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American Journal of Botany

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INVITED SPECIAL ARTICLE

For the Special Issue: Plant–Environment Interactions: Integrating Across Levels and Scales

Resource availability alters fitness trade-offs: implications for evolution in stressful environments

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Manuscript received 31 May 2019; revision accepted 16 September 2019.

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Citation: MacTavish, R. and J. T. Anderson. 2020. Resource availability alters fitness trade-offs: implications for evolution in stressful environments. *American Journal of Botany* 107(2): 308–318.

doi:10.1002/ajb2.1417

PREMISE: Industrialization and human activities have elevated temperatures and caused novel precipitation patterns, altering soil moisture and nutrient availability. Predicting evolutionary responses to climate change requires information on the agents of selection that drive local adaptation and influence resource acquisition and allocation. Here, we examined the contribution of nutrient and drought stress to local adaptation, and we tested whether trade-offs across fitness components constrain or facilitate adaptation under resource stress.

METHODS: We exposed 35 families of *Boechera stricta* (Brassicaceae) to three levels of water and two levels of nutrient supply in a factorial design in the greenhouse. We sourced maternal families from a broad elevational gradient (2499–3530 m a.s.l.), representing disparate soil moisture and nutrient availability.

RESULTS: Concordant with local adaptation, maternal families from arid, low-elevation populations had enhanced fecundity under severe drought over those from more mesic, high-elevation sites. Furthermore, fitness trade-offs between growth and reproductive success depended on the environmental context. Under high, but not low, nutrient levels, we found a negative phenotypic relationship between the probability of reproduction and growth rate. Similarly, a negative phenotypic association only emerged between fecundity and growth under severe drought stress, not the benign water treatment levels, indicating that stressful resource environments alter the direction of trait correlations. Genetic covariances were broadly concordant with these phenotypic patterns.

CONCLUSIONS: Despite high heritabilities in all fitness components across treatments, trade-offs between growth and reproduction could constrain adaptation to increasing drought stress and novel nutrient levels.

KEY WORDS abiotic stress; Brassicaceae; drought; fitness; genetic covariance; life history trade-offs; local adaptation; soil resource availability.

Natural populations evolve in response to abiotic and biotic agents of selection, which shape fitness trade-offs across environments (local adaptation) and across life history stages (life history evolution) (Roff, 2002). Global climate change has introduced novel environmental conditions through increasing temperatures, disrupted precipitation regimes, and increased frequency of extreme weather events (IPCC 2014). Climate change also influences the soil environment, elevating soil temperature and lowering moisture through increased evapotranspiration rates (Anderson, 1992; Rosenzweig and Hillel, 2000). Long periods of drought followed by

heavy precipitation have resulted in extreme soil moisture variability (Sheffield and Wood, 2008). Climate change will likely decouple plant–soil interactions; however, we know very little about the evolutionary consequences of this decoupling for plants (Bardgett et al., 2013; Classen et al., 2015; Yuan and Chen, 2015). Here, we examined the extent to which abiotic stresses associated with climate change influence local adaptation and life history trade-offs.

Variation in climatic, edaphic, and abiotic agents of selection across space can favor the evolution of local adaptation, such that ecotypes have enhanced performance in their home sites and reduced fitness in contrasting environments (Kawecki and Ebert, 2004). Disentangling the causal agents of local adaptation remains challenging because multiple interacting factors can contribute to fitness trade-offs across environments (Lowry et al., 2008; Wadgymar et al., 2017b). In some systems, variation in climatic factors has been directly linked to local adaptation (Liancourt et al., 2013; Anderson and Wadgymar, 2020). In other systems, variation in competitive interactions strongly influence local adaptation (Sambatti and Rice, 2006). Additionally, both climatic factors and soil environment can drive local adaptation for some species (Macel et al., 2007). Only through manipulative experiments will we gain insight into the causal agents of local adaptation, which is critical for predicting population persistence as advancing climate change may disrupt local adaptation, favoring foreign ecotypes that evolved under warmer and more arid conditions (Wang et al., 2010; Wilczek et al., 2014; Kooyers et al., 2019; Anderson and Wadgymar, 2020).

Abiotic and biotic conditions not only influence local adaptation, but they can also alter trade-offs between fitness components. Correlations across fitness components arise through variation in resource acquisition or allocation (Riska, 1986; Van Noordwijk and de Jong, 1986; Roff, 2002; Villellas and García, 2018). That is, individuals can vary in how they allocate limited resources to various critical functions like growth or reproduction; for example, high growth rates could come at a cost to reproduction (Stearns, 1989; Reznick et al., 2000; Roff, 2002; Villellas and García, 2018). Alternatively, individuals can vary in their capacity to acquire resources, such that some individuals have more resources to allocate to multiple functions, which would generate positive relationships between fitness components like growth and survival (Van Noordwijk and de Jong, 1986; Zera and Harshman, 2001). Trade-offs have emerged in response to altered conditions associated with climate change, such as new soil moisture levels (Rosenzweig and Hillel, 2000; Sheffield and Wood, 2008) and nutrient availability (Kuzyakov, 2010; Siemens et al., 2010). Drought stress has altered both the sign and magnitude of phenotypic and genetic correlations associated with fitness in barley (*Hordeum vulgare*; Shakhatreh et al., 2001). Additionally, water deficiency exposed a trade-off between stress tolerance (measured via growth rate) and herbivory defense (glucosinolate production) in natural populations of *Boechera stricta* (Siemens et al., 2012).

Physiological or phenotypic trade-offs could be highly plastic and evolutionarily labile when plants confront novel environments. In contrast, genetic trade-offs could impose more severe evolutionary constraints. Even when genetic variation exists in fitness components, trade-offs across traits can restrict adaptive evolution if genetic correlations across life history traits are antagonistic to the joint vector of selection; in contrast, genetic correlations can facilitate adaptation when selection operates in the same direction as the genetic correlation (Etterson and Shaw, 2001). Novel resource environments can alter genetic correlations of life history traits by inducing trade-offs under stress (Giesel, 1988; Krebs and Loeschcke, 1999; Ackermann et al., 2001; Sgro and Hoffmann, 2004). For example, the sign and magnitude of genetic correlations among traits of *Impatiens capensis* changed depending on intraspecific plant density and light environments (Donohue et al., 2000). Additionally, herbivore removals altered genetic correlations of herbivory tolerance and fitness in *Ipomoea herderacea* (Stinchcombe, 2002). Examining fitness trade-offs at the physiological and genetic levels will reveal how novel resource stress may alter evolutionary potential as climate change continues (Bemmels and Anderson, 2019).

