was performed to determine how 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 also examined seed weight differences by performing a single-factor ANOVA. A general linear model analyzed the mean seed weight for all *Poa* accessions. As average seed

weight directly corresponded to each accession, it was examined separately from other analyses to test for evidence of maternal effects.

## Results

### Emergence

Ninety percent of experimental pots had at least one 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%) and this was probably the result of poor seed viability at the time of collection. After removing MPG-5 from analyses, 98% of experimental pots were included in the competition study. The number of pots was only reduced for MPG-10 (34 control pots and 33 competition pots). 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 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;  $p = 0.4636$ ).

### Survival

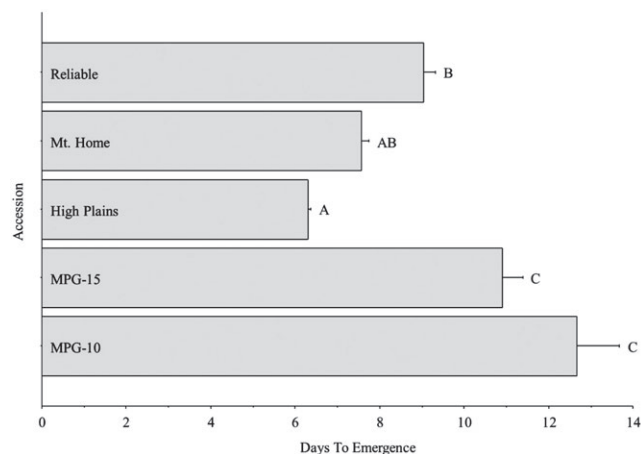
At the end of the study, Sandberg bluegrass survival was impacted by the main effects of accession and competition (Table 2). Wild and cultivated varieties of *P. secunda* had similar rates of survival ( $p = 0.8907$ ) and both groups had lower survival when in competition with *B. tectorum* (wild  $p = 0.0030$ ; cultivar  $p = 0.0148$ ). Among accessions, High Plains had the highest survival rate, but was only significantly greater than Reliable, which had the lowest number of survivors ( $p = 0.0433$ ; Fig. 2). Overall, plants in competition pots had lower survival than plants in control pots. There was no effect of competition with *P. secunda* on *B. tectorum* survival ( $p = 0.1695$ ).

### Plant Growth

*Poa secunda* plant growth was influenced by the interaction of accession, competition, and survey (Table 3). Overall, cultivars grew more rapidly than wild plants ( $p < 0.0001$ ). 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 (Fig. 3). Aboveground growth was consistent over time for all accessions for both competition treatments except for competing plants of MPG-10 and Reliable, which did not grow significantly larger between the last two surveys. Overall, cultivars High Plains and Mountain Home exhibited greater vigor than all other accessions, and this effect was consistent between control and competition

**Table 1.** ANOVA of *Poa secunda* average emergence among accessions and competition treatments.

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

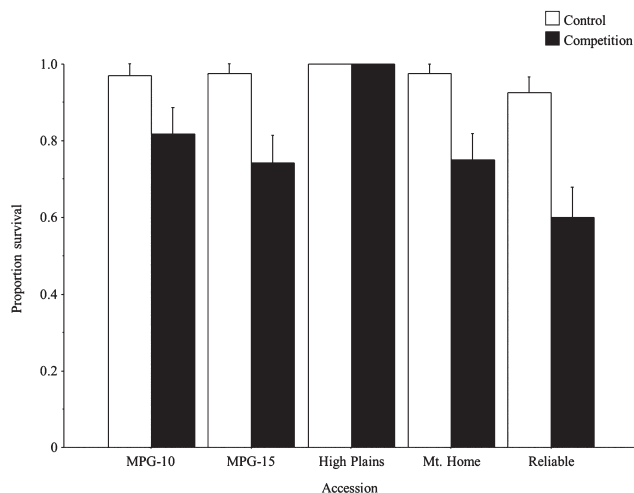
Figure 1. Average number of days until seedling emergence for each *Poa secunda* accession (+ 1 SE). Different letters denote significant differences among accessions ( $p \leq 0.05$ ).**Table 2.** ANOVA of *Poa secunda* survival at the end of the 16 week growing period.

