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Local climate and cultivation, but not ploidy, predict functional trait variation in *Bouteloua gracilis* (Poaceae)

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Abstract Efforts to improve the diversity of seed resources for important restoration species has become a high priority for land managers in many parts of the world. Relationships between functional trait values and the environment from which seed sources are collected can provide important insights into patterns of local adaptation and guidelines for seed transfer. However, little is known about which functional traits exhibit genetic differentiation across populations of restoration species and thus may contribute to local adaptation. Here, we report the results of a common garden experiment aimed at assessing genetic (including ploidy level) and environmental regulation of several functional traits among populations of *Bouteloua gracilis*, a dominant C4 grass and the most highly utilized restoration species across much of the Colorado Plateau. We found that leaf size and specific leaf area (SLA) varied significantly among populations, and were strongly correlated with the source population environment from which seeds were collected. However, variation in ploidy level had no significant effect on functional traits. Leaves of plants grown from commercial seed releases were significantly larger and had lower SLA than those from natural populations, a result that is concordant with the overall relation between climate and these two functional traits. We suggest that the patterns of functional trait variation shown here may extend to other grass species in the western USA, and may serve as useful proxies for more extensive genecology research. Furthermore, we argue that care should be taken to develop commercial seed lines with functional trait values that match those of natural populations occupying climates similar to target restoration sites.

Keywords Functional trait · Local adaptation · Seed increase · Seed transfer

Introduction

Using seed sources that are genetically adapted to target restoration sites has long been identified as important for restoration success (Langlet 1971; Lessica and Almendorf 1999) and for minimizing negative effects of gene flow between local, remnant, and imported gene pools (Hufford and Mazer 2003;

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McKay et al. 2005). Nonetheless, demand for native seeds of many species often exceeds the production capacity of local populations (Broadhurst et al. 2015), resulting in seed increase from one or a few sources in an agronomic setting. Native seed is needed for restoration and potentially for assisted migration, as many species are unlikely to keep pace with projected geographic shifts in their climate niche through natural dispersal alone (Jump and Peñuelas 2005; Aitken et al. 2008). Due to both logistics of seed increase and consequences of global environmental change, alternatives are needed to the "local is best" paradigm that guides restoration seed source selection.

Genecology researchers have taken us in the right direction by developing seed transfer zones for a selected set of species. Common garden (or provenance) trials have led to predictive models of tree- and stand-level performance for different genotype assemblages across broad environmental gradients that allow foresters to plant ahead of climate change (Rehfeldt et al. 1999; Wang et al. 2010). Guided by this work, an increasing number of studies on herbaceous plants have coupled data on historical source climate with plant performance in common garden settings to map seed transfer zones that minimize the risk of source to seeded site mismatch (e.g., Johnson et al. 2010; St Clair et al. 2013; Kilkenny 2015). While highly informative and adjustable to forecasted conditions, seed transfer zones derived from common garden experiments are time- and resource-intensive, and the results are likely to be specific to the species studied. Recently, Bower et al. (2014) provided a pragmatic approach to delineating provisional seed transfer zones for plants in the United States. Their zones are based on binning of two key climate variates (minimum temperature and aridity), and performed well in predicting patterns of trait variation among Great Basin populations of two species measured in common garden settings. The authors of this study acknowledged that their provisional approach will not be ideal for all species, particularly those which occupy regions characterized by seasonal variation in aridity. Nonetheless it provides a starting point for seed transfer guidelines that is validated by in-depth genecology research (Johnson et al. 2012, 2013; St Clair et al. 2013).

