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RESEARCH ARTICLE

Intraspecific trait variability in wild plant populations predicts neither variability nor performance in a common garden

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Dryland restoration requires plant materials capable of performing well despite difficult growing conditions. Selecting plant materials with higher intraspecific trait variability (ITV) may support successful outcomes by enhancing the performance of those materials in restoration settings. However, maintaining ITV from wild populations is not well understood and requires further investigation if ITV is to be incorporated into native plant materials, which are often developed from wild-collected seed grown in agricultural settings. We used two perennial plant species to explore whether (1) ITV measured at field sites predicts ITV in a common garden, (2) rankings of ITV among populations remain stable over time, and (3) higher levels of ITV promote survival and reproductive effort in a common garden. We measured ITV in specific leaf area and height for *Bouteloua curtipendula* and *Heterotheca villosa* at field sites and over 2 years in a common garden, as well as survival and flower production in the common garden. We also calculated climate distance between field sites, where seeds were originally sourced, and the common garden to account for the impact of climatic differences on ITV. We found that (1) ITV measured at field sites did not predict ITV in the common garden, (2) rankings of ITV across populations were inconsistent, and (3) relationships between ITV and performance were rare and differed by species. Our findings indicate that the utility of ITV in wild populations as a predictive tool may be limited.

Key words: Colorado Plateau, common garden, dryland restoration, native plant materials, plant functional traits

Implications for Practice

- Collecting and growing seed from a wild population does not result in individuals that collectively maintain correlated levels of intraspecific trait variability (ITV).
- The inherent complexity of factors influencing plant phenotypes (genetic, environment, genetic × environment, and maternal environment), in addition to unintentional impacts on genetic diversity during seed collection and plant propagation, likely erodes a consistent signal of ITV across populations.
- While high ITV may help increase the resilience of wild populations, we observed little impact of ITV on plant performance after 2 years in a common garden.
- Accounting for the similarity of climate between source populations of plant materials and restoration sites may support successful outcomes.

Introduction

Land managers in the southwestern United States face complex restoration challenges associated with interacting effects of increased drought, variable precipitation, rising temperatures, intensified land use, invasive species, and wildland fire

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(Hoover et al. 2019). Moreover, the speed of warming and associated increases in aridity (Zhang et al. 2021; Williams et al. 2022) are exacerbating difficulties for plant germination, growth, and survival and ultimately may lead to changes in community composition and ecosystem conversion (Munson et al. 2011; Winkler et al. 2019; Berdugo et al. 2022). Though there is evidence that increased seeding rate and larger seed sizes can support plant establishment in arid sites (Shackelford et al. 2021), climate trends will continue to impact plant establishment and survival. This reality necessitates exploring additional avenues for improving restoration effectiveness, like using plant materials that can navigate stressful conditions, either through adaptive or plastic responses.

A critical component of successful restoration is selecting appropriate plant materials that are genetically and ecologically suitable for intended restoration sites (Johnson et al. 2010; Oldfield 2019). Restoration practitioners often prioritize sourcing seeds from locally adapted plants, which are plants with advantageous, heritable traits associated with specific environmental conditions. Locally adapted plants typically outperform non-local plants (Leimu & Fischer 2008; Baughman et al. 2019) and are more likely to establish successfully and less likely to introduce maladapted genotypes in restoration settings (Miller et al. 2011; Bucharova et al. 2019). However, sourcing seeds from plants adapted to environmental conditions at a restoration site is challenging due to limited seed availability (National Academies of Sciences, Engineering, and Medicine 2023). In addition, future climatic conditions that push systems beyond what locally adapted plants have typically encountered require exploring restoration strategies that focus on aspects of plants beyond how "local" they are, including exploring how much trait diversity plants display (Rice & Emery 2003; Valladares et al. 2014; Espeland et al. 2017).

Plant functional traits offer a potential tool to build community resilience given the magnitude of disturbances and breadth of stressors associated with dryland restoration. Functional traits are easily measurable plant morphological and physiological characteristics that can help us understand taxon-independent ecosystem functioning and community responses to disturbance (Weiher & Keddy 1995; Violle et al. 2012; Funk et al. 2016). Most functional trait research focuses on variability among species, but recent attention has focused on intraspecific trait variability (ITV), which includes variation among and within populations of the same species (Mitchell & Bakker 2014; Zeldin et al. 2020; Westerband et al. 2021). Understanding ITV may be important for predicting adaptive capacity and future ecosystem functioning relative to anticipated environmental change (Jung et al. 2010; Siefert et al. 2015; Funk et al. 2017; Huxley et al. 2023). For example, plant communities in fire-adapted longleaf pine forests respond to altered fire regimes through changes in intraspecific trait expression based on measurements of specific leaf area (SLA) and leaf dry matter content, allowing species composition to remain stable (Mitchell et al. 2021). Similarly, ITV in leaf carbon content, leaf nitrogen content, SLA, and plant height shifts dynamically along stress gradients and can push species toward optimal traits that improve survival (Kitagawa et al. 2022). Furthermore, high ITV in cone serotiny can benefit *Pinus* populations located within marginal or disturbed environmental conditions, like those that are often present at restoration sites (Pelletier et al. 2023).

