

Estimating the capacity of *Chamaecrista fasciculata* for adaptation to change in precipitation

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Adaptation through natural selection may be the only means by which small and fragmented plant populations will persist through present day environmental change. A population's additive genetic variance for fitness ($V_A(W)$) represents its immediate capacity to adapt to the environment in which it exists. We evaluated this property for a population of the annual legume *Chamaecrista fasciculata* through a quantitative genetic experiment in the tallgrass prairie region of the Midwestern United States, where changing climate is predicted to include more variability in rainfall. To reduce incident rainfall, relative to controls receiving ambient rain, we deployed rain exclusion shelters. We found significant $V_A(W)$ in both treatments. We also detected a significant genotype-by-treatment interaction for fitness, which suggests that the genetic basis of the response to natural selection will differ depending on precipitation. For the trait-specific leaf area, we detected maladaptive phenotypic plasticity and an interaction between genotype and environment. Selection for thicker leaves was detected with increased precipitation. These results indicate capacity of this population of *C. fasciculata* to adapt in situ to environmental change.

KEY WORDS: Adaptation, additive genetic variance, heritability, natural selection, precipitation, quantitative genetics.

Recent research has documented rapid evolution in response to environmental change (Franks 2011; Geerts et al. 2015; Thomann et al. 2015; Hamann et al. 2018). These studies have demonstrated adaptation to novel environmental conditions under short timescales, by retrospectively evaluating the response to selection under environmental change in the recent past or by investigating the change in trait means. Few studies have prospectively estimated the capacity for wild populations to adapt to novel environmental conditions predicted for the future (but see Franks et al. 2013 and Bataillon et al. 2016), thus the rate at which populations could adapt to future environmental conditions is not well understood (but see Etterson and Shaw 2001 and Torres-Martínez et al. 2019).

Fisher's Fundamental Theorem of Natural Selection (FTNS; Fisher 1930) is a valuable conceptual tool that can be used to estimate a population's current capacity for adaptation (Shaw 2019). The FTNS predicts the genetically based change in mean fitness between the current generation and the progeny generation from the ratio of the current generation's additive genetic variance for fitness ($V_A(W)$) to its mean fitness (\bar{W} ; Shaw 2019). A *genetically* based change implies that the change in mean fitness observed in the progeny generation is due to a change in allele frequency, from differential transmission of alleles to the progeny generation, at loci that contribute to variation in fitness. Importantly, predictions from the FTNS are solely based on genetic changes due to natural selection in the environment of the

parental generation (Shaw 2019). Thus, the mean fitness of the progeny generation may likely differ from what is predicted by the FTNS because the environment in which the progeny develop will likely differ from the environment of the parental generation (Shaw 2019).

The fitness of an individual can be operationally defined as the number of offspring it contributes throughout its lifetime to the next generation. Populations that produce an average of one surviving offspring per individual are expected to maintain their population size ($\bar{W} = 1$). The population size increases or decreases when \bar{W} is greater than or less than 1, respectively. Whether a decreasing population ($\bar{W} < 1$) will be “rescued” from extirpation through adaptation resulting in $\bar{W} \geq 1$ depends on the magnitude of $V_A(W)/\bar{W}$.

Studies that directly estimate $V_A(W)$ in conjunction with \bar{W} are rare, and no studies have estimated $V_A(W)$ in environmental conditions predicted for the future (but see Torres-Martínez et al. 2019 for an example in the greenhouse using additive genetic variance for reproductive success as an estimate for $V_A(W)$). One reason these studies are rare is that it is argued that populations harbor little to no $V_A(W)$ because the constant process of natural selection would reduce variation to near zero through fixation of alleles that increase fitness (Barton and Keightley 2002). Additionally, Fisher (1930) may have curtailed interest in investigating the predictive power of the FTNS as he argued that an increase in population growth would degrade the environment through crowding. This could nullify any increase in fitness from natural selection, thus keeping the population growth rate constant or even diminishing it (Fisher 1930; Shaw 2019).

The annual prairie legume *Chamaecrista fasciculata* (Fabaceae) has been used to estimate genetic variation for fitness previously. Etterson's (2004a) pioneering study made use of a natural soil moisture gradient to assess potential for adaptation to changing climate in this species. She detected genetic variance in two populations when grown in a drier site. Recently, Sheth et al. (2018) and Kulbaba et al. (2019) directly estimated $V_A(W)$ and \bar{W} to quantify the rate of adaptation in multiple natural populations, and over multiple years, of *C. fasciculata*. Both studies found significant levels of $V_A(W)$ indicating capacity for ongoing adaptation of each population to its home environment.

Given this evidence for appreciable $V_A(W)$ in natural populations, our research objective was to use the FTNS to estimate the capacity for adaptation to change in climatic conditions of a population of *C. fasciculata* in the tallgrass prairie region of the Midwestern United States. Less than 1% of the tallgrass prairie remains relative to its historical extent. The remaining prairie is highly fragmented (Minnesota Prairie Plan Working Group 2018). Thus, prairie plant populations may be unlikely to respond

to changing climate via gene flow. Consequently, their persistence in the face of climate change will likely depend on adaptation in situ. The capacity for these populations to adapt in situ can be estimated using the FTNS. Estimates of $V_A(W)$ and \bar{W} , needed for the FTNS, are facilitated by the annual habit of *C. fasciculata*, which allows gathering of nearly complete lifetime fitness records for individuals at least through female gametes as male fitness is still challenging to estimate.

Climate change in the Midwest is expected to increase the intensity and overall amount, but decrease the frequency, of rainfall (Pryor et al. 2014). To estimate the adaptive capacity of *C. fasciculata* to changes in soil moisture, we manipulated incident rainfall using rain exclusion tents in the field. Our research is unique in that no other studies we are aware of have directly estimated $V_A(W)$ in conjunction with \bar{W} to determine the adaptive capacity of prairie plant populations to specific environmental variables manipulated in the field. In addition to the magnitude of $V_A(W)$, adaptive phenotypic plasticity could play a significant role in enabling populations to persist with environmental changes. Our experimental design allowed us to evaluate phenotypic plasticity, and genetic variation for phenotypic plasticity (as evidenced by genotype \times environment interactions), for fitness in relation to a specific component of climate, precipitation.

For plants, the trait specific leaf area (SLA) has been shown to be related to relative growth rate, stress tolerance, leaf longevity, and moisture availability (Scheepens et al. 2010). Thicker leaves (indicated by low values of SLA) may confer a fitness advantage in low-moisture environments because they tend to wilt less readily and transpire less water (Poorter et al. 2009). We evaluated the heritability of and selection on SLA to assess the capacity for adaptation through genetic change in this trait, and to enable an estimation of the rate of adaptation, to changes in soil moisture. We also assessed phenotypic plasticity of SLA, and whether it appeared to be adaptive, given that adaptive phenotypic plasticity may enhance populations' persistence through environmental change (Charmantier et al. 2008; Chevin and Hoffmann 2017). A significant genotype-by-environment ($G \times E$) interaction for SLA would indicate genetic variation for phenotypic plasticity of this trait.

