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RESEARCH ARTICLE

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Local adaptation of seed and seedling traits along a natural aridity gradient may both predict and constrain adaptive responses to climate change

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Abstract

Premise: Variation in seed and seedling traits underlies how plants interact with their environment during establishment, a crucial life history stage. We quantified genetic-based variation in seed and seedling traits in populations of the annual plant *Plantago patagonica* across a natural aridity gradient, leveraging natural intraspecific variation to predict how populations might evolve in response to increasing aridity associated with climate change in the Southwestern U.S.

Methods: We quantified seed size, seed size variation, germination timing, and specific leaf area in a greenhouse common garden, and related these traits to the climates of source populations. We then conducted a terminal drought experiment to determine which traits were most predictive of survival under early-season drought.

Results: All traits showed evidence of clinal variation—seed size decreased, germination timing accelerated, and specific leaf area increased with increasing aridity. Populations with more variable historical precipitation regimes showed greater variation in seed size, suggestive of past selection shaping a diversified bet-hedging strategy mediated by seed size. Seedling height, achieved via larger seeds or earlier germination, was a significant predictor of survival under drought.

Conclusions: We documented substantial interspecific trait variation as well as clinal variation in several important seed and seedling traits, yet these slopes were often opposite to predictions for how individual traits might confer drought tolerance. This work shows that plant populations may adapt to increasing aridity via correlated trait responses associated with alternative life history strategies, but that trade-offs might constrain adaptive responses in individual traits.

KEYWORDS
climate change, drought, intraspecific trait variation, life history strategies, local adaptation, *Plantago*, precipitation variability, seed size, trade-offs

Trait-based ecology aims to predict the outcome of an organism's interactions with the environment or other organisms as a function of its phenotype. Functional traits—important phenotypic characteristics affecting fitness—are believed to be multi-faceted proxies for alterative ecological or life history strategies (Kraft et al., 2015; Kunstler et al., 2016; Funk et al., 2017). While trait-based ecology holds promise for predicting how organisms might respond to changing ecological or environmental conditions, correlations among traits (Donovan et al., 2011) and their respective effects on vital rates may reduce the effectiveness of using individual traits to estimate adaptive capacity (Ahrens et al., 2020; Laughlin et al., 2020). For example, one of the most fundamental trade-offs expected in seed plants is that between seed number and seed size (Westoby et al., 1992). Given finite resources an individual may produce a greater number of smaller seeds or a smaller number of larger seeds (Smith and Fretwell, 1974). More smaller seeds are expected to maximize reproductive fitness under favorable conditions, whereas fewer larger seeds are expected to maximize offspring survival under harsh establishment conditions (Baker, 1972; Leishman et al., 2000; Leger et al., 2019), highlighting the context-dependent relationship between individual traits and fitness.

Seed size has received considerable attention in the literature as it influences myriad mechanisms underlying successful establishment, including dispersal ability, seed dormancy and germination timing, seedling growth rates, and survival probability under environmental hazards such as drought and competition (reviewed in Westoby et al., 1992; Leishman et al., 2000; Moles and Westoby, 2004). The transition from seed to seedling represents a vital stage in a plants' life history, one prone to high rates of mortality (Metz et al., 2018; Larson et al., 2020). Larger seeds are thought to be advantageous under harsh establishment conditions either via a seedling size effect in which larger seeds produce larger seedlings, a reserve effect in which larger seeds have greater energy reserves due to greater endosperm provisioning, or a metabolic effect in which a conservative growth strategy acts to ration seed resources (Leishman et al., 2000). These effects are typically most pronounced early in a plant's life; however, they can also have long-lasting effects on lifetime fitness (Halpern, 2005; Metz et al., 2010; Larios et al., 2014).

Despite evidence for increased seed mass facilitating the transition from seed to seedling, contrasting establishment conditions are likely to favor alternative seed and seedling life history strategies. For example, in benign or resource-rich habitats the increased dispersal ability of smaller seeds may outweigh potential fitness gains of producing larger seeds (Parciak, 2002). In addition to seed size, a suite of other seed and seedling traits that may be correlated with seed size can also directly affect fitness in harsh or variable environments. Increased dormancy and variation in germination timing may represent bet-hedging strategies facilitating drought avoidance at xeric sites or those with variable precipitation regimes (Clauss and Venable, 2000; Gremer and Venable, 2014). Rapid germination and growth following suitable conditions may represent a drought escape strategy (Duncan et al., 2019; Anstett et al., 2021). Following germination, other seedling traits including reduced specific leaf area, increased root length, and altered root composition can also be critical adaptations to drought (Harrison and LaForgia, 2019; Larson et al., 2020). Overall, different traits associated with drought avoidance, drought escape, and drought tolerance are likely to vary along environmental gradients, as selection may differentially favor alternative life history strategies based on abiotic conditions.

Many studies exploring correlations between seed and seedling traits have occurred across species (see Westoby et al., 1992; Leishman et al., 2000; Muller-Landau, 2010), as have many syntheses using functional traits to predict community-level responses to climate change (e.g., Venn et al., 2011; Soudzilovskaia et al., 2013; Bussotti et al., 2015; Ahrens et al., 2020). Alternatively, exploring trait-environment associations at the intraspecific level can reveal the outcome of evolutionary processes (Wellstein et al., 2013; Funk et al., 2017; Caruso et al., 2020; Laughlin et al., 2020), linking traits to fitness and informing expectations for how populations might evolve in response to climate change. One effective approach to understanding how past selection has shaped phenotypic variation, potential trade-offs among traits, and alternative life history strategies, is to explore intraspecific variation along natural environmental gradients (Petrů et al., 2006; Pratt and Mooney, 2013; Welles and Funk, 2021). Here, ecotypic differentiation across environments suggests that populations have evolved in response to abiotic drivers (Wellstein et al., 2013; Carvajal et al., 2017; Vázquez et al., 2017; Caruso et al., 2020). Despite the promise of leveraging trait variation across space to predict how individual populations might evolve across time (i.e., if local conditions change), explorations of intraspecific trait variation seem to be relatively lacking for seed traits (Westerband et al., 2021).

Seed and seedling traits are crucial in determining early survival, particularly under water-limited establishment conditions; however, life history traits are often correlated and may display distinct fitness trade-offs (Leishman et al., 2000; Donovan et al., 2011; Leger et al., 2019). Populations that have reached local optima under present-day conditions may thus be constrained in their capacity for specific traits to adapt independently to changing environmental conditions (Guo et al., 2000; Etterson and Shaw, 2001; Hellmann and Pineda-Krch, 2007), potentially reducing their evolutionary potential under future climate change. For example, populations from historically mesic sites may be unable to survive under increasingly xeric conditions imposed by rapid climate change (Barton et al., 2020), perhaps because they no longer harbor genetic diversity associated with drought tolerance. Furthermore, climate induced mismatches between establishment conditions that natural populations are now facing, and those under which they previously evolved (Tíscar et al., 2018), may hinder plants' recruitment abilities.