Leveraging functional traits to characterize species' recruitment niches and design interspecific seed mixes illustrates how trait-based frameworks may inform restoration approaches (Larson et al. 2023). Moreover, functional trait data can guide plant materials selection to match species to restoration sites and objectives (Fremout et al. 2022), and ITV can be used to identify populations better adapted to changing climate conditions (Roybal & Butterfield 2018), including extreme drought (Jung et al. 2014). For example, Klein and Mitchell (2023) measured traits, including above and belowground biomass, height, and SLA, under experimental drought conditions to understand how seed source environment influences phenotypic plasticity and performance. Despite debate over the role of functional traits in restoration planning (Gornish et al. 2023; Merchant et al. 2023), incorporating ITV into considerations for building seed mixes has the potential to increase restoration success (Zeldin et al. 2020). However, more information is needed to understand if ITV, as represented in wild populations, may be harnessed during native plant materials development (Basey et al. 2015; McCormick et al. 2021) to result in resilient restoration materials capable of withstanding difficult environmental conditions (Shackelford et al. 2021).

To investigate the fidelity of ITV and its role in promoting plant performance, we visited populations of two high priority restoration species in the southwestern United States from which seed collections had previously been made and collected ITV measurements across mature plants. We used seeds from these sites to establish a common garden experiment, within which we addressed the following questions: (1) Does ITV measured at field sites predict ITV in a common garden? (2) Are rankings of ITV consistent between field sites and the common garden? That is, are naturally variable populations also the most variable within the common garden and across years? (3) Do higher levels of ITV measured at field sites or in the common garden lead to improved plant performance (e.g. survival and reproductive effort) in a common garden setting? We accounted for the provenance of the wild-collected populations by including a calculation of climate distance between the wild population and common garden within our models. These data allowed us to assess whether selecting seed sources with high ITV for plant materials development may be expected to result in restoration materials with high ITV, and in turn, if more variable plant materials may support higher plant performance. Our research directly supports the goals of the National Seed Strategy for Rehabilitation and Restoration (Plant Conservation Alliance 2015) by detailing a key ecological mechanism (i.e. ITV) that may influence the development of native plant materials and support successful restoration outcomes.

Methods

Study Area and Seed Sources

The southwestern United States has growing restoration needs resulting from disturbance, oil and gas development, intensive

grazing practices, and the spread of invasive species (Copeland et al. 2017; Duniway et al. 2019; Winkler et al. 2019). Our research focuses on two geographically widespread perennial species native to the southwestern United States and prioritized for restoration: Sideoats grama (*Bouteloua curtipendula* [Michx.] Torr.; Poaceae) and Hairy goldenaster (*Heterotheca villosa* [Pursh] Shinners; Asteraceae). We did not track varieties of species under the assumption that gene flow occurs across populations regardless of subspecific delineation. We selected field sites by extracting climate data for available seed accessions and choosing those representing a diversity of climate space (see Section 2.5 below). Our final selection of field sites and seed accessions represents a diversity of elevations and latitudes (Table S1; Fig. S1); these gradients correlate with the major axes of climate variation across the region (see Massatti & Knowles 2020).

We obtained seeds from the Southwest Seed Partnership (https://southwestseedpartnership.org), the Bureau of Land Management (BLM) Colorado Plateau Native Plant Program, and the U.S. Geological Survey. Seeds were collected between 2015 and 2018 for *B. curtipendula* and 2013 and 2018 for *H. villosa* (Table S1). As we leveraged existing seed collections, the total population size and area covered by the populations are unknown. However, all collections were made following the BLM's Seeds of Success protocol, which involves sampling a minimum of 10,000 pure live seeds (PLS) from at least 50 plants per population; this protocol is expected to capture genetic variability within populations (Haidet & Olwell 2015). The PLS threshold (10,000 seeds) generally requires far more than 50 plants to be sampled, though we acknowledge that total population size may influence overall trait variability. Seeds were cleaned at the U.S. Forest Service Bend Seed Extractory and stored in a climate-controlled seed warehouse. We selected seeds from 10 populations of *B. curtipendula* in New Mexico and 18 populations of *H. villosa* from New Mexico, Arizona, southern Utah, and southern Colorado (Table S1; Fig. S1). In the context of our research, "population" refers to the individuals associated with different field sites from which plants were sampled.

Propagation and Common Garden

In March 2019, we planted 50 replicates per population (50 replicates × 28 populations) into a total of 1400 4-in. pots (Stuewe & Sons, Inc. Ray Leach RLC3R Conetainers). We planted five seeds per pot (7000 total seeds) and randomly thinned to one seedling per pot 1 month after sowing seeds. Seeds of *B. curtipendula* were cold stratified prior to planting. Plants were maintained in a greenhouse for 110 days before planting in a common garden in July 2019. We constructed the common garden at the Petchesky Conservation Center at the New Mexico Land Conservancy (35.6126, −106.0045) in Santa Fe, New Mexico. The general garden design was based on the RestoreNet gardens established by the U.S. Geological Survey Southwest Biological Science Center (Havrilla et al. 2020; Laushman et al. 2021). The garden is located at ca. 1993 m above sea level (a.s.l.) on a flat plateau dominated by sandy soils in a mixed grassland and pinyon-juniper woodland. We removed woody vegetation and applied herbicide prior to planting.

