

**Testing the cultivar vigor hypothesis: comparisons of the competitive ability of wild and cultivated populations of *Pascopyrum smithii* along a restoration chronosequence**

**Running head:** Cultivar persistence in restoration

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AP, KH, MP conceived and designed the research; MP performed the experiments; MP, KH analyzed the data; MP, KH, AP wrote and edited the manuscript.

**Abstract**

Restoration practitioners often rely on seeds of widely available cultivars representing native species but non-local germplasm. Cultivation improves the supply of plant materials and minimizes revegetation costs, but can also favor agronomic traits, and resulting vigor may affect the competitive ability and long-term persistence of cultivated genotypes at restoration sites. We compared cultivated, restored, and wild populations of *Pascopyrum smithii* (western wheatgrass) in a greenhouse study to test the extent to which cultivars outcompete local plants in biomass production, and to determine if morphological differences (including height and number of leaves) among cultivated and wild populations persist at restoration sites over time. We found evidence of vigor and greater competitive ability of cultivars in seed mass, growth rate, plant

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height and biomass and this advantage occurred when plants were grown alone or in competition with other seed sources. Cultivar vigor persisted at restoration sites over 30 years, but restored populations more closely resembled wild, local populations when cultivars were planted in closer proximity to nearby undisturbed sites. This study supports the cultivar vigor hypothesis and provides evidence for the long-term persistence of cultivated traits in the environment.

**Key words:** competition, grassland, greenhouse, local ecotype, plant materials

**Implications for Practice:**

- Cultivated varieties of native species planted in ecological restoration are often selected for agronomic traits and may outcompete nearby wild populations, potentially affecting community structure.
- Well-documented plantings along a time series or chronosequence may provide valuable evidence for long-term persistence of cultivars at restoration sites.
- Evidence of cultivar vigor and the persistence of cultivars in the landscape underscores the need for consideration of genetically appropriate plant materials in restoration programs.
- Understanding the consequences of mass reintroductions of plant materials will contribute to conservation of wild plant populations and improve risk assessment for revegetation outcomes in restoration.

**Introduction**

Ecological restoration is often dependent upon access to large quantities of native plant materials, and the source of propagules can significantly impact population fitness and

restoration outcomes (e.g., Gustafson et al. 2005; Byrne et al. 2011). Among populations of native species, genetic differentiation may result from adaptation to local environments, leading to higher fitness of seed sources in home sites (Kawecki & Ebert 2004). Use of local seed sources for revegetation is therefore often considered best practice to maintain adaptive variation and improve the odds of successful establishment (Linhart & Grant 1996; Hufford & Mazer 2003). Alternatively, non-local or composite seed sources may be recommended where restoration sites fall outside the range of historical environmental variability, and represent novel environments to which remnant, local populations may no longer be adapted (Broadhurst et al. 2008; Johnson et al. 2010).

In western North America, restoration practitioners often rely on seeds of widely available cultivars representing native species but non-local germplasm (Lesica & Allendorf 1999; Burton & Burton 2002). Cultivation improves the supply of plant materials and minimizes initial revegetation costs, but selection of cultivars can also favor agronomic traits such as prolific seed production, rapid germination (Schröder & Prasse 2013), altered stature (Lin et al. 1995), and increased biomass (Vander Mijnsbrugge et al. 2010; Dyer et al. 2016). As a result, cultivars may have a competitive advantage over wild plants of the same species, and their introduction risks introgression of undesirable genes or homogenization of gene pools through the swamping of local populations (Wilsey 2010; Lambert et al. 2011). For this reason, widespread use of cultivars in restoration, especially in the case of dominant species, may alter the structure of native plant communities and threaten ecosystem function (Whitham et al. 2006; Lankau & Strauss 2007, 2011; Gustafson et al. 2014). Despite these concerns, evidence for increased cultivar vigor relative to wild populations described as the “cultivar vigor hypothesis”, is mixed, and questions remain as to the competitive ability and long-term persistence of

cultivated genotypes at restoration sites (Wilsey 2010; Gibson et al. 2013; Carter & Blair 2013; Walker et al. 2014; Palik et al. 2016).

Patterns of intraspecific variation in competitive ability have been documented in numerous plant species, and competitive outcomes often depend on the source population (e.g., Mehrhoff & Turkington 1990; Violle et al. 2012). Relative competitive abilities among seed sources can be tested by comparisons of plants grown alone and in competition with individuals representing the same seed source, or an alternative seed source (Cahill et al. 2005). In this manner, the performance of cultivars and wild, local plants can be compared to test the hypothesis of greater cultivar vigor. Moreover, the inclusion in competition studies of plants derived along a chronosequence of restoration can determine whether cultivated traits persist in the environment or decline over time (Willand et al. 2013). If differences among wild and cultivated genotypes are no longer apparent at older restoration sites, evidence would suggest cultivars do not have a long-term advantage relative to wild, local plants, and it is unlikely that cultivated genotypes will swamp local genotypes among studied plant populations.