Plantago patagonica Jacq. [Plantaginaceae] is an annual forb that is currently widespread throughout arid areas across much of the U.S. (Flora of North America Editorial Committee, 1993 ongoing); however, it is unclear whether accelerated climate change in the Southwestern U.S. (Seager et al., 2007; Cook et al., 2015; Kogan and Guo, 2015) will outpace the ability of populations to adapt to increasing aridity, precipitation variability, and early season drought. To explore this potential, we assess genetic-based trait variation for several traits that may be associated with climate adaptation. We focus on traits that are biologically relevant to seedling establishment, a life history stage we expect to be particularly sensitive to increasing drought and precipitation variability. We ask: (1) if traits commonly associated with alternative drought strategies—seed size, germination timing, and specific leaf area—show evidence of local adaptation along a natural aridity gradient? (2) whether populations from locations with variable precipitation regimes show evidence of increased seed size variation? and (3) which seed and seedling traits best predict survival under extreme early-season drought? Our goal is to assess patterns of local adaptation and potential trade-offs among seed and seedling traits, and to leverage trait-environment associations to predict how plant populations might evolve under increasingly arid conditions associated with climate change in the Southwestern U.S. *P. patagonica* is an ideal study system to address these questions as it is geographically and climatically diverse and is thus expected to harbor substantial intraspecific trait variation. The species' restoration potential is currently being explored (Massatti et al., 2019), thus findings from this work may have important implications for restoration efforts of degraded drylands.

MATERIALS AND METHODS

Study system

We used *Plantago patagonica* to study local adaptation of seed and seedling traits. The species inhabits sandy soils and open sites throughout much of the United States (Flora of North America Editorial Committee, 1993 ongoing), and in the Southwestern U.S. it is widespread across a broad range of elevations (400–2100 m in Arizona alone) (Huisinga and Ayers, 1999). Within the semi-arid Colorado Plateau it occurs across a wide variety of locations and climates (Figure 1). *P. patagonica* is largely inbreeding and shows greater reproductive effort and higher seed weights compared to other outcrossing congeners (Sharma et al., 1999). Populations from different source climates across the Colorado Plateau show patterns of local adaptation with respect to germination requirements (Seglias et al., 2018), and seeds have been found to be relatively abundant in the seedbank (Bernstein et al., 2014; Haight et al., 2019).

Seed collections

For our study we obtained seeds from 12 native populations of *P. patagonica* from across the Colorado Plateau ecoregion in Arizona and Utah (Figure 1A). First, in 2019 we collected seeds from eight populations by collecting mature seeds directly from senesced plants, sampling the full spatial extent of each population, and seeds from approximately 30 maternal plants per population, each separated by at least 2 m from one another. In addition, we acquired field-collected seeds from four additional populations from the Colorado Plateau Native Plant Program (CPNPP) and the Bureau of Land Management (BLM) that were collected in 2014. These collections represent bulk samples of seeds from hundreds of maternal lines per population.

Greenhouse refresher generation

We planted field-collected seeds from all 12 populations in the greenhouse at Northern Arizona University in a 50:50 potting soil:sand mix in SC10 pots (164 mL). We planted seeds from an average of 33 maternal lines per population for populations collected in 2019; seeds from the four populations collected in

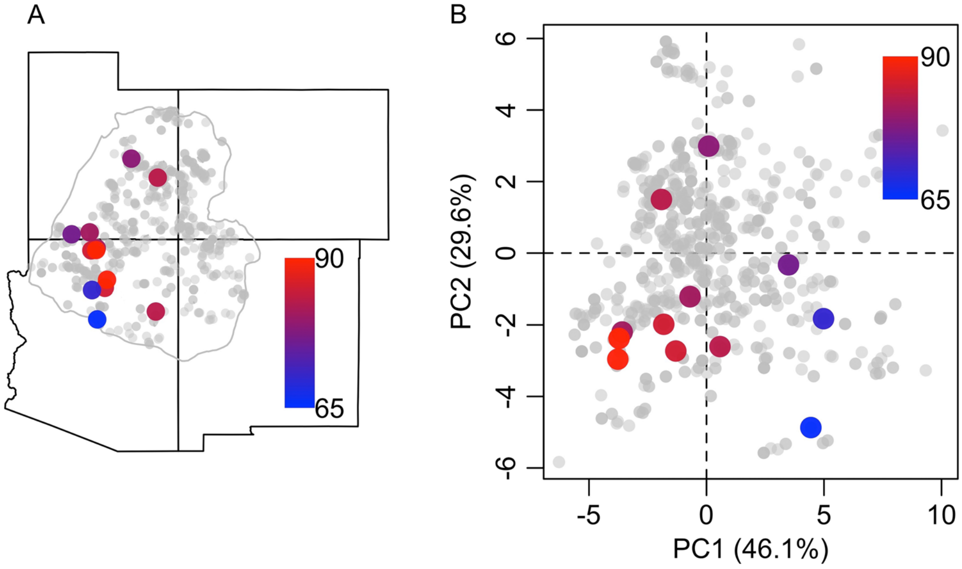

FIGURE 1 Geographic and climatic variation among *P. patagonica* populations on the Colorado Plateau. (A) Regional distribution (gray points) and seed collection locations of 12 focal populations (colored points); gray points represent georeferenced records (GBIF, 2022; SEINet Portal Network, 2022). (B) Principal Component Analysis based on 19 bioclimatic variables from WorldClim showing the climate space occupied by *P. patagonica* on the Colorado Plateau (gray points), and the portion occupied by our 12 focal populations (colored points). Colors depict the Thornthwaite aridity index at each site; warmer colors/higher values represent more arid sites.

2014 represented bulk samples of approximately 500 individuals per population. On average we planted 133 seeds per population for a total of approximately 1600 seeds. To minimize maternal and storage effects, we grew plants under shared environmental conditions for one generation, watering every other day, allowing them to autonomously self-fertilize, produce seeds, and senesce. We randomly selected 24 individual plants (i.e., subsequent maternal lines) from each of the 12 populations to serve as seed sources for the subsequent experiments. As maternal effects (Donohue, 2009; Yin et al., 2019) and storage effects (Rogalski, 2015) can dramatically affect offspring phenotypes, this refresher step ensures that phenotypic trait variation observed in experimental plants largely reflects underlying genetic variation as opposed to phenotypic plasticity.

We stored the seeds from the refresher generation at room temperature in the dark and did not apply any vernalization or cold stratification to the seeds before initiating the greenhouse experiments the following year. This was a logistical constraint and not a biological consideration. The interaction between source climate and cold stratification conditions may affect germination likelihood in *P. patagonica* (Seglias et al., 2018); however, we do not expect this to differentially affect germination timing among non-dormant seeds (see below).

Seed imaging

We placed all seeds from each maternal plant ($n = 24$ per population) concave-side down on a piece of white paper and took photographs using a Canon Powershot SX120IS (Canon, Inc., Ota, Tokyo, Japan) from a fixed distance of 20 cm under standardized light conditions. We used a custom *Analyze Particles* script in *ImageJ* (Schneider et al., 2012) to calculate the area of each individual seed.

To determine whether seed area was a reliable proxy for seed mass, we weighed 216 randomly selected seeds using a Mettler Toledo microbalance (Mettler Toledo, Inc. Columbus, Ohio, USA) (6 seeds from each of 36 maternal lines, 2–4 maternal lines per population, while sampling seeds from all populations), and calculated seed area as above. We conducted a Pearson's correlation test (*cor.test* function) in R (R Core Team, 2021) to assess the correlation between seed area and seed mass. We also modeled this relationship using a linear mixed model (*lmer* function from the *lme4* package, Bates et al., 2015) with a fixed effect for seed area and a random effect for population. We calculated partial R^2 from the linear mixed model using the *partR2* function from the *partR2* package (Stoffel et al., 2021). We also assessed the relationship between seed size and seed number using a Pearson's correlation test as well as using a linear mixed model as above.