Functional ecology may provide another bridge between genecology and practical needs for restoration seed selection. Functional traits are organismal characteristics that mediate responses to, and effects on, the local environment (Lavorel and Garnier 2002), and have been proposed as useful links between environmental responses, species interactions, and ecosystem functioning in a restoration context (Funk et al. 2008; Sandel et al. 2011). Community ecology has relied heavily on functional trait analysis to address a variety of questions over the past decade (McGill et al. 2006), resulting in extensive descriptions of trait–environment relationships across species and how these relationships shape community composition. While intraspecific variation in functional traits is not as thoroughly described, initial data indicate that the strength of trait–environment correlations within species are of the same magnitude as those among species (Read et al. 2014). In addition, ecological genetic research on important restoration plant species demonstrates clear evidence of genetic regulation of population differences for a wide variety of important functional traits (e.g., Parsons et al. 2011). Focusing on heritable functional traits under selection would facilitate rapid seed source selection, and provide a predictive link between population success and restoration of specific ecosystem functions (Funk et al. 2008).

In this study, we use a common garden experiment to examine the extent to which functional traits vary among populations of a perennial grass species, *Bouteloua gracilis* (blue grama grass). In addition we ask how trait variation relates to the source environment of these populations. *B. gracilis* is a dominant species across much of the Colorado Plateau of the southwest United States and is in high demand for restoration projects across the region (Peppin et al. 2010). In addition to its regional importance and broad climate niche, *B. gracilis* has at least two other characteristics that are common among many restoration grass species, one biological and the other economic. First, at least three ploidy levels have been identified in natural populations of *B. gracilis*, a degree of variability that is not uncommon in grasses (Wood et al. 2009). Ploidy variation can have significant effects on plant anatomy, morphology, and physiology that is independent of genic variation (Comai 2005), but the ecological impacts of these effects are not well understood. Second, several commercial seed sources exist for *B. gracilis*, but these sources may exhibit a narrow range of functional trait values relative to the distribution of *B. gracilis* in the region, thus having restricted utility in restoration. Thus, we predict that ploidy, local climate of source populations, and selection for agronomic seed increase may all influence variation in functional trait values among sources of *B. gracilis*.

Methods

Study species and region

Bouteloua gracilis is a perennial C4 grass species distributed across the Interior West and Great Plains of the United States and analogous, adjacent regions of Canada and Mexico. It is dominant in many areas of Colorado Plateau, where it forms extensive, low-lying mats of vegetation. The ability to regenerate from seed, develop extensive clonal growth, and withstand intensive grazing make *B. gracilis* a highly desirable restoration species for degraded rangelands on the Colorado Plateau. Substantial morphological variation exists among populations, which often differ substantially in climate, grazing intensity and/or competitive environment, suggesting that local adaptation is important for the species. Some work has examined the genetic basis of among population variability (e.g., Riegel 1940), but additional study is warranted. The potential importance of local adaptation in *B. gracilis* coupled with its importance as a restoration species for the Colorado Plateau guided the focus of this study.

Seed sources and common garden

Seeds of *B. gracilis* were obtained through direct collection from populations distributed across the Colorado Plateau and several outlying locations (see Fig. S1) and two existing sources (see Table S1). Seeds noted as derived from Seeds of Success (SOS) accessions were collected as per their protocol (http://www.blm.gov/wo/st/en/prog/more/fish__wildlife_and/plants/seeds_of_success/protocol.html) and were obtained directly from the SOS program or via the Germplasm Resources Information Network (GRIN, http://www.ars-grin.gov/). Seeds of cultivars were obtained from GRIN, and the location (GPS coordinates) of their source populations was estimated from information provided in National Resource Conservation Services publications. Details on the cultivars are provided in Table S1. All other seeds were field collected by the authors from at least ten maternal plants with a minimum distance between these plants of 10 m. These latter seeds were pooled to be consistent with the SOS and commercial materials. Twenty-five seeds were sown in 1″ container trays on a misting bench in a greenhouse where the minimum daily temperature was 65 °C. At sowing (January 30 and 31, 2012), seeds were randomly assigned to containers, and the trays were shuffled haphazardly on the misting bench every 3 days. Twelve to fifteen seedlings per populations were transplanted to the common garden, located within the Southwest Experimental Garden Array site (http://www.sega.nau.edu/) at the Arboretum at Flagstaff from July 26 to 28, 2012. The site was prepared by clearing all above-ground and as much below-ground vegetation as practical. The cleared area was covered with black landscape cloth to inhibit weed incursion. Seedlings were randomly transplanted with 45 cm spacing, and the garden was watered until the soil was saturated on the day of planting and 3 days later, with no subsequent watering.