Alternatively, if differences in seeded and wild populations persist over time among reclamation and undisturbed sites, and nearby wild populations grow to resemble cultivated varieties, cultivated genotypes may have a long-term impact on population fitness and the surrounding plant community.

In this study, we compared growth traits and competitive ability of restored and wild populations of *Pascopyrum smithii* collected along a restoration chronosequence to determine: (1) to what extent cultivars outcompete local plants, supporting the hypothesis of greater vigor of cultivars relative to wild populations, and (2) whether differences among cultivated and wild populations persist over time. Our objective was to investigate the potential for cultivated

genotypes to swamp local populations in landscapes subject to large-scale restoration. Despite widespread planting of cultivated varieties of native species, little is known about their potential to alter plant population and community dynamics (Gustafson et al. 2004; Lambert et al. 2011; Dyer et al. 2016). Studies to determine the extent to which cultivars remain in the landscape contribute to the identification of genetically appropriate seed sources for ecological restoration and improve guidelines for restoration seed sourcing (see review in Johnson et al. 2010).

## Methods

### *Study Site*

The Dave Johnston Mine (DJM), located near Glenrock, Wyoming in the Powder River Basin, produced 104 million tons of coal during its operation from 1959 to 2000 (Fig. 1; Osmonson et al. 2011). Post-mining reclamation occurred over a period of more than 30 years, and seeded species consisted primarily of a mix of warm and cool season grasses, but also included a small number of forbs and shrubs (Chet Skilbred, PacifiCorp, personal communication). Reclaimed areas were closed to grazing by livestock, but remained accessible to wild ungulates, including *Antilocarpa americana* (pronghorn) and *Odocoileus hemionus* (mule deer). The former coal mine site is currently an operational wind farm, and large areas of the original restoration chronosequence remain intact. Annual precipitation near Glenrock ranges from 254–355 mm and the average annual temperature is 8.86 °C. Elevation is approximately 1500 m and surrounding rangelands represent a sagebrush-steppe ecosystem supporting domestic livestock as well as wildlife. Sampled sites consist of shallow soils with a sandy loam texture (Wick et al. 2009) and the reclaimed area occurs in a matrix of relatively undisturbed rangeland.

### *Study Species and Seed Collections*

*Pascopyrum smithii* (Rydb.) A. Löve (western wheatgrass) is a cool-season, C<sub>3</sub>, perennial grass species native to North America (Dorn 1992). Plants are wind pollinated and evidence supports an outcrossed mating system (Jones & Larson 2005). Western wheatgrass is commonly planted in revegetation programs due to the soil stabilizing properties of its rhizomatous root system and forage value for livestock and wildlife (Ogle et al. 2009). Several cultivars of *P. smithii* are commercially available, including the cultivar ‘Rosana,’ which is commonly planted in the Intermountain West (Jones & Larson 2005). Rosana was originally collected near Forsyth, Montana in 1959 and released for commercial production in 1972 after selection for traits such as rapid establishment and seedling vigor (Alderson & Sharp 1994; Winslow 2010).

Although the species seeded in post-mining reclamation at the DJM varied over time, western wheatgrass was consistently included in the seed mix. Between 1972 and 2001, approximately 600 hectares were planted with over 5000 lbs. of the Rosana cultivar, allowing comparisons of reclaimed populations over large time intervals. For this study, we collected seeds in August of 2014 from three sites along the restoration chronosequence originally planted in 1979, 1988, and 1998 and likely representing a mix of original cultivars as well as their progeny and other seed sources. These source populations were compared with a commercial source of Rosana provided by the same company (Granite Seed, Denver, CO) that supplied the DJM, and seeds collected from two wild populations located on nearby, undisturbed rangeland (Table 1). Wild populations were collected in cooperation with local land managers to minimize the risk that plantings had occurred at those sites, and were representative of the surrounding landscape. Seed collections from a minimum of 40 plants were made along two or more 50 m transects to sample a large area of each undisturbed or reclaimed site, including each site along

the restoration chronosequence. Sampling along each transect was designed to minimize collecting seeds from related individuals. All seeds were cleaned and stored at room temperature (20–25°C) for several months prior to planting this experiment. Voucher specimens were collected for each population and submitted to the Rocky Mountain Herbarium (Laramie, WY).