In this study, we asked the following questions for a wild population of *C. fasciculata*: (1) Is there appreciable $V_A(W)$ in differing rainfall conditions in the field? (2) If so, what is the predicted change in mean fitness between the parental and progeny generation (i.e., rate of adaptation) in each condition, based on the FTNS? (3) Is there appreciable selection on SLA in differing rainfall conditions in the field? (4) If so, what is the heritability of this trait and what is the predicted change in SLA between the parental and progeny generation? (5) Is there phenotypic plasticity for SLA, and is it adaptive? (6) Is there a $G \times E$ interaction for mean lifetime fitness and for SLA?

Methods

STUDY SPECIES

This research focuses on *Chamaecrista fasciculata* (partridge pea), an annual herbaceous legume native to North America. *C. fasciculata*'s life history and floral traits make it amenable to research employing a quantitative genetic framework. *C. fasciculata*'s floral attributes facilitate hand pollination to generate pedigreed offspring as a basis for obtaining accurate estimates of $V_A(W)$. Flowers are hermaphroditic, last one day, and are singly pollinated by bees whose buzzing stimulates the release of pollen from the tips of anthers (Fenster 1991). *C. fasciculata* has a high outcrossing rate (80%; Fenster 1991); to the extent that selfing occurs, it generally results from pollinator movement between flowers on the same plant (Fenster 1995); pollinations can be controlled in the greenhouse.

PEDIGREE GENERATION

A paternal half-sibling pedigree was used to estimate $V_A(W)$ from the covariance between noninbred half-siblings, which is equal to $\frac{1}{4} V_A$ (Falconer and Mackay 1996, Ch. 10). A pedigree that is restricted to full-siblings (in the absence of selfing) confounds V_A with dominance variance and maternal effects, thereby reducing the accuracy of the V_A estimate, because the covariance of full-siblings is equal to $\frac{1}{2} V_A + \frac{1}{4} V_D + V_M$ (Falconer and Mackay 1996, Ch. 10). Pedigreed seed was produced following Kulbaba et al. (2019) from seed collected by Dr. V. Eckard in 2013 from the Conard Environmental Research Area in Kellogg, Iowa (41°40'44.2"N 92°51'24.9"W). We used a single population of *C. fasciculata* to keep the space and time requirements for pedigree generation feasible. The incidence of selfing was mitigated by conducting hand pollinations in the greenhouse. Pollen tubes were removed from the flowers of the sire and pressed to release pollen. The extruded pollen was collected in a petri dish and transferred to the fresh stigmas of the open flowers on designated recipients with the tip of the toothpick. A magnifying lens was used to ascertain that the pollen was on the stigma, and the peduncle was marked. After accounting for mortality in the greenhouse, the final pedigree consisted of 18 paternal half-sibling families and 52 maternal full-sibling families.

FIELD EXPERIMENT

With the goal of determining the capacity of *C. fasciculata* to adapt to changes in rainfall, we established ten 2 m² plots spaced 1.5 m apart in an urban grassland on the University of Minnesota Twin Cities campus (44°58'34.2"N 93°13'08.3"W) in the summer of 2016. Each plot was randomly assigned a treatment, with five plots receiving full rainfall and five receiving reduced rainfall. The reduced rainfall treatment consisted of deploying exclusion shelters before specific storms (17 rainfall events were ex-

cluded; Fig. 1). The shelters were removed the next day to minimize shading, passive warming, and altered humidity and wind (Beier et al. 2012). The proximity of the study site to campus enabled us to effectively deploy the rain exclusion shelters and minimize the time they remained assembled after storms.

Rain exclusion shelters consisted of four polyvinyl chloride (PVC) pipe legs of varying lengths that enabled angling of the shelters west to southwest, and to direct the flow of water into a rain catchment barrel at the west corner of the shelter. The shortest leg, in the west corner, was 100-cm long, and the longest, in the east corner, was 171-cm long. We deployed the shelters by attaching the top of the shelter to the PVC legs. The top of the shelter was composed of 2 m² 1-inch PVC frame to which we fastened 3 mil clear overwintering film (RKW Klerks, Chester, SC, USA), which excluded rain but allowed penetration of photosynthetically active radiation.

Rain exclusion shelters were deployed after seeds germinated from June 30 to September 25 to reduce rainfall by 40% to simulate drought like conditions predicted to be more common in the future (Pryor et al. 2014). We placed a rain gauge in the center of each exclusion plot to confirm the efficacy of the shelters, and we placed a rain gauge in the center of the field to determine rainfall at the site. The total reduction in rainfall from June to October was calculated as the ratio of the summed recorded rainfall in the uncovered gauge on the days shelters were deployed to the total rainfall for the season, which was the sum of the rainfall in the uncovered gauge for the season.

MEASURING SOIL MOISTURE

To quantify the difference in soil moisture between plots receiving full rain and those from which rain was excluded, we recorded volumetric water content by placing one EC-5 decagon soil moisture probe (Decagon Devices, Pullman, WA) connected to a HOBO USB micro station data logger (Onset Computer Corporation, Bourne, MA, USA) in the center of two full rain and two rain reduction plots.

FIELD PLANTING DESIGN

Into each plot, 208 scarified *C. fasciculata* seeds from 52 full-sibling families representing 18 paternal half-sibling groups were planted into bare soil June 8–10, 2016. Seeds were assigned randomized positions in a hexagonal array in each plot to maintain consistent density (Shaw 1987a). In each plot, planting positions were spaced 20 cm apart and at each planting position four seeds from the same full-sibling family were spaced 5 cm apart and later thinned to one germinant per planting position. After thinning, 52 seeds, one representing each full-sibling family, remained. Two rows of nonexperimental *C. fasciculata* seeds from the same population were planted in between the plot edge and the experimental plants to maintain a consistent density for