The common garden consisted of a 25 × 50-m area protected by fencing. The area contained 41 2 × 2-m plots with 27–36 individual plants per plot (though 1 plot only had 10 plants), spaced 30-cm apart, for a total of 1400 individuals. We used a randomized planting design with blocking at the species level, wherein individuals from each population were randomly assigned. We weeded other plants that occurred within experimental plots. We implemented supplemental watering at the garden for approximately 1 month after planting to reduce transplant shock. We reinstated weekly supplemental watering in August–September 2020 due to a 40% decline in average monsoonal precipitation. We obtained precipitation data from the National Oceanic and Atmospheric Association's National Climatic Data Center (https://www.ncei.noaa.gov/cdo-web) from a station located approximately 22-km from the common garden (station id: GHCND:USW00023049).

Trait Measurements: Field Sites

Under the assumption that ITV may be informative when selecting populations for native plant materials development, we focused on collecting data for functional traits that can be easily assessed by field crews. We collected leaf samples to calculate SLA and measured the height of adult plants at every field site from which seeds were collected. SLA is a fundamental axis of the leaf-economic spectrum; lower SLA generally correlates with more conservative resource strategies, while higher SLA correlates with more acquisitive resource strategies (Reich 2014). We measured height from the soil surface to the tallest natural point on the plant without extending stems or leaves. Plant height is often associated with competition for light (Craine & Dybzinski 2013). Data collection took place from June to October 2019. We collected 10 leaves and height data from 25 plants per population (25 × 28 populations = 700 plants), following established collection protocols (Cornelissen et al. 2003; Perez-Harguindeguy et al. 2016).

Trait Measurements: Common Garden

In the common garden, we measured SLA, plant height, flower count (fecundity), and the number of surviving individuals following standardized trait measurement protocols (Cornelissen et al. 2003; Perez-Harguindeguy et al. 2016). We measured height as described above in September 2019 (year 1) and July 2020 (year 2). We monitored survival in September 2020 and counted flowers in September 2019 and September 2020. We collected one leaf per plant for SLA measurements in September 2019 and July 2020. We measured height and collected leaves from all surviving individuals (see Table S1 for survival proportions).

We scanned leaves collected at field sites on an Epson flatbed scanner to facilitate SLA measurements. We then dried leaves for 24 hours at 40°C before measuring dry mass (g). We averaged weights and leaf areas of the 10 leaves per individual from

field populations. We processed leaf scans for leaves collected at field sites using ImageJ (v.1.51; Schneider et al. 2012) to generate accurate leaf area measurements. We calculated leaf area for leaves collected from individuals in the common garden using a CI-203 Handheld Laser Leaf Area Meter (CID Bioscience; Camas, WA, U.S.A.).

Quantifying Climate Distance

To quantify the climate space associated with each seed source, we used ClimateNA 30-year normal data (800-m resolution; Wang et al. 2016) and performed a spatial principal component analysis (PCA) using the "princomp" function in R (center = T, scale = T; R Core Team 2023). These data represent the climate conditions of seed collection sites averaged from 1990 to 2020 and are similar to data used in the construction of empirical and provisional seed transfer zones, which are commonly used to select the seed sources used in native plant materials development. To calculate climate distance between field sites and the common garden, we calculated Euclidean distance between each field site's principal component (PC) values and the PC values of the garden; we used the first seven PC axes because they cumulatively explained greater than 99% of variation across the climate layers (Table S2).

Statistical Analyses

All analyses were performed in R version 4.3.2 (R Core Team 2023). We quantified the amount of ITV within populations using the coefficient of variation (CV; Tables 1 & S3). We also calculated mean trait values (Tables 1 & S4). We first used Spearman correlations to test whether CVs measured in the field were correlated with CVs measured across years in the common garden. Next, we used the Friedman test (a nonparametric alternative to the Analysis of Variance) to quantify whether there were significant differences in ITV distributions between field sites, and each year in the common garden. That is, to understand whether the amount of variation expressed differed between field site and each year in the common garden. Finally, we quantified whether there were significant changes in the rankings between populations for ITV at the field sites and each year in the common garden using Kendall's coefficient of concordance (W). Values of W closer to 1 indicate that there is higher concordance in rankings between groups, whereas values of W closer to 0 indicate substantial shifts in ranking between groups.

We used linear mixed effects models to understand how ITV for SLA and plant height related to survival and fecundity. For all models, we included scaled CV of SLA or height in each year and the scaled climate distance between the field site and the common garden as fixed effects, and population identity as a random effect to control for lack of independence between repeated measurements. We included a measure of climate distance within our models to account for the potential impact of climate distance on patterns of ITV. We used binomial regression to model survival and zero-inflated negative binomial regression to model the number of flowers produced in the common garden. We tested each variable individually, using separate models to look at the relationships between ITV and different performance metrics for both species. Specifically, we analyzed whether, after accounting for climate distance: (1) CVs calculated from traits measured at field sites successfully predicted the proportion of individuals surviving and the number of flowers produced in year 2 and (2) CVs for SLA and height in both year 1 and year 2 in the common garden were related to survival and flower production in year 2. We also ran models excluding climate distance (Figs. S2 & S3) to further explore relationships between ITV and performance and see whether results remained relatively stable. Independent variables were scaled for all analyses. All analyses were performed using the *lme4* (Bates et al. 2015) and *pscl* (Zeileis et al. 2008; Jackman 2020) packages in R (R Core Team 2023), and all model diagnostics were performed using the DHARMa package (Hartig 2022). For all models, variance inflation was checked using the vif() function in the car package (Fox & Weisberg 2019). No model coefficients exceeded a variance inflation of 2, so all coefficients were retained in each model.