Climate data

To characterize the overall climatic conditions at each of the 12 *P. patagonica* seed collection locations, we extracted data for 19 bioclimatic variables from the *WorldClim* climate database (Fick and Hijmans, 2017) using the *getData* function from the *raster* package (Hijmans, 2022). To characterize the aridity at each site, we downloaded the Thornthwaite aridity index (Thornthwaite, 1948) representing the degree of water deficit below water need, and a climate moisture index (Willmott and Feddema, 1992; Vörösmarty et al., 2005) from the ENVIREM (Environmental Rasters for Ecological Modeling) database (Title and Bemmels, 2018). To determine historic variability in precipitation regimes, we downloaded annual precipitation data from 1967 to 2017 from each site from PRISM (PRISM Climate Group, 2014).

Greenhouse experiments

Germination

Following one generation under shared environmental conditions in the greenhouse (see above), we randomly selected 144 seeds (6 seeds from each of the 24 maternal lines) from each of the 12 populations ($n = 1728$ seeds in total). To approximate the physical effects of seed transport and dispersal in native habitats, we manually scarified each seed by gently rubbing it in a circular motion between two sheets of 150-grit sandpaper for 10-seconds. We planted the seeds in potting soil in 72-cell germination trays (4 cm × 4 cm × 5 cm cells, 80 cm^3), randomizing all populations and maternal lines across rows in the germination trays. For four weeks (1 to 28 June 2021), we saturated trays via daily misting, maintaining the plants under shared conditions (12–25°C, 43% mean relative humidity, 14.5 hours of ambient daylength). We randomized the position of trays on benches every 3–5 days throughout the experiment. We censused seeds daily, recording the germination date of each seed.

Determining specific leaf area

Four weeks after initially planting seeds we measured the height of all germinants. We collected one leaf (2nd or 3rd true leaf) from each germinant that was at least 5 mm tall ($n = 307$ seedlings). We immediately calculated the fresh area of each leaf using *Leafscan* for iOS (Anderson and Rosas-Anderson, 2017). We then dried all leaves at 70°C for 24 hours and measured dried leaf mass on a microbalance. We calculated specific leaf area (SLA) as leaf area (in mm^2) divided by leaf dry mass (in mg).

Terminal drought experiment

After four weeks of daily misting, which maintained continual soil moisture in the germination trays, we imposed a severe drought by completely halting daily watering. We monitored the seedlings daily for an additional four weeks, recording the number of days until death. We intended to simulate a situation in which seeds received inducive germination cues followed by a complete lack of precipitation, a biologically realistic scenario associated with increased precipitation variability in the Southwestern U.S. (Seager et al., 2007; Coats et al., 2013; Cook et al., 2015). A seedling was scored as dead when it was no longer green and if a leaf broke when bent. To determine whether germinant size influenced the dry-down rate of individual tray cells, we measured the soil moisture content of 144 cells (108 cells randomly sampled with respect to plant height, and 36 empty cells lacking a seedling) after one week of the drought treatment, using a Vegetronix VG-METER-200 soil moisture meter (Vegetronics, Riverton, Utah, USA).

Seed size and growth rates

We sowed the 216 seeds for which we quantified mass in potting soil in germination trays and misted daily as above. We censused germination daily and recorded the height of all plants 18 days after the onset of inductive germination conditions. For a cohort of 62 seeds that germinated on the same day (7 days after the onset of germination conditions), we calculated growth rates as ln (plant height in mm – 0 [plant height at the time of germination])/(Julian day 195 [measurement date] – Julian day 184 [germination date]), representing average growth rates as calculated 11 days after germination.

Statistical analyses

Characterizing overall climatic differences between sites

To determine how the 12 populations of *P. patagonica* differed in overall climate space, and to determine what portion of total climatic variation across the Colorado Plateau ecoregion our sampling captured, we conducted Principal Components Analysis (PCA) based on 19 bioclimatic variables using the *prcomp* function in R.

Seed number-seed size correlations

We assessed the relationship between seed size and seed number in 291 maternal plants using Pearson's correlation. Additionally, to account for a population-level effect we also used a linear mixed model (*lmer* function) to model seed size, fitting a fixed effect for seed number and a random effect for population.

Modeling seed and seedling traits across a natural aridity gradient

We used linear mixed models (*lmer* function) to model three traits—seed size, days to germination, and specific leaf area (SLA)—as a function of the aridity experienced by the 12 populations of *P. patagonica.* For seed area, we fit a fixed effect for aridity of the source location (Thornthwaite aridity index) and random effects for both population and maternal line. For germination timing, we again fit a fixed effect for aridity, and random effects for population, maternal line, and germination tray. We also modeled the likelihood of germination under our experimental conditions (*glmer* function from the *lme4* package; binomial model family with logit link) with the same model specifications as above. For SLA, we fit a fixed effect for aridity, and random effects for population, maternal line, and germination tray. We used the *ggpredict* function from the *ggeffects* package (Lüdecke, 2018) to calculate estimated marginal means and to generate model predictions. To corroborate these analyses, we replicated the same models substituting the climatic moisture index from ENVIREM in place of the Thornthwaite aridity index.

Determining seed size variation and variation in historical precipitation patterns

To test the hypothesis that populations experiencing greater variability in historical precipitation regimes display greater variation in seed sizes, we used measurements of annual precipitation from 1967 to 2017 to calculate a coefficient of variation (COV; standard deviation divided by the mean) representing the variability of annual precipitation patterns at each *P. patagonica* site. Next, we calculated the COV for seed size for each maternal plant (24 per population), representing the degree of variation in seed size when plants were grown under shared environmental conditions. We used a linear mixed model (*lmer* function) to model seed size variation, fitting fixed effects for both precipitation variability and aridity of the source climate and a random effect for population. We again generated model predictions using *ggpredict.*

Modeling growth rates

We modeled the growth rates of *P. patagonica* seedlings using a linear mixed model (*lmer* function), fitting a fixed effect for seed mass and random effects for population, maternal line, and germination tray. We built a single model for a cohort of 62 seedlings that germinated on a single day, and thus experienced identical growing conditions for the duration of their lifetimes. We generated model predictions as above.

Modeling seedling survival under experimental drought

To test the hypothesis that seedlings from populations experiencing greater aridity show greater resilience to early-season drought, we modeled days to death under experimental drought. We fit a mixed effects survival model using the *coxme* function from the *coxme* package (Therneau, 2022), fitting fixed effects for germination date, plant height at the onset of drought (a proxy for overall seedling size), and aridity of a plant's source climate, and random effects for population, maternal line, and germination tray. We generated a Kaplan-Meier survival curve using the *Surv* and *survfit* functions from the *survival* package (Therneau, 2021), and visualized survival curves for three arbitrary height classes of seedings (<5 mm, 5–10 mm, and >10 mm tall). For the subset of seedlings for which we had SLA data ($n = 296$), we conducted another survival analysis in the same manner, fitting an additional fixed effect for SLA.

We determined whether plant height influenced soil moisture availability in individual germination cells using a linear mixed model (*lmer*), modeling soil moisture (volts) with a fixed effect for seedling height and a random effect for germination tray.