### ***Experimental Design***

We conducted the greenhouse study to assess differences in morphology and competitive ability among differently-aged, restored and wild populations of *P. smithii*. The experiment was designed as a randomized complete block design with three blocks. Seeds were sown into trays containing a 1:2 ratio of sand and potting medium and placed on a greenhouse mist bench. Lots of twenty seeds were weighed for each population prior to sowing to test potential maternal effects (Roach & Wulff 1987). After approximately two weeks, seedlings from each population and block were selected at random and planted into medium (3.8 cm diameter, 21 cm depth) conetainers™ (Stuewe & Sons, Corvallis, Oregon, USA). Pots were watered every two days. A total of 378 pots representing each source population (n=6 sources, with 63 replicates of each) were planted with a single seedling in the center of the pot. Competition pots were planted with two seedlings of similar size and at equal distances in each pot, representing all possible combinations of the six source populations (n=21 combinations, with 9 replicates of each) for a total of 189 pots. Competing plants were distinguished by randomly marking one plant in each pot with an orange plastic ring placed around the base of the plant that did not interfere with plant growth. Plants were fertilized weekly using Jack's 15-5-15 Cal-Mag applied with a mechanical dispenser (Dosatron) at a ratio of 1:100.

We measured initial plant height (from the base of the seedling to the tip of the longest leaf) once seedlings were transplanted to the small containers. Thereafter, plants were evaluated approximately every 10 days for height (cm), width (cm), and total number of leaves. Leaf number data were only collected for the first four surveys to ensure accuracy. Prior to the fourth survey, plants were transplanted into larger (6.35 cm diameter, 25.4 cm depth) containers to prevent root binding. All plants were transplanted at the same time, with minimum disturbance to seedlings. A total of 10 surveys were conducted over the course of the three-month study. At the end of the study, plants were harvested and aboveground biomass was dried in an oven at 60°C and weighed to the nearest 0.001 g (Mettler Toledo, Columbus, Ohio, USA).

### ***Data Analysis***

To test for maternal effects, differences in average seed weight among the six source populations were examined with a single-factor ANOVA using a general linear model. In a pilot study of *P. smithii* plants, regression analysis of the product of plant height and plant width was significantly correlated with total aboveground biomass (dried weight,  $r^2 = 0.72$ ,  $p < 0.0001$ ). The product of these two variables represented plant growth, and data were cube-root transformed to normalize residuals and meet assumptions of ANOVA (Zar 2010). Subsequently, plant growth and leaf number data (square-root transformed) were analyzed in separate tests using a repeated measures model in SAS software (Proc MIXED, SAS Institute Inc., Cary, NC, USA). Blocks were considered to be random while the source population and competition treatment were fixed factors. Initial plant height measured at the start of the experiment was included as a covariate. A first-order autoregressive covariance structure was incorporated into each analysis to account for correlation among repeated measurements and degrees of freedom were calculated using the



Satterthwaite approximation (Littell 2006). A total of 3022 and 7545 observations from 756 individuals were included in repeated measures analysis of leaf number and plant growth, respectively, representing all relevant surveys and excluding missing observations.

Given that plant height, or stature, may distinguish cultivated and wild populations of *P. smithii*, we conducted a mixed-model ANOVA using height for survey no. 9, the survey at which plant productivity was greatest and most representative of overall growth observed prior to plant senescence. We hypothesized that cultivars would differ from wild populations due to a harvest advantage of taller plants in cultivation. These results were compared with plant growth data.

Total aboveground biomass was analyzed with a mixed-model ANOVA, including the fixed factors of competition treatment and source population. Initial plant height served as the covariate and blocks were considered random effects. Preliminary tests indicated biomass measurements met assumptions of analysis of covariance and transformations were unnecessary. Degrees of freedom were estimated using the Satterthwaite approximation. In each analysis, we compared differences among source populations and competition treatments using least square means that were adjusted for multiple comparisons using the Tukey-Kramer procedure (Zar 2010). We also contrasted biomass among plants grown singly and plants grown in competition using Mantel tests to determine if differences among source populations when plants were grown alone in pots correlated with differences among source populations in competition (Miller & Schemske 1990).

Lastly, we calculated the distance among paired collection sites to further test differences among reclaimed and undisturbed source populations. We conducted Mantel tests to determine to what extent population differences in biomass were a function of site proximity using distance matrices and either biomass of plants grown alone in pots, or plants grown in competition. We

hypothesized that differences in growth and competitive ability along the restoration chronosequence were correlated with space (or the potential for gene flow among source populations) as well as time (Garant et al. 2006).

