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Expression of additive genetic variance for fitness in a population of partridge pea in two field sites

Seema Nayan Sheth,[1,2,3] **Mason W. Kulbaba,**[1] **Rachel E. Pain,**[1] **and Ruth G. Shaw**[1]

[1] *Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, Minnesota 55455*

[2] *Department of Plant and Microbial Biology, North Carolina State University, Raleigh, North Carolina 27695*

[3] *E-mail: Seema_Sheth@ncsu.edu*

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Despite the importance of adaptation in shaping biological diversity over many generations, little is known about populations' capacities to adapt at any particular time. Theory predicts that a population's rate of ongoing adaptation is the ratio of its additive genetic variance for fitness, $V_A(W)$, to its mean absolute fitness, $\overline{W}$. We conducted a transplant study to quantify $\overline{W}$ and standing $V_A(W)$ for a population of the annual legume *Chamaecrista fasciculata* in one field site from which we initially sampled it and another site where it does not currently occur naturally. We also examined genotype-by-environment interactions, $G \times E$, as well as its components, differences between sites in $V_A(W)$ and in rank of breeding values for fitness. The mean fitness indicated population persistence in both sites, and there was substantial $V_A(W)$ for ongoing adaptation at both sites. Statistically significant $G \times E$ indicated that the adaptive process would differ between sites. We found a positive correlation between fitness of genotypes in the "home" and "away" environments, and $G \times E$ was more pronounced as the life-cycle proceeds. This study exemplifies an approach to assessing whether there is sufficient $V_A(W)$ to support evolutionary rescue in populations that are declining.

KEY WORDS: Adaptation, aster models, breeding values, *Chamaecrista fasciculata*, $G \times E$, quantitative genetics.

Adaptation, in the sense of fitness of organisms to their environments as a result of evolution by natural selection, has been extensively documented across the tree of life (Darwin 1859; Schluter 2000; Hoekstra et al. 2006). Over long timescales, natural selection can lead to vast diversifications within and among clades, while adaptive divergence among populations within species can be realized over dozens of generations, or fewer (e.g., Antonovics and Bradshaw 1970). The current profound insight into the ubiquity and importance of adaptation in structuring biotic diversity has derived largely from retrospective studies of patterns of organisms' attributes in relation to the conditions they inhabit (or inhabited). These insights can be further deepened through direct study of the process of natural selection, requiring a prospective approach that can indicate populations' capacities to adapt at the pace of environmental changes, now far exceeding past rates (Shaw and Etterson 2012).

As a conceptual tool to study the adaptive process directly, Fisher's (1930) Fundamental Theorem of Natural Selection (FTNS) predicts a population's genetically based change in mean fitness from one generation to the next under its current conditions as the ratio of its additive genetic variance for fitness, $V_A(W)$ (i.e., the variance of breeding values for absolute fitness), to its mean absolute fitness, $\overline{W}$ (Fisher 1930; Ewens 2004). This expression offers the opportunity for predicting not only whether a population has capacity for adaptation, but also how much genetically based change in mean fitness can be expected under the prevailing conditions. As a corollary to the FTNS, it has been deemed likely that consistent natural selection favoring genotypes of high fitness depletes $V_A(W)$, such that any given population is expected to harbor little $V_A(W)$ in its native habitat (Fisher 1930; Charlesworth 1987; Bradshaw 1991; but see Zhang 2012). Cases of very rapid adaptation to an environmental change (e.g., Bradshaw and Holzapfel 2001; Grant and Grant 2002; Franks et al. 2007) imply the persistence of standing genetic variation that can support immediate responses to natural selection under novel conditions. Further, environments that fluctuate in time or across space may impose balancing selection and actually maintain $V_A(W)$ in natural populations (Mitchell-Olds et al. 2007). Whereas theoreticians and philosophers have devoted considerable attention to the FTNS (Charlesworth 1987; Ewens 1989; Frank and Slatkin 1992; Okasha 2008), it has rarely been applied empirically to quantify the immediate potential of natural populations for ongoing adaptation, whether to their current, or to novel, conditions. Consequently, there exists a paradox of expected low $V_A(W)$ based on theory, in the face of empirical evidence of rapid adaptation and thus presumably abundant $V_A(W)$. An open question is the extent to which populations express $V_A(W)$ in the context of environmental conditions that typically prevail on them or in novel conditions, and further, whether populations in decline harbor sufficient $V_A(W)$ to support evolutionary rescue in the face of environmental changes (Gomulkiewicz and Holt 1995).