Natural selection operates strongly on fitness components (Price and Schluter, 1991), rapidly reducing genetic variation in survival, fecundity, and other traits that are tightly linked to lifetime fitness. Therefore, fitness components typically have reduced heritability values relative to morphology or other traits that are more distantly related to fitness (Mousseau and Roff, 1987). Genetic variation in fitness is crucial for natural populations to adapt to current environmental conditions, as the adaptive potential of populations is proportional to genetic variation in lifetime fitness (Sheth et al., 2018). Novel conditions can induce the expression of cryptic genetic variation, thereby enhancing the capacity of populations to adapt to environmental change (Hoffmann and Merilä, 1999; McGuigan et al., 2011; Paaby and Rockman, 2014). Alternatively, new stressful conditions could depress fitness and genetic variation in fitness (Hoffmann and Merilä, 1999; Bemmels and Anderson, 2019), restricting adaptive potential. Evaluating the extent of heritability in fitness components under novel environments will enable robust predictions about the potential for populations to adapt to climate change factors (Sheth et al., 2018; Bemmels and Anderson, 2019).

This study investigates the effects of resource availability in the context of climate change on fitness trade-offs and heritabilities. We evaluated local adaptation to drought and nutrient stress using, *Boechera stricta* (Brassicaceae), a perennial forb native to high elevation sties in the Rocky Mountains. We predicted that low-elevation populations, which evolved under reduced water availability relative to their high-elevation counterparts, would have elevated fitness in water-limited treatments and high-elevation populations would express the greatest fitness under well-watered conditions. Similarly, we hypothesized that high-elevation populations that evolved in nutrient-poor soils would have greater performance under nutrient limitation. We also tested the extent to which the environmental context influence life history trade-offs. We hypothesized that allocation of limited resources results in trade-offs across fitness components. Additionally, we examined whether stressful environments enhance or restrict the adaptive potential of populations by comparing genetic variation under stressful and benign conditions. By exposing *B. stricta* individuals from a broad elevational gradient to variation in soil nutrient and soil water stress in the greenhouse, we directly tested the extent to which global change influences correlations between fitness components.

MATERIALS AND METHODS

Focal system

Boechera stricta (Brassicaceae) is a short-lived perennial forb that grows in montane habitats of the Rocky Mountains in North

America, from Utah to Alaska (Rushworth et al., 2011). The Colorado Rocky Mountains are home to genetically diverse populations of *B. stricta* (Kiefer et al., 2009). Natural populations of *B. stricta* are adapted to local environments across latitudes, elevations, and soil water gradients (Anderson et al., 2013, 2015; Lee and Mitchell-Olds, 2013; Anderson and Wadgymar, 2020). *Boechera stricta* is primarily self-pollinating (average F_{IS} = 0.89, Song et al., 2006) and has gravity-dispersed seeds. In this species, foliar N content increases with elevation (Anderson and Gezon, 2015). In addition, in this region, soil moisture increases and soil nitrate availability declines with elevation (Ranelli et al., 2015). Taken together, these data suggest that natural populations could differ in nutrient acquisition and allocation strategies.

The direct effects of climate change can disrupt soil biogeochemical cycling of organic carbon and inorganic nutrients (Seneviratne et al., 2010; St. Clair and Lynch, 2010), and limit phosphorous and nitrogen availability to plants (Agren et al., 2012). A simulation model found that increased mean annual temperatures reduced soil available phosphorous primarily by decreasing organic phosphorous (Hou et al., 2018). Elevated temperature and increased precipitation accelerate organic matter turnover (Conant et al., 2011; Fyfe et al., 2017), releasing plant available nitrogen (Kuzyakov, 2010). In northern latitudes and alpine regions, variability in snow pack exposes soil to an increased number of freeze–thaw cycles, prematurely releasing nitrogen before plants emerge (Henry, 2008; Groffman et al., 2011; Templer et al., 2017; Gao et al., 2018). These abiotic stresses imposed by climate change could alter fitness tradeoffs across environments and across life history.

Experimental design

Before initiating this experiment, we collected seeds from natural populations that span a broad elevational gradient (2499–3530 m a.s.l.) around the Rocky Mountain Biological Laboratory (Gothic, Colorado, United States; Appendix S1) to capture genetic variation in resource acquisition and allocation strategies. We grew field-collected seeds for one generation in the greenhouse to standardize maternal effects and generate full-sibling maternal families to use in our experiments.

To evaluate the consequences of resource supply for phenotypic and genetic correlations, we experimentally manipulated water and nutrient resource availability in the greenhouse at the University of Georgia. We quantified fitness components to examine life history trade-offs such as growth vs. survival. In March 2017, we exposed plants from 35 maternal families (one family per source population) to factorial manipulations of three water levels and two nutrient availability levels. As very young seedlings would not have survived water stress, we first germinated seeds in benign conditions, misting with water daily to ensure survival to the juvenile stage. When individuals were 8 weeks old, we randomized plants into a factorial experiment, assigning six siblings per family to three water and two nutrient availability treatments (N = 6 siblings × 35 families × 3 water levels × 2 nutrient levels = 1260 individuals). In 51 cases, seeds failed to germinate or seedlings died before randomization, resulting in a total of 1209 experimental plants (Appendix S2). Water treatment levels included control (watered 7 days/week), moderate drought (watered 2 days/week), and severe drought treatments (watered 1 day/week).

Hand watering delivered ~3 mm of water per treatment application, such that control, moderate drought, and severe drought treatments received ~90, 24, and 12 mm of water per month, respectively. As a point of comparison, average annual summer (June–August) precipitation from 2000 to 2018 at the Rocky Mountain Biological Laboratory (elevation: 2895 m a.s.l.) was 51.20 ± 18.30 mm (mean ± SD), with a range of 29.21–90.80 mm (barr, 2019; Gothic, CO, USA, long-term weather data). We verified the efficacy of our water treatments by sampling soil moisture as percentage volume water content (%VWC) before the weekly nutrient application with a Hydrosense II (Campbell Scientific, Logan, UT, USA) from four randomly selected individuals per block (Appendix S1). No visible size differences were detected at the time of collection of data on volumetric water content (R. MacTavish, personal observations). At a mid-elevation (2890 m a.s.l.) field common garden at the Rocky Mountain Biological Laboratory, summer volumetric water content averaged 10% (SD: 5%; range 0–39%) from 2014 to 2018. Thus, the moderate drought stress (mean ± SE: 10.51% ± 2.33%) reflects average soil water availability in the field, and the well-watered (17.52% ± 2.71%) and severe drought stress (4.65% ± 1.71%) fall within the range of variability in the field.