Determining the direct and indirect effects of source climate and seedling traits on survival

We used structural equation modeling (SEM) to decompose the relative contributions of source climatic aridity and plant traits to survival timing in the terminal drought experiment. SEMs consider the correlation structure among predictors (e.g., germination date and seedling height were co-linear as individuals that germinated earlier had a longer growth period prior to the onset of drought) and facilitate the partitioning of direct and indirect effects of predictors on response variables. We implemented SEMs using the *sem* function in the *lavaan* package in R (Rosseel, 2012). As our response variable, days to death under experimental drought, was left-skewed (some individuals died relatively quickly after the onset drought), we used bootstrapping ($n = 10{,}000$) and a Bollen-Stine test (Bollen and Stine, 1992) to compute P-values of test statistics. Our model considered five paths: (1) source aridity directly affects survival time (potentially via unmeasured physiological mechanisms such as water use efficiency); (2) source aridity affects germination timing; (3) source aridity affects plant height (potentially via seed size effects and associated growth rates); (4) germination timing affects plant height; and (5) plant height affects days to death (potentially due to other size-related traits such as root length or root area). We assessed model fit using a chi-square test, the Comparative Fit Index (CFI), Root Mean Square Error of Approximation (RMSEA), and Standardized Root Mean of Square Residuals (SRMR) via the *summary* and *fitMeasures* functions within *lavaan*. We visualized the SEM paths using the *semPaths* function from the *semPlot* package (Epskamp, 2022), and the *mark_sig* function from the *semptools* package (Cheung and Lai, 2021) in R.

We repeated the same SEM pipeline for the subset of the data for which we had specific leaf area (SLA) data, adding two additional direct paths to the model: (6) source aridity affects SLA and (7) SLA affects survival time (potentially via reduced transpiration), while also accounting for the correlations between (8) SLA and germination time and (9) SLA and height, reflecting potential differences in SLA when measured across stages of early leaf development.

RESULTS

Seed size correlations

We found a strong correlation between seed area and seed mass based on the raw data (Pearson's $r = 0.87$, $P < 0.001$; Appendix S1), as well as when we took population into account (partial $R^2 = 0.73$, $P < 0.001$), indicating that seed area was a reliable proxy for seed mass. Among plants grown under well-watered conditions in the greenhouse for one generation, we found some evidence for a weak seed size-seed number trade-off (Pearson's $r = -0.13$, $P = 0.02$); however, this relationship was not significant when accounting for population ($P = 0.70$).

Do traits associated with drought strategies show evidence of local adaptation along a natural aridity gradient?

Inconsistent with the hypothesis that *P. patagonica* populations from more arid environments produce larger seeds, seed size decreased as the aridity of the source climate increased (effect size = −0.017; $P = 0.002$). There was a 20% decrease in seed size across the full aridity gradient, with average seed size ranging from 2.02 mm^2 in the least arid site to 1.61 mm^2 in the most arid site (Figure 2A). We observed a similar trend in the linear mixed model based on the climate moisture index ($P = 0.003$; data not shown).

Seeds from populations experiencing more arid conditions germinated earlier under shared greenhouse conditions than those from less arid sites (effect size = −0.173; $P = 0.012$). On average, seeds from the most arid end of the gradient germinated four days earlier (9.79 days after the onset of inductive germination conditions) compared to those from the least arid site (13.94 days) (Figure 2B). Results were again consistent in the model based on the climatic moisture index ($P = 0.012$; data not shown). Under our storage conditions (room temperature in the dark, no cold stratification between the refresher generation and the subsequent experiments conducted the following year) and greenhouse germination conditions (daily misting), there was no effect of aridity of the source climate on the probability of germination ($P = 0.43$).

Contrary to the hypothesis that seedlings from more arid environments produce leaves with lower specific leaf area (SLA), our data supported the opposite trend as SLA increased along the aridity gradient (effect size = 0.122;

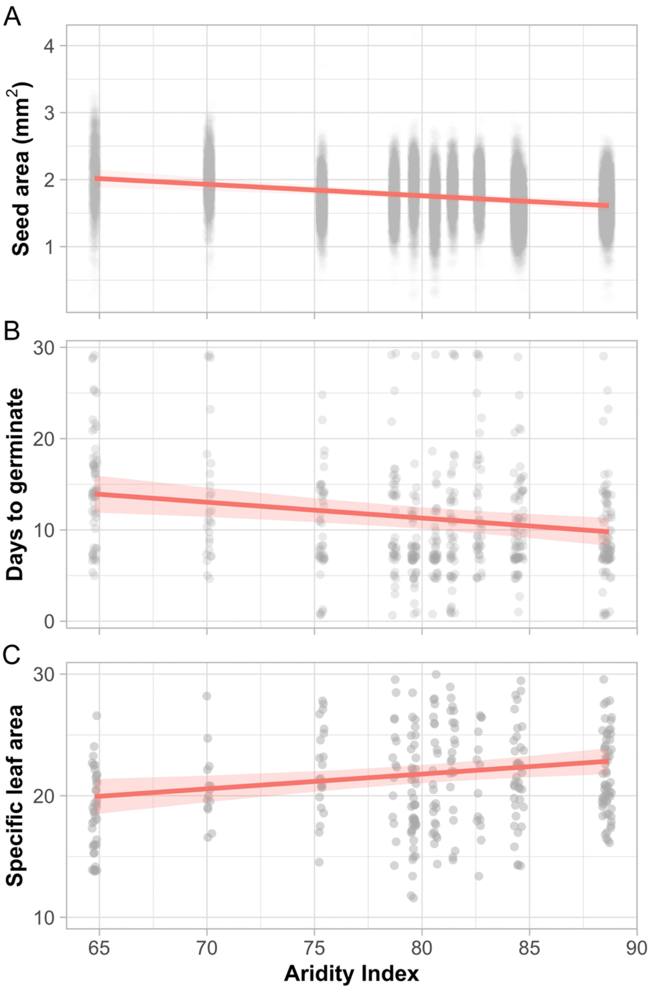

FIGURE 2 Trends in seed and seedling traits among 12 populations of *P. patagonica* from across an aridity gradient on the Colorado Plateau when grown under shared greenhouse conditions. The x-axis (Thornthwaite aridity index) is a measure of the degree of water deficit below water need; higher numbers reflect more arid conditions. Points in each panel represent individual seeds ($n = 33{,}093$ imaged seeds), germinants ($n = 535$), and seedlings ($n = 307$), respectively. Trend lines represent model predictions with shaded 95% confidence intervals. (A) Seed size decreased as aridity increased; (B) Seeds from more arid locations germinated earlier under consistently well-watered greenhouse conditions; (C) Under shared greenhouse conditions, specific leaf area of seedlings increased with the aridity of a population's source climate.

$P = 0.02$). We observed a 15% increase in SLA from the least arid to the most arid end of the aridity gradient (Figure 2C). Again, results were consistent in the model based on the climatic moisture index ($P = 0.03$; data not shown).

Overall, we observed substantial trait variation at the population level for all three seed and seedling traits (Figure 2), reflecting substantial underlying genetic variation. The breadth of intraspecific trait variation within every individual population spanned a much greater range than did mean predictions across populations (Figure 2). Thus, every population harbored at least some genetic variation consistent with that of populations from both extremes of the aridity gradient.

Do populations experiencing greater annual variation in precipitation show increased seed size variation?

Populations of *P. patagonica* from sites that have experienced higher coefficients of variation in annual precipitation over the past 50 years (1967–2017) were comprised of individuals that also showed greater coefficients of variation for seed size (effect size = 0.479; $P = 0.03$). Along the precipitation variation gradient spanned by the 12 focal populations, the average seed size COV was 13% for the population from the least variable site compared to 20% for the population experiencing the most variable long-term precipitation regime (Figure 3).

Do larger seeds grow into larger seedlings?

Among a cohort of 62 seeds that germinated on the same day, and thus experienced identical environmental conditions throughout their lives, there was a significant effect of seed mass on growth rate after 11 days (effect size = 0.07; $P = 0.03$), with larger seeds growing into taller seedlings (Figure 4).