## Results

### *Seed Weight*

Differences in average seed weight were significant among the source populations ( $p < 0.0001$ ; Fig. 2). Seeds of the cultivar Rosana were significantly larger ( $p < 0.0001$ ) than those collected from the restoration plantings and the surrounding wild populations, indicating potential maternal effects resulting from commercial production. Seeds collected from sites at the DJM were not significantly different in weight from those of the wild populations ( $p = 0.2257$ ), suggesting there was no maternal advantage of seed weight for plants growing at reclamation sites relative to plants growing in nearby, undisturbed rangeland.

### *Plant Growth and Height*

Differences in growth among *P. smithii* plants were a function of source population, competition treatment, survey date, and initial plant height (Table S1;  $p = 0.0085$ ). There was no significant effect of block in the full model, and the block term was removed from subsequent analyses. Overall, the Rosana cultivar grew significantly larger than all other seed sources (Fig. 3;  $p < 0.0001$ ). Plants sourced from reclamation sites at the Dave Johnston Mine also grew significantly larger than plants sourced from two, nearby undisturbed sites ( $p < 0.0001$ ) primarily as a result of the relatively shorter plants from population EastG, and plants grown in competition were significantly smaller than plants grown alone for all populations sampled (Fig.

3;  $p < 0.0001$ ). There was a significant effect of survey date reflected in both two-way interactions of survey and competition or population, as well as a significant three-way interaction of source population, competition and survey. There was no significant effect of the source population  $\times$  competition interaction ( $p = 0.3689$ ), indicating source populations grew at similar rates between competition treatments and suggesting that the three-way interaction was a function of the survey date, or plant growth over time.

Upon closer examination, plant growth differed significantly among all paired survey dates (least square means, Tukey-Kramer test,  $p < 0.0001$ ). Results of contrasts indicated the cultivar Rosana grew significantly faster than all other source populations except for the comparison of Rosana with the population most recently planted along the chronosequence (DJM98,  $p = 1.000$ ). In addition, growth of Rosana individuals was lowest when competing with another Rosana plant or an individual representing DJM98. Comparisons between the two undisturbed sites suggested these populations also differed in plant growth rate over time ( $p < 0.0001$ ). Lastly, the Rosana cultivar proved significantly taller than wild populations (Fig. 4;  $p < 0.0001$ ). Rosana did not differ in height when compared to DJM98 ( $p = 0.9886$ ), but was taller when compared with DJM79 ( $p = 0.0555$ ) and DJM88 ( $p = 0.0191$ ).

### ***Leaf Number***

Leaf number was affected by the source population and competition treatment, but not their interaction, and initial plant height was not significant and was removed from analysis (Table S2). The average number of leaves was lower in the competition treatment ( $p < 0.0001$ ) and plants representing the Rosana cultivar had on average a greater number of leaves than all other source populations ( $p = 0.0207$ ). This affect was primarily due to differences among Rosana,

DJM88 and the EastG wild population (Fig. 4B). The difference among cultivar plants and wild populations was not apparent along the chronosequence, and populations of planted cultivars sampled along the restoration chronosequence had similar leaf numbers relative to populations from undisturbed sites ( $p = 0.9005$ ). The average leaf number did not differ between the two wild populations ( $p = 0.2073$ ).

### ***Biomass***

Results of analysis indicated final aboveground biomass was a function of initial plant height, source population, competition treatment, and the interaction between source and treatment (Table S3). Similar to plant growth data, average biomass of Rosana was significantly greater than biomass of all other seed sources ( $p < 0.0001$ ), and plants in competition were significantly smaller than plants grown alone in pots ( $p < 0.0001$ ). In this case, the source population  $\times$  competition interaction was significant ( $p = 0.0452$ ), indicating the effect of competition on biomass depended on the seed source. Rosana biomass was lowest when grown in competition with Rosana or DJM98 (Fig. S1). Average biomass did not differ significantly between the two wild populations ( $p = 0.3450$ ; Fig. 4C). Average biomass did differ significantly in pairwise comparisons of wild populations, Rosana, and all populations along the chronosequence, with the exception of DJM88 and RanchR, two sites in close proximity to one another. Upon further examination, the significant difference in biomass among Rosana and plants sourced from sites along the restoration chronosequence was solely an effect of Rosana and DJM88, indicating average biomass did not change over time but instead remained constant among Rosana, DJM79 and DJM98 plants regardless of competition treatment. Other factors such as proximity to wild populations may have impacted the average biomass of population DJM88. When comparing

biomass of plants grown alone versus plants in competition, we found a significant positive correlation indicating relative competitive abilities of source populations remained consistent across competition treatments ( $r = 0.8282$ ,  $p = 0.0239$ ).