Whatever the magnitude of $V_A(W)$ in a population's prevailing environment, its expression may differ between environments (Hoffmann and Merilä 1999; Etterson 2004b; Shaw and Shaw 2014). There are conflicting hypotheses about additive genetic variance in novel or even unfavorable environments relative to a population's local home environment or a favorable environment, with predictions ranging from greater, less, or equal heritability in stressful versus favorable environments (Hoffmann and Merilä 1999). A meta-analysis of wild animal populations indicated lower heritable variation for morphological traits in unfavorable relative to favorable environments, but little difference in heritability for fitness between environments varying in quality (Charmantier and Garant 2005). Beyond the differences in the magnitude of $V_A(W)$ and thus potential rates of adaptation between environments, divergent selection may favor contrasting alleles and genotypes in the respective environments, such that the correlation between breeding values for fitness, as expressed in different environments, is less than 1. Together, differences in $V_A(W)$ and breeding values for fitness between environments contribute to genotype-by-environment interactions ($G \times E$). Evidence about differences between environments in the expression of breeding values for fitness and $V_A(W)$, including how these attributes develop over the lifespan, would shed light on how the process of adaptation may vary across geographic and environmental space.

One impediment to studying the adaptive process involves logistical and statistical challenges in quantifying $V_A(W)$ and $\overline{W}$ (but see Etterson 2004b). Obtaining the data required for estimating lifetime fitness demands resources that are available for very few long-lived species. Even for short-lived species, statistical challenges of making inferences about lifetime fitness arise from its multimodal distribution, which no standard probability distribution approximates (Wagenius et al. 2010). An individual's lifetime fitness results from fitness components expressed at several life-history stages (e.g., survival to reproduction and total fecundity over possibly multiple reproductive events). Because these distinct components of fitness typically do approximately conform to parametric distributions, they are often analyzed separately without accounting for the dependence of fitness components at later life-history stages on those earlier in the life cycle. In recent years, aster models (Geyer et al. 2007; Shaw et al. 2008) were developed to jointly model individual lifetime fitness accounting for the dependence of each stage on earlier stages (e.g., total fecundity at a certain stage is conditional on surviving to that stage) and using appropriate statistical distributions for each fitness component (e.g., Bernoulli distribution for probability of survival and Poisson distribution for components of reproductive output such as number of fruits) conditional on survival to that stage. These models have been expanded to include random effects (Geyer et al. 2013), allowing for estimates of genetic components of variance for fitness. Thus, aster models provide a powerful and unprecedented opportunity to directly study the adaptive process in natural populations.

In this study, we assess the standing $V_A(W)$ for ongoing adaptation to each of two sites in the partridge pea, *Chamaecrista fasciculata* (Fabaceae), an annual legume native to central and eastern North America. Specifically, we performed crosses to obtain seeds of known pedigree from a population in eastern Minnesota. Subsequently, we planted these pedigreed seeds out into two field sites with contrasting soil and community composition: a "home" site very near the population from which seeds originated, and an "away" site (where the species does not currently occur naturally) just a few kilometers from the source population, to allow evaluation of interaction between genotype and site. We then censused fitness components at each site throughout the growing season, and used aster models to address the following objectives: (1) estimate mean lifetime fitness corresponding to the population's growth rate in each site; (2) estimate the population's $V_A(W)$ in each site, to evaluate its capacity for ongoing adaptation to each habitat; (3) characterize genetic variation in response to the site differences, that is $G \times E$ with respect to lifetime fitness, and (4) evaluate breeding values for fitness and the extent to which they differ between sites, to assess whether such differences in fitness expression are more prominent during certain stages of the life cycle.

Methods

STUDY SYSTEM AND SEED COLLECTIONS

Chamaecrista fasciculata is a bee-pollinated, hermaphroditic, annual legume with a range spanning from the prairies of the northern Great Plains in Minnesota to Central Mexico (Irwin and Barneby 1982). *Chamaecrista fasciculata* has been the subject of many studies on local adaptation (Galloway and Fenster 2000; Etterson 2004a,b; Abdala-Roberts and Marquis 2007; Stanton-Geddes et al. 2012a,b), mutualism (Keller 2014; Pain et al. 2018), and phenological traits (Kelly 1992; Wadgymar et al. 2015a,b; Wadgymar and Weis 2017), making it an ideal system for studying capacity for adaptation and $G \times E$. In the fall of 2013, seed pods from 200 maternal plants were collected from a population of *C. fasciculata* at Grey Cloud Dunes Scientific and Natural Area (44°46′32“N, 93°01′38″W; hereafter “Grey Cloud”). Grey Cloud is a 237-acre remnant of restored, sand barrens prairie along the east bank of the Mississippi River in east-central Minnesota. Recognition that $V_A(W)$ could be negligible in the population’s home environment motivated assessment of $V_A(W)$ for that population in another site, enabling an evaluation of capacity for ongoing adaptation to a novel site. Directly opposite Grey Cloud, along the west bank of the Mississippi River is the Flint Hills Resources Refinery at Pine Bend (44°46′32“N, 93°01′38″W; hereafter “Flint Hills”), which owns several hundred acres of wild lands, including a former sand-gravel prairie that had become dominated by bromegrass and other invasive species. This site at Flint Hills was chosen for its close proximity to Grey Cloud and differences in soil and vegetative composition and the absence of *C. fasciculata*. The “home” site is near the species’ northern range edge, where *C. fasciculata* is more likely to occupy open habitats with relatively low competition and sandy soils and rarely occurs in adjacent areas with loamy soil (Stanton-Geddes et al. 2012a). The “away” site has relatively loamy soil and a taller, denser vegetation community, leading to potentially elevated competition but also greater nutrient availability. Prior to this study, the “home” site was mowed; the “away” site was disked, and locally sourced seeds representing numerous prairie species were sown as a background matrix.