Table 1. Summary of minimum and maximum mean trait values and coefficients of variation for specific leaf area (SLA) and height (cm) for populations of focal species. Coefficient of variation (CV) explains the degree of variation around the trait mean within populations. Larger values indicate greater intraspecific trait variability within populations.

Scientific name	*Trait*	*Mean trait values*	*CV*
Heterotheca villosa	Field SLA	67.64–139.37	0.30–0.69
	2019 SLA	102.41–127.38	0.19–0.36
	2020 SLA	52.99–93.89	0.13–0.35
	Field height	7.28–48.90	0.16–0.33
	2019 height	2.88–5.83	0.27–0.60
	2020 height	10.44–29.77	0.23–0.44
Bouteloua curtipendula	Field SLA	66.86–138.56	0.26–0.62
	2019 SLA	114.32–143.64	0.25–0.37
	2020 SLA	60.80–78.85	0.27–0.48
	Field height	27.40–50.68	0.15–0.28
	2019 height	13.41–20.61	0.49–0.73
	2020 height	13.51–31.66	0.36–0.64

Results

Wild populations of *Bouteloua curtipendula* ($n = 10$), from which seeds were sourced, ranged in elevation from 1292 to 2195 m a.s.l. (mean = 1872 m a.s.l.) and varied in distance from 7.34 to 436.29 km (mean = 105.59 km) away from the common garden (Table S1). These populations represented a climate space with climate distances ranging from 0.14 to 3.79 (mean = 1.36; Table S1). For *B. curtipendula*, total survival within populations ranged from 34 to 85% (mean = 70% survival). Populations of *Heterotheca villosa* ($n = 18$) represented a larger elevation gradient, a wider geographic expanse, and a broader climate space relative to the populations of *B. curtipendula*. Seed source populations ranged in elevation from 1370 to 3078 m a.s.l. (mean = 2096 m a.s.l.) and varied in distance from 1.56 to 562.93 km away from the common garden (mean = 237.22 km). Climate distance ranged from 0.008

to 7.056 (mean = 2.33; Table S1). For *H. villosa*, total survival within populations ranged from 26 to 92% (mean = 64% survival).

ITV Across Settings and Over Time

Intraspecific trait variability (ITV) measured at field sites did not predict ITV in either year 1 or year 2 in the common garden for either species or either trait (Table S5). In addition, rankings of trait variability, as determined from the CV calculated at field sites, were inconsistent across settings and over time in the common garden (Tables 1 & S3; Fig. 1). Plant height within *H. villosa* showed the greatest concordance between rankings ($W = 0.43$; Fig. 1), but this value is low. For all traits and both species, rankings of variability shifted over time and relative to traits collected in the field. However, measurements across populations generally corresponded between the field, year 1, and year 2. For example, height CVs for both species generally increased between the field and year 1 in the common garden, with the average height CV across populations increasing from 0.20 to 0.64 for *B. curtipendula* and from 0.26 to 0.36 for *H. villosa*. For both species, this was followed by a small decrease in year 2, where the average height CV decreased to 0.48 for *B. curtipendula* and 0.33 for *H. villosa* (Table S3; Fig. 1). Alternatively, SLA CVs for both species generally decreased between the field and year 1 and values remained fairly stable from year 1 to year 2 (Fig. 1).

ITV and Plant Performance

Survival. We identified few significant relationships between ITV and plant survival. Higher SLA variability in 2020 (year 2)