### ***Spatial Variation***

Mantel tests demonstrated a significant relationship between population distance and biomass among non-competing plants ( $r = 0.5087$ ,  $p = 0.0167$ ) suggesting that populations sourced closer to each other were more similar than populations located farther apart. Results were not significant, however, for comparisons of competing plants ( $r = 0.5087$ ,  $p = 0.2250$ ). Effects of competition on biomass were likely much greater than the effect of proximity of source populations.

### **Discussion**

The “cultivar vigor hypothesis” proposes that cultivated varieties of native plants have an increased ability to capture resources, providing a competitive advantage relative to wild, local genotypes (Wilsey 2010). While our study was limited to available populations along a 30-year chronosequence, results support the cultivar vigor hypothesis for the Rosana cultivar of *Pascopyrum smithii*. On average, the commercially-sourced cultivar had significantly larger seeds, more rapid growth, superior height, and greater biomass production relative to plants sourced from wild populations. This advantage was apparent both when plants were grown alone and when plants were grown in competition. As a result, the *P. smithii* cultivar is favored in both competitive and non-competitive environments, increasing the potential that community dynamics are altered at sites seeded with cultivated varieties of this dominant, rhizomatous grass

species (Miller & Schemske 1990; Bolnick et al. 2011). Cultivated plants also had a larger average number of leaves, but this difference was not consistent among cultivated and wild source populations. Overall, our findings are in agreement with traits screened in the original Rosana source population, including rapid establishment and seedling vigor (Winslow 2010; Ogle et al. 2009).

Cultivar seeds grown in commercial fields may be larger than seeds derived from non-commercial populations as a result of differences in the maternal growing environment (Roach & Wulff 1987). While commercially supplied Rosana seeds in this study were significantly larger than any other source, the average seed weight of collections from restored sites representing Rosana plantings over two decades did not differ from wild populations. Yet plants from those populations were more vigorous on average than plants derived from wild populations. This result suggests that the greater vigor of plants from restored sites was not a result of maternal seed provisioning. However, maternal effects may influence plant traits beyond seed size (Bischoff & Müller-Schärer 2010) and it is feasible that maternal traits such as adult plant size or competitive ability contributed to cultivar vigor in sampled populations (e.g. Espelend & Hammond 2013). Further testing is therefore needed to distinguish maternal effects and adaptive traits (Mousseau & Fox 1998). We note our study occurred in a common greenhouse environment with seedlings that were germinated prior to competition testing, reducing the effect of environmental variation among sources.

Other studies have found mixed evidence of cultivar vigor when testing morphological and physiological differences among cultivated and wild grasses. Gustafson et al. (2004) studied competition among *Andropogon gerardii* local, non-local, and cultivated seed sources, and found evidence of cultivar vigor relative to wild local and non-local populations. Lambert et al. (2011)

found evidence of a cultivar advantage for physiological traits measured in three dominant tallgrass prairie species. Similarly, Palik et al. (2016) compared local genotypes to cultivars of *Panicum virgatum* to assess the potential for cultivated populations to become invasive, and found two of four cultivars were more vigorous, and those cultivars were most recommended for planting by seed suppliers. In contrast, no evidence of vigor in plant growth was discovered in comparisons of commercial and wild sources of the native bunchgrass, *Elymus glaucus* (Fonseca et al. 2014), and comparison of *Sorghastrum nutans* seed sources detected no differences in primary production, net mineralization rate, or soil carbon accrual among cultivated and wild genotypes (Baer et al. 2013). Additional research is needed to assess not only cultivar vigor, but also the consequences of selected traits for competitive interactions and plant community composition in restored systems. Further studies would benefit from field experiments to compare competitive outcomes of cultivars and wild populations in field conditions.

Our second objective was to determine if traits associated with the Rosana cultivar persisted in the environment. Rosana sourced from commercial suppliers was virtually indistinguishable from DJM98, the most recently planted population along the chronosequence (established 15 years prior to this study). This suggests that DJM98 plants continue to represent the Rosana cultivar. The DJM88 population least resembled traits of Rosana cultivars, suggesting some evidence for introgression of wild populations at restoration sites after 26 years. However, few differences were apparent between the commercially grown Rosana and the oldest chronosequence population, DJM79. Persistence of planted populations in the broader landscape likely depends on the distance from nearby wild populations as well as the time since planting, and evidence suggests that the proximity of DJM88 to nearby undisturbed sites facilitated gene flow in that location (Loveless & Hamrick 1984). To summarize, we found evidence of a faster

growth rate, taller stature and greater biomass in populations seeded at the DJM, contrasting with the smaller stature and lower biomass of local, wild populations. Given these data, traits attributed to the Rosana biotype have persisted for over 30 years at this restoration site.

