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Genetic Basis and Consequences of Niche Construction: Plasticity-Induced Genetic Constraints on the Evolution of Seed Dispersal in *Arabidopsis thaliana*

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abstract: Because seed dispersal influences the environment experienced by seeds, that environment can change as dispersal evolves. The evolutionary potential of dispersal can in turn change as dispersal evolves, if its expression of genetic variation depends on the postdispersal environment. We examined whether seed dispersion patterns have a detectable genetic basis (and therefore evolutionary potential) and determined whether that genetic basis changed depending on one postdispersal environmental factor: conspecific density. We grew replicates of 12 ecotypes of *Arabidopsis thaliana* at high and low density and measured seed dispersion patterns and maternal traits associated with dispersal under controlled conditions. We found density-dependent ecotypic variation for maternal traits that influence dispersal. Significant genetic variation for postdispersal sibling density was detected only when plants were grown at high density, suggesting that if dispersal evolves to result in lower postdispersal densities, the expression of genetic variation for dispersal would be reduced. This dynamic could lead to a plasticity-induced constraint on the evolution of dispersal. The ability of organisms to alter the environment they experience and the ability of that environment to evolve can alter evolutionary dynamics by augmenting or reducing evolutionary potential and thereby facilitating or constraining evolutionary responses to selection.

Keywords: evolutionary constraints, habitat choice, habitat selection, maternal effects, phenotypic plasticity.

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The ability of organisms to alter the environment they experience has been termed "niche construction" (Odling-Smee et al. 1996). Niche construction can occur through direct habitat modification, habitat choice, or resource garnering and depletion. Plants can alter the environment they experience through resource use, architectural responses to environmental cues, germination cueing, and seed dispersal (Bazzaz 1991; de Kroon and Hutchings 1995; Huber et al. 1999; Donohue 2003).

Seed dispersal is the most mobile stage in a plant's life history, excepting pollen dispersal in outcrossing species, and for many species, it is the only mobile stage. It thereby provides plants the opportunity to change the environment experienced in the next generation, enabling, for example, escape from pathogens associated with maternal plants (Burdon and Chilvers 1975; Augspurger 1983), escape from adverse environmental conditions or predators at the maternal home site (Janzen 1971, 1972; Wilson and Janzen 1972; Liew and Wong 1973; Peroni 1994; Lott et al. 1995), or escape from sibling competition (Baker and O'Dowd 1982; Rees and Brown 1991; Augspurger and Kitajima 1992; Gibson 1993*b*; Donohue 1997). Directed dispersal, especially by animals, can effectively provide seeds with nurturing conditions more favorable than surrounding environments (e.g., Beattie and Lyons 1975; Gibson 1993*a*; reviewed in Howe and Smallwood 1982; Willson and Traveset 2000). Thus, traits of plants that influence their dispersal ability influence the environment experienced by offspring and thereby contribute to niche construction.

One fundamental question is whether niche construction itself has evolutionary potential in natural plant systems. The environments that plants inhabit are typically considered to be purely ecological and beyond the control of the plants. If niche-constructing characters of plants have a genetic basis and can evolve, however, then the propensity of plants to experience specific environments can evolve (Donohue 2003). We examined the genetic basis of one niche-constructing plant character: seed dispersal.

Seed dispersal is a complex, composite character that is notoriously difficult to quantify, and it has therefore eluded genetic investigation in a comprehensive manner. To our knowledge, no quantitative genetic study has yet attempted to examine the genetic basis of seed dispersion patterns themselves, although some admirable studies have examined specific plant characters demonstrated or hypothesized to be associated with dispersal ability (Erskine 1985; Venable and Burquez 1990; Robertson et al. 1997; Liljegren et al. 2000). It is important to measure the evolutionary potential of niche-constructing characters such as dispersal because if dispersal and niche-constructing characters in general have a genetic basis and can evolve, then their evolution can influence the evolutionary dynamics of other traits and even of themselves.

Niche construction alters evolutionary dynamics in three ways. First, it can alter the agents of natural selection that an organism is exposed to. If niche construction causes greater consistency in environmental conditions over time, then it can also promote adaptation and specialization (Levins 1968; Holt 1987; Rosenzweig 1987; Brown 1990).

Second, plastic phenotypes can change according to the environment that an organism creates for itself. For example, in annual mustards, dispersing to low density caused plant morphology to change significantly because plant morphology is highly plastic in response to density (Donohue 1999; Wender et al. 2005). Similarly, the timing of dispersal influenced fundamental life-history expression in *Campanula americana*, with early dispersal leading to an annual life history and later dispersal leading to a biennial life history (Galloway 2002). Therefore, niche construction can influence patterns of morphological and life-history expression in a general manner.

Third, niche construction has the potential to influence the expression of genetic variation. Environment-dependent genetic expression is extremely common (e.g., Mazer and Wolfe 1992; Dorn et al. 2000; Munir et al. 2001). Therefore, the ability of organisms to alter the environment they experience can alter their evolutionary potential. If niche construction alters the environment in a manner that enhances the expression of genetic variation, then it can increase the ability to respond to natural selection, but if the environment reduces the expression of genetic variation, niche construction can impose genetic constraints on the response to selection. Therefore, niche construction can facilitate or constrain adaptive evolution by influencing the expression of genetic variation.