We applied two nutrient treatments once weekly as a mixture of water-soluble Peters Professional General Purpose Fertilizer 20N-10P-20K (Scott's Co., Marysville, OH, USA) at 110 ppm N (1×; 1 ppm = 1 mg/L), and 1100 ppm (10×). We selected fertilizer concentrations to be stressful vs. moderate (low vs. medium) based on previous studies of nutrient stress in *B. stricta* (Siemens et al., 2010, 2012). We applied high nutrient levels early in life history to simulate nutrient pulses that occur at snowmelt when seedlings first emerge (Groffman et al., 2001, 2011; Gavazov et al., 2017) and to enhance seedling establishment (Villar-Salvador et al., 2012; Gan et al., 2015). After vernalization, we reduced nutrient levels to a low (1×) of 5 ppm N and high (10×) of 50 ppm N through the remainder of the study to reflect high vs. low values documented across elevational gradients (Ranelli et al., 2015; He et al., 2016; Drollinger et al., 2017).

We rotated blocks around the greenhouse benches weekly to minimize non-experimental environmental variation. Juvenile plants received 3 weeks of watering treatments with nutrient application before an 8-week vernalization at 4°C in June 2017, when water was supplied equally across treatments by bottom watering. Vernalization is necessary to induce flowering in this system (Anderson et al., 2011). After observing furled leaf development at the beginning of the second growing season, we applied a micronutrient mixture containing only Mg and Ca to all plants once every 8 weeks at 110 ppm in water.

Fitness components—We measured the following fitness components: survival to the end of the 20-week experiment, the probability of reproduction, fecundity among individuals that reproduced, and growth rate. We quantified fecundity as the number of mature siliques (fruits) per individual, and relative growth rate (RGR) using initial and final leaf lengths: (ln Final leaf length – ln Initial leaf length)/Elapsed time in months.

Statistical analyses—To evaluate whether populations from different elevations have adapted locally to abiotic conditions, we evaluated fitness as a function of elevation of origin, drought treatment, nutrient treatment, and all two- and three-way interactions. As our fecundity data were zero-inflated, we adopted a hurdle model approach, in which we first tested the probability of reproduction in a logistic regression framework (logit link)

and then used a gamma distribution (log link) to test fecundity (number of fruits) among individuals that successfully reproduced. We analyzed data at both the individual- and the family-level in Proc Glimmix (SAS ver. 9.4, SAS Institute, Cary, NC, USA), with random effects for source population (both analyses) and block (individual-level analysis). To analyze the probability of reproduction at the family-level, we summarized the number of individuals that successfully reproduced over the number of individuals planted for each source population. We generated family-level LSMEANs for fecundity (number of fruits) in generalized linear mixed models in Proc Glimmix with a random effect for block. Family- and individual-level analyses generated nearly identical results; we present the family-level analyses in the Results and the individual-level analyses in Appendix S3.

To assess whether life history trade-offs varied across environmental contexts, we analyzed trade-offs as a function of drought treatment, nutrient treatment, and drought × nutrient interactions. We modeled phenotypic correlations using family-level LSMEANs as well as individual-level data in a mixed linear model framework by regressing one trait against another in SAS 9.4 (Proc Glimmix), with fixed effects for drought and nutrient environments, and all two- and three-way interactions among drought treatment, nutrient treatment, and trait values. We incorporated maternal family as a random effect to account for nonindependence among families exposed to different treatments (both analyses) and block as a random effect in the individual-level models. We tested trade-offs between the probability of reproduction and RGR, as well as fecundity (number of fruits among individuals that reproduced) and RGR. We were unable to model trade-offs between survival and other fitness components because we have no fecundity or growth data on individuals that died. As we used the same data to evaluate two trade-offs, we adjusted our alpha level ($\alpha = 0.05/2 = 0.025$) to correct for multiple comparisons (Chen et al., 2017).

We estimated broad-sense heritability and analyzed genetic correlations with a Bayesian approach known as the animal model, implemented in the MCMCglmm package of R 3.5.2 (Wilson et al., 2010). This approach uses a mixed model restricted maximum likelihood (REML) process to analyze individual-level data while considering genetic relationships between individuals. We extracted **G** matrices (genetic variance and covariance matrices) to examine genetic trade-offs in different environments and determined statistical significance as 95% credible intervals not overlapping zero (Wilson et al., 2010). In *B. stricta* and other selfing species, selection operates on total genetic variance, not simply additive genetic variance (Roughgarden, 1979).

We estimated broad-sense heritability for fitness components by fitting univariate models with random effects for individual plant ("animal" in the coding for the MCMCglmm models) and block across the six resource supply environments (3 water × 2 nutrient). This analytical approach links phenotypic data to a pedigree file, which identifies the parents of each individual plant, thereby enabling estimation of heritability. We then compared genetic covariance across the six resource supply environments (3 water × 2 nutrient) using MCMCglmm posterior mean and credible intervals to construct distributions and test for overlapping regions at $\alpha = 0.05$. After testing each trade-off × drought and nutrient combination, we found no significant differences due to treatment for any trade-offs. Therefore, we used results from our phenotypic correlations described above as a guide to examine whether drought influenced genetic covariance for reproduction vs. RGR and fecundity vs. RGR. To do so, we fitted multivariate models of fitness component trade-off × drought treatment to model the *G*-matrix across watering treatment. We could not analyze trade-offs between survival and other fitness components because we lacked fecundity and growth data on plants that died during the experiment.

RESULTS

Fitness consequences of abiotic stress

The probability of reproduction varied significantly as a function of nutrient stress and nutrient × source elevation in both family-level (Table 1; Fig. 1) and individual-level (Appendices S4 and S5) analyses. In the high nutrient treatment, the probability of reproduction increased significantly with elevation of origin for both analyses, but we found no relationship between this fitness component and source elevation in the low nutrient treatment (source elevation × nutrient treatment: $F_{1, 164} = 6.23$, $p = 0.0135$, Fig. 1).