Many studies have compared restored and remnant wild population genetic diversity, often finding restored populations are less diverse than nearby wild populations (e.g., Gustafson et al. 2002; Dolan et al. 2008; Fant et al. 2008). However, few have attempted to document not only the composition, but also the fate of native plant materials seeded at restoration sites. Gustafson et al. (2001) found evidence for persistence of introduced *Andropogon gerardii* genotypes at tallgrass prairie restoration sites for at least 20 years, although authors did not test cultivar vigor. Rydgren et al. (2015) determined that three of five species seeded on spoil heaps persisted in large numbers 20–30 years post-restoration with little increase in cover, but authors did not differentiate seed sources. Chamberlain et al. (2012) examined persistence of cultivated and locally harvested sources of *Andropogon gerardii* and *Sorghastrum nutans* under rotational grazing and detected no differences in persistence over two years, but did not follow plantings any longer. Our study therefore represents one of the first to track the long-term persistence of cultivars in ecological restoration. The use of a well-documented chronosequence was essential to assess changes in planted populations of *P. smithii* over time (Baer et al. 2002).

Results that support not only cultivar vigor in *P. smithii*, but also increased competitive ability and persistence of cultivated traits raise concerns about the long-term effects for plant community dynamics at restoration sites (Wilsey 2010). Vigorous, cultivated genotypes may pose a risk for swamping wild populations, and potentially invading new regions previously unoccupied by that species (Palik et al. 2016). In addition, large-scale seeding of cultivars may impact soil nutrient availability through increased root allocation and nutrient uptake (Klopf &



Baer 2011), invertebrate richness through enemy release (Vandeghechuchte et al. 2012), and competitive interactions between forbs and dominant grasses (Walker et al. 2014). In this study, sampled nearby, undisturbed populations of *P. smithii* did not resemble cultivars more than 30 years after restoration plantings. Instead, we discovered that plants at the DJM88 site, representing the mid-point of the chronosequence, more closely resembled nearby wild (RanchR) populations. This result suggests that despite the large-scale revegetation program at the DJM, the surrounding matrix of wild populations maintains a pool of local diversity and may have the potential to swamp cultivars in the relatively smaller mine site. In addition, we cannot determine whether *P. smithii* cultivars or local populations are better adapted to site conditions. Traits required for population persistence in arid environments, such as the root to shoot ratio, often differ from traits selected in cultivation, and further investigation is needed to identify the impacts of cultivar vigor over time (Kulpa & Leger 2013).

In summary, our evidence points to persistence of the Rosana cultivar long after initial plantings, with the potential for swamping by local genotypes that are more abundant in the area and possibly better suited to local environmental conditions (Hufford & Mazer 2003). However, complete integration has not occurred within a time frame of 30 or more years post planting as evidenced by the persistence of Rosana cultivar traits. We studied traits in a limited number of source populations grown in a controlled environment. Interpretation of results would improve by pairing phenotypic studies with studies of genetic markers distinguishing cultivars and wild populations (underway in *P. smithii*), and ultimately linking intraspecific variation to community structure (Crutsinger et al. 2006). Furthermore, molecular marker studies could determine the genetic basis for intracultivar variation and contribute to predictions of the likelihood of swamping or other risks of large-scale cultivar introductions at restoration sites.

Wild source populations included in this experiment differed from DJM populations, but may not have captured the range of phenotypic variation represented in the broader environment. Nevertheless, the close match in measured traits among commercial Rosana and DJM populations suggests that significant differences exist among cultivated and wild genotypes, and those differences persist over many years. Our understanding of the fate of cultivated varieties in the landscape will improve with a growing number of studies that test cultivar vigor in a range of species and also examine the consequences of large-scale seeding efforts for native plant community dynamics (Kettenring et al. 2014). Given the potential for genetic swamping and loss of allelic variation among local populations, caution should be exercised when selecting seed sources in restoration, and careful records of seed sources and planting locations will assist with assessment of restoration success, and long-term outcomes for plant community diversity (Knapp & Rice 1994).

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Table 1. Source population, location of origin (including latitude and longitude where available), the collection status of each population, and the representative genotype for original cultivars, three mine sites and two wild populations of *Pascopyrum smithii*.