PEDIGREED CROSSES

In March 2014, we surface sterilized six seeds from each individual collected from Grey Cloud using an 8.9% bleach solution and sterile water and 70% ethanol rinse. We used 100 grit sandpaper to scarify the seeds, let them imbibe in sterile water for three days, and then planted them in small peat pots. Seeds from 167 individuals germinated. We randomly chose one seedling per individual to represent a distinct family and transplanted that seedling to a large tree pot with 1 teaspoon of Osmocote® slow release fertilizer (14:14:14) after it had five true leaves (~1.5 months after germinating). We grew all transplants in the University of Minnesota Plant Growth Facilities greenhouse under 16:8-h photoperiod. We crossed plants according to a nested paternal half-sibling design, in which independent sets of three dams were randomly assigned to each sire. After accounting for mortality in the greenhouse, the final pedigree consisted of 42 paternal half-sibling families and 124 maternal full-sibling families. Manual crosses were performed daily and all nonpollinated flowers were removed.

EXPERIMENTAL PLANTING DESIGN

Seeds within a given full-sibling family were combined and randomly distributed among 12 envelopes with five seeds each, half to be planted at Grey Cloud and the other half at Flint Hills in the fall of 2014. We then randomly assigned each envelope to a position and planted them in randomly designated rows, minimally two meters apart in a randomized block design (eight blocks at Grey Cloud and two blocks at Flint Hills). Within rows, planting positions were marked by nails two meters apart. From each envelope, seeds were planted with forceps less than 1 cm under the soil surface, 10 cm apart along the row and centered at the nail. Each envelope of seeds was planted in the same fashion every two meters along the row. Ultimately, we collected fitness data for 3658 seeds from 42 sires and 123 dams planted at Grey Cloud and 3569 seeds from 42 sires and 121 dams planted at Flint Hills.

FITNESS SURVEYS

We recorded plant presence for every seed planted at Grey Cloud and Flint Hills on June 1st and 2nd 2015, respectively. A plant was present if the cotyledons had emerged. We conducted two additional censuses measuring presence on June 15–16 and June 29–30. Censuses were performed July 29–30 and September 1–4, where we recorded presence, flowering, and herbivory. We recorded a plant as flowering if there were open flowers on the plant or evidence of flowering from previous days (e.g., wilted flowers, pedicels, or pods). Herbivory consisted of deer or rodent browsing, where stems were partially eaten. We performed a sixth census on September 14–16, where we recorded presence and number of ripe pods collected for all positions where plants had been recorded as present in previous censuses. Many plants were damaged by rodent herbivory prior to this census, leaving stems with ripe pods broken next to the live plant. When the origin of the segment of stem with pods still attached was certain, pods were collected and recorded as pods collected off the ground. We conducted a final census of all positions September 29–October 1, recording presence, flowering, number of ripe pods collected, number of fully elongated green pods collected, number of pods collected off the ground, and number of immature pods and/or pedicels from dehisced pods remaining on the plant. We collected ripe pods from the plant and the ground between censuses, throughout the month of September. After completing the final censuses, we obtained the total number of pods produced by each plant as the sum of pod types described above. We included immature pods in our total pod count because we assumed that pods that were immature at the time of the final census would mature before the end of the growing season. Similarly, we included pods collected off the ground in our total pod count because these pods escaped seed predation.