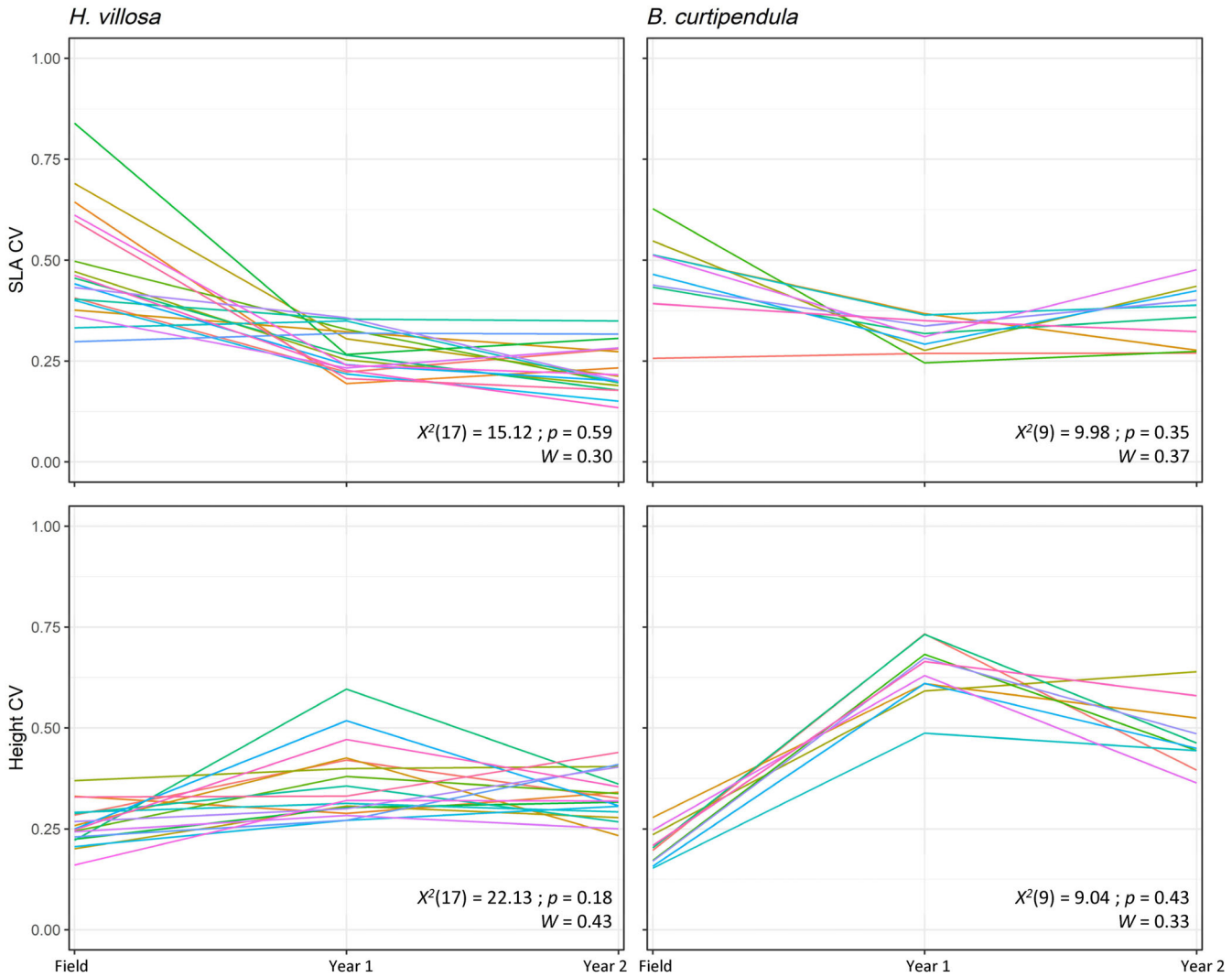


Figure 1. Change and concordance (Kendall's *W*) in ranked coefficient of variation (CV) for height and specific leaf area (SLA) across populations of *Heterotheca villosa* (left panels) and *Bouteloua curtipendula* (right panels) in the field and across 2 years at a common garden. Line colors distinguish different populations. Rankings were determined by Friedman's test and the calculation of Kendall coefficient of concordance (*W*). All tests are with $\alpha = 0.05$; higher values of *W* indicate greater concordance in rankings of variability between measurements.