Family- and individual-level analyses of fecundity (number of fruits) among individuals that successfully reproduced generated nearly identical results (Tables 1 and Appendix S4; Fig. 2 and Appendix S6). A significant interaction between source elevation and nutrient treatment ($F_{1, 115} = 10.09$, $p = 0.0019$) revealed a positive relationship between fecundity and elevation of origin

TABLE 1. Local adaptation: Fitness trade-offs across nutrient and drought treatments for the probability of reproduction (a binary variable indicating whether a plant successfully fruited) and fecundity (number of fruits among individuals that fruited). This table presents type III sums of squares from analyses testing fitness as a function of nutrient treatment, drought treatment, source elevation and all two and three-way interactions, showing numerator and denominator degrees of freedom (df), *F*-values and *p*-values. We computed the significance of the random effect of population with a likelihood ratio test using a one-tailed χ^2 with one degree of freedom (Littell et al., 1996).

	Probability of reproduction			Fecundity (no. fruits)		
Predictor	**df**	***F***	***p***	**df**	***F***	***p***
Nutrient treatment	1, 164	10.47	**0.0015**	1, 115	10.87	**0.0013**
Drought treatment	2, 164	2.98	0.054	2, 115	5.43	**0.0056**
Nutrient × Drought	2, 164	1.84	0.16	2, 115	1.07	0.35
Source elevation	1, 164	0.80	0.37	1, 115	3.15	0.079
Source elevation × Nutrient treatment	1, 164	6.23	**0.0135**	1, 115	10.09	**0.0019**
Source elevation × Drought treatment	2, 164	3.00	0.053	2, 115	7.09	**0.0013**
Source elevation × Nutrient × Drought	2, 164	1.95	0.14	2, 115	1.39	0.25
Population	1	χ^2 =177.4	**<0.0001**	1	χ^2 =13.2	**0.0001**

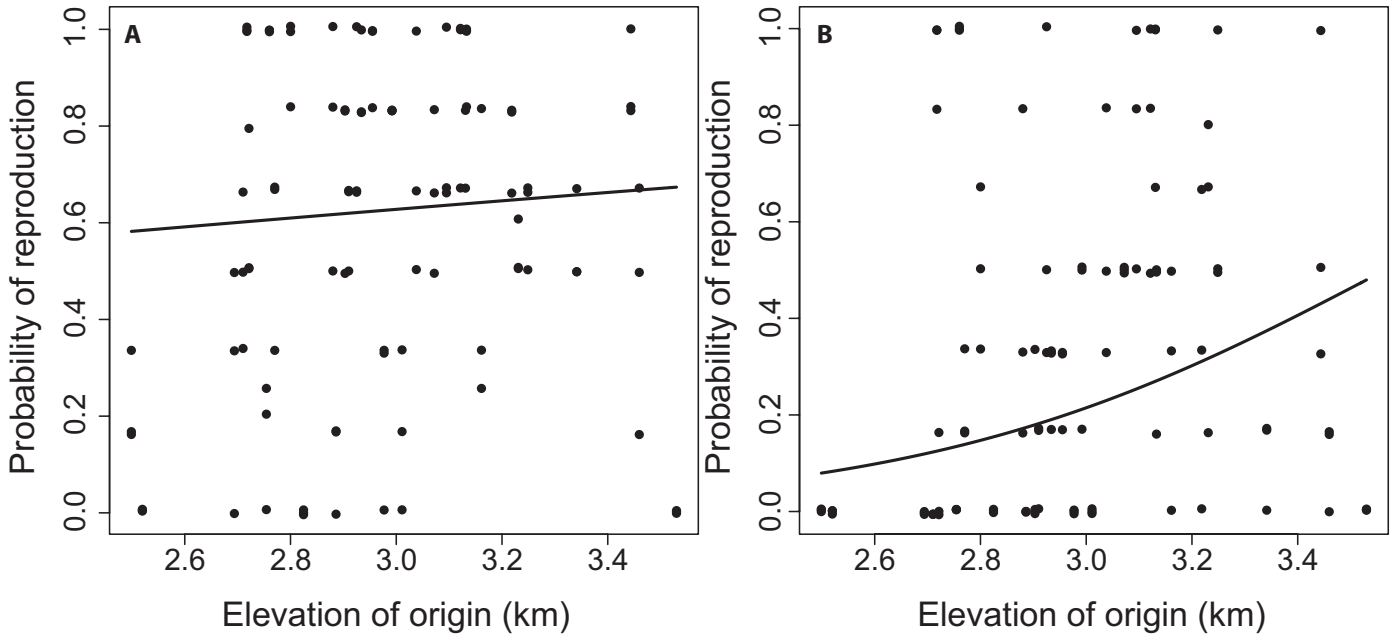

FIGURE 1. Family-level analyses revealed a significant interaction between nutrient treatment and source elevation for the probability of reproduction. Under low nutrient levels (A), there was no evidence that the source elevation influenced reproductive success. In contrast, under higher nutrient levels (B), the probability of reproduction increased with source elevation. Data points represent family-means.