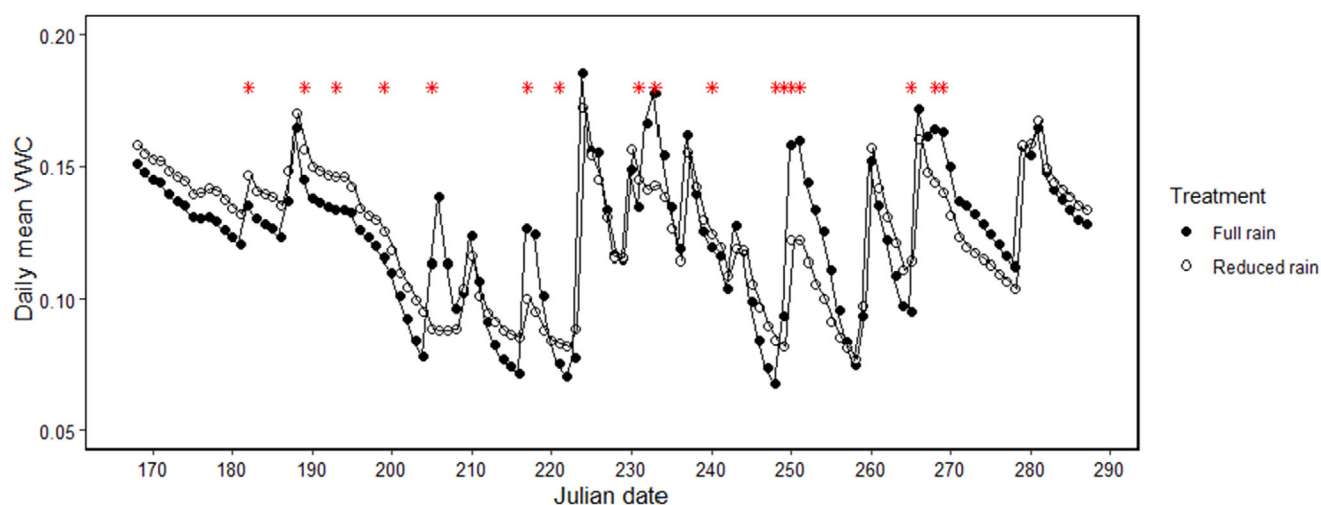


Figure 1. Average daily volumetric water content (VWC) from EC-5 decagon soil moisture probes and HOBO USB micro station data loggers averaged over two probes in the full rain and reduced rain plots from June to October 2016. Filled circles indicate plots receiving full rainfall and open circles represent plots from which rain was excluded. Stars indicate days when rainfall was excluded.

experimental plants and to attenuate edge effects of rainfall and competition (Langton 1990). A 4-foot-tall chicken wire fence was erected around the site perimeter to minimize prevalent rabbit herbivory and the plots were kept weed free.

FITNESS AND TRAIT DATA COLLECTION

To gain insight into the current degree of adaptation of *C. fasciculata* to reduced soil moisture, we obtained measures of components of fitness throughout the lifetime of all plants. Emergence data were collected approximately three weeks after planting, and we thinned at that time. Each plant that remained after thinning was followed throughout the growing season. At the end of the season, as pods ripened, seeds were collected and counted. To obtain SLA, we harvested the third most fully expanded leaf from the top of the plant midway through the growing season. Each leaf was pressed between two moist paper towels and kept in a cooler to prevent wilting after harvesting. Preparatory to measuring leaf area, the leaflets, which were exhibiting paraheliotropism when harvested, were cut from the petiole to keep them flat. We measured leaf area with a LI-C3000 area meter (LI-COR, Lincoln, Nebraska USA). Thereafter, the leaflets were placed in a manila coin envelope, dried at 90° F, and weighed when dry to determine dry weight. SLA is obtained as the ratio of leaf area to leaf dry weight ($\text{cm}^2 \text{g}^{-1}$).

STATISTICAL ANALYSES

All data and R markdown for the results reported here are available at: <https://doi.org/10.5061/dryad.34tmpg4hx>. We estimated additive genetic variance for fitness ($V_A(W)$) and population mean lifetime fitness (\bar{W}) using aster models from the aster package in R software version 3.6.2 (R Core Team 2019). Aster mod-

els were developed to account for the nonconformity of lifetime fitness to known statistical distributions (Geyer et al. 2013). Aster models appropriately model the distribution of each life history variable and account for the dependency of each life history stage on earlier stages in a joint analysis that produces valid standard errors for mean fitness. In our analyses, the aster graphical model for lifetime fitness included emergence, modeled as a Bernoulli distribution, and the number of seeds produced modeled as a Poisson distribution.

ANALYSIS OF MEAN LIFETIME FITNESS, ADDITIVE GENETIC VARIANCE FOR FITNESS, AND PREDICTED PROGENY MEAN FITNESS

We obtained estimates of $V_A(W)$ in each treatment using random effect aster models (Geyer and Shaw 2013). Because of their comparable magnitude, we were able to estimate dam and sire effects in the same random effects aster model as one term, parental variance, by equating the variance attributable to dam and sire effects, as noted in Falconer and Mackay (1996) example 10.4 (Sheth et al. 2018; Kulbaba et al. 2019). The analysis in aster, like those in all generalized linear mixed models (glmm), proceeds on a transformed scale. To obtain estimates of $V_A(W)$, from parental variance, on the original measurement scale, we applied a nonlinear back transformation of the values using fitness values from the plot that had the median fitness value among the five plots in that treatment (as in Kulbaba et al. 2019). We obtained estimates of \bar{W} for each treatment using fixed effect aster models. Plot was included as a fixed factor in all aster analyses and we evaluated its significance using likelihood ratio tests. The change in mean fitness between the progeny and parental generation for

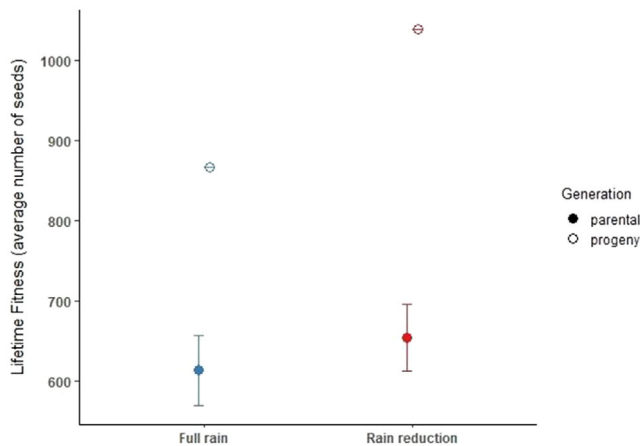


Figure 2. Estimated mean lifetime fitness of parental generation (closed circles with standard error) obtained from fixed effect aster models and predicted fitness of the progeny generation (open circles without standard error) in the full rain and rain reduction treatment. Predicted mean fitness of the progeny generation was calculated using Fisher's fundamental theorem of natural selection: $V_A(W)/\bar{W} + \bar{W}$ where \bar{W} equals mean fitness and $V_A(W)$ is the additive genetic variance for fitness. The plot with the median mean fitness value in each treatment was used as the basis for estimating $V_A(W)$, which was estimated from random effect aster models.

each treatment was predicted as $V_A(W)/\bar{W}$, and mean fitness of the progeny generation as $V_A(W)/\bar{W} + \bar{W}$ (Fisher 1930).

ANALYSIS OF GENOTYPE-BY-ENVIRONMENT INTERACTION ($G \times E$) FOR LIFETIME FITNESS

To test for a $G \times E$ interaction, we jointly analyzed data for both treatments using random effects aster models. Treatment and plot were modeled as fixed factors, and dam, sire, and the interaction between sire and treatment were random factors. We evaluated the significance of the interaction with a likelihood ratio test.

There are two contributors to $G \times E$ interactions—the first is a difference in genetic variance between environments and the second is a difference in rank of breeding values between environments (Conner and Hartl 2004, Ch. 5). Breeding values are the effect of an individual's alleles on its offspring's trait value (Falconer and Mackay 1996, Ch. 7). To visualize the type of $G \times E$ interaction, we plotted estimated breeding values for fitness for each paternal half-sibling group for the two treatments using dot plots. Breeding values were extracted from the random effect aster models for each treatment (Geyer et al. 2012). We calculated Pearson's product-moment correlation coefficient (r) as an indicator of the similarity between breeding values between treatments (Kulbaba et al. 2019), acknowledging that it only ap-

proximates the association between breeding values because it does not account for the uncertainty in their estimates.