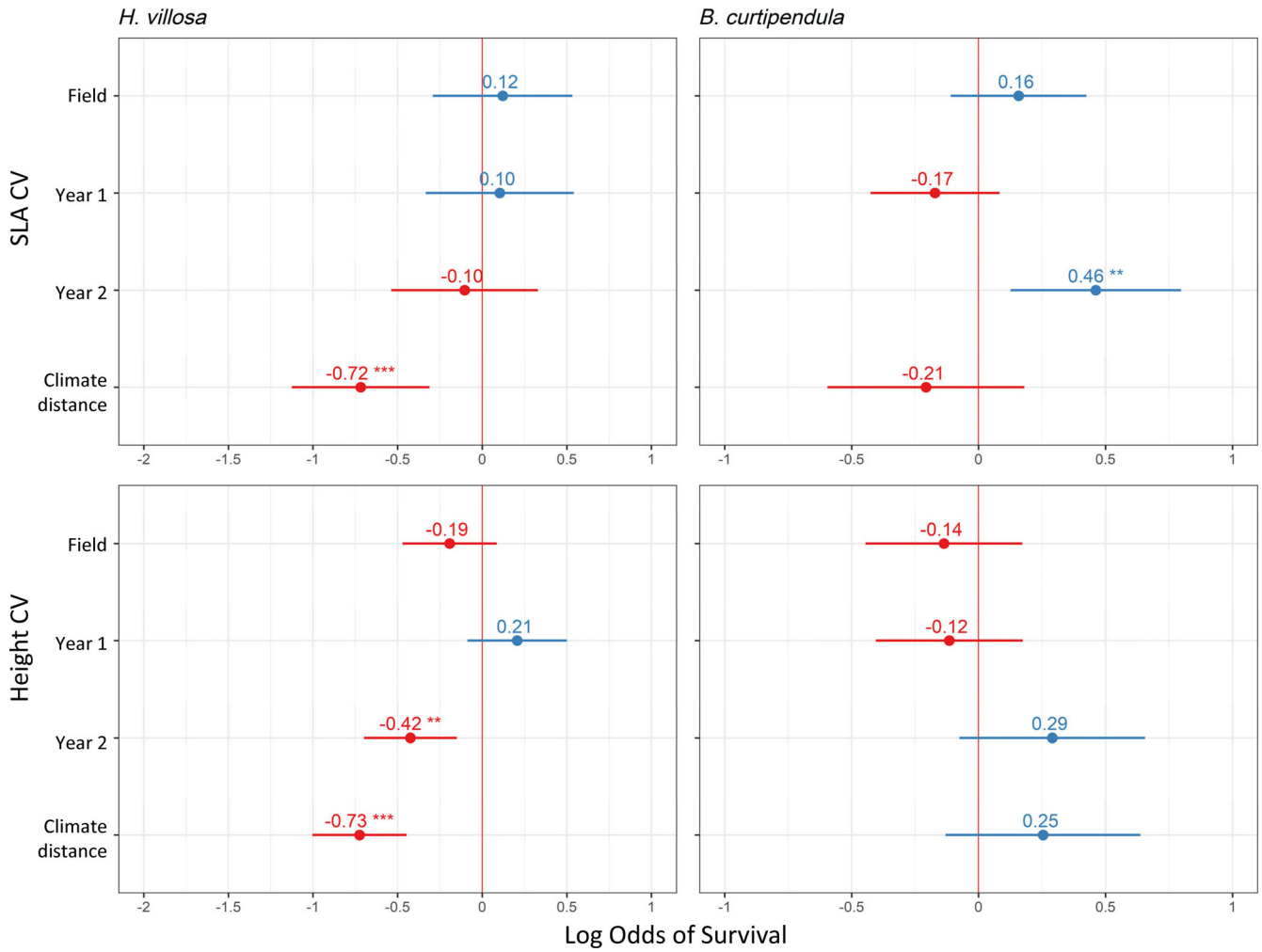


Figure 2. Scaled model estimates (± SE) for 2020 survival in *Heterotheca villosa* and *Bouteloua curtipendula* in response to trait variation in specific leaf area (SLA) and height measured in field populations in the common garden in 2019 (year 1) and 2020 (year 2), and in response to the climate distance between the wild population and the common garden. Red values (left of zero) represent negative relationships, and blue values (right of zero) represent positive relationships. When error bars do not cross zero, the relationships are significant. Significant p values at $\alpha = 0.05$ are indicated by asterisks (** = 0.01, *** = 0.001).

was related to greater survival for *B. curtipendula* in the same year (Est. ± Standard Error of the Mean [SEM] $= 0.46 \pm 0.17$, $p = 0.007$; Table S6; Fig. 2). Similarly, higher variability of plant height in year 2 explained decreased *H. villosa* survival (Est. ± SEM $= -0.42 \pm 0.14$, $p = 0.00245$). Notably, ITV data collected from field sites did not inform survival in the common garden for either species. However, climate distance between the field site and the common garden had a negative effect on the survival of *H. villosa* in both the SLA and height models, meaning that more similar environmental conditions promoted higher *H. villosa* plant performance (Table S6; Fig. 2). We ran models that excluded climate distance to ensure results remained relatively stable. We found one consistent relationship: higher variability in SLA in year 2 was related to greater survival for *B. curtipendula* in the same year (Est. ± SEM $= 0.36 \pm 0.14$, $p = 0.00875$; Table S7). In the models excluding climate distance, we also found that higher variability in height in year 1 was related to greater survival for *H. villosa* in year 2 (Est. ± SEM $= 0.46 \pm 0.22$, $p = 0.0388$; Table S7; Fig. S2). Similar to models including climate distance, ITV data from field sites was not related to survival within the common garden.

Fecundity. Neither variability in SLA nor variability in height were significant predictors of flower production for either species. However, greater climate distance between the field site and garden in both the SLA and height models had a negative effect on flower production for *B. curtipendula*, meaning that more similar climatic conditions bolstered *B. curtipendula* plant performance by promoting higher fecundity (Table S6; Fig. 3). While no relationships between variability and performance were identified when including climate distance, we identified two significant patterns between ITV and flower production when excluding climate distance. High variability in SLA in year 2 was related to increased flower production for *H. villosa* (Est. ± SEM $= 0.18 \pm 0.08$, $p = 0.0332$;