DATA ANALYSES

To estimate $\overline{W}$ and $V_A(W)$ in each site, as well as assess evidence for $G \times E$, we used aster models (Geyer et al. 2007; Shaw et al. 2008) in the R 3.4.4 (R Core Team 2018) package "aster" (Geyer 2018). Specifically, we used unconditional aster models to assess the direct relationship between the expected value of the measure specified for overall fitness (in this study, fruit number) and the explanatory variables in each model (Shaw and Geyer 2010). The graphical model for fitness (Fig. 1) included germination and flowering modeled with Bernoulli distributions, and fruit number modeled with a Poisson distribution. We consider random only those factors necessarily treated as random to address the questions at hand. In contrast to normal effects models, which naturally accommodate random effects, practitioners are advised to minimize the use of random factors in generalized linear-mixed models, including aster models (Bolker et al. 2009; Geyer et al. 2013). Thus, in the full model, block, and site were included as fixed factors and parental (genetic) effects as random. To evaluate the fixed effect factors, larger models were tested against submodels using likelihood ratio tests, as follows: to test site, a submodel without block was tested against a submodel without block and site; to test block, the full model was tested against the submodel lacking block. Preliminary analyses that included either sire or dam as random effects showed each factor to be statistically significant. As a computational economy, we employed a model that equated the variances attributable to sires and dams, hereafter termed parental variance, permitting estimation of sire plus dam variance as a single parameter. The interaction between parental effect and site ($G \times E$) was treated as random. Because there was significant $G \times E$ (described below), we also conducted site-specific aster analyses to estimate $\overline{W}$ (including block as a fixed factor) and $V_A(W)$ (including block as a fixed factor and parental effects as a random factor) expressed at each site.

We quantified $\overline{W}$ and standard errors for each site, as follows. For Grey Cloud, we used the median estimate of mean fitness among the eight blocks, that is the estimate for block 7. As the Flint Hills site only had two blocks we arbitrarily chose block 1. To obtain estimates of $V_A(W)$ for each site, we transformed estimates of $V_A(W)$ from the canonical to mean value parameter scale with a mapping function that adds a component of a fixed effect (consistent with mean fitness calculation: block 7 for Grey Cloud and block 1 for Flint Hills) to each random effect (Geyer and Shaw 2013; de Villemereuil et al. 2016). These converted effects represented genetic effects (analogous to breeding values) on the mean value parameter scale, and were used to estimate $V_A(W)$. We generated 95% confidence intervals for estimates of $V_A(W)$ using a double parametric bootstrap (DiCiccio et al. 1996). We used the outer bootstrap ($n = 100$) to bootstrap the estimate. To obtain a measure of scale (standard deviation) for each value obtained in the outer bootstrap, we ran an inner bootstrap ($n = 31$). We generated a bootstrap-*t* distribution as the array of 100 bootstrap iterates, each taken as a difference from the original estimate and divided by its own standard deviation. We obtained 95% CIs from this distribution. Therefore, the total number of bootstrap iterations is the product of the numbers of outer and inner bootstrap iterations ($n = 3100$).

To visualize the nature of $G \times E$ with respect to fitness expressed through different stages of the life cycle (i.e., germination vs flowering vs fruit number) in the two sites, we constructed separate mixed-effects aster models truncating the graphical model to end with flowering. We also estimated germination probability as the proportion of planted seeds that germinated for each sire at each site in 2015. Using estimates of genetic effects that we obtained from these truncated graphical models, we then plotted the estimated genetic effect expressed in Flint Hills against that expressed in Grey Cloud for each sire. Because these genetic effects are estimated with inherent uncertainty, Pearson product-moment correlations and their tests are not statistically valid. Yet we include these correlations only as coarse indicators and urge caution in their interpretation. All data and scripts associated with this study are available at https://bitbucket.org/snsheth/gxeanalysis.

Results

SUMMARY OF FITNESS DATA AND HERBIVORY

Probabilities of germination and flowering were higher at the home site, Grey Cloud, while fruit numbers were higher at the away site, Flint Hills. Of the total number of seeds planted at Grey Cloud, 721 (19.7%) germinated, 621 (17.0%) flowered, and 336 (9.2%) produced fruits. Of the total number of seeds planted at Flint Hills, 564 (15.8%) germinated, 418 (11.7%) flowered, and 363 (10.2%) produced fruits. At Grey Cloud, of all plants setting fruit, the observed number of fruits per plant ranged from 1 to 185 (mean ± 1 standard error = 8.8 ± 0.8 fruits), and at Flint Hills, fruit number ranged from 1 to 91 (mean ± 1 standard error = 11.4 ± 0.8 fruits).

Early- and late-season herbivory differed between the two study sites. Early in the season, 14% of all plants at Grey Cloud showed signs of herbivory, while 71% of all plants at Flint Hills underwent herbivory. In contrast, late in the season, herbivores damaged 54% of all plants at Grey Cloud, but only 5% of plants at Flint Hills.