PHENOTYPIC PLASTICITY OF SLA

For SLA, we evaluated its phenotypic plasticity, which is the difference in trait expression between environments (Conner and Hartl 2004, Ch. 5), using mixed effect linear models. SLA was the response variable with treatment as a fixed factor and dam and sire as random factors. We used a likelihood ratio test to determine if the difference in mean SLA between treatments was significant. Two SLA values with a leaf mass less than 10 mg were removed from the analysis. The extremely small denominator values gave rise to SLA values four standard deviations from the mean, which inflated the sampling variance.

PHENOTYPIC SELECTION ANALYSES OF SLA

The selection differential (S) and curvature of the selection surface (γ) for SLA were estimated for each treatment separately using fixed effect aster models following Shaw et al. (2007) and Geyer and Shaw (2010). The selection differential is estimated as the slope of the linear regression of fitness on a trait (Conner and Hartl 2004, Ch. 6). Significant quadratic predictors in the regression of fitness on the trait indicate curvature in the fitness landscape. We used likelihood ratio tests to determine significance of linear and quadratic terms. Significant curvature with the inflection point within the range of phenotypic trait values indicates disruptive selection (positive curvature) or stabilizing selection (negative curvature). Coefficients and standard errors for S and γ were estimated following Geyer and Shaw (2010) using aster models.

ESTIMATING HERITABILITY AND RESPONSE TO SELECTION OF SLA

The response to selection, which is the change in the mean trait value between the parental and progeny generation, was predicted as the product of narrow sense heritability (h^2) and S , via the breeders equation: $R = h^2 S$ (Falconer and Mackay 1996, Ch. 11). Narrow sense heritability for a trait is the quotient of V_A (additive genetic variance) and V_P (phenotypic variance; Falconer and Mackay 1996, Ch. 8). To obtain an estimate of V_A for SLA in each treatment, we partitioned the phenotypic variance of SLA using the quantitative genetics software Quercus with the program nf3.p (Shaw and Shaw 1994), which implements the method of restricted maximum likelihood (Shaw 1987b). We used likelihood ratio tests to determine the significance of variance components. Significance testing revealed V_M (variance due to a common environment) was not statistically significant ($P > 0.05$), so we proceeded with a smaller model including only V_A and V_E (variance due to environments unique to individuals). We modeled V_P as the sum of V_A and V_E .

Table 1. Summary output from aster models testing the significance of plot and treatment (fixed factors), and sire, dam, and the interaction between sire and treatment (random factors) on lifetime fitness. Significance of the parental effect (random factor) in the treatment-specific models on individual lifetime fitness was also evaluated. Factors in each model are denoted as fixed (F) or random (R). Statistical significance of fixed effects was assessed from likelihood ratio tests with sub models, and random effects were assessed from summary output of aster analyses with all terms for each model. *P*-values less than 0.05 are considered significant.

Model	Test degrees of freedom	Test deviance	<i>P</i> -value
Full model with both treatments (for evaluation of $G \times E$): Fitness \sim Treatment + Plot + Sire + Dam + Sire \times Treatment			
Treatment (F)	1	0.28	0.6
Plot (F)	8	1652.50	$<2.2 \times 10^{-16}$
Sire (R)	–	–	0.008
Dam (R)	–	–	$<2 \times 10^{-16}$
Sire \times Treatment (R)	–	–	1.4×10^{-9}
Rain reduction random effect model for additive genetic variance for fitness: Fitness \sim Plot + Parental effect			
Plot (F)	4	1127.80	7.3×10^{-243}
Parental effect (R)	–	–	$<2 \times 10^{-16}$
Rain reduction fixed effect model for mean fitness: Fitness \sim Plot			
Plot (F)	4	19.70	0.0006
Full rain random effect model for additive genetic variance for fitness: Fitness \sim Plot + Parental effect			
Plot (F)	4	7332.30	0
Parental effect (R)	–	–	$<2 \times 10^{-16}$
Full rain fixed effect model for mean fitness: Fitness \sim Plot			
Plot (F)	4	1545.30	$<2.2 \times 10^{-16}$

Going forward, significance testing was only conducted on V_A as this component determines the rate of adaptation and trait heritability (Falconer and Mackay 1996, Ch. 8). Feasibility constraints were imposed so that variance estimates were ≥ 0 . Standard errors for V_A were estimated as the square root of the sampling variance as estimated by Quercus.

G \times E INTERACTION FOR SLA

We evaluated a possible $G \times E$ interaction for SLA using a likelihood ratio test. SLA was the response variable with treatment as a fixed effect and dam, sire, and the interaction between treatment and sire as random effects. We used Quercus to estimate the additive genetic covariance (COV_A), which indicates the direction of the linear relationship between breeding values for SLA in the two treatments, and the additive genetic correlation (r_A) to help determine the type of interaction; r_A less than 1 corresponds to a shift in rank of breeding values between treatments (Falconer and Mackay 1996, Ch. 19). The test of the hypothesis: $COV_A = 0$ was conducted using the same method to evaluate significance

of V_A . To visualize the type of $G \times E$ interaction, we plotted the sire group breeding values for SLA between the two treatments. Sire breeding values were estimated using Quercus by finding individual breeding values for all the observed individuals and then averaging by family.

Results

SOIL MOISTURE BETWEEN TREATMENTS

In a summer of exceptionally great precipitation, the research site received 61.2 cm of rain from June to October 2016. In June–October 2016, rainfall was 37.5% more than the average from 1895 to 2019 (PRISM 2019). Altogether, 40% of incident rain (24.1 cm) was excluded from the rain reduction treatment. Because the year's rain was extreme, plants in the rain reduction treatment received rainfall levels closer to the historical summer averages, whereas the full rain treatment was representative of increased rainfall. The rain reduction treatment was effective at reducing soil moisture, as evidenced

