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Plasticity in native perennial grass populations: Implications for restoration

Erin K. Espeland[1] | Richard C. Johnson[2] | Matthew E. Horning[3]

[1]Pest Management Research Unit, USDA-ARS, Sidney, MT, USA

[2]Plant Germplasm Introduction and Testing Research Unit, USDA-ARS, Pullman, WA, USA

[3]Deschutes National Forest, USDA Forest Service, Bend, OR, USA

Correspondence
Erin K. Espeland, USDA-ARS Pest Management Research Unit, Sidney, MT, USA.
Email: erin.espeland@ars.usda.gov

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Abstract

Increasing the evolutionary potential of restored populations has become a viable objective of restoration activities. Choosing plant materials genetically adapted to the restoration environment is critical for success, and phenotypic plasticity may also contribute to establishment and persistence in disturbed environments. To select seed sources for restoration informed by plasticity, we must answer the question: Do some source environments produce more plastic genotypes than others? Using a dataset of maternal families from 130 western US source populations of the perennial bunchgrass *Poa secunda*, we used variance components to determine the contribution of source population to phenotypic plasticity in two common gardens over two growing seasons. Compared with the genetic contribution to phenotypes, plasticity explained a large fraction of phenotypic variation and was particularly strong for phenology (timing of reproductive events) traits. Plasticity values among phenology traits were also highly correlated. For the morphological traits (panicle length, leaf size) and survival, the genetic contribution to the phenotype was greater than the plastic contribution, but plasticity values among these traits were not highly correlated. Seeds collected from warm and dry locations produced plants with more plasticity in phenology, panicle number, and biomass; cool and wet locations were associated with more plasticity in leaf size, panicle length, plant habit (prostrate or erect), and survival. Plasticity may complement genetic variation for adaptation in restoration materials in some traits.

KEYWORDS

adaptive plasticity, genecology, intraspecific variation, phenotypic integration, Sandberg bluegrass

1 | INTRODUCTION

Plants have the capacity to sense and respond to their environment. Plasticity, or the gene-by-environment interaction, is a deviation of the expression of a genotype (i.e. phenotype) from the mean phenotype across all environments (Bradshaw, 1965; Scheiner & Goodnight, 1984) and is an important component of evolutionary potential: phenotypic variation linked to fitness variation describes the opportunity for selection at the population level (e.g. Espeland & Rice, 2012). In addition to choosing adapted restoration materials, evolutionary potential of restored populations is becoming increasingly important for creating resilient populations in the context of climate change, other anthropogenic disturbances, and continual introductions of invasive species (e.g. Jump & Penuelas, 2005; Sgro, Lowe, & Hoffmann, 2011). Studies showing that plasticity is favored under climate change scenarios are accumulating (reviewed in Franks, Weber, & Aitken,

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2013; Nicotra et al., 2010; Matesanz, Gianoli, & Valladares, 2010). Also, plant populations with greater plasticity have higher population growth rates (Davidson & Nicotra, 2012; Lavergne & Molofsky, 2007; Leffler, Monaco, & James, 2011; Muth & Pigliucci, 2007; Skalova, Havlickova, & Pysek, 2012; but see Peperkorn, Werner, & Beyschlag, 2005). Understanding the contribution of plasticity to plant traits responsible for establishment and persistence (Albert, Grassein, Schurr, Vielledent, & Voille, 2011) benefits strategic choices of seed sources for restoration. Seed source choices are becoming more sophisticated with the application of seed zones and other climate model-driven approaches (e.g. Bower, St. Clair, & Erickson, 2014; Espeland & Rice, 2012; Johnson, Horning, Espeland, & Vance-Borland, 2015; Kramer, Larkin, & Fant, 2015) and projected future climate scenarios (e.g. Vitt, Havens, Kramer, Sollenberger, & Yates, 2010). In these cases, care is taken to choose seed source populations that are pre-adapted to the restoration site (but see Jones, 2013).