What traits predict seedling survival under extreme drought?

After planting seeds and growing seedlings under well-watered greenhouse conditions for four weeks, seedlings had reached an average height of 10 mm (6 mm 1st quartile, 10 mm mean, 14 mm 3rd quartile), with more extreme individuals ranging from 0 to 22 mm

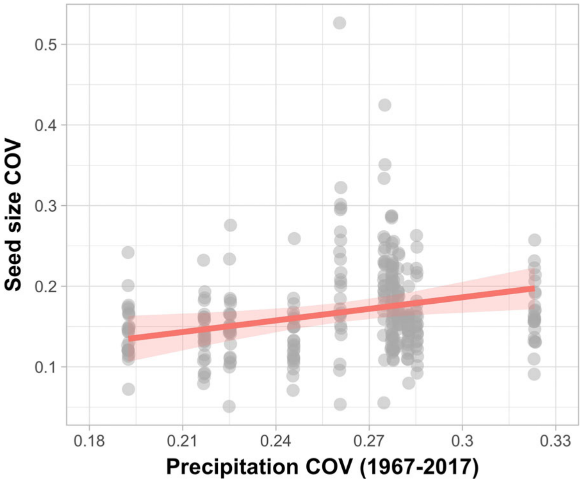

FIGURE 3 Seed size variation among 12 populations of *P. patagonica* from sites on the Colorado Plateau experiencing differing degrees of variability in annual precipitation over the past 50 years. Points depict the coefficient of variation (COV) of seed size within individual maternal plants. The red trend line shows model predictions with shaded 95% confidence intervals.

(95% quantiles). After ceasing watering, seedlings survived 8 to 24 days of drought in 80 cm^3 germination cells. Plant height at the onset of drought was a significant predictor of increased survival or decreased mortality (effect size = –0.084; $P < 0.001$), whereas aridity of the source climate had no effect ($P = 0.440$). Taller seedlings showed dramatically greater resilience to drought compared to shorter seedlings (Figure 5). For example, after 15 days of drought, less than 50% of seedlings <5 mm were still alive compared to more than 90% of seedlings >5 mm tall. After 20 days of experimental drought, only 4% of seedlings <5 mm tall had survived, compared to 18% of seedlings 5 to 10 mm, and 42% of those >10 mm tall (Figure 5). Germination date was insignificant in the full model ($P = 0.20$); however, we note that this resulted because of the co-linearity between plant height and germination date. When we removed plant height from the model, earlier germination was also significantly associated with increased survival (effect size = 0.065; $P < 0.001$; also see results from the structural equation models below).

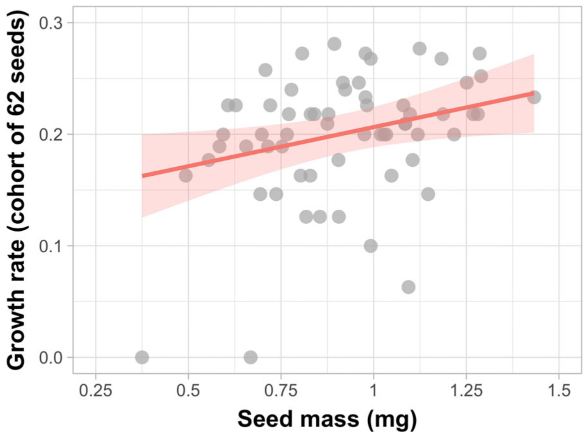

FIGURE 4 The growth rates of 62 *P. patagonica* seedlings that germinated on the same day, as calculated after 11 days of growth. Points represent individual seedlings; trend lines show model predictions with shaded 95% confidence intervals.

In the second survival model based on the dataset for which we had SLA data ($n = 296$ seedlings); plant height was again a significant predictor of mortality timing (effect size = –0.043; $P = 0.02$), whereas both source aridity ($P = 0.81$) and SLA ($P = 0.81$) were insignificant.

Seedling height had no effect on soil moisture in the germination cells one-week into the drought experiment ($P = 0.62$), indicating that individual grid cells were not drying down at different rates, which if this had been the case, would have rendered our results conservative.

Our first structural equation model captured the direct effects of climatic aridity on seedling survival

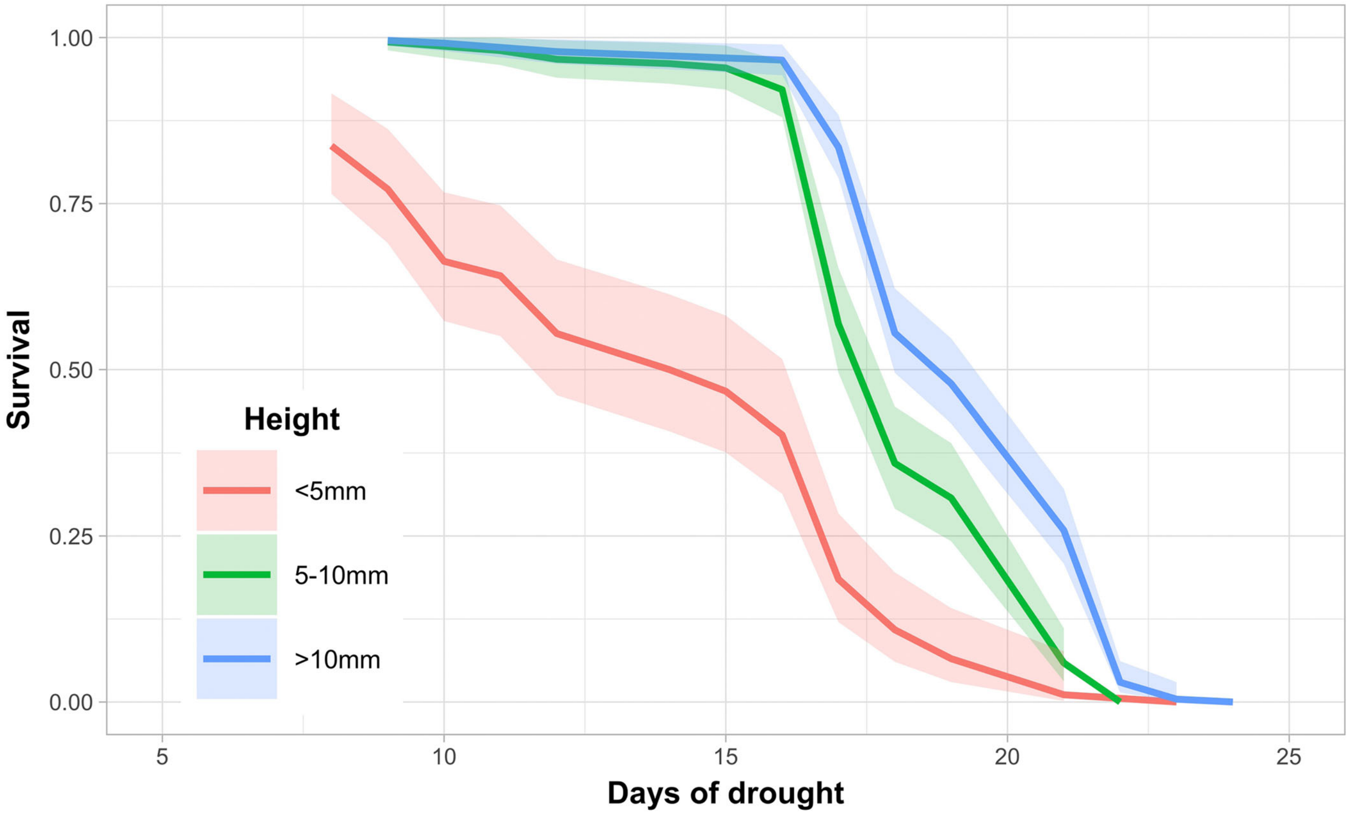

FIGURE 5 Survival curves generated with data from 489 *P. patagonica* seedlings subjected to terminal experimental drought in the greenhouse. Seedling height at the onset of drought was a significant predictor of mortality timing. Lines depict survival probabilities for three arbitrary height classes of seedlings (<5 mm tall, $n = 95$ seedlings; 5–10 mm, $n = 155$ seedlings; >10 mm tall, $n = 239$ seedlings) with shaded 95% confidence intervals.