FULL ASTER MODEL INCLUDING BOTH SITES FOR EVALUATION OF G × E

There was a statistically significant genotype-by-site interaction in the full aster model including site as a fixed effect (Table 1).

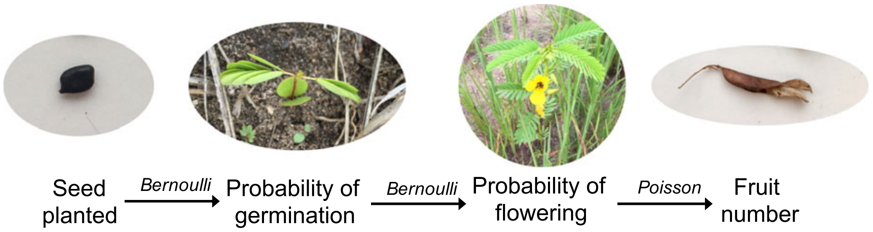

Figure 1. Aster graphical model for all analyses. Nodes represent fitness components as response variables, and arrows correspond to conditional distributions. Probabilities of germination (0 for absence and 1 for presence of seedling during any census) and flowering (0 for no flowers; 1 for one or more flowers) were modeled with a Bernoulli distribution, and fruit number (total number of pods at the end of the growing season) was modeled with a Poisson distribution. Photos of seed and fruit by Anna Peschel, and photos of seedling and flowering plant by SNS.

Table 1. Summary of output from aster models testing the fixed factors of block and site, and the random factors of parental effects and the interaction between site and parental effects, on individual fitness.

Model	Test df	Test deviance	*P*
Full model with both sites (for evaluation of $G \times E$)			
Block (F)	8	137.25	<0.0001
Site (F)	1	45.104	<0.0001
Parental effects (R)	–	–	<0.0001
Site × Parental effects (R)	–	–	<0.0001
Grey Cloud (home) full model (for estimation of $\overline{W}$)			
Block (F)	7	188.12	<0.0001
Flint Hills (away) full model (for estimation of $\overline{W}$)			
Block (F)	1	0.56557	0.452
Grey Cloud (home) full model ending in fruit number (for evaluation of $V_A(W)$ and breeding values for fitness between sites)			
Block (F)	7	186.18	<0.0001
Parental effects (R)	–	–	<0.0001
Flint Hills (away) full model ending in fruit number (for evaluation of $V_A(W)$ and breeding values for fitness between sites)			
Block (F)	1	3.5695	0.0589
Parental effects (R)	–	–	<0.0001
Grey Cloud (home) full model ending in flowering (for evaluation of breeding values for fitness between sites)			
Block (F)	7	17.916	0.0124
Parental effects (R)	–	–	<0.0001
Flint Hills (away) full model ending in flowering (for evaluation of breeding values for fitness between sites)			
Block (F)	1	0.98024	0.3221
Parental effects (R)	–	–	<0.0001

Factors in each model are denoted as fixed (F) or random (R). The full model including both sites was used to evaluate $G \times E$, site-specific mixed effects models allowed for estimation of $V_A(W)$, and site-specific fixed effects models permitted estimation of $\bar{W}$. Statistical significance of each predictor variable was assessed using likelihood ratio tests comparing the full model to submodels that dropped each term sequentially, with the exception of parental effects, which were assessed solely based on *P*-values from summary output of aster analyses. For the analysis including both sites, the block and the interaction terms were tested against the full model, and the effect of site was tested by comparing the full model with site but without block to the full model without site and block.

Block, parental effects, and site were also statistically significant (Table 1).

FIXED EFFECTS ASTER MODELS FOR ESTIMATION OF $\bar{W}$ AND STANDARD ERROR

Taking all the fitness components into account via aster, Flint Hills exhibited higher $\bar{W}$ (1.107 ± 0.086 fruits per seed planted) than Grey Cloud (0.620 ± 0.109 fruits per seed planted). Because the fruits are multi-seeded (mean ± 1 standard error = 8.81 ± 0.22 seeds per fruit at Grey Cloud and mean ± 1 standard error = 7.13 ± 0.16 seeds per fruit at Flint Hills), these estimates of $\bar{W}$ on the basis of fruit counts imply that the population in both sites would increase. The effect of block was only statistically significant at Grey Cloud (Table 1).