Fitness variation (i.e. opportunity for selection), mean fitness, genetic variation, and heritability of traits are all important contributors to evolutionary potential (e.g. Broadhurst et al., 2008; Ghalambor, McKay, Carroll, & Reznick, 2007; Kettenring, Mercer, Reinhardt Adams, & Hines, 2014; Sgro et al., 2011). Plasticity influences the mean and variation in fitness. In some cases, plasticity may be functionally heritable via genetics (e.g. Schlichting, 2008), epigenetics (Nicotra et al., 2010), and/or a high correlation between the environments of parent and progeny (as in Espeland & Rice, 2012). Genetic assimilation of plasticity can occur when selection reinforces reductions in fitness variation (Eshel & Metessi, 1998; Pal & Miklos, 1999). Plasticity may increase evolutionary rates and promote adaptation in changing environments (Bonduriansky, Crean, & Day, 2012; Eshel & Metessi, 1998; Laland, Sterelny, Odling-Smee, Hoppitt, & Uller, 2011; Pal & Miklos, 1999;). The clear advantage of increasing evolutionary potential to overcome maladaptation to new environments has been shown in numerous studies on genetic diversity (e.g. Lavergne & Molofsky, 2007; Matyas, 1996) and effective population size (e.g. Ellstrand & Elam, 1993; Willi & Hoffmann, 2009).

We know little about the genotypes that do well in restoration of disturbed sites; in contrast to the large literature affirming local adaptation (Hereford, 2009; Joshi et al., 2001; Leimu & Fischer, 2008; Linhart & Grant, 1996), other studies show that local collections perform suboptimally when transplanted to nearby locations (e.g. Bischoff, Steinger, & Muller-Sharer, 2010; Grady et al., 2011; Rehfeldt, Ying, Spittlehouse, & Hamilton, 1999; but see Bucharova et al., 2016). Plant seed used for restoration is often chosen from local populations (Broadhurst et al., 2008; USDI & USDA 2002; Vander Mijnsbrugge, Bischoff, & Smith, 2010), assuming widespread local adaptation in plants (Hereford, 2009; Joshi et al., 2001; Leimu & Fischer, 2008; but see Gibson, Wagner, Espeland, & Nelson, 2016). Seed zone research for restoration links genetic adaptation to climate (e.g. Bower et al., 2014; Johnson et al., 2015; Kramer et al., 2015), and in these cases, a nearby, natural population is likely to contain genotypes adapted to the climate of the restoration site. However, restoration sites may not be ecologically similar to nearby, natural populations (e.g. Bischoff et al., 2006; Jones, 2013; Lesica & Allendorf, 1999; Montalvo & Ellstrand, 2000), with disturbance levels, light availability, and temperature extremes higher within restoration sites (e.g. Kettenring & Galatowitsch, 2011). In absence of reliable information on the genetic variation required for successful establishment within restoration projects and for future resilience of restored populations, maximizing evolutionary capacity with plasticity and increased genetic diversity within adaptive zones may be the most risk-averse approach to choosing seed sources for restoration.

The adaptive advantage of any factor, including plasticity, can be difficult to support experimentally because some traits may only be adaptive under specific circumstances (e.g. Espeland & Rice, 2007). Some environments are more likely to promote the evolution of plasticity than others. Plasticity is favored in unpredictable and stressful environments (Cowling, Ojeda, Lamont, Rundel, & Lechmere-Oertel, 2005; Dyer, Hardison, & Rice, 2012; Pichancourt & Van Klinken, 2012; Scheiner, 1993). Consequently, we expect to see greater plasticity in those unpredictable and stressful environments, but plasticity may not always be adaptive (Nicotra et al., 2010). For example, stress can reduce phenotypic variation because limited resources reduce variance in growth (e.g. Waller, Dole, & Bersch, 2008).

Here, we use a genecology dataset to understand the generation and maintenance of phenotypic plasticity within populations of a commonly used restoration species. Genecology studies identify the degree of phenotypic variability among plants from different source populations. Plants are grown from seeds of known origin (characterized by available climate data in conjunction with latitude, longitude, and elevation) and evaluated in common gardens. Aspects of their phenology, morphology, and production are tracked over time and in differing environments represented by different sites and years. When phenotypes of the plants in the common gardens group within climatic conditions of the seed source environments, local adaptation is inferred and seed transfer zones are recommended within the boundaries of these climatic conditions. Genecology studies are common in forestry research (Rehfeldt & Jaquish, 2010) and are becoming more common for herbaceous rangeland species (Bower et al., 2014; Kramer et al., 2015). Genecology studies offer a survey of the phenotypic variability within a species and provide a methodology for examining interactions among traits at different garden sites. The inferred link between phenotypic groupings within common gardens to the scale of local adaptation illustrates the climate factors that are most likely to drive plasticity and local adaptation across a wide number of species.