Ploidy and functional trait measurements

Preliminary analysis, motivated by published cytogenetic studies (Snyder and Harlan 1953; Tsuchiya et al. 1992), indicated that the studied samples of *B. gracilis* contained multiple cytotypes (diploid, tetraploid, and hexaploid), which are apparently derived from autopolyploidy. Ploidy was determined for a subset ($n = 97$) of plants by comparing past literature reports (Snyder and Harlan 1953; Tsuchiya et al. 1992) to results of flow cytometry using fresh leaf material at the U.S. Forest Service's Provo Shrub Sciences Lab in Provo, UT (for flow cytometry methods see Sanderson 2011). Analyzed samples aligned clearly with past work, where the base has been identified as $x = 10$ and diploid ($2n = 20$), tetraploid ($2n = 40$), pentaploid ($2n = 50$), and hexaploid ($2n = 60$) plants have been uncovered. No pentaploid and only two hexaploid plants were typed here, and the hexaploids came from two different populations widely separated geographically. Only diploids (23 plants) and tetraploids (72 plants) were included in further analyses. Although known to occur in nature, with the exception of the two populations with hexaploids (and tetraploids), none of our populations had more than one cytotype. Ploidy data for each population are reported in Table S1.

On August 5, 2013 (ca. 1 year after transplanting), three leaf functional traits were measured on 3–6 plants (mean ± 1SE = 5 ± 0.2) from each of 34 populations (171 plants total), including three Natural Resource Conservation Service (NRCS) cultivars (Table S1). Specific leaf area (ratio of area to dry mass; SLA), leaf dry matter content (LDMC), and leaf size (one-sided area) were measured following the standard protocols of Pérez-Harguindeguy et al. (2013). LDMC and SLA are both generally associated with photosynthetic capacity, relative growth rate, and leaf longevity (Cornelissen et al. 2003), but are regulated by construction costs related to water and carbon economies, respectively. LDMC generally responds to variation in water availability and likelihood of physical damage (Cornelissen et al. 2003), and is related to water use efficiency (Butterfield and Briggs 2011), but is unrelated to temperature variation (Albert et al. 2010). In contrast, SLA generally responds strongly to variation in temperature and light availability across a broad range of species (Poorter et al. 2009). Thus, LDMC and SLA may vary independently in response to different dimensions of climate. Leaf size generally increases with water availability and decreases with temperature, due to effects of leaf size on boundary layer thickness and rates of photosynthesis and transpiration that have environmentally dependent effects on carbon economy (Givnish 1984).