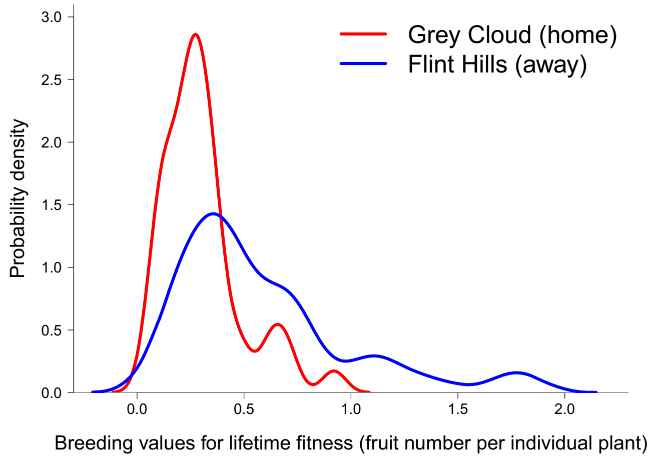

Figure 2. The probability density distribution of breeding values for lifetime fitness expressed as number of fruits per individual at Grey Cloud and Flint Hills.

MIXED EFFECTS ASTER MODELS FOR ESTIMATION OF $V_A(W)$

Considering each site separately, there was statistically significant $V_A(W)$ at both, with the point estimate at the away site greater than that at the home site, but confidence intervals overlapping (Grey Cloud: 1.672, 95% confidence interval: 0.183, 3.765; Flint Hills: 2.534, 95% confidence interval: 1.148, 6.078; Fig. 2). At Grey Cloud, block and parental effects were statistically significant, and at Flint Hills, block was not statistically significant and parental effects were statistically significant (Table 1). The rate of adaptation, as predicted by the ratio of $V_A(W)$ to $\bar{W}$, was similar for both sites (Grey Cloud: 2.864; Flint Hills: 2.289 fruits per seed planted).

MIXED EFFECTS ASTER MODELS TO ASSESS HOW BREEDING VALUES FOR FITNESS VARY BETWEEN SITES

A positive relationship was apparent throughout the lifespan between fitness expressed in the two sites through germination (Fig. 3A; $r = 0.778$), flowering (Fig. 3B; $r = 0.788$), and fruit production (Fig. 3C; $r = 0.402$). However, between the two sites the genetic effects on fitness appeared to be most closely correlated early in the life cycle. Genetic effects on fitness through fruit production included cases of maximal fitness in one site associated with relatively low fitness in the other (Fig. 3C), but there was no indication of a general tradeoff in fitness expression between sites. At both sites, the variance in fitness due to parental effects was statistically significant in aster models ending in the probability of flowering, but the effect of block was only statistically significant at Grey Cloud (Table 1).

Discussion

A population's basis for immediate adaptation depends on the ratio of its $V_A(W)$ to its $\bar{W}$ (Fisher 1930), yet empirical estimates of this ratio for natural populations are scarce, precluding evaluation of capacity for ongoing adaptation and prediction of the rate of change in mean fitness. In this study, we quantified $\bar{W}$ and standing $V_A(W)$ for ongoing adaptation for a population of *C. fasciculata* in one field site from which it was originally sampled and another nearby site. We examined $G \times E$, considering both differences between the sites in the expression of $V_A(W)$ and the relationship between breeding values for fitness as expressed in the two sites. At both sites, $\bar{W}$ was greater than 1 (accounting for ~7–9 seeds per fruit) and there was substantial $V_A(W)$ for fitness. Further, there was significant $G \times E$, indicating that adaptation would differ genetically between sites even though there was no evidence of genetic specialization to the "home" site. Below, we discuss each of these results in turn considering the biotic conditions we observed at each field site, and highlight their importance for understanding a population's potential for ongoing adaptation to prevailing environments across space.

$G \times E$ AND VARIATION IN BREEDING VALUES FOR FITNESS BETWEEN ENVIRONMENTS

The finding of statistically significant $G \times E$ for fitness indicates that ongoing adaptation in the two sites would differ genetically. Of the two possible contributors to $G \times E$, we detected evidence for differences between sites in both $V_A(W)$ and ranking of breeding values for fitness. The magnitude of $V_A(W)$ was somewhat greater in the novel Flint Hills site than in the home Grey Cloud site. Moreover, whereas the null hypothesis of additivity of effects of genotype and environment implies a correlation of 1 between breeding values (Falconer 1952), there was considerably less correspondence between breeding values as expressed in the two sites (Fig. 3). These findings indicate that the genetic response to natural selection would differ between sites. Even so, we found no evidence for fitness tradeoffs between sites. Instead, breeding values were positively correlated between sites. Thus, genetic specialization to the environment characterizing each site was low, and we would not expect that adaptation to one site would entail decline in mean fitness in the other site. Given that *C. fasciculata* often inhabits disturbed prairies (Kelly 1992; Stanton-Geddes et al. 2012a) and has been regarded as a pioneer species (Henson et al. 2013), low genetic specialization may be consistent with generalist characteristics posited for many colonizing species (Baker 1965). These findings bring attention to the scale of our study—given the proximity of the two sites (6 km), they share many environmental attributes, despite having distinct soil types and plant community compositions.