Source	Latitude	Longitude	Status	Genotype
Rosana	*	*	Cultivar	Rosana
DJM98	43.00523	-105.793659	Chronosequence	Rosana
DJM88	43.07966	-105.855797	Chronosequence	Rosana
DJM79	43.06646	-105.859516	Chronosequence	Rosana
EastG	43.08929	-105.826533	Undisturbed	Wild
RanchR	43.09639	-105.857449	Undisturbed	Wild

Figure 1. Collection location for all source populations. On the left, stars indicate the original collection site of Rosana in 1959 near Forsyth, Montana and to the south, the location of the Dave Johnston Coal Mine (DJM) near Glenrock, Wyoming. To the right are seeded restoration areas at the DJM with points indicating each collection site. Populations RanchR and EastG represent wild populations. Populations DJM79, DJM88, and DJM98 represent planted restoration populations established in 1979, 1988, and 1998 respectively.

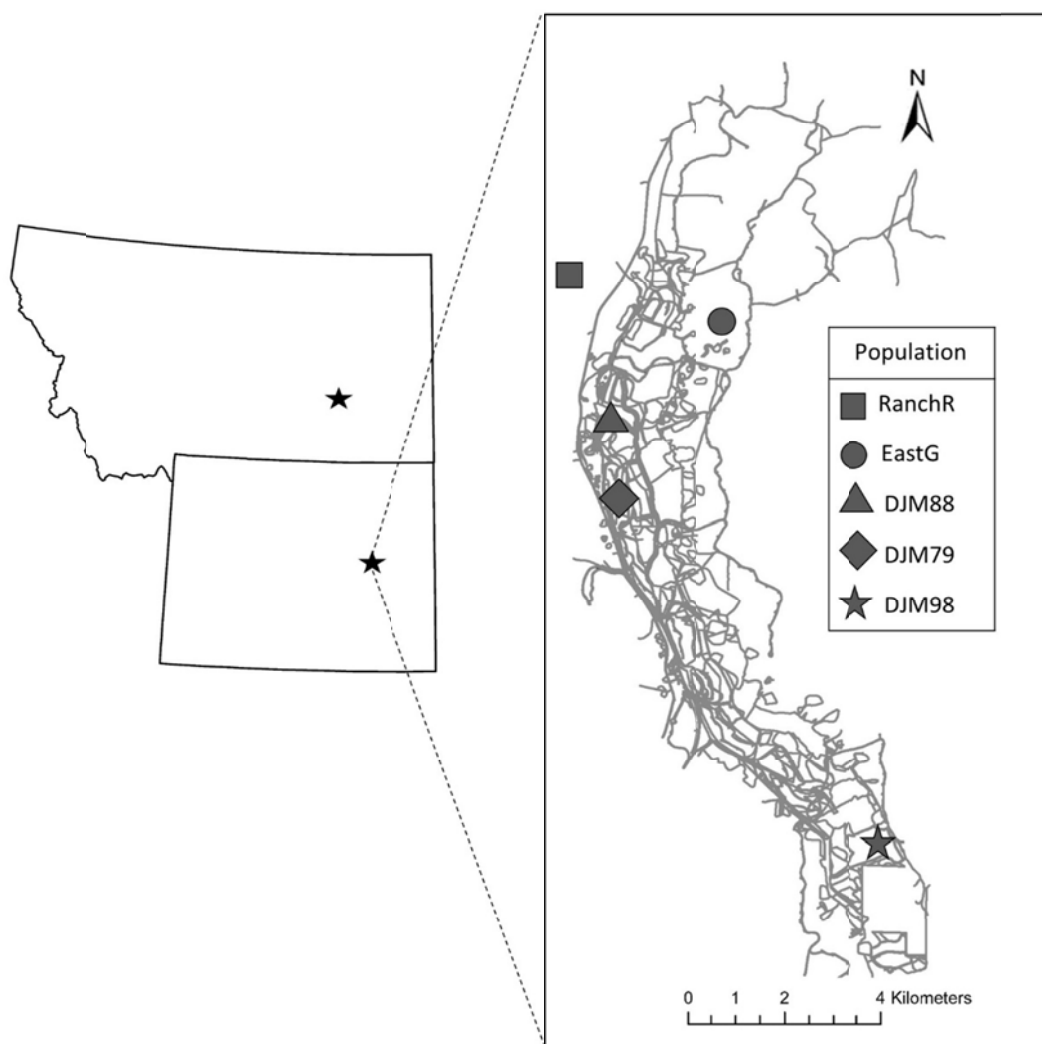


Figure 2. Box plots for seed weight of the six source populations of *P. smithii*. The length of each box represents the interquartile range, whiskers delimit the 10<sup>th</sup> and 90<sup>th</sup> percentiles and the line within each box represents the median seed weight.