Statistical analysis

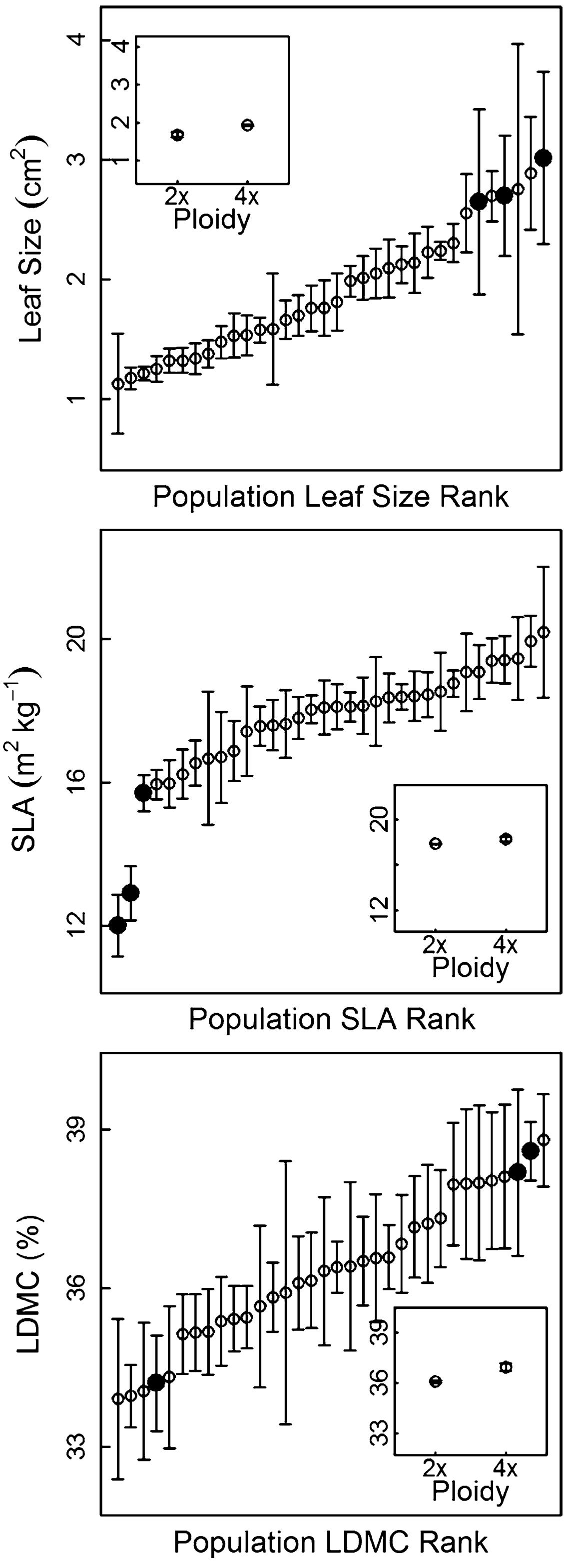
The effects of ploidy and population source were tested in a two-step approach. Because ploidy data were only available for a subset of plants, both ploidy and population could not be analyzed simultaneously without significant loss of statistical power. Thus, a Welch's two sample *t* test for unequal sample size was first performed on each functional trait with ploidy level (diploid, tetraploid) as the predictor variable. Because there was no significant effect of ploidy on any of the three functional traits measured (see Results below), one-way analysis of variance was used to test the effect of population on functional trait values. Only plants from natural populations were included (population $n = 31$) in this analysis, and data were first assessed for homoscedasticity and normality. To test the hypothesis that plants grown from commercially produced seed are functionally different from those of natural populations, a Welch's two sample *t* test with unequal sample size was then performed on each trait, with seed source (natural, commercial) as the predictor variable.

To test the hypothesis that trait values from natural populations are related to their source environment, multiple regressions were conducted for each trait using seven bioclimatic variables (mean annual temperature, monthly temperature range, temperature seasonality, temperature of wettest quarter, mean annual precipitation, precipitation seasonality and precipitation of warmest quarter). These climate variables represent orthogonal axes of climate variation across the study region (Butterfield 2015), and were acquired from WorldClim (Hijmans et al. 2005). The most parsimonious models were selected using all-subsets regression and adjusted R^2, with either individual samples or population means as the response variables. Commercial populations were not included in the regression analysis. All analyses were conducted in R version 3.1.1.

Results

Even when excluding commercial plants [which were drawn from outside the core regional focus of this study (Fig. S1)], population was found to have a significant effect on two of the three functional traits measured, but ploidy level did not (Fig. 1). Both leaf size ($F_{30,130} = 3.4$, $P < 0.001$) and SLA ($F = 1.6$, $P = 0.048$) exhibited greater variation among populations than within, but not among ploidy levels ($t_{29} = -1.1$, $P = 0.28$; and $t_{31} = 0.62$, $P = 0.54$, respectively). LDMC did not vary significantly among populations ($F_{30,130} = 1.1$, $P = 0.40$) or among ploidy levels ($t_{35} = 1.3$, $P = 0.20$). Leaves of plants from commercially available seed sources were on average 53% larger ($t_{9.5} = 3.1$, $P = 0.012$) with 26% lower SLA ($t_{10.3} = -7.0$, $P < 0.001$) than those from natural populations, whereas LDMC of commercial plants was on average greater by only 2% ($t_{11} = 1.1$, $P = 0.30$).