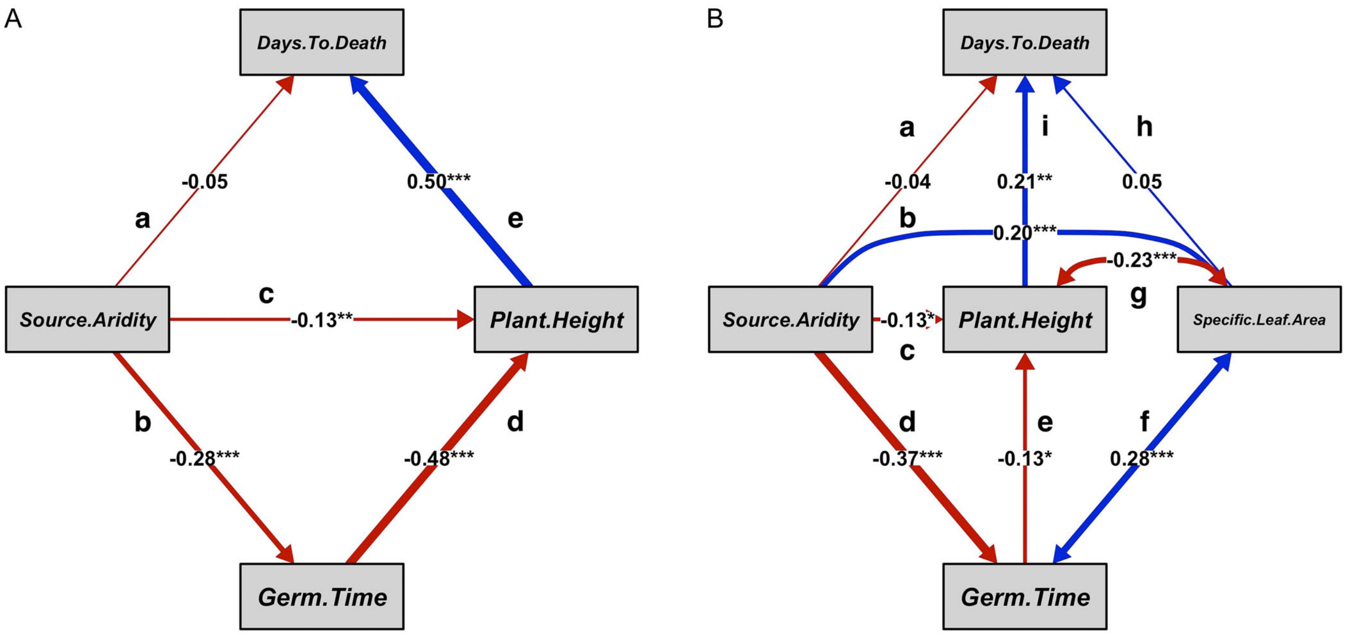

FIGURE 6 Path diagrams of structural equation models (SEMs) indicating the relationships among predictors of seedling survival under terminal drought. (A) SEM without SLA data based on 474 observations; (B) SEM with SLA data based on 296 observations. Single-headed arrows indicate causal relationships; doubled-headed arrows indicate correlations; arrow widths correspond to standardized effect sizes (also shown numerically); arrow color indicates the sign of influence (red for negative, blue for positive), which is only interpretable in the context of how predictors were measured; asterisks represent significance; letters specify individual paths.

under drought, as well as indirect effects mediated through two plant traits (Figure 6A). Climatic aridity of source populations had a relatively small and insignificant direct effect on days to death (Figure 6A; Table 1). Conversely, its two indirect effects, either mediated through plant height (Figure 6A, path "ce") or mediated through germination timing and then plant height (Figure 6A, path "bde"), were both significant and of equivalent magnitude (Table 1), suggesting two potentially alternative mechanisms underlying seedling survival under drought. The first structural equation model adequately fit our data. The chi-square test statistic indicated a good model fit ($X^2 = 3.772$, $P = 0.195$; P-values > 0.05 indicate adequate fit in this test), and other assessment metrics also indicated good fit (CFI = 0.99, RMSEA = 0.076, SRMR = 0.021).

A secondary SEM based on the 296 individuals for which we had specific leaf area (SLA) data (Figure 6B) also had a good fit ($X^2 = 0.0124$, $P = 0.935$; CFI = 1.00, RMSEA = 0.00, SRMR = 0.005), and corroborated findings from the survival analysis and the first SEM, indicating no significant direct effects of source climate or SLA on survival timing (Table 1). As in the first SEM, plant height strongly affected survival timing (Table 1), and germination timing was marginally significant through two indirect paths (paths "dei" and "ei" in Figure 6B). In this model, SLA was significantly correlated with both germination timing and plant height, with lower SLA associated with both earlier germination times and taller seedlings (Figure 6B).

DISCUSSION

We explored genetic-based intraspecific trait variation in several seed and seedling traits associated with alternative drought and life history strategies in 12 populations of the annual plant *Plantago patagonica* from across a natural aridity gradient. Every population displayed substantial trait variation for all the traits we quantified (Figures 2 and 3), reflecting substantial underlying genetic diversity. We found evidence of clinal variation for three traits—seed size, germination timing, and specific leaf area—consistent with local adaptation to the abiotic environment. Patterns for both seed size (populations from more arid locations produced smaller seeds) and specific leaf area (populations from more arid locations produced seedlings with higher SLA) were opposite to those found for many drought-adapted species in which large seed size (Hallett et al., 2011; Lowry et al., 2015; Leger et al., 2019; Larson et al., 2020; Wang et al., 2020) and low SLA (Wellstein et al., 2017; Andivia et al., 2021) are associated with drought tolerance. Conversely, seeds from more arid sites germinated substantially earlier under shared conditions than those from less arid sites, consistent with a drought escape strategy mediated by accelerated phenology (Dickman et al., 2019; Duncan et al., 2019).

Populations that had experienced more variable historical precipitation regimes showed increased seed size variation, suggestive of a diversified bet-hedging strategy in unpredictable environments or those with fluctuating selection pressures (Venable and Lawlor, 1980; Rice and

TABLE 1 Direct and indirect effects from the structural equation models (SEMs). Direct effects relate to single paths in the SEMs depicted in Figure 6; indirect effects pertain to paths mediated through multiple predictors. Standardized coefficients allow for a comparison of the relative magnitude of different paths. Rows in bold indicate statistically significant effects; rows in italics indicate marginally significant effects.