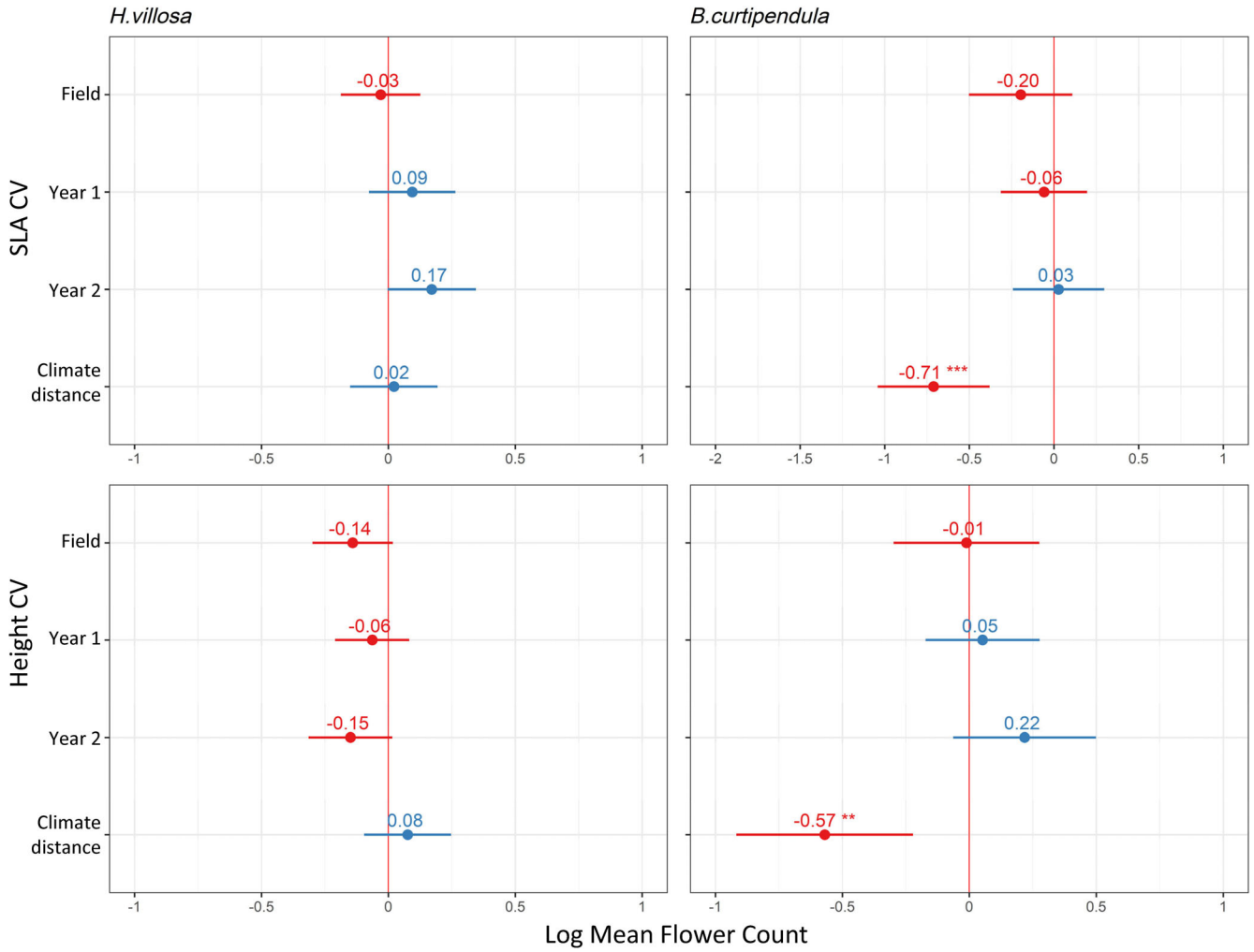


Figure 3. Scaled model estimates (± SE) for 2020 flower production in *Heterotheca villosa* and *Bouteloua curtipendula* in response to trait variation in specific leaf area (SLA) and height measured in field populations in the common garden in 2019 (year 1) and 2020 (year 2), and in response to the climate distance between the wild population and the common garden. Red values (left of zero) represent negative relationships, and blue values (right of zero) represent positive relationships. When error bars do not cross zero, the relationships are significant. Significant p values at $\alpha = 0.05$ are indicated by asterisks (** = 0.01, *** = 0.001).

Table S7; Fig. S3) and high variability in height in year 2 was related to increased flower production for *B. curtipendula* (Est. ± SEM = 0.31 ± 0.15, $p = 0.0387$; Table S7; Fig. S3). Regardless, no relationships were identified between ITV measurements at field sites and flower production in the common garden, similar to models including climate distance.

Discussion

Variation in plant functional traits can indicate greater adaptive capacity to stressful or challenging environmental conditions, which means ITV may be a useful tool for restoration practitioners (Roybal & Butterfield 2018). We used multiple populations of two perennial species primarily sourced from across the Arizona-New Mexico Plateau and the Colorado Plateau to understand (1) whether variation in plant functional traits in wild populations predicts trait variation in a common garden, (2) whether rankings of trait variability among populations are stable across settings and over time, and (3) whether ITV is a reliable indicator of plant performance. By quantifying ITV in wild populations and an experimental setting, we found that (1) ITV was not correlated between the field sites and the common garden, (2) rankings of trait variability across populations were not consistent between settings or across years at the common garden, and (3) ITV was an inconsistent predictor of plant performance. While ITV may be important for species to navigate environmental variability and disturbances within wild populations, our results suggest that patterns of ITV are unstable from wild to experimental populations.

ITV Across Settings and Over Time

We identified no relationships between ITV measured at field sites and variation in SLA or plant height measured in young plants in the common garden. In addition, ITV rankings in the

garden were inconsistent when compared to ITV measured from wild populations at field sites where seeds were originally sourced. Our results support similar research that identifies a weak relationship between ITV measured across settings compared to mean trait values (Dostál et al. 2020). While we focus on trait variation and its ability to predict plant performance herein, we note that relationships between mean trait values and performance have a strong foundation within the scientific literature (Poorter & Bongers 2006).

ITV and Plant Performance

Survival during establishment is an early indicator of the suitability of plant materials in restoration contexts (Lauenroth & Adler 2008; James et al. 2011). Thus, tracking survival is important, particularly in dryland restoration where successful outcomes can be difficult to achieve (Baughman et al. 2019; James et al. 2019). Both species demonstrated high survival in the common garden. By leveraging differences in ITV across populations and given the hypothesized role of variability in supporting performance (Westerband et al. 2021), we tested whether ITV in functional traits was correlated with plant survival. Our models incorporating variation in SLA and plant height across wild populations (field sites) and experimental sites, as well as among years, did not identify a role for ITV measured in wild populations in the survival of individuals within our common garden. It is difficult to assess whether relationships between trait variation within the garden and survival are meaningful. For example, the importance of ITV in SLA for *Bouteloua curtipendula* survival in 2020 may reflect different physiological tolerances between the species we studied (Mundim & Pringle 2018). *Bouteloua curtipendula* utilizes the C_4 photosynthetic pathway, which is correlated with greater tolerance of heat and water stress, while *Heterotheca villosa* utilizes the C_3 pathway. Under the right combination of weather variables in 2020, this difference may have led to slightly higher survival rates via a larger number of viable trait and allocation strategies for *B. curtipendula*. Similarly, reduced survival predicted by high ITV in plant height for *H. villosa* in 2020 may reflect the species' growth allocation strategy during establishment. In other words, survival was more difficult for *H. villosa* populations with higher height variability (e.g. Tyler et al. 2008).