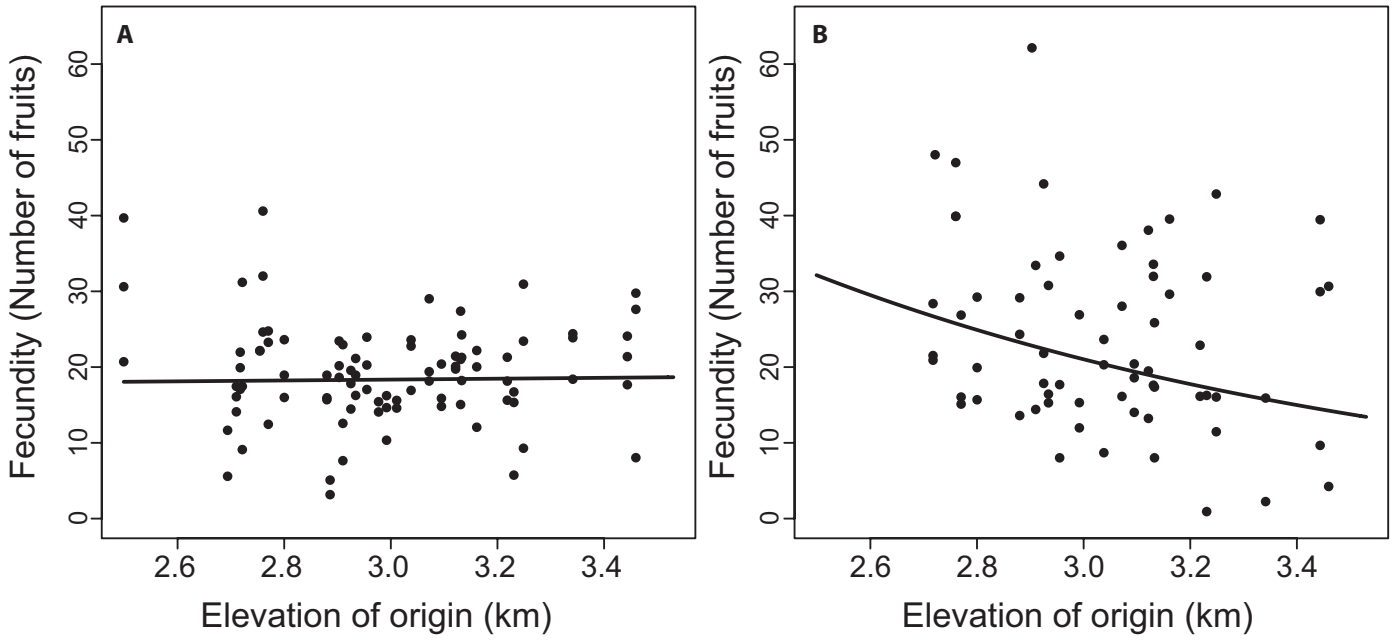

FIGURE 2. Fitness trade-offs across nutrient levels also emerged for the fecundity component of fitness (number of fruits among individuals that reproduced successfully). We found no relationship between source elevation and fecundity in the low nutrient treatment (A). In contrast, in the higher nutrient treatment, fecundity declined with source elevation (B). Data points represent family-level LSMEANs for fecundity.

in the high nutrient treatment and no relationship in the low nutrient treatment (Fig. 2). This fecundity pattern in the high nutrient treatment is in the opposite direction from what we found for the probability of reproduction. The fecundity analysis also uncovered a significant interaction between source elevation and drought treatment ($F_{2, 115} = 7.09$, $p = 0.0013$). Concordant with expectations, under severe drought stress, fecundity declined with source elevation in both family- and individual-level analyses (Fig. 3; Appendix S7), such that plants from arid, low-elevation population exhibited enhanced fitness in severe drought conditions relative to those from humid, high-elevation populations. We found no significant relationship between fecundity and source elevation under moderate drought and well-watered conditions (Fig. 3, Appendix S7).

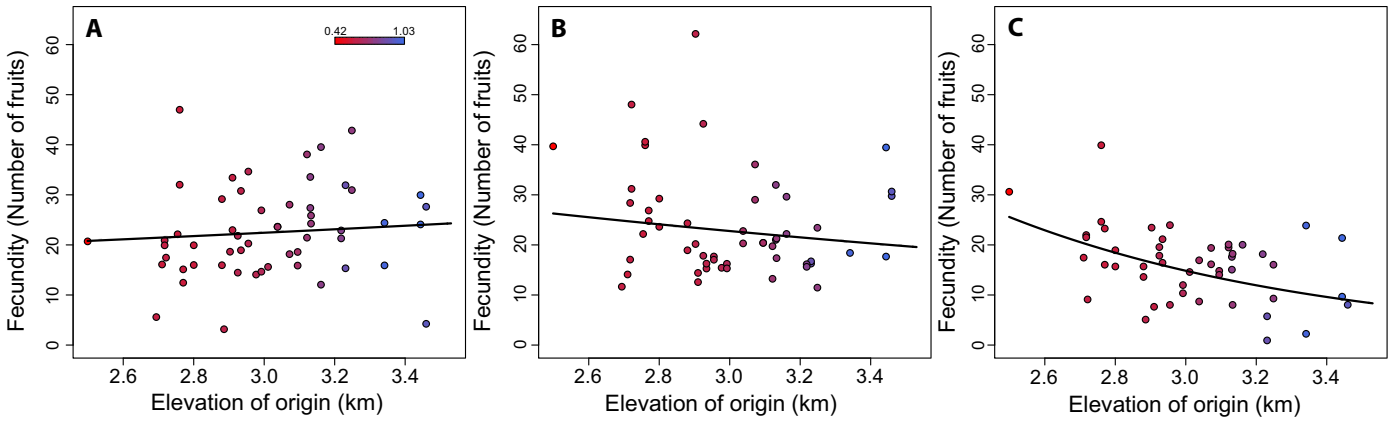

FIGURE 3. Fecundity trade-offs across drought treatments. Under control well-watered conditions (A) and moderate drought stress (B), fecundity was not associated with source elevation. However, under severe drought (C), fecundity declined with increasing source elevation. We color-coded the data points to indicate the aridity index (mean annual precipitations/mean annual potential evapotranspiration) of each population based on climatic data extracted from WorldClim, with arid, low-elevation populations indicated with red and mesic, high-elevation populations indicated with blue. Data points represent family-level LSMEANs for fecundity.

Phenotypic correlations

Resource supply altered the magnitude of life history trade-offs. Nutrient availability influenced the relationship between reproductive success and RGR at both the family-level (nutrient treatment × RGR: $F_{1, 163} = 5.91$, $p = 0.016$; Table 2, Fig. 4) and individual-level (nutrient treatment × RGR: $F_{1, 998} = 9.22$, $p = 0.0025$; Appendices S8 and S9). Plants in both nutrient treatments showed a negative relationship between the probability of reproduction and RGR, yet higher nutrient levels intensified the magnitude of this negative pattern (Fig. 4).

Water availability influenced the relationship between fecundity and RGR, at the family level (drought treatment × RGR: $F_{2, 114} = 5.48$, $p = 0.0054$; Table 2), such that a negative relationship emerged only under severe drought and no significant relationship appeared under moderate drought stress or well-watered conditions (Fig. 5). Individual-level analyses did not find this drought × treatment interaction, instead a negative relationship emerged between fecundity and RGR across all treatments (main effect of RGR: $F_{1, 458} = 13.88$, $p = 0.0002$; Appendices S8 and S10).

Heritability

Broad-sense heritability values ranged from 0.033 to 0.997 (Table 3). Consistent with expectations, the lowest heritability values were for fecundity (all treatments) and survival (all drought treatments under low nutrient levels). For all fitness components, we found high overlap in 95% credible intervals across treatment levels, except for survival, for which heritabilities were depressed in the low nutrient treatment relative to the high nutrient treatment. Thus, our data set provides no evidence that abiotic stress either enhances or depletes genetic variation in fitness traits.

Genetic covariances

We found significant negative genetic covariances indicative of trade-offs between growth and the probability of reproduction under severe water stress in low nutrient conditions, and under all watering treatments (control, moderate drought and severe water stress) at the moderate nutrient level (Table 4). Our analyses did not reveal any significant genetic covariances between growth and fecundity among individuals that successfully reproduced.