Leaf size and SLA were significantly correlated with aspects of source climate among plants collected from natural populations (Fig. 2). Leaf size was significantly correlated with 6 of the 7 climate variables included (all but monthly temperature range), and the most parsimonious model (Table S2)



◀**Fig. 1** Functional trait variation within and across populations (and ploidy races) of *B. gracilis*. *Circles* and *error bars* represent population (ploidy) means and two standard errors, respectively. *Closed circles* represent the three commercial releases. Only natural populations were used in statistical analysis

included positive relationships with mean annual temperature, mean annual precipitation and precipitation seasonality (population $R^2_{\mathrm{adj}} = 0.56$, individual $R^2_{\mathrm{adj}} = 0.25$; both $P < 0.001$); SLA was negatively correlated with mean annual temperature (population $R^2 = 0.44$, individual $R^2 = 0.13$; both $P < 0.001$), and uncorrelated with any of the other climatic variables (Table S2). No climatic variables were significantly correlated with LDMC (Table S2).

Discussion

The relationships between leaf size and SLA with source climate observed in *B. gracilis* correspond well with what we know about the general functional significance of these traits in herbaceous plants of semi-arid regions, and this correspondence suggests that *B. gracilis* is locally adapted to the climate drivers evaluated, or to factors that covary with them. The increase in leaf size with increasing annual precipitation and precipitation seasonality (increase in proportion of precipitation that falls during the growing season) correspond with relationships between boundary layer dynamics and water loss (Givnish 1984), with larger leaves perhaps having lower water use efficiency but potentiating greater net carbon gain under relatively wetter conditions. The decrease in SLA with increasing annual temperature likely reflects greater leaf longevity and water use efficiency in warmer environments, coupled with selection for minimal construction costs and high rates of return on high SLA leaves in colder environments with shorter growing seasons (Wright et al. 2004). Similar patterns have been found for SLA in other C4 grasses (Aspinwall et al. 2013) and herbaceous species (Kraft et al. 2014), and a genetic basis for a significant fraction of the variation in SLA but a lack of detectable genetic variation for LDMC has been demonstrated in other herbaceous species (e.g., Agrawal et al. 2008). The relatively stronger covariation of SLA to envi-