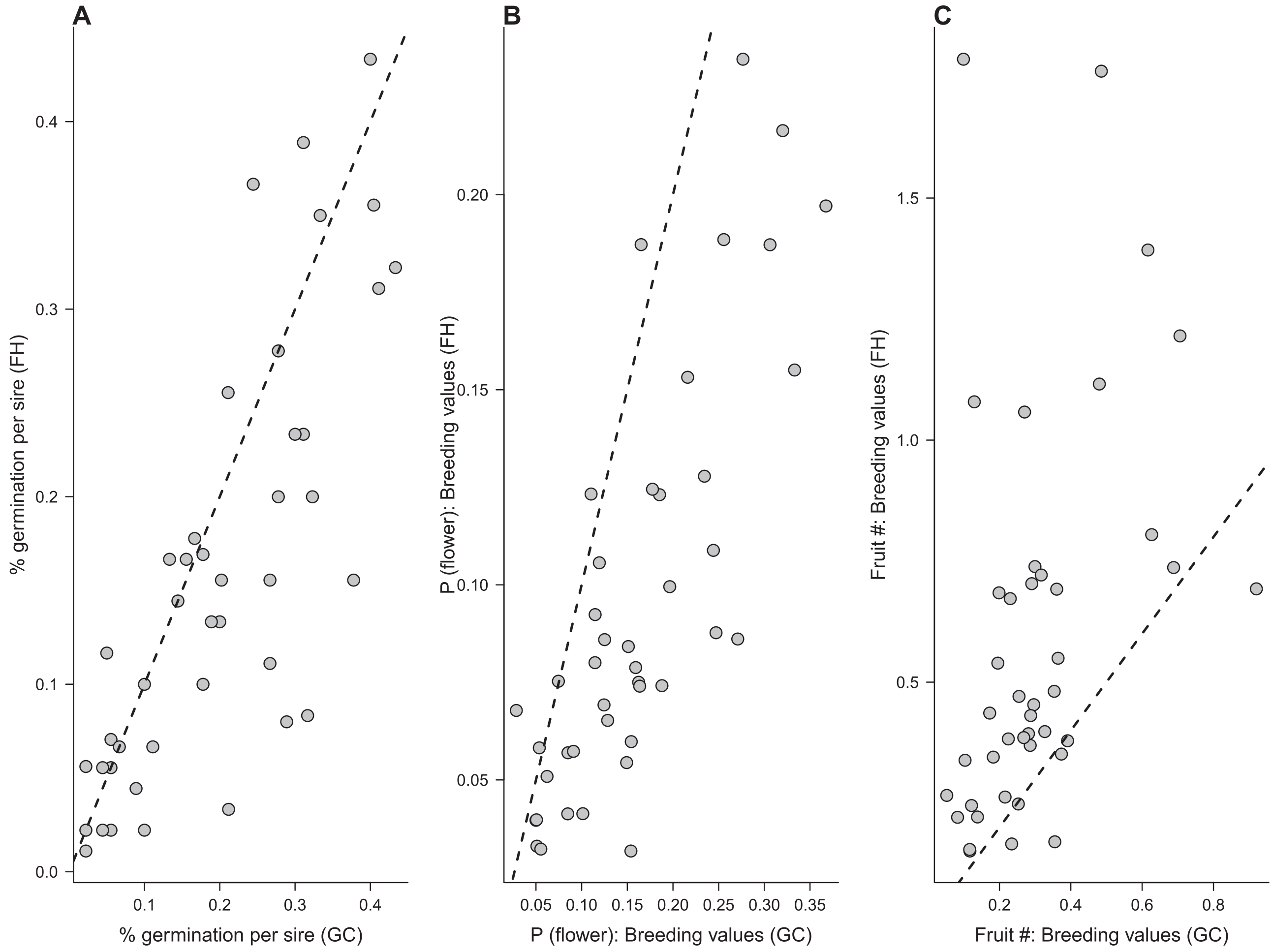

Figure 3. **Relationships of fitness expressed as probability of germination (A), probability of flowering (B), and fruit number (C) between sites. Dashed lines show 1:1 relationships between breeding values at Grey Cloud and breeding values at Flint Hills. In each panel, each point represents a unique sire.**

Interestingly, $G \times E$ became more apparent at later life-history stages. Specifically, there was a strong positive correlation between sites for fitness expressed as germination probability, whereas this association was weakest for overall fitness expressed as number of fruits (taking into account survival to reproduction). This pattern implies that natural selection varies through the life span. Plants at Flint Hills suffered from deer herbivory early in the growing season prior to the onset of flowering, whereas those at Grey Cloud were subject to severe herbivory by small mammals late in the season after peak flowering and many fruits had begun to mature (SNS & REP, pers. obs.). Thus, it is possible that in the absence of herbivore pressure, the correlation in fitness between sites would have remained strong for fruit counts.