TABLE 2. Phenotypic associations of fitness components varied with treatment in family-level analyses. This table presents type III sums of squares from analyses evaluating the context dependent nature of phenotypic correlations, showing numerator and denominator degrees of freedom (df), *F* values and *p* values. We adjusted our alpha level (α = 0.05/2 = 0.025) to correct for multiple comparisons (analysis of two trade-offs in one data set). Significant *p*-values that fall below our adjusted α are in bold. We computed the significance of the random effect of population with a likelihood ratio test using a one-tailed χ^2 with one degree of freedom (Littell et al., 1996).

	Probability of reproduction vs. RGR			Fecundity vs. RGR		
Predictor	**df**	***F***	***P***	**df**	***F***	***P***
RGR	1, 163	12.22	**0.0006**	1, 114	8.96	**0.0034**
Drought	2, 163	2.84	0.061	2, 114	4.46	**0.014**
Nutrient	1, 163	4.41	0.037	1, 114	0	0.95
Drought × RGR	2, 163	3.17	0.045	2, 114	5.48	**0.0054**
Nutrient × RGR	1, 163	5.91	**0.016**	1, 114	0.03	0.87
Drought × Nutrient	2, 163	0.52	0.60	2, 114	0.23	0.80
Drought × Nutrient × RGR	2, 163	0.57	0.57	2, 114	0.23	0.80
population	1	$\chi2$ =168.9	**<0.0001**	1	$\chi2$ =5.39	**0.010**

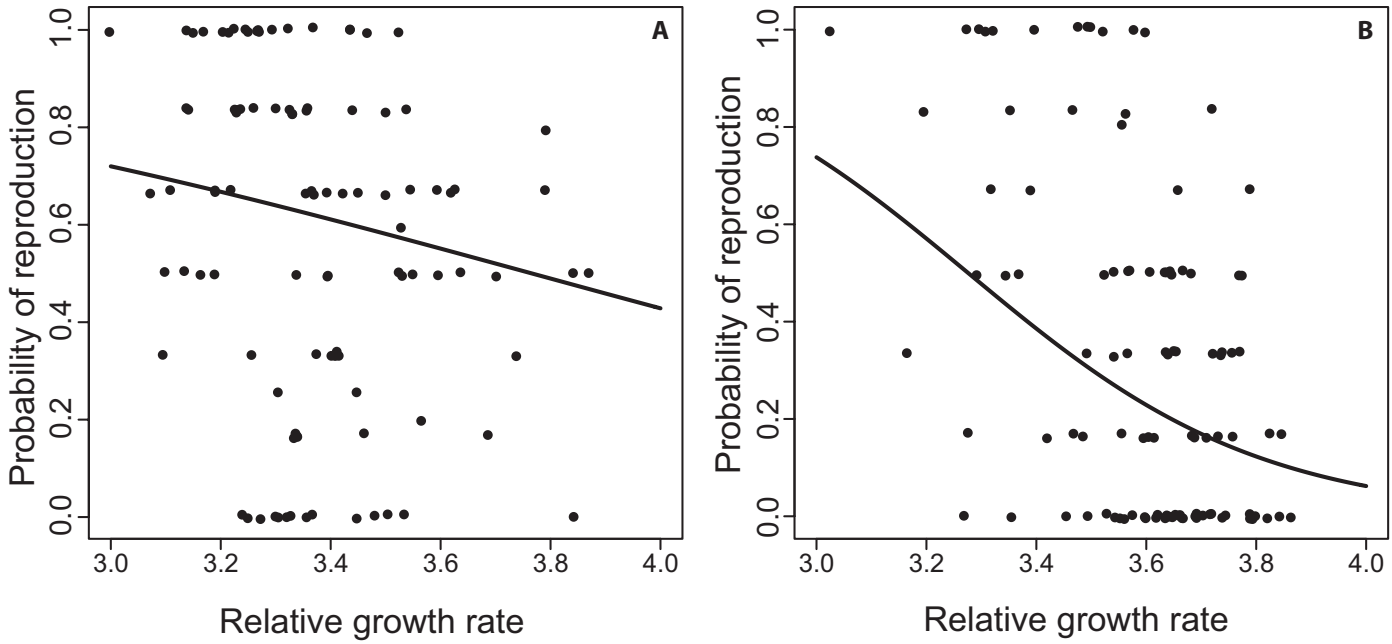

FIGURE 4. Phenotypic correlations at the family-level between the probability of reproduction and relative growth rate revealed no significant relationship under low nutrient levels (A) and a negative association between these fitness components under higher nutrient levels (B). Data points represent family-level LSMEANs for relative growth rate and family-means for the probability of reproduction (number of individuals that reproduced/number planted for each family).

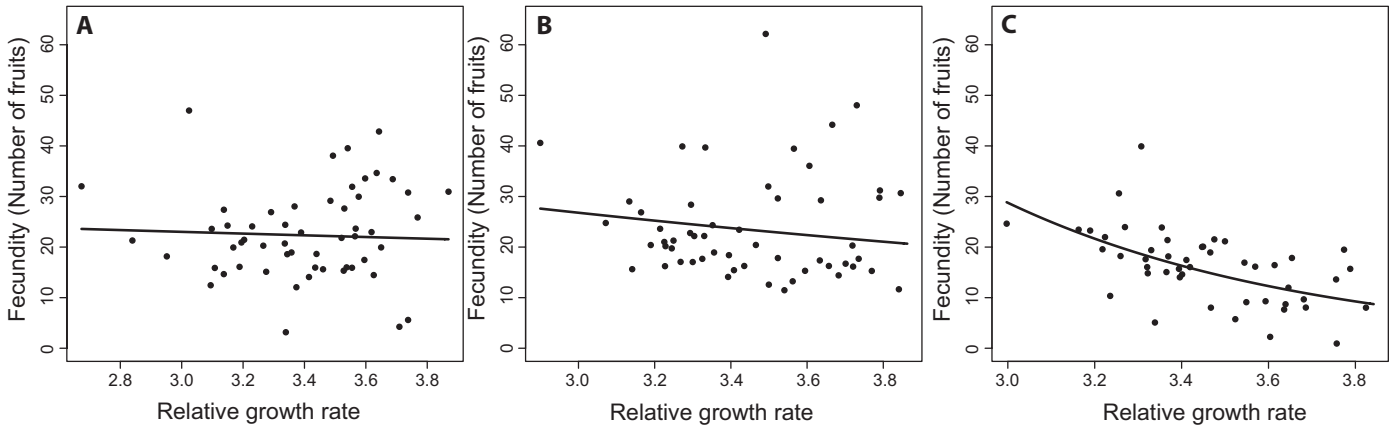

FIGURE 5. Phenotypic correlations at the family-level between fecundity (number of fruits among individuals that reproduced successfully) and relative growth rate revealed context-dependent relationships. Under control conditions (A) and moderate drought (B), we found no significant relationship. However, under severe drought, a trade-off emerged across these two fitness components (C). Data points represent family-level LSMEANs for relative growth rate and fecundity.