Within a species, source populations may vary in their plasticity (Droste, Flory, & Clay, 2010; Dyer et al., 2010; Hyldgaard, Sorrell, Olesen, Riis, & Brix, 2012). Genecology studies may use hundreds of populations planted in a single common garden, but several common gardens situated in different climates must be used to apply their results over a species range (Clausen, Keck, & Hiesey, 1948; Gibson et al., 2016; Núñez-Farfán & Schlichting, 2001) because trait expression is usually modified by the environment (Edwards & Weinig, 2011) that can also change among years. Given the emphasis on local seed collections and local adaptation in plants used for restoration, we hypothesized that phenotypic variation across common gardens would

be largely explained by genetics (e.g. Johnson et al., 2015), but that plasticity is also important. We also hypothesized that populations in abiotically stressful locations would contain more plasticity (Dyer et al., 2010) than populations in nonstressful locations. We tested these hypotheses using a genecology dataset collected over 2 years in two common gardens placed in different environments.

2 | MATERIALS AND METHODS

Poa secunda J. Presl (Poaceae) is a cool-season perennial bunchgrass native to the western portion of North America. Its identity has been plagued by taxonomic ambiguity and revision (Majerus, Holzworth, Tilley, Ogle, & Stannard, 2009). Kellogg (1985) concluded that among various forms, only *Poa curtifolia* Scribner represented a separate evolutionary lineage. In this study, *P. secunda* germplasm collections corresponded to *Poa sandbergii* from Cronquist, Holmgren, Holmgren, Reveal, and Holmgren (1977) as given by Majerus et al. (2009). As in Johnson et al. (2015), our study excludes the taller and later summer flowering variants Big bluegrass, Canby's bluegrass, Pacific bluegrass, Nevada bluegrass, and Alkali bluegrass (Majerus et al., 2009). These variants are extremely uncommon in our collection area and were not encountered during collection trips (Figure 1).

Poa secunda is a facultative apomictic with seeds predominantly formed asexually as clones (Kellogg, 1987). Here, we examine plasticity

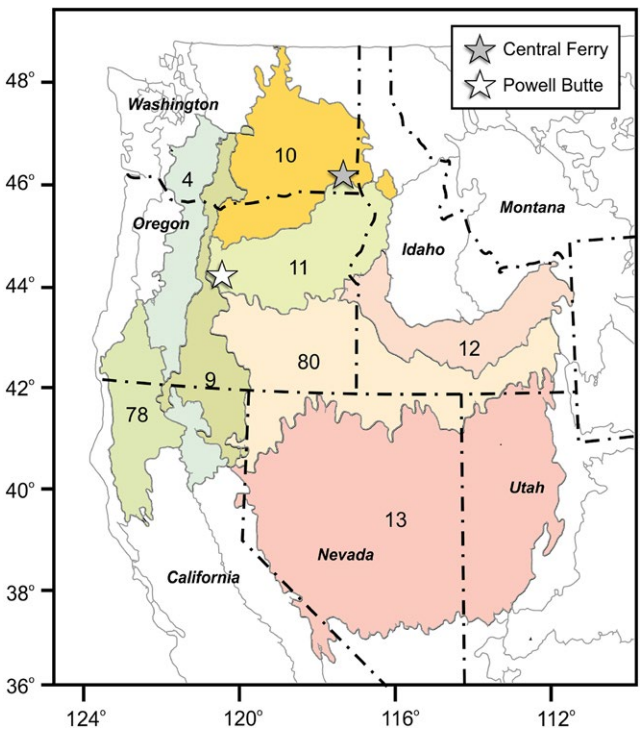

FIGURE 1 Ecoregions (Omernik, 1987) from which 130 source populations were collected (4—Cascades, 9—Eastern Cascades Slopes and Foothills, 10—Columbia Plateau, 11—Blue Mountains, 12—Snake River Plain, 13—Central Basin and Range, 78—Klamath Mountains/California High North Coast Range, 80—Northern Basin and Range); common garden locations are indicated with stars

at the level of maternal family (as in Dyer et al., 2010). Because apomixis usually predominates in this species, resulting in minimal outcrossing, we expect low genetic variation within most maternal families. Indeed, genetic variation within seed source families in this experiment did vary but was usually very small (Johnson et al., 2015, this study).