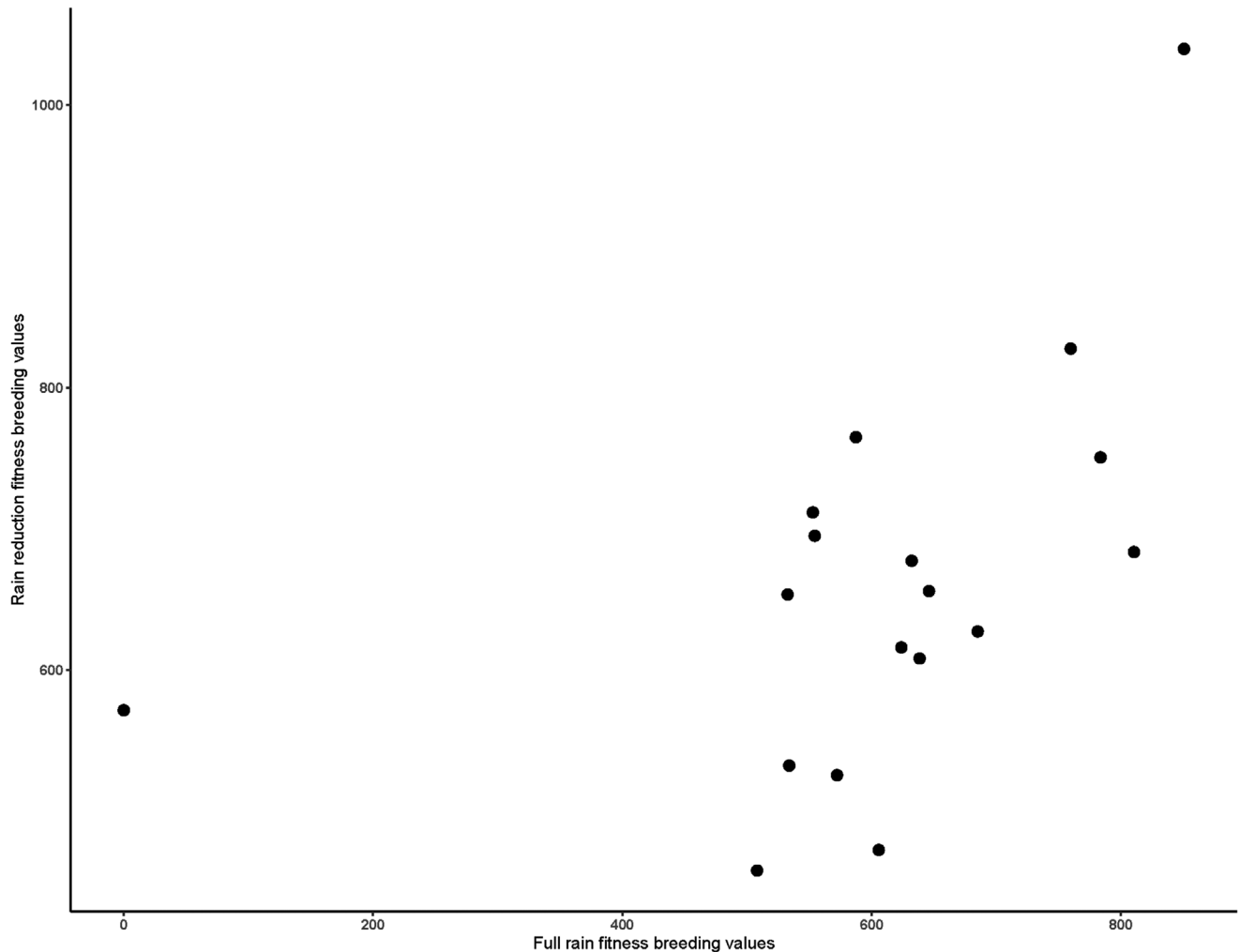


Figure 3. Correlation of breeding values for mean lifetime fitness in the full rain and rain reduction treatment. Each point represents the estimated breeding value for mean lifetime fitness for one of the 18 sire groups in each treatment. The Pearson's correlation coefficient (r) of breeding values between treatments is 0.44. This value presents a very approximate sense of the relationship between sire breeding values between treatments because it does not account for the error in estimating the breeding values.

by lower volumetric water content in the rain reduction treatment during storms when rain exclusion tents were deployed (Fig. 1).

MEAN LIFETIME FITNESS (\bar{W})

Mean lifetime fitness of the pedigree generation was higher in the rain reduction treatment than in the full rain treatment when comparing the mean fitness value that was the median value for mean fitness among the five plots in each treatment (654 ± 42 SE and 613 ± 43 SE average seeds per plant, respectively; Fig. 2). When averaged across all plots in each treatment, mean lifetime fitness in the rain reduction treatment was also higher than in the full rain treatment (591 ± 22 SE and 575 ± 23 SE). However, likelihood ratio tests of the treatment effect did not detect a statistically significant difference in mean fitness between treatments ($\chi^2 = 0.28$, $P = 0.6$; Table 1).

ESTIMATION OF ADDITIVE GENETIC VARIANCE FOR LIFETIME FITNESS

We detected large and highly significant values of additive genetic variance for lifetime fitness in both treatments as evidenced by significant parental effects in both models ($P < 2 \times 10^{-16}$ for both treatments; Table 1). Estimates of $V_A(W)$ were 62.6% larger for the rain reduction treatment than the full rain treatment ($252,000 \pm 49,000$ SE and $155,000 \pm 30,000$ SE, respectively). Plot effects were also significant in both models indicating spatial variation in lifetime fitness across the study site (rain reduction: $\chi^2 = 1127.8$, $P < 7.3 \times 10^{-243}$; full rain: $\chi^2 = 7332.30$, $P = 0$; Table 1).

PREDICTED PROGENY MEAN LIFETIME FITNESS

Average fitness of the parental generation, as well as the predicted mean fitness of the progeny generation, in both treatments, was

Table 2. Results from comparisons of mixed effect linear models employing likelihood ratio tests to evaluate the significance of treatment (fixed effect) and the interaction between sire and treatment (random effect) as predictor variables with SLA as the response variable. The significance of treatment was evaluated by comparing a model with sire (random effect), dam (random effect), and treatment to a model without treatment. Similarly, the significance of the interaction between treatment and sire was evaluated by comparing a model with sire, dam, treatment, and the interaction to a model without the interaction. Terms are considered significant when the *P*-value from model comparison is less than 0.05.

Model	Test degrees of freedom	Test deviance	<i>P</i> -value
SLA ~ Sire + Dam + Treatment	1	16.60	4.6×10^{-5}
SLA ~ Sire + Dam + Treatment + Treatment \times Sire	1	3.27	0.07

Table 3. Results from comparisons of mixed effect linear models employing likelihood ratio tests to determine the significance of the interaction between specific leaf area (SLA) and treatment. Significance of treatment was evaluated by comparing a model with sire (random effect), dam (random effect), and treatment to a model without treatment. Significance of the interaction between treatment and SLA was evaluated by comparing a model with sire, dam, treatment, and the interaction to a model without the interaction. Terms are considered significant when the *P*-value from model comparison is less than 0.05.

Model	Test degrees of freedom	Test deviance	<i>P</i> -value
Fitness ~ Intercept + SLA + Treatment	1	1373.3	$<2.2 \times 10^{-16}$
Fitness ~ Intercept + SLA + Treatment + SLA \times Treatment	1	20.41	6.3×10^{-6}

well above one suggesting that the populations will increase in size, in the next generation. The predicted change in mean fitness between the parental and progeny generation was 52% larger in the rain reduction treatment than in the full rain treatment (385 and 253 average seeds per plant, respectively). Accordingly, predicted mean fitness of the progeny generation was 20% larger in the rain reduction than in the full rain treatment (1039 and 866 average seeds per plant, respectively; Fig. 2), which indicates a greater rate of genetic adaptation in the rain reduction treatment.