	Effects	Path	Standardized coefficient	*p*-value
Model 1	**Direct Effects**			
no SLA data	Days.To.Death ~ Source.Aridity	a	−0.050	0.202
no. obs. = 474	**Germ.Time ~ Source.Aridity**	**b**	**−0.280**	**<0.001**
	Plant.Height ~ Source.Aridity	**c**	**0.133**	**0.004**
	Plant.Height ~ Germ.Time	**d**	**−0.480**	**<0.001**
	Days.To.Death ~ Plant.Height	**e**	**0.500**	**<0.001**
	Indirect Effects			
	Source.Aridity -> Germ.Time -> Plant.Height -> Days.To.Death	**bde**	**0.067**	**<0.001**
	Source.Aridity -> Plant.Height -> Days.To.Death	**ce**	**−0.066**	**0.006**
	Germ.Time -> Plant.Height -> Days.To.Death	**de**	**−0.240**	**<0.001**
Model 2	**Direct Effects**			
with SLA data	Days.To.Death ~ Source.Aridity	a	−0.036	0.530
no. obs. = 296	**Specific.Leaf.Area ~ Source.Aridity**	**b**	**0.199**	**<0.001**
	Plant.Height ~ Source.Aridity	**c**	**−0.131**	**0.025**
	Germ.Time ~ Source.Aridity	**d**	**−0.368**	**<0.001**
	Plant.Height ~ Germ.Time	**e**	**−0.129**	**0.028**
	Days.To.Death ~ Specific.Leaf.Area	h	0.054	0.454
	Days.To.Death ~ Plant.Height	**i**	**0.208**	**0.001**
	Indirect Effects			
	Source.Aridity -> Specific.Leaf.Area -> Days.To.Death	bh	0.011	0.495
	Source.Aridity -> Plant.Height -> Days.To.Death	*ci*	*−0.027*	*0.063*
	Source.Aridity -> Germ.Time -> Plant.Height -> Days.To.Death	*dei*	*0.010*	*0.057*
	Germ.Time -> Plant.Height -> Days.To.Death	*ei*	*−0.027*	*0.051*

Dyer, 2001; Gremer et al., 2016). Our common garden experiments uncovered a seemingly paradoxical pattern—larger seeds grew into taller seedlings, which in turn survived experimental drought at a much higher rate than shorter seedlings—yet seeds from naturally arid locations were markedly smaller than those from less arid sites when grown under shared conditions. Our findings suggest that trade-offs and trait correlations have likely shaped the evolution of life history strategies in *P. patagonica*.

Alternative life history strategies: Establishment vs. dispersal

Theory suggests that parental investment strategies must strike an optimal balance between offspring size and offspring number (Smith and Fretwell, 1974), yet this trade-off is likely resource dependent (Venable, 1992) and thus highly sensitive to environmental conditions (Paul-Victor and Turnbull, 2009). Empirical data often show no evidence of a seed size-seed number trade-off (e.g., Michaels et al., 1988; Sober and Ramula, 2013), as we found here in plants grown in the greenhouse under well-watered and low-competition conditions. Patterns emerging under non-limiting experimental conditions may not accurately reflect field conditions, therefore it remains unknown whether reduced seed size in plants from more arid sites (Figure 2A) is offset by relatively greater seed production (compared to large-seeded individuals) under resource-limited field conditions. Interpreted in the context of our experiments, smaller seeds would seem to confer some intrinsic fitness advantage or to be associated with others trait that do.

Smaller seeds (even if fewer in number) may be more efficient dispersers than larger seeds (Greene and Johnson, 1993; Eriksson and Jakobsson, 1999), thus conflicting selection pressures for dispersal and seedling establishment (those favoring small and large seeds, respectively) may shape observed trait variation across environments or temporally fluctuating conditions (Parciak, 2002; Sober and Ramula, 2013). We did not assess this phenomenon directly so we can only speculate; however, in *P. patagonica* from arid sites on the Colorado Plateau, selection pressures for dispersal to more favorable microsites may be stronger than those favoring more efficient establishment at microsites already inhabited by maternal plants and other seeds in the seedbank. Field sites often have low vegetation cover (K. Christie, personal observation), thus seedlings likely face relatively little competition or shading during establishment, a common correlate of larger seeds in interspecific comparisons (Westoby et al., 1992; Leishman et al., 2000). Moreover, smaller seeds may have a higher likelihood of penetrating the soil and amassing in the seed bank (Chambers et al., 1991; Khurana and Singh, 2001), potentially linking smaller seeds to a drought avoidance bet-hedging strategy. Lastly, smaller seeds are often more likely to escape seed predation (Maron et al., 2012; Dylewski et al., 2020), and thus incorporate into the seed bank (Connolly et al., 2014). Further experiments are needed to determine which, if any, of these mechanisms act in *P. patagonica*.

Bet-hedging strategies and environmental variability

Annual plants inhabiting arid or unpredictable environments are faced with a challenging life history predicament—does germinating in a given year and potentially facing stochastic hazards maximize fitness, or does remaining dormant until more favorable conditions exist represent a better strategy (Rees, 1994; Iler et al., 2021)? Smaller seeds may be more likely to postpone germination in any given year compared to larger seeds, which presumably can establish more efficiently in water-limited environments (Venable and Brown, 1988; Rubio de Casas et al., 2017). We did not find a difference in the likelihood of germination among *P. patagonica* populations inhabiting different climates; however, we did not impose any specific vernalization cues to the stored seeds, so this pattern may not accurately reflect natural germination conditions for all populations. Alternatively, natural selection may favor advanced phenology in response to limited water availability (Anderson et al., 2012), either via earlier flowering (Franks et al., 2007) or through earlier seedling emergence (Verdú and Traveset, 2005; Dickman et al., 2019). In the case of *P. patagonica* seeds from the semi-arid Colorado Plateau, we see a pattern of earlier germination in populations from more arid source locations when exposed to favorable germination conditions (Figure 2B). This result is consistent with findings from other arid adapted plant populations (Vaughn and Young, 2015; Thomson et al., 2017; Leger et al., 2019), in which an expedited life cycle following germination is favored by natural selection (Caruso et al., 2020). Such an opportunistic strategy could be advantageous for utilizing suitable, but limited, germination windows. Overall, the seed size—climate association together with the seed size—germination timing association may represent different components of a correlated life history response, as both smaller seeds (Figure 2A) and earlier germination (Figure 2B) were significantly associated with increased aridity.

We did not directly test the relationship between seed size and germination timing with our data (i.e., we did not weigh individual seeds in the full experiment consisting of 1728 seeds), yet we can infer this relationship as seeds from arid sites were smaller and also germinated earlier than seeds from less arid sites (see Figure 2A, B). This correlation has interesting ramifications for how populations may adapt to seasonal environments, as greater variation in seed size may also increase variation in the timing of germination (Metz et al., 2018; Martins et al., 2019). We found a significant relationship between precipitation variation over the past 50 years and genetic-based variation in seed size across populations (Figure 3). A similar pattern has been found in the tropical vine *Dalechampia scandens* L. [Euphorbiaceae], for which meaningful precipitation variation occurs at the scale of months (Pélabon et al., 2021). Our result suggests that past variation in precipitation may have selected for increased seed size variation, highlighting one potential mechanism underlying intra-annual diversifying bet-hedging in environments with unpredictable precipitation patterns. Additionally, strong competition is expected to select for invariably large seeds able to maximize competitive establishment, whereas reduced competition at more arid sites should free individuals to produce a greater diversity of seeds sizes with the ability to establish under a greater range of environmental conditions (Violle et al., 2009). Thus, our observed result may stem from the interaction of abiotic and biotic selection pressures. Overall, our findings indicate that average aridity as well as precipitation variability both represent important selective forces structuring local adaptation across abiotic gradients (Pratt and Mooney, 2013; Muir and Angert, 2017; Blumenthal et al., 2021).