Effect	DF	$\chi^2$	Prob. > $\chi^2$
Accession	4	10.23	0.0367
Competition	1	12.39	0.0004
Accession × competition	4	2.31	0.6780

treatments. *Bromus tectorum* plant growth increased over time ( $p < 0.0001$ ) but did not differ between control and competition treatments ( $p = 0.1993$ ).

### Biomass

*Poa secunda* aboveground biomass was influenced by accession and competition (Table 4). Cultivars produced greater aboveground biomass than wild plants in control pots ( $p < 0.0001$ ). 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 influenced only by competition ( $p = 0.0152$ ). However, *B. tectorum*

Figure 2. Average proportion survival per *Poa secunda* accession between non-competing and competing plants at the end of the 16 week growth period (+ 1 SE).**Table 3.** Repeated measures ANOVA of seed source and competition treatment effects on *Poa secunda* plant growth 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 4.** ANOVA of *Poa secunda* average aboveground biomass.

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

produced significantly greater biomass in competition pots relative to control pots (335 versus 315 mg between competition and control pots, respectively).

### Seed Weight

Average seed weight differed among *Poa* accessions ( $p < 0.0001$ ). Results of pooled contrasts indicated 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,

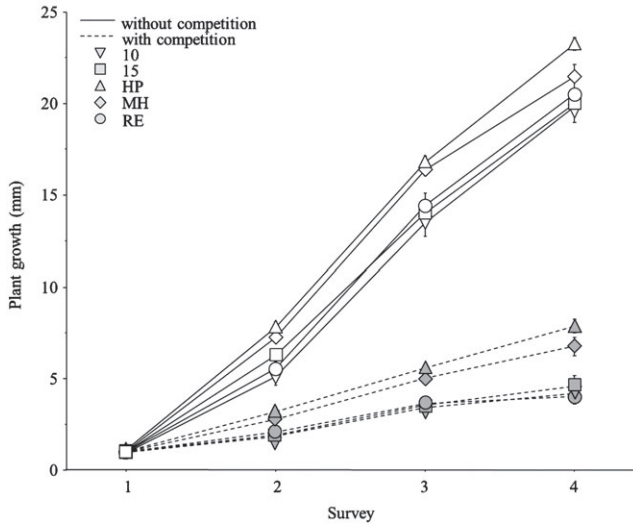


Figure 3. Average plant growth (estimated by plant width) per *Poa secunda* accession between non-competing (solid line) and competing plants (dashed line) measured at four surveys over a 16 week growth period ( $\pm 1$  SE).

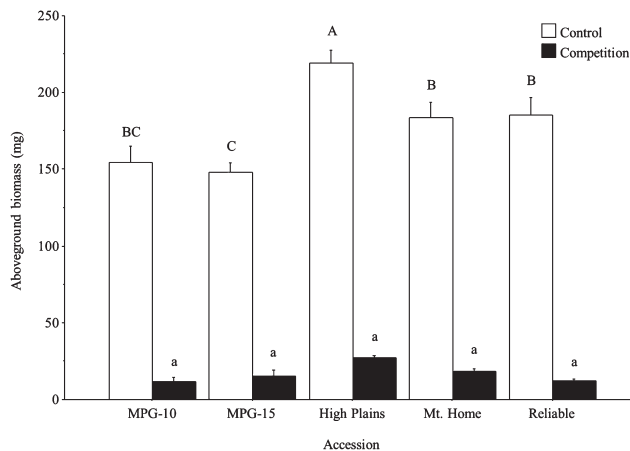


Figure 4. Average aboveground biomass of *Poa secunda* per accession between control (white) and competing plants (black) ( $\pm 1$  SE). Different uppercase letters denote significant differences among non-competing accessions ( $p \leq 0.05$ ). Different lowercase letters denote significant differences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

MPG-15, and MPG-10 (Fig. 5). 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 2013). We found significant differences between cultivated and wild accessions in control pots for all measured variables except survival, where differences were