G \times E FOR LIFETIME FITNESS

There was a significant G \times E interaction for lifetime fitness (Table 1). To check whether the interaction was primarily due to one outlying sire group (21), whose mean fitness was exceptionally greater in the rain reduction treatment than the full rain treatment, we repeated this analysis eliminating that family and found that the interaction remained significant ($\chi^2 = 2162$; $P < 0.0001$). We detected evidence for both contributors to a G \times E interaction as there was greater $V_A(W)$ in the rain reduction treatment and breeding values for fitness differed in rank between treatments (Figs. 3 and S1). Sire breeding values between treatments are moderately positively correlated ($r = 0.44$; Fig. 3), and along with the finding of a significant G \times E interaction, these results suggest that the genetic contribution of individual sires to the fitness of their offspring was only moderately consistent between treatments.

PHENOTYPIC PLASTICITY OF SLA

We detected evidence for phenotypic plasticity in SLA as model comparison revealed significant differences in SLA between treatments ($\chi^2 = 16.60$, $P = 4.6 \times 10^{-5}$, Table 2). SLA values were 9.7% larger in the full rain treatment (indicating thinner leaves) than in the rain reduction treatment ($335.3 \text{ cm}^2 \text{ g}^{-1} \pm 6.7 \text{ SE}$ and $305.7 \text{ cm}^2 \text{ g}^{-1} \pm 4.3 \text{ SE}$, respectively). Lower values of SLA were associated with higher fitness in the full rain treatment, but the plastic response of plants in the full rain treatment was toward higher values of SLA. Additionally, although we did not detect a significant difference in fitness between treatments ($\chi^2 = 0.28$, $P = 0.6$; Table 1), mean fitness was lower in the full rain treatment than the rain reduction treatment. Together, these results suggest maladaptive phenotypic plasticity of SLA in the full rain treatment.

PHENOTYPIC SELECTION ANALYSES OF SLA

We detected evidence for variable selection between treatments as comparison of aster models revealed a significant interaction between treatment and SLA in predicting fitness ($\chi^2 = 20.41$, $P = 6.3 \times 10^{-6}$; Table 3). We did not detect evidence of selection on SLA in the rain reduction treatment; comparison of models with and without SLA as a fitness predictor showed no improvement in the model ($\chi^2 = 1.49$, $P = 0.2$; Table 4). However, for the full rain treatment, comparison of aster models with and without the linear term revealed the linear term to be significant ($\chi^2 = 10.56$, $P = 0.001$; Table 4) as well as the quadratic term ($\chi^2 = 951.4$, $P < 2.2 \times 10^{-16}$; Table 4). The negative linear term suggests selection on SLA for lower trait values ($S = -0.0805 \pm 0.0088 \text{ SE}$; Table 5), whereas the positive quadratic term ($\gamma = 0.0766 \pm 0.0036 \text{ SE}$;

Table 4. Summary from model comparison employing likelihood ratio tests of fixed effect aster models to determine if specific leaf area (SLA) is under selection. A significant linear term indicates directional selection and the sign of the term indicates the direction of selection. A significant positive quadratic term suggests disruptive selection and a significant negative quadratic term suggests stabilizing selection. Lifetime fitness is the response variable with SLA values as the linear predictor variable and the squared SLA values (SLA^2) as the quadratic predictor variable. Significance of the linear term was evaluated by comparing a model with the intercept and the linear term to a model with only the intercept. Similarly, significance of the quadratic term was evaluated by comparing a model with the linear and quadratic term to a model without the quadratic term. Asterisk (*) denotes significance. *P*-values less than 0.05 are considered significant.

Full rain treatment			
Model	SLA estimate (<i>P</i> -value)	SLA ² estimate (<i>P</i> -value)	Test deviance (<i>P</i> -value)
Fitness ~ Intercept + SLA	−0.0053(0.083)	NA	10.56 (0.001*)
Fitness ~ Intercept + SLA + SLA ²	−0.486 ($<2 \times 10^{-16}$ *)	0.0630 ($<2 \times 10^{-16}$ *)	951.4 ($<2.2 \times 10^{-16}$ *)
Rain reduction treatment			
Model	SLA estimate (<i>P</i> -value)	SLA ² estimate (<i>P</i> -value)	Test deviance (<i>P</i> -value)
Fitness ~ Intercept + SLA	−0.0017(0.180)	NA	1.49(0.2)
Fitness ~ Intercept + SLA + SLA ²	0.0139(0.141)	−0.0021(0.109)	2.54(0.1)

Table 5. Sample size (*N*) used to obtain variance estimates for specific leaf area (SLA). Mean SLA value in each treatment with standard error in parentheses. Phenotypic variance (V_P) of SLA is the sum of V_A and V_E . Estimates of additive genetic variance (V_A), environmental variance (V_E), and their standard errors (in parentheses) for SLA were calculated using the software Quercus with the nf3.p program. Significance of variance components was only calculated for V_A and was determined by log-likelihood ratio tests. The selection differential (*S*) and the quadratic selection coefficient (γ) were calculated using aster models. Narrow sense heritability (h^2) for each treatment was calculated as the quotient of V_A and V_P and is significant if the additive genetic variance of SLA for the treatment is significant. The response to selection, *R*, for SLA in each treatment was calculated as the product of *S* and h^2 . * denotes significance at $P < 0.05$, ** at $P < 0.01$, and *** at $P < 0.001$.

Treatment	<i>N</i>	Mean SLA (SE)	V_P SLA	V_A SLA (SE)	V_E SLA (SE)	<i>S</i> (SE)	γ (SE)	h^2	<i>R</i>
Full rain	131	335.3(6.8)	6366.07	4800** (1800)	1500(1200)	−0.0805*** (0.0087)	0.0087*** (0.0035)	0.76**	−0.061
Rain reduction	112	305.7(4.1)	1961.86	40(340)	1910(423)	−0.029(0.002)	NA	0.023	−0.00067

Table 5) suggests disruptive selection, as the inflection point is centered over the trait distribution (Fig. 4A). We removed the two most extreme points on either end of the trait distribution to determine if they were largely responsible for inducing curvature in the fitness function but through model comparison found the linear term to be significantly negative ($\chi^2 = 355.7$, $P = 2.2 \times 10^{-16}$, $S = -0.388 \pm 0.013$ SE) and the quadratic term to be significantly positive ($\chi^2 = 122.4$, $P = 2.2 \times 10^{-16}$, $\gamma = 0.542 \pm 0.012$ SE).