Trade-offs between seed size and seedling growth rates

Larger *P. patagonica* seeds produced taller seedlings after approximately two-weeks of growth (Figure 4), consistent with a seedling size effect (Stanton, 1984; Krannitz et al., 1991; Gomaa and Picó, 2011) potentially facilitating improved initial establishment (Leishman et al., 2000). If larger seedling size is mediated by a reserve effect in which larger seeds have greater energy reserves, we would also expect this effect to be most pronounced early in a seedling's life before reserves are depleted. Across species, larger-seeded species seem to obtain an initial advantage in seedling size, yet they also tend to have slower relative growth rates such that their size advantage attenuates later in life and smaller-seeded species then catch up (Swanborough and Westoby, 1996). We found a somewhat analogous pattern at the intraspecific scale in *P. patagonica*; smaller seeds, despite their slower growth rates early in life, germinated earlier, a mechanism potentially stabilizing fitness differences between small and large seeded individuals. We were unable to incorporate seed size into our SEMs; however, when mediated through source aridity, seedlings had two roughly equivalent paths to higher survival (Figure 6A, Table 1)—germinate earlier (path "bde") or be taller (path "ce"), a phenotype associated with larger seeds.

The paradox of specific leaf area

One interesting and potentially counterintuitive finding from our study was that plants from more arid sites had higher specific leaf areas (SLAs) than those from less arid sites (Figure 2C). On one hand, lower SLA is typically associated with drought tolerance and resource-conservative life history strategies (Ackerly et al., 2002), whereas higher SLA is often associated with faster growth rates (Tjoelker et al., 2005; Villar et al., 2005) and resource-acquisitive strategies (Grotkopp and Rejmánek, 2007). Even if higher SLA might make leaf tissue more susceptible to transpiration and water loss under drought (Ackerly et al., 2002; Greenwood et al., 2017; Wellstein et al., 2017), species facing drought may leverage faster growth rates to build additional root tissues (Pérez-Ramos et al., 2013; Puglielli et al., 2015). Thus, based on leaf water relations alone, the pattern of increasing SLA as climates becomes more arid (Figure 2C) would seem maladaptive, yet this may be part of a correlated life history strategy in which individuals from arid sites are able to germinate early and allocate resources to roots as necessary. Alternatively, higher SLA in more arid sites may simply reflect a genetic constraint or correlation to another favorable phenotype. Our SEM indicated a strong correlation between SLA and both germination timing and plant height (Figure 6B), with younger, shorter plants having higher SLA and older, taller plants having lower SLA. This finding renders the clinal trend observed across populations (Figure 2C) conservative, as plants from more arid sites germinated earlier, were older at the time we censused SLA, and thus might be expected to display lower SLA as a result of the developmental stage at which they were censused. We can only speculate here as we did not measure root mass directly; however, the fact that more arid populations showed higher SLA than less arid populations warrants additional exploration, whether it be counter-gradient variation in the greenhouse or a seemingly counterintuitive drought strategy.

Drought is inevitable—to avoid, to escape, or to tolerate?

Plant populations in the Southwestern U.S. are expected to continue to face severe drought and precipitation variability associated with global climate change (Seager et al., 2007; Coats et al., 2013; Cook et al., 2015), and precipitation and evapotranspiration commonly predict the strength of selection faced by natural populations (Siepielski et al., 2017). Our results in *P. patagonica* mirror a more general trend associated with abiotic selection pressures in plants—selection for larger plant size and earlier phenology (Caruso et al., 2020)—highlighting two alternate, but not mutually exclusive, life history strategies for annual plants facing arid conditions.

Another recent study examining intraspecific trait variation along a steep aridity gradient found no evidence of ecotypic differentiation with respect to Leaf-Height-Seed (LHS) traits (Westoby, 1998; Westoby et al., 2002), suggesting that such traits may be relatively unimportant for climate adaptation compared to phenological or reproductive allocation traits (Kurze et al., 2017). We found that two traits associated with the LHS scheme—specific leaf area and seed size—showed clinal variation, but not in the directions we originally predicted. Interpreting reduced seed size and increased specific leaf area in more arid sites as climate adaptations only makes sense in view of correlated trait responses consistent with alternative life history strategies. Examining individual traits in isolation (e.g., smaller seeds and thus shorter seedlings were less resilient to drought) may have mis-evaluated the cumulative fitness effects of other correlated traits (e.g., smaller seeds germinated earlier giving them a phenological head start). Plant height—attained either due to larger seeds with higher seedling growth rates, or via accelerated germination allowing individuals to grow taller prior to the onset of drought—predicted survival in our terminal drought experiment. This finding highlights the indirect relationship between both seed and leaf traits on fitness under drought. We unfortunately did not measure root traits, so it is unclear here if larger or longer roots (traits potentially associated with taller seedlings) might represent a mechanistic link between plant height and increased fitness under drought (Harrison and LaForgia, 2019; Garbowski et al., 2020; Larson et al., 2020).

CONCLUSIONS

Our study explored seed size variation at the intraspecific scale, employing a common garden approach to understand genetic-based trait variation along a natural aridity gradient. This approach allowed us to generate predictions for how natural populations are expected to evolve under increasingly arid conditions associated with climate change in the Southwestern U.S. The substantial degree of intraspecific trait variation within individual populations of *P. patagonica* from the Colorado Plateau suggests that sufficient genetic variation exists to fuel future adaptive evolution. We found four possible ways in which *P. patagonica* populations may be locally adapted to the aridity and precipitation variability of their source environments. First, seeds from more arid sites were smaller, and secondly, they germinated more rapidly in response to consistent germination cues. These traits may be adaptive as we have discussed above, and populations may in fact continue to evolve further along these trajectories if sites become increasingly arid. Conversely, smaller seeds and earlier germination might only confer fitness benefits if growing conditions following germination remain suitable. Early emergence may in fact represent a liability if germination triggering events are followed by prolonged droughts (Vieira et al., 2008; Larson et al., 2020), an increasingly likely scenario given the climate trajectory in the Southwestern U.S. (Cook et al., 2015). Our experiments showed that reduced seed size (and thus seedling size) may carry establishment costs in water-limited conditions and thus may only be adaptive if associated with increased seed production or the ability to reproduce via an accelerated lifecycle. Third, *P. patagonica* seedlings from more arid sites had higher specific leaf areas than those from less arid sites, possibly facilitating faster growth prior to the onset of drought. Such a resource-acquisitive strategy might only prove effective however, if compensatory growth outweighs the cost associated with increased transpiration. Thus, while currently observed clinal patterns predict how traits might evolve in response to increasing aridity, our results also highlight how individual traits in and of themselves may be constrained and/or hinder adaptation if they are unable to shift as part of correlated responses. Lastly, we found evidence of increased genetic-based seed size variation in populations that had experienced historically variable precipitation regimes, consistent with selection shaping a diversified bet-hedging strategy. Such a bet-hedging strategy hinges upon genetic variation for seed size which could be depleted by strong directional selection associated with climate change (e.g., if only larger seeds are able to successfully establish during drought), highlighting the precipitous balance natural populations in increasingly arid environments currently face.

AUTHOR CONTRIBUTIONS

K.C., L.M.H., and D.B.L. conceptualized the study; N.R.P. and K.C. conducted experiments and collected data; K.C. analyzed the data; K.C. wrote the manuscript with comments from all authors.

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DATA AVAILABILITY STATEMENT

Data and analysis code are archived in the Dryad Digital Repository: https://doi.org/10.25338/B85D2X (Christie et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Relationship between seed mass and seed area.

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