Wild-collected seeds were maintained by their maternal family identity throughout this study (e.g. seeds from each maternal plant in the field were collected and stored individually), and field collections were made from two maternal plants from each of 130 source populations in the spring of 2007 (Figure 1). Specific locations and detailed methods can be found in Johnson et al. (2015). Seeds were germinated in boxes in winter at room temperature and then planted into 5 × 5 × 5 cm containers, grown in a greenhouse, watered to keep pots moist, and periodically fertilized. Seedlings were placed in a lath house the following spring (March 2008), 2 weeks before they were planted in common gardens (Figure 1).

The common gardens were located at Central Ferry WA and Powell Butte OR. Central Ferry is a low elevation (209 m), warm site in the Snake River Canyon within the Columbia Plateau ecoregion and Powell Butte a cooler, higher elevation (941 m) site in the high desert of central Oregon in the Blue Mountain ecoregion (Omernik, 1987). The 30-year (1981–2010) mean annual temperature at Central Ferry is 12.0°C and is 9.2°C at Powell Butte. The 30-year averages (or, normals over the reference period 1980–2010, Wang, Hamann, Spittlehouse, & Murdock, 2012) for precipitation are 352 and 269 mm, respectively. The two common gardens do not span the environmental variation for *P. secunda*, because there are twelve recommended seed zones for this species across the eight ecoregions where source collections were made (Figure 1, Johnson et al., 2015). Therefore, our measurements of plasticity are likely less than the full capacity of the species.

Two maternal plants from each source population were represented in six blocks at the two sites. Thus, six plants from each maternal family and 12 from each population source were grown for a total of 1,560 plants at each site. We measured phenology and growth traits in the first and second full-growing seasons after transplantation. There were fifteen measured variables: six phenological traits (heading date, bloom date, maturation date, days from heading to bloom, days from heading to maturation, days from bloom to maturation) and nine morphology, or growth, traits: plant habit (erect to prostrate), culm length, panicle length, number of panicles, leaf size, leaf shape (length-to-width ratio), survivorship, basal diameter, and aboveground biomass. Trait means are reported in Johnson et al. (2015); in that study, over two-thirds of the phenotypic variation observed within the common gardens was attributed to source population climates.

2.1 | Data analysis

Variance components were estimated using PROC MIXED (SAS v9.2, SAS Institute, Cary, NC USA) with all experimental factors treated as random. Then, plastic and genetic components were computed for each plant trait, as outlined by Scheiner and Goodnight (1984). We made two sets of estimates. In one set, variance components

among plants over all source populations were estimated to obtain an overall assessment of plastic and genetic components. Families were nested within populations over all 129 sources with surviving plants; genetic components were source population and family within source population. The plastic components were the growth environments (planting sites and years) and interactions with growth environments, resulting in the model,

$$\sigma^2 p = \sigma^2 s + \sigma^2 l + \sigma^2 f(l) + \sigma^2 s * l + \sigma^2 s * f(l) + \sigma^2 y + \sigma^2 s * y + \sigma^2 l * y + \sigma^2 y * f(l) + \sigma^2 s * l * y + \sigma^2 s * y * f(l) + \sigma^2 r \quad (1)$$

where the variance for each factor was defined as, p for total phenotypic, s for site (or common garden location, $N = 2$), l for source population ($N = 129$), $f(l)$ for maternal family within source population ($N = 2$), y for year ($N = 2$), and r for replications (blocks within sites, $N = 6$) and the residual error.

A second set of plastic and genetic estimates were made independently for each of the 129 source populations as

$$\sigma^2 p = \sigma^2 s + \sigma^2 f + \sigma^2 s * f + \sigma^2 y + \sigma^2 s * y + \sigma^2 f * y + \sigma^2 s * f * y + \sigma^2 r. \quad (2)$$

For each set of estimates, plasticity was estimated as the ratio of the sum of plastic variation to total phenotypic variation, and genetic variation was the ratio of the sum of genetic variation to total phenotypic variation (Scheiner & Goodnight, 1984). For Equation 1, the genetic component was represented by sources and families; for Equation 2, the genetic component was represented by families only. We determined the relationship between genetic and plastic components and relationships among genetic traits and plastic traits using Pearson linear correlations.