ESTIMATION OF HERITABILITY AND RESPONSE TO SELECTION OF SLA

We detected significant V_A for SLA from likelihood-ratio tests with output from the Quercus analysis in the full rain treatment (LR = 14.73, $P < 0.01$; Table 6) resulting in a significant heritability of 0.76 (Table 5), indicating appreciable potential for adaptive evolution of SLA in the full rain treatment. The response to selection from the breeder's equation estimates a decrease in SLA value of 0.061 in the full rain treatment in the

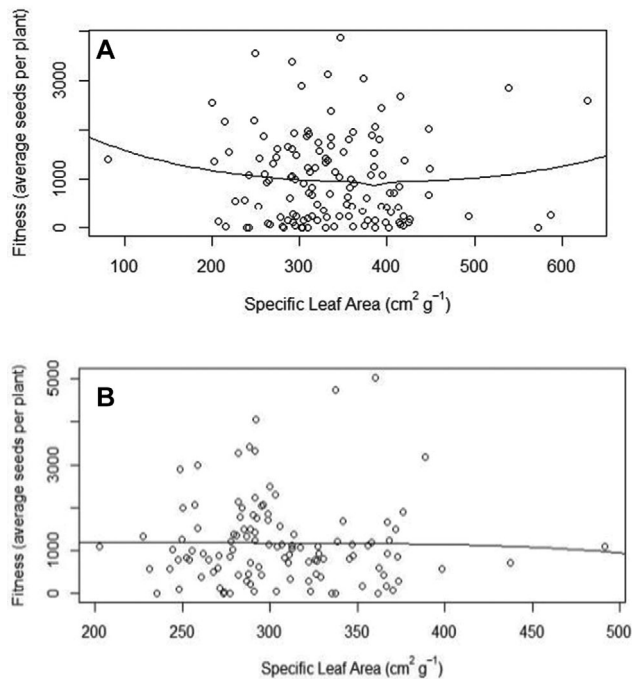


Figure 4. Relationship between fitness and specific leaf area (SLA) for (A) full rain treatment and (B) rain reduction treatment. Open circles represent SLA values for each individual measured, and the solid line represents the fitness function. In the full rain treatment, the fitness function is significantly quadratic with positive curvature representative of disruptive selection. No detectable selection was found in the rain reduction treatment, but the fitness function shown is a negatively linear.

progeny generation (Table 5). We did not detect significant V_A for SLA in the rain reduction treatment ($LR = 0.6572$, $P > 0.05$; Table 6).

G × E INTERACTION FOR SLA

The value of the likelihood-ratio test comparing mixed linear models with and without the interaction between sire and treatment was slightly above the critical value of 0.05 ($\chi^2 = 3.27$,

$P = 0.07$; Table 2). This result provides marginal evidence of heritable genetic variation in phenotypic plasticity of SLA. We found positive, but nonsignificant, COV_A of SLA as expressed in the two treatments ($LR = 0.6564$, $P > 0.05$; Table 6). Thus, there is weak evidence for a positive association of breeding values between treatments (Figs. 5 and S2). Additionally, the estimate for r_A , even though not significant, was equal to one.

Discussion

Persistence of natural populations exposed to environmental change will likely depend on their continued adaptation. Predicting the capacity of populations to adapt to future climate change will aid in their conservation, especially for populations that are not able to migrate to more favorable climates (Staudinger et al. 2013). The presence of $V_A(W)$ within a population is essential for ongoing adaptation, and the ratio $V_A(W)/\bar{W}$ determines the rate of genetically based adaptation (Fisher 1930). We found large and significant $V_A(W)$ for a population of *C. fasciculata* in both an atypically wet environment and a reduced rain environment more closely reflecting the population's normal climatic conditions. We also detected evidence of variable selection on SLA but found selection to only be significant in the full rain treatment, which indicates potential for adaptation of SLA only in the full rain treatment. Although our predictions of adaptation are contingent on the environmental conditions of the study (such as study site location and precipitation treatments), our results suggest that this population has the capacity to adapt in situ to variable precipitation predicted for the Midwest region of the United States (Pryor et al. 2014) over short time scales.

Our estimates of \bar{W} are two orders of magnitude larger, and our estimates of $V_A(W)$ are five orders of magnitude larger, than those estimated from comparable studies in native prairie (e.g., Sheth et al. 2018; Kulbaba et al. 2019), likely because we weeded plots and protected the plants from rabbit herbivory. The ample

Table 6. Significance tests for genetic variance components of SLA obtained from Quercus software with the nf3.p program. Significance testing for variance components was conducted by comparing the log-likelihood of models with and without a given parameter in a log-likelihood ratio test (LRT). LRT values are significant when they are greater than the chi-square value at a given P -value. * denotes significance of LRT value and therefore the parameter. V_A = additive genetic variance; V_M = variance due to a common environment; COV_A = additive genetic covariance. The addition of V_M was not found to be significant, so V_M was excluded from models to assess significance of V_A in each treatment as well as the COV_A between treatments.

Parameter	Variance value	LRT value	Degrees of freedom	Chi-square value	P -value
V_M SLA	NA	0.9024	3	7.81	0.05
V_A SLA full rain treatment	4843.01	14.73*	1	6.63	0.01
V_A SLA rain reduction treatment	45.34	0.6572	1	3.84	0.05
COV_A SLA	468.81	0.6564	1	3.84	0.05