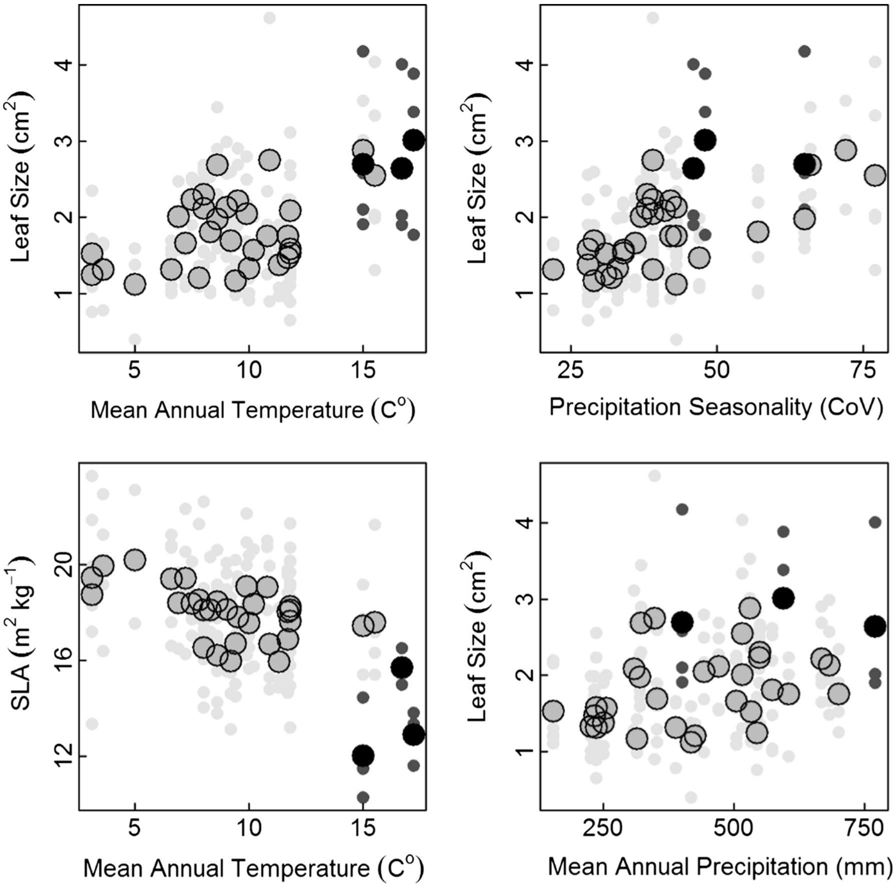


Fig. 2 Trait–environment relationships for leaf size and specific leaf area (SLA). These specific climate variables are presented based on model selection results reported in Table S1. *Small* and *large circles* represent individual plant and population mean values, respectively. *Dark circles* represent commercial releases

ronmental variation, relative to LDMC, has also been observed for a suite of herbaceous species in Europe (Jung et al. 2010), though genetic and environmental effects on trait variation were not differentiated. It may be that SLA, a structural trait, is more heritable than LDMC because the latter can more quickly change to track short-term physiological status (Ackerly et al. 2000), whereas the former trait is determined earlier during leaf development.

While increases in ploidy are common within plant species and can have a gross impact on diverse morphological, anatomical, and physiological features (Hegarty and Hiscock 2008), only a few studies have documented a direct relation between ploidy increase and ecological adaptation (e.g., Ramsey 2011). Here, as in many other studies (reviewed in Madlung 2013), ploidy variation could not be linked to ecological differentiation, or more specifically in this study, to traits that can be sensibly linked to ecology. None of the morphological or anatomical traits measured were different between diploid and tetraploid plants, even though ploidy increase generally leads to increased cell size (not evaluated here). Ecological equivalence of ploidy races is consistent with the complex spatial distribution of cytotypes of *B. gracilis*, with diploid and tetraploid races exhibiting no clear spatial segregation across the part of the species' range sampled here (Wood, unpubl. data). In a study similar to ours, Aspinwall et al. (2013) reported that octoploids of switchgrass (*Panicum virgatum*) had greater SLA than did tetraploids; however, the authors concluded that genotypic variation that could be linked to climate was largely independent of a ploidy effect. The lack of a link between ploidy and ecology within many plant species (Madlung 2013) seems somewhat surprising given the often gross impacts of whole genome duplication on the organism (Comai 2005), but perhaps reflects plants' general ability to maintain homeostasis through plastic control of diverse traits that affect physiology; for example, tetraploids may deploy fewer, larger stomates to maintain similar gas exchange rates as their diploid progenitors. For *B. gracilis*, the geographic distribution of cytotypes, with diploid and tetraploid races having similar, widespread distributions across the core study area, may also indicate that many of the tetraploid plants sampled for the current study are derived from relatively old mutational events, which may have allowed sufficient time for selection to counteract any maladaptive effects intrinsic to ploidy increase (Otto and Whitton 2000).