For each source population (Equation 2), a matrix of plastic and genetic variation estimates for each of the fifteen measured dependent variables were developed and related to climate variables (see below) from each source population using Pearson linear correlations. With 24 climate variables and 15 measured traits, we examined 360 responses. Because this is exploratory research, we set the false discovery rate (FDR) for all correlations at 10% (Benjamini & Hochberg, 1995), accepting that 10% of the instances where we reject the null hypothesis, the null hypothesis is actually true. For this procedure, p-values of all tests are ranked, where the smallest p-value has a rank (i) =1. Q is calculated for each test by dividing i by the number of tests and then multiplying by the FDR. When $p < Q$, the null hypothesis is rejected. We report Q in the text and report raw p values in tables.

For each source population, climate averages were extracted from ClimateWNA climate data rasters (Wang et al., 2012; http://www.genetics.forestry.ubc.ca/cfcg/ClimateWNA/ClimateWNA.html) for the time period spanning 1981–2010. We used 21 climate variables designated by Wang et al. (2012) as "annual variables" including directly calculated means for annual temperature, warmest and coldest months, continentality, annual and summer precipitation, and annual and summer heat to moisture indices. Additional derived variables included average degree days, frost-free days, day ending the frost-free period, precipitation as snow, 30-year minimum and maximum temperature extremes, and evaporative demand indices.

3 | RESULTS

With source locations included in the model across sites and years, plasticity contributes more to phenotypic variation than genetics (Table 1): exceptions were panicle length, leaf size, and survival. There was an inverse relationship between genetic variation and plasticity ($r = -.66$, $p = .01$). Most of the genetic variation was associated with source populations which strongly differed for phenotypic traits (Johnson et al., 2015). Within maternal family, we found relatively little genetic variation, with most well below 5%. Among the traits listed in Table 1, between 56 and 80 source populations exhibited genetically based phenotypic variation within families. This supports our assumption of relatedness among plants from a given source, consistent with a relatively large degree of apomixis.

Correlations between plasticity and geographic-climate variables for 129 source populations were not significant for basal diameter, heading to bloom date, leaf shape, and number of panicles. Table 2 shows significant relationships ($Q < 0.0061$) between climate variables and plastic traits that have more than one significant correlation. We found one singular correlation between culm length plasticity and elevation (0.25). Significant correlations (Table 2) between phenology plasticity and longitude, mean annual temperature, mean warmest month temperature, continentality, annual heat moisture index, summer heat moisture index, number of degree days above 5°C, number of degree days above 18°C, extreme maximum temperature, Hargreaves

TABLE 1 Plastic and genetic percentages of total phenotypic variation over 129 locations from the intermountain West grown in common gardens at two sites over 2 years

Trait	% Plastic	% Genetic	% Source population	% Family
Head date	72.8	15.8	13.7	2.1
Bloom date	80.5	10.9	9.9	1.0
Maturity date	49.8	9.0	8.4	0.6
Days head to bloom	53.7	11.9	8.2	3.7
Days head to maturity	80.6	5.0	3.7	1.3
Days bloom to maturity	82.7	4.2	3.4	0.8
Habit	35.9	16.2	9.8	6.4
Culm length	46.1	13.8	10.1	3.7
Panicle length	*12.1*	*43.8*	*35.9*	*7.9*
# Panicles	40.2	4.6	3.1	1.6
Leaf size	*16.4*	*42.5*	38.5	4.0
Survival	*10.4*	*14.0*	*10.1*	*3.9*
Basal diameter	46.4	6.1	4.7	1.4
Biomass	66.2	8.6	7.6	1.0

"Population" reflects the genetic component of seed collection source population. "Family" reflects the genetic component of maternal families. Traits where genetic contribution to phenotypic variation is greater than the plasticity contribution are italicized.

reference evaporation, and Hargreaves climatic moisture deficit were positive (0.22–0.34). Significant correlations between phenology plasticity and mean annual precipitation, mean summer precipitation, and precipitation as snow were negative (−0.24–0.40). With the exception of biomass, significant correlations between morphology plasticity and elevation, mean coldest month temperature, mean annual precipitation, mean summer precipitation, and precipitation as snow were positive (0.22–0.30) while correlations with latitude, longitude, mean warmest month temperature, continentality, number of degree days above 5°C, and extreme maximum temperature were negative (−0.23–0.29). Slopes of biomass plasticity grouped with morphology.