$\overline{W}$ AND V_A (W) AT EACH SITE

Mean fitness indicated population persistence at both sites, with higher fitness in the "away" versus the "home" site. While fruit counts were higher at Flint Hills, where many plants recovered following early deer browsing, germination, and flowering probabilities were higher at Grey Cloud, where the severity of early-season deer herbivory was less, competition was lower and the vegetation cover was sparser. Small mammalian herbivores at Flint Hills could have been less common or preferred other plant species. Either way, the two sites differ in herbivory late in the season, causing the direction of mean performance in each site to be reversed early versus late in the growing season. Similar to our findings, another study of *C. fasciculata* conducted at a small spatial scale found high reproductive output but low survival at the end of the growing season at one of the sites and attributed this decline in survival to gopher herbivory (Abdala-Roberts and Marquis 2007). Aside from differences in the type and timing of herbivory between sites, differences between sites in vegetation cover and nutrient availability may also explain the observed differences in fitness. Lower competition and sparser vegetation at Grey Cloud may have promoted germination and flowering, whereas greater nutrient availability at Flint Hills may have played a role in higher fruit numbers for the plants that did flower.

We detected substantial $V_A(W)$ at both sites, countering a common view that there is little standing genetic variance for fitness, at least in the native habitat. This would correspond to an expectation of negligible $V_A(W)$ at Grey Cloud. Though the estimate of $V_A(W)$ was smaller at Grey Cloud than at Flint Hills, the confidence intervals for the two estimates overlapped. Moreover, the prediction for the change in mean fitness was somewhat greater for Grey Cloud, though the values for the sites were similar (somewhat over two fruits per plant).

CONCLUSIONS

Our detection of $V_A(W)$ and $G \times E$ for fitness illustrates the power of our experimental quantitative genetic approach coupled with aster analysis. Direct measures of the process of genetic selection are not often undertaken (Austen and Weis 2016). In contrast with our finding of substantial $V_A(W)$ in two sites, a study of a natural population of the collared flycatcher suggested a negative relationship between the heritability of morphological traits and their association with lifetime reproductive success, and found a heritability of 0 in lifetime reproductive success (Gustafsson 1986). Further, Hayward et al. (2018) recently found no evidence of $G \times E$ for fitness in the Soay sheep population, despite evidence for environmentally varying selection on morphology and life-history. These authors suggested that populations generally lack $G \times E$ for fitness on relevant environmental scales. In view of our findings, we doubt this conclusion and urge the value of expanding efforts to assess $V_A(W)$ across a range of environmental conditions. In this context, we underscore the importance of an experimental approach. Like other quantitative traits such as morphology, behavior, physiology, and disease susceptibility, expression of individual fitness is highly sensitive not only to environmental variation on coarse scales, as we have studied here in the effects of different sites, but also on finer scales not readily amenable to direct experimental study (but see Antonovics et al. 1987; Stratton 1994). A crucial value of the experimental approach we have used is the randomization of genotypes over microenvironmental variability, which may otherwise be confounded with genetic variability, obscuring the true genetic effects on fitness.

Consistent with population persistence and ample capacity for immediate adaptation, we documented $\bar{W}$ above replacement levels and substantial $V_A(W)$ in both study sites. Quantification of $V_A(W)$ allows us to predict rates of adaptation, and work is currently underway to address two key questions. First, we are examining the extent to which realized rates of adaptation correspond to the prediction from the ratio of $V_A(W)$ to $\bar{W}$. Second, we aim to determine whether $V_A(W)$ is sufficient to support evolutionary rescue when individuals in a population fail to replace themselves (on average). This work has important implications for populations' capacities to adapt to environmental changes, including temporal changes in climate (Shaw and Etterson 2012).

AUTHOR CONTRIBUTIONS

R.G.S. conceived of the project, S.N.S., R.E.P., and R.G.S. collected the data, M.W.K. and S.N.S. analyzed the data, S.N.S. led the writing of the article with substantial contributions from all coauthors.

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DATA ARCHIVING

All data and scripts associated with this manuscript are available at https://bitbucket.org/snsheth/gxeanalysis. Data have also been archived at https://doi.org/10.5061/dryad.kv27n5g.

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