In contrast to ploidy level, cultivation status was strongly related to leaf size and SLA. The greater size and lower SLA of the cultivated releases studied here correspond with the hot local temperatures of the environments from which they were developed. Although we cannot directly assess effects of cultivation because we did not include natural population analogs of the commercial plants, the SLA values of two of the cultivars deviate from the SLA-MAT relationships for natural populations, assuming a linear relationship (Fig. 2). This deviation suggests that development of these cultivars may have involved selection for decreased SLA. This inference is not conclusive, and more research needs to be conducted to assess the effects of cultivar selection and seed increase on functional traits of *B. gracilis*. Regardless, the releases studied here may be maladapted to most environments where *B. gracilis* presently occurs on the Colorado Plateau, and highlights the need for development of additional seed sources of *B. gracilis* for use in restoration on the Colorado Plateau.

Implications

If the correlations between functional traits and source climate reported here for *B. gracilis* were found to be general across a selected set of grass species used for restoration, then results could be extrapolated to others for which we lack direct genetic data. That is, seed sources could be selected based on readily measured functional traits, a strategy which may provide a cost-effective alternative to in-depth common garden experiments. However, two recent studies suggest that the picture may be more complicated than we might hope. In a review of common garden studies conducted on forest tree species in Europe, Bussotti et al. (2015) concluded that the heritable functional traits that determine responses to the environment vary substantially from species to species, and are influenced by evolutionary history and species-specific ecology. While not explicitly accounting for genetic contributions to intraspecific trait variation, de Frenne et al. (2013) conducted a meta-analysis of intraspecific trait responses to variation in latitude and temperature in North American and Europe. They found that most species exhibited no response to variation in latitude across five functional traits, and that nearly identical numbers of species exhibited positive or negative responses for height and SLA to variation in temperature. Both of these studies indicate that intraspecific trait–environment relationships can be highly complex, and that general patterns may not exist.

Variability in trait–environment relationships should not, however, deter attempts to develop predictive models. Evolutionary history (Ackerly and Reich 1999), growth form and environment (Wright et al. 2004) can all influence trait–trait and trait–environment relationships. For example, the decrease in SLA with increasing temperature found here is common among herbaceous plants, particularly in water-limited systems, but counters the general positive trend for vascular plants as a whole (Wright et al. 2004). The increase in leaf size with increasing MAT is also opposite of the pattern found across populations of *Oryza rufipogon* (Zhou et al. 2013), a wetland grass species, suggesting that leaf size plays very different roles in nutrient versus water-limited systems. Nonetheless, it is not unreasonable to predict that many C4 grasses that inhabit semi-arid regions of western North America should exhibit similar patterns of local adaptation in specific functional traits. In addition, a consistent relation between climate and functional trait values in C3 grasses is worth evaluating. Although C3 grasses have distinct photosynthetic physiology, they often span gradients in growing season temperature (and length) similar in breadth to those of C4 grasses. Indeed, in a study of the C3 grass, *Elymus elymoides*, SLA was negatively correlated with maximum temperature at source (Parsons et al. 2011), as was found here for *B. gracilis*. Focused estimates of the sign and magnitude of trait–environment relationships will improve our ability to match sources of restoration species to target sites. Finally, patterns of functional trait variation across species can guide the assembly of seed mixes with compatible trait values (Lessica and Almendorf 1999).

Identifying the environmental-dependence of functional trait variation could improve seed selection in several ways. First, efforts to increase intraspecific diversity of restoration seed resources could focus on filling the observed breadth of functional trait values within a species, rather than climate or geographic space. Functional traits are the proximate determinants of population success and could be used to develop seed transfer guidelines that identify the range of suitable trait values for areas with high restoration need. Further efforts to assess how functional trait and classical empirical seed transfer zone approaches can complement one another are warranted. Second, functional trait-based selection of restoration seed sources could be expanded to address factors such as specific abiotic challenges, competitive ability with invasives, and desired ecosystem services (e.g., erosion control, forage production) for restoration sites where key predictors of success may not be predictable from historical climate at target sites. In conclusion, functional trait-based approaches to restoration, in conjunction with genecology research, have the potential to improve both the outcomes and predictability of restoration efforts, though additional research on the genetic controls on specific functional traits across a variety of plant groups and environments is needed.

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