Most of the correlations we report in Table 2 had opposing slopes for morphology traits (except biomass) compared to phenology traits, supporting the possibility of different influences on plasticity (Table 2). In contrast to all other morphology traits (habit, panicle length, and leaf size), plasticity in biomass always had the same slope direction as plasticity in phenology. Survival had the same slope direction as morphology. It appeared that, warmer and drier environments, characterized by higher annual (AHM) and summer (SHM) heat moisture indices, may promote plasticity in phenology and biomass (positive slopes) and decrease plasticity in survival and morphology (negative slopes). Cooler and wetter environments, then, could be associated with increased plasticity in survival and morphology and decreased plasticity in phenology and biomass accumulation. Correlations were low, indicating a great deal of plasticity is unexplained by source environment.

There were far fewer significant associations among genetic traits (each family within the source populations) than among trait plasticity (Table 3). All significant correlations among genetic traits ($Q < 0.028$) were positive, and mostly involved morphology traits. Most significant correlations ($Q < 0.004$) among traits for plasticity were positive except for the association between survival and maturity date. Correlation coefficients were largely in the same range within plastic and genetic traits.

4 | DISCUSSION

Multiple, recent publications have cited the importance of understanding how plant traits predict success in restoration environments (Chivers, Jones, Broadhurst, Mott, & Larson, 2016; Espeland et al., 2017; Jones, 2013; Leger & Baughman, 2015). Understanding source population effects on mean trait expression (such as in genecology experiments) and on variation in trait expression (this study) will help practitioners select materials that are adapted to disturbed sites and that contain enough plasticity to ensure adaptive capacity through environmental change.

TABLE 2 Pearson correlation coefficients between plasticity of plant traits measured in common gardens and environmental variables from 129 source populations that had more than one significant correlation (climate variables are 30-year averages from 1980 to 2010)

	Phenology				Morphology				
Climate¶	Bloom	Maturity	Bloom to maturity	Head to maturity	Habit	Panicle length	Survival	Biomass	Leaf size
Latitude					−0.32***				
Longitude			0.26**		−0.27**				−0.27**
Elevation					0.22*				
MAT	0.22*								
MWMT	0.24**	0.22*				−0.24**			
MCMT					0.23*				0.22*
TD			0.33****	0.27**	−0.32***			0.24**	
MAP			−0.40****	−0.28**			0.30***	−0.28**	
MSP	−0.26**	−0.25**				0.31***	0.25**		
AHM	0.24**	0.25**	0.34****	0.22*			−0.29***	0.27**	
SHM	0.24**	0.26**	0.24**			−0.23**	−0.24**		
DD5	0.25**					−0.23**			
DD18	0.27**								
PAS	−0.24**					0.28**			
EXT	0.25**	0.23**			−0.23**				
Eref	0.31***	0.24**							
CMD	0.31***	0.28**	0.28**						

Only significant correlations are shown, and *p* values are untransformed.

¶Definitions for climate abbreviations (Wang et al., 2012): MAT, mean annual temperature; MWMT, mean warmest month temperature; MCMT, mean coldest month temperature; TD, continentality; MAP, mean annual precipitation; MSP, mean summer precipitation; AHM, annual heat moisture index; SHM, summer heat moisture index; DD5, number of degree days above 5°C; DD18, number of degree days above 18°C; PAS, precipitation as snow; EXT, extreme maximum temperature; Eref, Hargreaves reference evaporation; CMD, Hargreaves climatic moisture deficit.

*$p < .05$, **$p < .01$, ***$p < .001$, ****$p < .0001$.