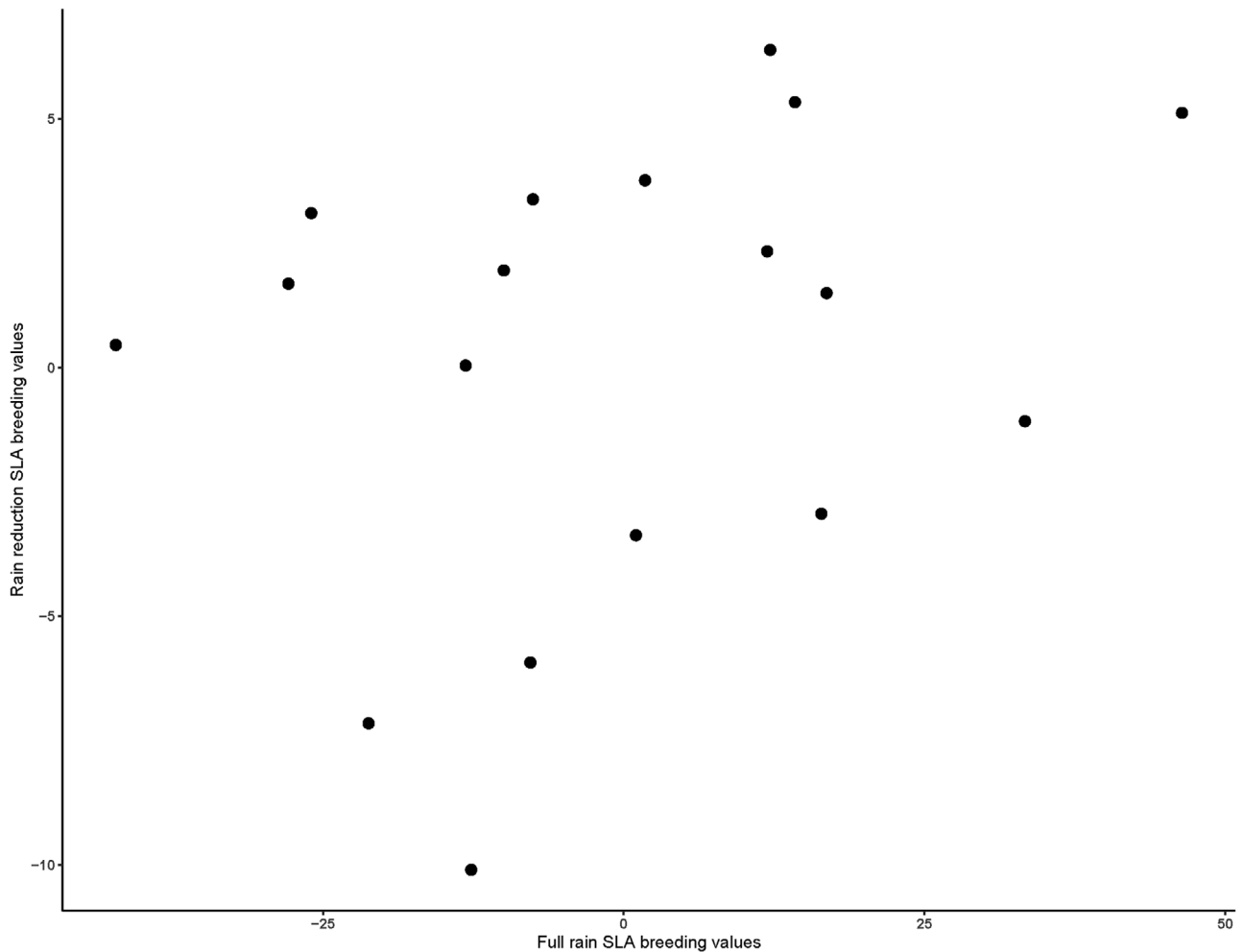


Figure 5. Correlation of breeding values for SLA in the full rain and rain reduction treatment. Each point represents the estimated breeding value for mean SLA for one of the 18 sire groups in each treatment. Given the greater variance in the full rain treatment, the positive but nonsignificant additive genetic covariance ($COV_A = 468.81$; $LR = 0.6564$, $P > 0.05$) provides weak evidence for a positive association of sire breeding values between treatments.

$V_A(W)$ in both treatments suggests that there is sufficient standing genetic variation for a genetic response to natural selection and that the population possesses the capacity to adapt to both environments over short time spans. We also found a significant $G \times E$ interaction for lifetime fitness between treatments. Sire group breeding values were only moderately positively correlated ($r = 0.44$) between treatments, indicating that a sire group's fitness in full rain conditions was a weak predictor of its fitness in reduced rain conditions. These results suggest that although there is substantial $V_A(W)$ in both environments to respond to selection, the genetic basis of the response to natural selection will differ depending on the environment.

We found greater $V_A(W)$ in the less stressful environment (rain reduction treatment representative of historical norms) compared to the more stressful environment (full rain treatment). High rainfall is a putatively stressful environment for *C. fasciculata*,

which tends to occupy well-drained sandy soils (McGregor and Barkley 1986). In contrast to our results, Etterson (2004a) found V_A for fecundity of *C. fasciculata* increased in response to greater soil moisture. Individuals from dry Southern populations had greater V_A for fecundity when grown in more moisture-rich Northern sites, compared to V_A for fecundity when grown in their home sites (however, fitness at the home site was always highest). Additionally, Torres-Martínez et al. (2019) found greater V_A for reproductive success in the annual herb *Las-thenia fremontii* subject to the more extreme rainfall events. In our study, even though the population in the stressful environment had less $V_A(W)$, the prediction for the progeny generation mean fitness is well above replacement, which indicates population growth and, thus, likely persistence. Increased rainfall may reduce the mean fitness and adaptive capacity of this population compared to historical conditions, but its mean fitness

implies potential population growth and its substantial $V_A(W)$ implies capacity to adapt to high rainfall at least in the short term.

We detected variable selection on SLA as there was a significant treatment \times SLA interaction effect on fitness. We only detected significant selection in the full rain treatment, and we detected positive quadratic selection (indicative of disruptive selection); however, the curvature was quite small. The breeder's equation ($R = h^2 S$) predicts a decline in mean SLA in the progeny generation (i.e., in the direction of mean SLA in the rain reduction treatment) of $0.061 \text{ cm}^2 \text{ g}^{-1}$, which is a 0.018% decrease in the trait mean. Thus, although there is potential for adaptive evolution of SLA with increased precipitation, adaptation will proceed slowly. We acknowledge that the response to selection could differ from our prediction because we did not take into consideration correlations with other traits that may slow or reverse the rate of adaptation in the full rain treatment (Via and Lande 1985; Etterson and Shaw 2001).

Adaptive phenotypic plasticity may be a means by which populations can persist as the climate changes (Charmantier et al. 2008; Chevin and Hoffmann 2017). For populations where the rate of genetic change is slow, adaptive phenotypic plasticity could buffer the population from the negative effects of a changing environment. However, in our study we found evidence for maladaptive phenotypic plasticity in SLA—that is, selection in the full rain treatment favored lower values of SLA and the plastic response was toward higher values of SLA. Additionally, mean fitness was lower in the full rain compared to the rain reduction treatment. Thus, we did not find evidence that phenotypic plasticity in SLA would buffer the population against effects of increased precipitation. Our results differ from Etterson (2004b) who found phenotypic plasticity for SLA in *C. fasciculata* to be adaptive, albeit across a much starker environmental gradient.

The significant $G \times E$ interaction for SLA indicates there is additive genetic variance for plasticity. Thus, sire groups vary in plasticity of SLA between environments. The positive COV_A for SLA between treatments suggests that the marginally significant $G \times E$ interaction for SLA may be largely due to the difference in genetic variance rather than independent expression of breeding values between treatments. The estimated variance of SLA breeding values is 106.8 times larger in the full rain treatment, which indicates a greater range of trait values upon which selection can act, and therefore a greater potential for adaptation of this trait in wetter environments.

Climate change is reshaping ecosystems worldwide. We have few tests of the capacity of natural populations to adapt to changes in specific climatic variables. Here, we directly manipulated precipitation and found abundant and significant additive genetic variation for fitness in a population of the widespread

annual plant, *C. fasciculata*. We also found significant and heritable selection on SLA in the wet environment, but maladaptive phenotypic plasticity. Although we cannot comment on the adaptive capacity of all populations of *C. fasciculata*, our results provide insight into its capacity for adaptation in situ. More studies are needed that directly estimate $V_A(W)$ in environments predicted for the future as a basis for improving our understanding of populations' adaptive capacity in the wild under novel and rapidly changing environments.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

AP designed the experiment, analyzed the data, and wrote the manuscript in consultation with RS. AP collected data with assistance from EB.

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DATA ARCHIVING

Data and R Markdown files are available on Dryad: <https://doi.org/10.5061/dryad.34tmg4hx>.

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Supporting Information

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

Figure S1. Lines connect breeding values for mean lifetime fitness for each of the 18 sire groups between treatments.

Figure S2. Lines connect breeding values of mean SLA for each of the 18 sire groups between treatments.