DISCUSSION

In our study, drought and nutrient stresses contributed to local adaptation and the environment affected phenotypic correlations and genetic covariances between fitness components. Field studies have documented local adaptation to elevation in this system (Anderson et al., 2015; Wadgymar et al., 2017a; Anderson and Wadgymar, 2020). Concordant with expectations, in this greenhouse experiment, we found that low-elevation ecotypes had elevated fecundity under drought stress compared with high-elevation ecotypes. This trade-off indicates that water stress contributes significantly to local adaptation in these populations. The results of our tests for local adaptation to nutrient stress were more equivocal. Contrary to predictions, the probability of reproduction increased with source elevation under higher nutrient levels. However, patterns were consistent with expectations when we examined fecundity among individuals that successfully reproduced: Fecundity declined with source elevation under higher nutrient levels, which could reflect local adaptation to high soil nutrient levels in low elevation locations. Both nutrient and drought treatments influenced the relationships between growth and reproductive success.

TABLE 3. Broad-sense heritability (H^2) estimates across six resource combinations (3 water × 2 nutrient). Lower and Upper 95% credible intervals are represented as L95 and U95, respectively.

		RGR			Fecundity			Probability of reproduction			Survival		
Drought	**Nutrient**	H^2	**L95**	**U95**	H^2	**L95**	**U95**	H^2	**L95**	**U95**	H^2	**L95**	**U95**
Watered	Low	0.457	0.220	0.713	0.109	0.022	0.209	0.720	0.392	0.992	0.033	3.20e-5	0.170
Moderate	Low	0.282	0.109	0.479	0.098	0.022	0.193	0.849	0.571	0.995	0.048	1.07e-4	0.290
Severe	Low	0.198	0.053	0.352	0.117	0.022	0.222	0.875	0.505	0.996	0.031	3.90e-5	0.130
Watered	Moderate	0.360	0.137	0.612	0.137	0.024	0.257	0.843	0.620	0.966	0.839	0.571	0.990
Moderate	Moderate	0.275	0.096	0.465	0.138	0.033	0.258	0.810	0.565	0.962	0.823	0.457	0.980
Severe	Moderate	0.293	0.107	0.498	0.174	0.044	0.314	0.997	0.994	1.000	0.642	0.321	0.960

TABLE 4. Genetic covariances within each watering treatment for two fitness trade-offs: relative growth rate (RGR) vs. the probability of reproduction and RGR vs. fecundity (no. of fruits produced among individuals that reproduced). We show genetic covariances between traits with lower and upper 95% credible interval values. Bold indicates significance.

		RGR vs. probability of reproduction			RGR vs. Fecundity		
Drought	**Nutrient**	**Covariance**	**L95**	**U95**	**Covariance**	**L95**	**U95**
Watered	Low	−6.75	−20.84	1.00e-01	−0.03	−0.07	0.001
Moderate	Low	−1.31	−5.27	5.50e-01	−0.02	−0.06	0.015
Severe	Low	**−1.19**	**−3.30**	**−2.16e-03**	−0.02	−0.05	0.002
Watered	Moderate	**−2.19**	**−5.44**	**−1.90e-01**	−0.01	−0.05	0.031
Moderate	Moderate	**−2.03**	**−6.14**	**−1.20e-01**	−0.02	−0.08	0.019
Severe	Moderate	**−1.70**	**−4.31**	**−8.00e-02**	−0.03	−0.08	0.018

Our findings highlight that variation in resource allocation and fitness trade-offs depend on the environment (Riska, 1986; Van Noordwijk and de Jong, 1986; Houle, 1991; Roff, 2002). In the sand cricket, *Gryllus firmus*, negative genetic correlations between key traits only emerged under food restriction, indicating that low resource supply induced life history trade-offs (King et al., 2011). Few studies have empirically tested the effect of resource supply on phenotypic or genetic correlations of fitness components, although the environment clearly influences the direction and magnitude of other trait correlations (Sgro and Hoffmann, 2004). Service and Rose (1985) found that limiting food resources shifted the magnitude of genetic correlations between fecundity and starvation resistance for *Drosophila melanogaster*. Despite significant heritability in fitness components under severe water restriction in this study, phenotypic trade-offs between growth and reproduction could constrain adaptation in stressful environments if selection favors both increased growth and fecundity. Climate change has already caused severe winter and summer droughts in many regions, including the native range of *B. stricta* (Rangwala et al., 2012; IPCC, 2014; Fyfe et al., 2017). Our results suggest that families with high growth rates may have reduced fecundity during years of drought stress, which will intensify as climate change continues (Rangwala et al., 2012; IPCC, 2014; Fyfe et al., 2017; Schlaepfer et al., 2017). Furthermore, our results suggest that low-elevation ecotypes, which are adapted to dry conditions, could have a fitness advantage over higher-elevation ecotypes under increasing drought stress. Future studies will evaluate the extent to which fitness trade-offs restrict lifetime fecundity under drought.

Other studies have also observed that life history trade-offs can emerge under stressful conditions. For example, Villellas and Garcia (2018) examined the context-dependent nature of fitness trade-offs across natural populations of *Plantago major*. In their study, costs of reproduction manifested only in habitats with low soil fertility (Villellas and García, 2018). Thus, stress could induce life history trade-offs that are not apparent when resource levels are abundant. Interestingly, Villellas and García (2018) found greater evidence for costs of reproduction under increased precipitation, which could have been due to flooding stress in populations exposed to elevated precipitation. Populations of *Plantago coronopus* under drought stress in the greenhouse displayed negative genetic correlations between fitness components (Hansen et al., 2013). Additionally, Sherrard et al. (2009) found that water stress increased negative genetic correlations between physiological traits in *Avena barbata*. Stressful conditions likely reduce the amount of resources that individuals can acquire while simultaneously altering associations between fitness components and potentially reducing adaptive potential.