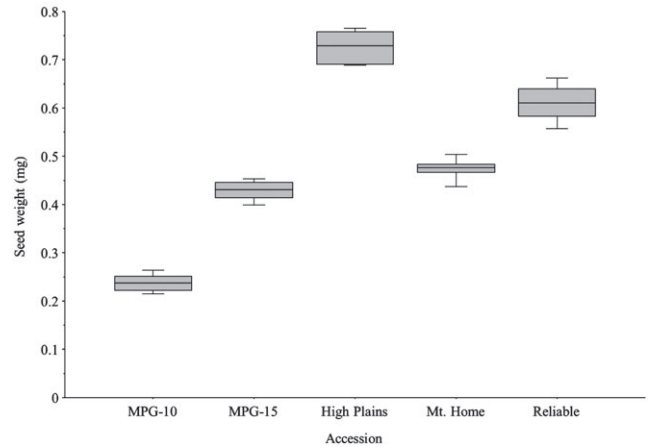


Figure 5. Box-and-whisker plots of *Poa secunda* seed weight among accessions. The median value is indicated by the central horizontal line, and the lower and upper quartiles by the corresponding horizontal ends of the box. The whiskers indicate the range of the data. All accessions are significantly different from one another ( $p \leq 0.05$ ).

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 plants were consistently greater than measures for other cultivated and wild accessions. Traits measured in the remaining cultivars were generally similar to, or greater than, the wild accessions. The greater vigor noted in native cultivars, however, may not be universal. A recent study determined that the source of seeds (wild or cultivated) of exotic species had no impact on measured traits, and exotics routinely outperformed native species (Wilsey et al. 2015).

Observed differences in *P. secunda* emergence and growth were likely due, in part, to maternal effects resulting from differences in seed weight (Roach & Wulff 1987). Seeds of the High Plains cultivar weighed more than seeds of all other accessions, and average seed weight for pooled 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 indicates that accession differences are due to multiple traits, rather than seed mass alone.

Contrary to our expectations, *P. secunda* 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 cultivars (High Plains and Mountain Home). In this case, both cultivars presented some evidence of greater tolerance of cheatgrass, and Mountain Home is noted for its use in reseeded post-fire restoration sites dominated by *B. tectorum*

(Lambert et al. 2011b). For survival and aboveground biomass, however, cultivars and wild accessions had similar values when in competition with *B. tectorum*. Regardless of source, there were significantly fewer survivors, reduced growth, and smaller aboveground biomass for *Poa* in competition compared to control pots. 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.

This study detected variation in emergence, survival and growth among cultivated and wild *P. secunda* seed sources in the first growing season. To determine the long-term effects of seed source and competition on *P. secunda* fitness, this research would benefit from further study in the field over multiple growing seasons. Vegetation at restoration sites is expected to experience increased competition over time, and fitness differences among seed sources may be more apparent in later life stages and for reproductive traits (Rice & Knapp 2008). 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) showed that local collections of *P. secunda* increased flower production when in competition with *B. tectorum* by allocating less energy to leaf production relative to non-competing plants.

Overall, *Bromus tectorum* survival and growth did not differ between competition treatments, although we noted greater aboveground biomass of cheatgrass 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 adapted to invasion by *B. tectorum* at their location of origin (Rowe & Leger 2011). Alternatively, Lowe et al. (2003) and Vasquez et al. (2008) reported an increase in *B. tectorum* biomass in competition with native perennial grasses, and hypothesized this was the result of greater use of available resources, so that the rapid growth rate of *Bromus* contributed to a positive feedback mechanism between size and resource uptake. The feedback loop was particularly evident with increasing available nitrogen. Field research is needed to evaluate the competitive response of *P. secunda* when grown in the presence of *B. tectorum* in local soils at restoration sites.

To conclude, evidence indicates that the source of seeds selected for restoration can influence seedling establishment and performance (McKay et al. 2005; Hufford & Mazer 2012).

When grown alone, native *P. secunda* cultivars were more vigorous than wild populations, although some wild accessions performed as well as cultivated accessions. Variation noted among individual *P. secunda* accessions, however, suggests that knowledge of early growth traits of different cultivated or wild populations may improve initial establishment at restoration sites. Additionally, the use of multiple wild or cultivated accessions may increase the odds that more vigorous genotypes such as High Plains are included in the seed mix (Lesica & Allendorf 1999; Kettenring et al. 2014). Despite consistent evidence for increased early vigor, cultivars did not perform better on average than wild populations when grown with exotic, invasive *B. tectorum*. Further study is needed to determine if increased vigor of native seed sources will improve initial establishment and long-term survival in the presence of exotic species (Wilsey et al. 2015). Given that intraspecific variation in performance among seed sources may alter patterns of dominance in native plant communities, we recommend the use of representative local or regional seed sources when feasible (Klopf & Baer 2011; Gustafson et al. 2014; but see Baer et al. 2014). 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.

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