TABLE 3 Pearson correlation coefficients among plasticity of plant traits measured in common gardens that correlated with climate variables (bold, lower half) and among genetic contributions to the same plant traits for comparison (upper half)

	Bloom	Maturity	Bloom to maturity	Head to maturity	Biomass	Habit	Panicle length	Survival	Leaf size
Bloom	1						0.24**		
Maturity	**0.33*****	1						0.42******	
Bloom to maturity	**0.40******		1	0.41******					
Head to maturity	**0.26****	**0.20***	**0.75******	1		0.20*	0.47******		
Biomass			**0.42******	**0.38******	1		0.40*		0.27**
Habit		**0.22***	**−0.20***			1			
Panicle length							1		0.40******
Survival		**−0.25****	**−0.19***					1	
Leaf size	**0.18***	**0.19***				**0.27****			1

Only significant relationships are shown, and untransformed *p* values are indicated.
*$p < .05$, **$p < .01$, ***$p < .001$, ****$p < .0001$.

The generally small genetic contribution of maternal family to phenotypic variation means that families within most populations were only slightly different from each other. Although facultative to some degree, we expected strong apomixis in *P. secunda* to result in small differences in genetic variation within families collected at the same source population. Most of the genetic variation was found among the source populations rather than within, however, the small number of families per population ($N = 2$) means that our interpretation of these results is limited for a given source population. We previously reported that genetic variation in *P. secunda* (Johnson et al., 2015) indicated that 77% of phenotypic variation was attributable to source collection location (i.e. genetically based) within gardens and years. In this study, we examined the variation in phenotypes (plasticity) across gardens and years, encompassing spatial and temporal variation, and, in this case, plasticity represents the majority of variation when compared with the genetic contribution, especially for phenology traits. Thus, our hypothesis that genetics would represent the largest part of phenotypic variation was not supported in this study. Indeed, the opposite was true in the majority of cases.

Here, we show that seed sources from warm and dry climates were associated with plasticity in phenology (bloom to maturity) while cool and wet seed source locations were associated with plasticity in panicle length and survival in *P. secunda*. Therefore, we found qualified support for our second hypothesis: collections from more extreme, or stressful, climates (higher heat: moisture indices) tended to be more plastic for phenology. However, we also found more plasticity for morphology and more plasticity in survival in nonstressful (wetter, cooler) environments. A trade-off between phenology and morphology traits is well characterized for trees (e.g. Gömöry & Paule, 2011; Matyas, 1996). In herbaceous species, opposing patterns of plasticity for growth and phenology has been observed in a clonal aquatic plant species (Dorken & Barrett, 2004) and an invasive perennial forb (Colautti, Eckert, & Barrett, 2010), but positive correlations between growth and phenology have also been found (Edwards & Weinig, 2011; Sun & Frelich, 2011). Given the demonstrated benefit of phenological plasticity to persistence during climate change (Franks et al., 2013; Matesanz et al., 2010), selecting more plastic seed sources for these traits may be appropriate for restoration. However, plasticity in both morphology and phenology has been suggested to be beneficial under climate change scenarios (Nicotra et al., 2010); therefore, the balance between the two may warrant further investigation.

Many of studies of plasticity are performed by examining the slope or direction of the change in trait means in two environments, but we analyzed four study environments (two gardens in 2 years) giving a broader perspective. Because plasticity in aboveground biomass may be positively correlated with plasticity in phenology of *P. secunda*, comparisons to other work are complicated. Positive associations among traits for plasticity may be due to correlated selection for plasticity or because of developmental constraints (e.g. Pigliucci, 2003, 2005).

Plasticity in phenology imparts persistence with climate change patterns (reviewed in Matesanz et al., 2010; Nicotra et al., 2010; and Pau et al., 2011). It is likely that there is less competition for light in plant communities in warmer parts of the *P. secunda* range that encompass the arid and semi-arid portions of the Great Basin (Figure 1), but there may be more competition for light in the cooler and wetter portions of its range where denser vegetation could be supported. Therefore, plasticity for habit, leaf size, and panicle length may be adaptive in cool/wet environments where species cover, and therefore competition, tends to be greater. Plasticity in habit, panicle length, and leaf size is adaptive in environments where light is a limiting resource (Schmitt, Dudley, & Pigliucci, 1999). In our study, plasticity in panicle length, habit, leaf size, and survivorship was significantly correlated with climate conditions at source populations. Plasticity in panicle length, survivorship, and biomass accumulation has been shown to be important for fitness in degraded landscapes (Matesanz et al., 2010).