Reproduction is another important measure of performance because it reflects a species' potential for persistence in a restoration setting, even if survival of individual plants is relatively low. We focused on flower production as a metric of reproductive effort instead of seed production because seeds can be reduced in the absence of pollinators for *H. villosa* (Herron-Sweet et al. 2016). In addition, cross pollination in the garden among distantly related populations or between populations with ploidy variation (i.e. *B. curtipendula*; Siqueiros-Delgado et al. 2017) may influence the production of viable seeds (McKay et al. 2005; Frankham et al. 2011; Kramer et al. 2018). Neither species showed a significant relationship between flower production and trait variation that was measured at field sites or within the garden. The shifting importance of growth versus reproduction in young transplants, as well as our use of supplemental water, may have masked any biologically relevant signal. For example, in 2019, we used supplemental watering to maximize survival and reduce transplant shock, which may have buffered phenotypes that might otherwise have been selected against (e.g. Abella et al. 2015) or artificially supported a more homogenous number of flowers across populations. Similarly, we may have reduced selection pressure in 2020 when we used supplemental watering later in the growing season (during anthesis) to approximate average regional growing conditions due to extreme drought.

Climate Distance and Plant Performance

We included a measure of climate distance within our models to account for the potential impact of differences in climate between the source population and the common garden on patterns of ITV. Climate distance and ITV are related because ITV can help plant populations succeed in non-local, or climatically dissimilar, environments (Mitchell et al. 2021; Kitagawa et al. 2022). In addition, including a climate distance measurement also allowed us to understand the relationship between climate and performance. We show clear, negative signals of increasing climate distance on survival for *H. villosa* and on flower production for *B. curtipendula*. That is, as seeds were collected at greater climatic distances from the common garden, performance declined, which is similar to relationships identified during the course of common garden analyses to construct empirical seed transfer zones (St. Clair et al. 2013). That said, excluding climate distance from our models resulted in additional instances of ITV improving plant performance across species. This suggests climate distance largely masks the influence of ITV in predicting performance, which is an expected outcome in dryland plant systems that are largely dominated by interannual climate variability (Gherardi & Sala 2019).

Our findings align with meta-analyses on local adaptation in similar systems (Hereford 2009; Baughman et al. 2019) that describe the importance of local adaptation in predicting performance. For flower production, the significant negative effect of seed collection distance is important in a restoration context, as delayed, early, or absent floral resources may lead to significant phenological mismatch between plants and their mutualists (Bucharova et al. 2022). Since climate matching plays a role in predicting performance for both *H. villosa* and *B. curtipendula*, efforts to restore for future climates may benefit from matching using predicted climate scenarios (Sgrò et al. 2011; Weeks et al. 2011; Burrows et al. 2014), though methodological development and testing will be critical to provide guidance (e.g. Lotterhos 2024).

Experimental Limitations

Multiple factors could impact the relationships we observed between ITV measured in the field and performance in a new setting. We acknowledge that phenotypic diversity may have been influenced by our methodology, which included collecting seeds from wild populations, growing plants within a greenhouse, and transplanting plugs into our common garden where unrealistic conditions were maintained through weeding and watering (Abella et al. 2015; Passaretti et al. 2020). In addition,

trait measurements were limited by our study timeframe; given that our focal species are perennial, characterizing flower production early in these species' lives may be skewed, as many perennial species are not highly reproductive in their first 2 years of growth (Friedman 2020). Furthermore, it will be important to track ITV within experimental studies to understand if patterns remain stable as an experimental population matures.

ITV and Native Plant Materials Development

This study explores assumptions that high ITV in wild populations is indicative of higher variability in experimental populations and vice versa (Dostál et al. 2020). Examining this assumption is important because identifying populations with highly variable, potentially adaptive traits is relevant for seed sourcing decisions, restoration planning, and native plant materials development (Broadhurst et al. 2008; Espeland et al. 2017). However, effectively selecting for trait variation and maintaining variation from seed collection through planting is not well understood for a broad range of species (McCormick et al. 2021). We observed instability of rankings among populations within *H. villosa* and *B. curtipendula*, suggesting that field-based ITV measurements for these species are not useful predictors to support the development of morphologically variable native plant materials from single source populations. However, the impact of other native plant materials development strategies on ITV, such as pooling wild-collected seed sources (Bucharova et al. 2019; Erickson & Halford 2020), requires additional investigation. While pooling seed sources after agricultural increase may increase ITV if trait means within seed sources vary, pooling seed sources before agricultural increase may homogenize the gene pool for outcrossing species, resulting in unclear expectations for ITV and patterns of local adaptation. Moreover, future work is required to decipher the potential maternal effects that can influence phenotypes across multiple generations (e.g. Boyd et al. 2007). Together, these avenues for future research may provide a richer and more informed context for ITV that warrants its inclusion within restoration planning.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Map of seed collection sites.
Figure S2. Log odds of survival without climate distance.
Figure S3. Log mean flower count without climate distance.
Table S1. Details about seed collection sites.
Table S2. Principal component (PC) loadings.
Table S3. Coefficients of variation for trait measurements.
Table S4. Mean and standard deviation of trait measurements.
Table S5. Spearman correlation between coefficients of variation for trait measurements.
Table S6. Statistics from linear mixed effects models with climate distance.
Table S7. Statistics from linear mixed effects models without climate distance.

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