Genetic covariances were broadly congruent with phenotypic patterns for the trade-off between the probability of reproduction and growth rates. At the genetic and phenotypic levels, we found that individuals with high growth rates had reduced probability of reproduction under higher nutrient levels. In contrast, genetic and phenotypic patterns differed for the trade-off between fecundity and growth. At the phenotypic level, allocation to growth reduced fecundity under severe drought; however, we found no evidence for significant genetic covariances between these fitness components under any treatment. We hypothesize that resource limitation drives the negative phenotypic correlations between growth and reproductive success in our study. In contrast, negative genetic covariances may result from intrinsic mechanisms including linkage and pleiotropy (Flatt and Hayland, 2011). Furthermore, negative genetic correlations can constrain evolution toward an optimal combination of trait values, potentially limiting a population's adaptive potential (Lande, 1982; Etterson and Shaw, 2001).

Fitness components experience strong selection, which leads to the expectation that genetic variation and heritability should be low for traits strongly associated with lifetime fitness (Mousseau and Roff, 1987). Consistent with this prediction, heritability estimates were lower for fecundity than growth and the probability of reproduction, yet heritabilities in these three fitness components did not vary with environment. In contrast, heritabilities in survival were

substantially lower under low nutrient levels than high nutrient levels across all drought treatments. Overall, this regional pool of plants appears to have sufficient genetic variation for adaptive responses to ongoing selection, but limited heritability could constrain adaptation to low nutrient levels (see also Bemmels and Anderson, 2019). By exposing plants to stresses in the greenhouse that reflect conditions they experience in the field, we have increased the likelihood that our results reveal meaningful eco-evolutionary dynamics that occur in nature (Poorter et al., 2016). We focused this study on maternal families collected across a broad elevational and resource gradient to increase the genetic variation within our experiment. Future studies will test the extent to which genetic trade-offs and limited genetic variation could constrain within population adaptation to novel environments under field conditions.

CONCLUSIONS

By isolating the effects of nutrient and drought stresses on fitness in a diverse regional pool of accessions, our greenhouse experiment revealed local adaptation to severe drought, relatively high heritabilities across fitness components and environments, and fitness trade-offs at the phenotypic and genetic levels in distinct environments. In our study, resource supply altered the associations between fitness components. Under benign water supply and moderate drought stress, we found no relationship between fecundity and growth. In contrast, as drought increased in severity, we uncovered trade-offs, such that allocating resources to growth reduced investment in fecundity. Longitudinal studies have revealed that high interannual variability of water supply may obscure trade-offs (Agrawal et al., 2010; Zust and Agrawal, 2017). Our results show that water stress can shift genetic associations between fitness components, potentially constraining ongoing adaptation to stressful conditions despite significant heritability in fitness components (Hellmann and Pineda-Krch, 2007). As climate change continues to expose plants to stressful resource environments, genetic trade-offs that did not previously exist under benign conditions could restrict adaptive potential.

ACKNOWLEDGMENTS

We thank Suni Thakhur, Mike Boyd, Cherien Abou-harb, Alex Dos Santos, Mariana Gonzalez, Marisa Sheres, and Kevin Turner for assistance in the greenhouse and Jordan Bemmels for help with the statistical models and comments on a previous draft of the manuscript. We are grateful to Susana Wadgymar, Lisa Donovan, Nina Wurzburger, Shu-Mei Chang, and Andrea Sweigart for valuable discussions about this project. Funding was provided by a RC Lewontin grant from the Society for the Study of Evolution (to R.M.) and the National Science Foundation (DEB-1553408 to J.T.A.). We are grateful to the two anonymous reviewers and Associate Editor Gina Baucom for their feedback on a previous version.

AUTHOR CONTRIBUTIONS

R.M. and J.T.A. designed the study and acquired funding; R.M. carried out the study and collected all data; R.M. and J.T.A. analyzed data; R.M. and J.T.A. wrote the manuscript.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

APPENDIX S1. Spatial coordinates of selected populations spanning an elevational gradient in Gunnison County Colorado (USA).

APPENDIX S2. Genotypes with fewer than six siblings per genotype treatment combination.

APPENDIX S3. Soil moisture as percentage volumetric water content (%VWC).

APPENDIX S4. Individual-level analyses of fitness trade-offs across nutrient and drought treatments for the probability of reproduction.

APPENDIX S5. Individual-level analyses of fitness trade-offs across nutrient levels were highly congruent with family-level analyses.

APPENDIX S6. Individual-level analyses of fecundity trade-offs across nutrient levels.

APPENDIX S7. Individual-level analyses of fecundity trade-offs across drought treatments.

APPENDIX S8. Phenotypic associations of fitness components varied with treatment in individual-level analyses.

APPENDIX S9. Phenotypic correlations at the individual-level between the probability of reproduction and relative growth rate.

APPENDIX S10. Phenotypic correlations at the individual-level between and relative growth rate.

APPENDIX S11. This is a .csv file with the family-level data for recreating Tables 1 and 2. The columns including source population identifier ("Population"), drought treatment ("Drought_treatment"), nutrient treatment ("Nutrient_treatment"), the number of individuals planted into the experiment ("Number_planted"), the number of individuals that successfully reproduced ("Number_reproduced"), LSMEANs relative growth rate ("RGR"), standard error in relative growth rate ("RGR_SE"), LSMEANs number of fruits produced by individuals that successfully reproduced ("fecundity"), standard error in fecundity ("fecundity_SE"), aridity index ("Aridity_Index"), and the source elevation in meters of all individuals in the study ["Source_elevation(m)"].

APPENDIX S12. This is a .csv file with the individual-level data for recreating Tables S3 and S4, as well as heritability and genetic variance-covariance matrices. The columns including source population identifier ("Population"), experimental block identified ("Block"), unique plant identifier ("Plant_ID"), drought treatment ("Drought_treatment"), nutrient treatment ("Nutrient_treatment"), concatenated treatment ("Treatment"), survival ("Survival"), reproductive success ("Reproduction", with values of 0 indicating failure to reproduce and values of 1 indicating successful reproduction), number of fruits produced by individuals that successfully reproduced ("fecundity"), relative growth rate ("RGR"), aridity index ("Aridity_Index"), and the source elevation in meters of all individuals in the study ["Source_elevation(m)"].

APPENDIX S13. Pedigree text file for running MCMCglmm scripts. This text file lists the unique plant identifier as "animal", the maternal parent as "dam" and the paternal parent as "sire". Since *Boechera stricta* is a selfing species, maternal and paternal parents are identical.

APPENDIX S14. heritabilities_MacTavish_Anderson.R: This file contains the R script for calculating heritabilities, using the pedigree file and the individual.txt file.

APPENDIX S15. genetic_covariances_MacTavish_Anderson.R: This R script contains the code for all genetic variance–covariance models in this manuscript.

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