Of the 46 significant relationships among climate variables and measured traits, we expect 4.6 to be false discoveries. The clear separation in the direction of multiple relationships between phenology and morphology is striking and remains robust when controlling Type I error. Because our common gardens did not represent extremes within the species range (Figure 1), we have likely underestimated the degree of plasticity in this species (e.g. Valladares, Gianoli, & Gómez, 2007).

Because we relate plasticity in common gardens to maternal environments in this study, we are in effect reporting on effects of the maternal environment, or, transgenerational plasticity (e.g. Dyer et al., 2010) that may or may not be genetically determined (e.g. Van Kleunen & Fischer, 2005). The degree to which the plasticity we found would be maintained in subsequent generations is unknown and will depend on the amount of plasticity that is genetically based.

Natural selection acts on fitness variation linked to phenotypic variation. Even when phenotypic expression is driven by plasticity, selection can reinforce adaptive phenotypes that are driven by plasticity and lead to genetic assimilation (Eshel & Metessi, 1998; Laland et al., 2011; Pal & Miklos, 1999). Thus, for highly plastic traits like phenology, we could assume that plasticity has the potential to contribute as much or more to adaptation in restoration than genetic variation.

The ploidy level, mating system, genetic diversity, and generation time of a plant species will affect the likelihood of adaptive plasticity as well as its importance in promoting population maintenance. It is reasonable to expect that clonality leads to greater plasticity than sexual reproduction (e.g. Schlichting, 1986), but there has been little research on this topic (Van Kleunen & Fischer, 2005). Greater ploidy levels offer more opportunities for epigenetic interactions that influence plasticity (Chen, 2007). Most of the research performed on population-level plasticity in plants has focused on weeds and annuals (Dyer et al., 2010; Van Kleunen & Fischer, 2005; but see Espeland & Hammond, 2013; Espeland, Perkins, Johnson, & Horning, 2016), and while weeds might require plasticity to maintain their success in ruderal environments (e.g. Schlichting, 1986), outcrossing, short-lived species may require less plasticity for persistence than long-lived self-fertilizing perennials (e.g. Van Kleunen & Fischer, 2005). Plasticity in traits important for restoration success has been found for self-fertilizing cultivars of perennial grasses, but not for an outcrossing, genetically diverse, prevariety germplasm (Espeland et al., 2016). Our study illustrates the importance of plasticity to persistence and evolution of local seed sources in restoration environments and propagule increase fields (Dyer, Knapp, & Rice, 2016; Espeland et al., 2017; Nevill et al., 2016); other research has shown the importance of plasticity to large-scale restoration seeding with cultivars (Espeland et al., 2016).

There are a large number of number of genecology datasets that have accumulated over the decades, and some fraction of these studies have been conducted in more than one common garden location. At least ten datasets with more than one common garden location for herbaceous species in the western United States are available (http://www.fs.fed.us/wwetac/threat_map/SeedZones_Intro.html) and can be investigated for the contribution of source climate to plasticity when family structure is included. Often, plasticity is indicated in the results of genecological studies (Johnson & Vance-Borland, 2016; Johnson et al., 2015), but the phenomenon has not been explored in detail. The generality of trade-offs that we found between phenology and morphology can be ascertained by exploring these available datasets and could have important ramifications for evolutionary mechanics across plant species as a whole (e.g. Gibson et al., 2016). Genecology datasets have also been underutilized for their potential to illustrate correlations among functional traits and to predict adaptation to climate change (Aspinwall et al., 2013). Our results show that, for *P. secunda*, we cannot choose sources that supply plasticity to restoration populations without choosing the type of plasticity most appropriate for persistence in the restoration environment. This research underscores the importance of understanding the relationship of seed source populations to plant traits when strategically selecting seed to increase restoration success.

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AUTHOR CONTRIBUTIONS

EE, RJ, and MH conceived and designed the research; EE, RJ, and MH performed the experiments; RJ analyzed the data; EE, RJ, and MH wrote and edited the manuscript.

ORCID

Matthew E. Horning http://orcid.org/0000-0003-4583-2807
Erin K. Espeland http://orcid.org/0000-0001-8541-3610

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