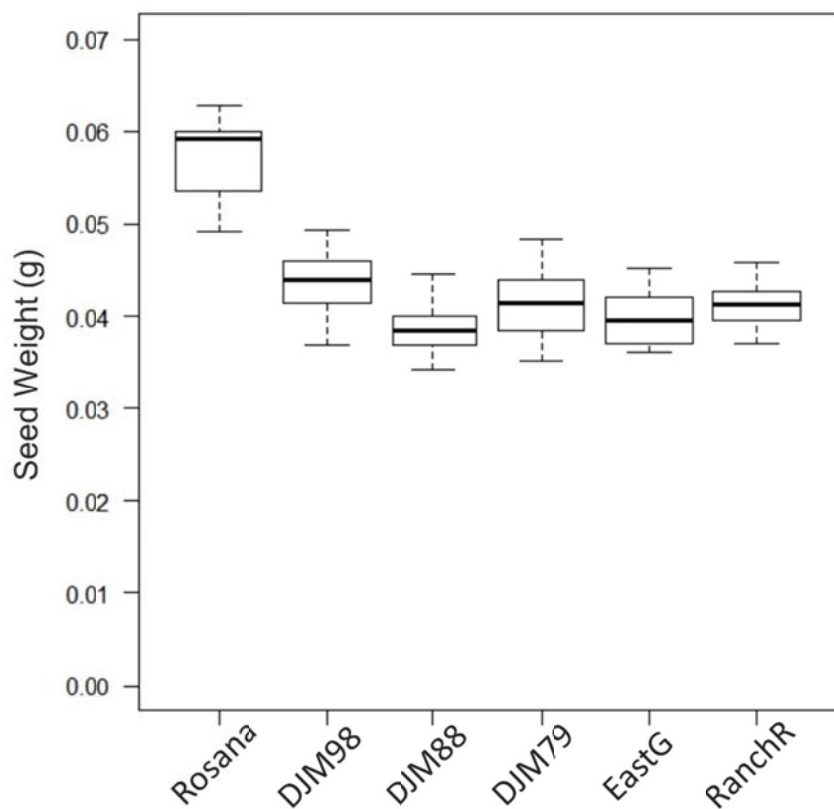


Figure 3. Plant growth (area in  $\text{cm}^2$ ) over ten surveys ( $\pm$  SE) for six seed sources of *P. smithii* grown alone or in competition. Note differences in y-axis scale between graphs.

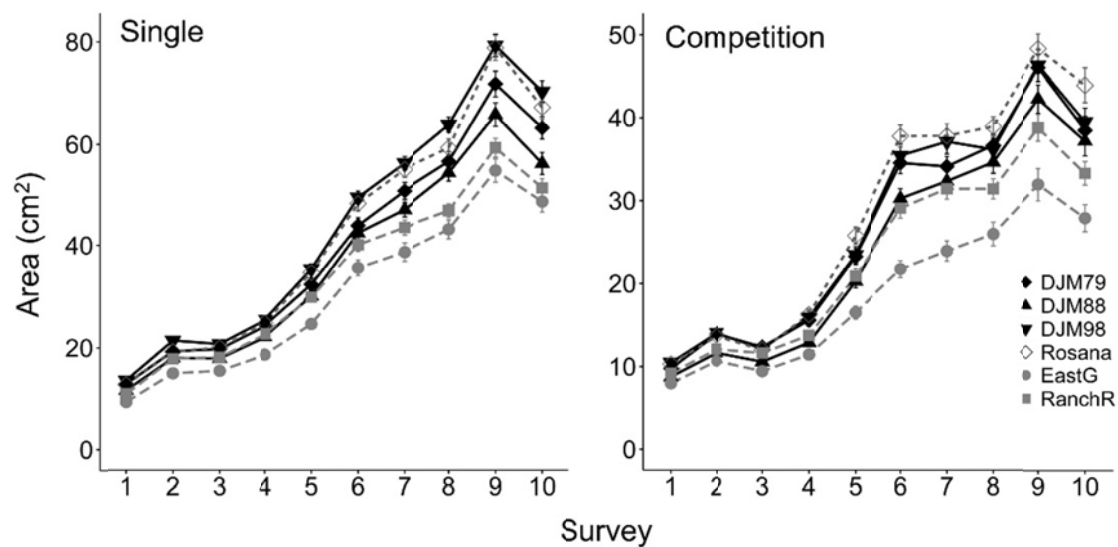




Figure 4. Variation among *P. smithii* seed sources grown alone or in competition for: (A) maximum height at survey 9, (B) mean leaf number at survey 4, and (C) average biomass. Seed sources include chronosequence populations (DJM98, DJM88, DJM79), the cultivar Rosana, and local populations (EastG, RanchR).