We investigated the genetic basis of the niche-constructing character of seed dispersal and how its genetic basis changes depending on the postdispersal environmental factor of conspecific density. Dispersal ability can influence the conspecific density experienced by seeds (reviewed in Howe and Smallwood 1982; Willson and Traveset 2000). Postdispersal density in turn influences plant fitness, frequently with natural selection favoring dispersal to lower density (e.g., Burdon and Chilvers 1975; Augspurger and Kitajima 1992; Donohue 1997). By examining the genetic basis of dispersal at different densities, we examined the potential for dispersal to influence its own genetic basis as it evolves in response to selection, and we tested whether its evolution could constrain or augment its evolutionary potential over time.

The necessary first step to characterizing the genetic basis of seed dispersion patterns is to test whether a genetic basis of this complex trait is detectable at all using genetically variable material. If a genetic basis can be detected, then we can examine which maternal traits contribute to that genetic basis and how the genetic basis varies with environmental conditions. In this study, we deliberately increased our ability to detect a genetic basis for seed dispersion patterns so we could detect maternal characters that are genetically associated with seed dispersion patterns and increase our ability to resolve how the genetic component of variation in dispersal changes with density.

We used *Arabidopsis thaliana* for this study. A related article (Wender et al. 2005) identified morphological traits associated with dispersal at high and low density in *A. thaliana*. Here we present a genetic analysis of those traits, their genetic correlations with dispersal, and a genetic analysis of seed dispersion patterns themselves in high and low density. The previous study also documented that high density resulted in lower fitness, suggesting that, all else being equal, natural selection may favor lower postdispersal density, but of course, field studies are required to test that hypothesis. For illustrative purposes, however, we can ask here whether dispersal has the genetic variation required to respond to selection, and if so, how the genetic basis of dispersal would change if dispersal did evolve to create lower postdispersal density.

We addressed the following specific questions: Are maternal traits that influence dispersal genetically variable, and does the degree of genetic variation for these traits depend on density? Are maternal traits genetically correlated with dispersal at high and low density? Is there detectable genetic variation for seed dispersion patterns themselves, and does this genetic variation vary with density? Can density-dependent genetic expression of plant traits and dispersal constrain or facilitate the evolution of dispersal?

Methods

To increase our resolution of the genetic basis of seed dispersion patterns, we deliberately increased the chance of sampling genetically diverse material and minimized

environmental variance in dispersal. We sampled ecotypes in a manner likely to increase the genetic component of phenotypic variation by selecting ecotypes that differ in phenotypic characters hypothesized to be associated with dispersal ability. The morphological variation increased the statistical power to detect associations between plant phenotypes and seed dispersion patterns and to characterize patterns of plasticity of diverse genotypes. After we identified plant characters associated with dispersal in the diverse ecotypes, we measured these same characters on a sample of genotypes collected from one natural population in order to quantify the genetic variation for these characters within a population.

We reduced environmental variance by measuring seed dispersion patterns under controlled conditions. Studies under controlled conditions enabled us to precisely manipulate density to determine its effect on specific plant characters, on seed dispersion patterns, and on the genetic variation for seed dispersion patterns. Such studies would have been prohibitively difficult in the field because the seeds of *Arabidopsis thaliana* are tiny, making their recovery nearly impossible, and seedling distributions would be almost equally difficult to quantify under a natural canopy. In addition, many seedlings die very soon after germination (K. Donohue, unpublished data), and such early mortality would confound estimates of seed dispersion patterns with environment-dependent seedling mortality. These studies of seed dispersal under controlled conditions are therefore the necessary first step toward identifying relevant mechanisms of dispersal variation in *A. thaliana* for future studies under more ecologically realistic environments and for characterizing environment-dependent genetic expression.

Study System

Arabidopsis thaliana, a weedy mustard (Brassicaceae), displays a winter annual, spring annual, and autumn-flowering life history (Napp-Zinn, 1976; Thompson 1994; Nordborg and Bergelson 1999; Griffith et al. 2004). Native to Western Eurasia, it has successfully populated much of North America, Asia, Europe, and North Africa (Sharbel et al. 2000; Hoffman, 2002). Like many related pest and crop species of the Brassicaceae, *A. thaliana* has dehiscent siliques, and its seeds are passively dispersed by wind or are transported with soil. *A. thaliana* is autogamous and exhibits a high rate of self-fertilization in the field (Abbott and Gomes 1989) leading to high homozygosity in natural populations (Todokoro et al. 1995; Berge et al. 1998; Bergelson et al. 1998). Broad-sense heritability estimates therefore accurately estimate the genetic variance that contributes to responses to selection in inbred lineages.

Experimental Treatments

We measured seed dispersion patterns of replicates of 12 ecotypes grown at high and low density under controlled conditions. Five of the ecotypes were supplied by the Arabidopsis Biological Resource Center at Ohio State University (BAUK-CS952, BUR-CS1028, EDI-CS1122, TAD-CS929, and TEO-CS1550). Seven additional ecotypes were collected from North America by K. Donohue (one each from Rhode Island, Tennessee, and Michigan; two each from Massachusetts and Kentucky; see Griffith et al. 2004 for more information on these populations). We also grew replicates of 16 genotypes of one ecotype collected from Montague, Massachusetts, under high and low density and measured traits associated with seed dispersion patterns.

We grew all plants in a common greenhouse environment for two generations before the experiment to minimize random maternal effects on plant traits. Ten replicates of each ecotype were grown in two density treatments. The low-density treatment had one plant per 2.5-inch pot. The high-density treatment consisted of a single plant of a given ecotype in a 2.5-inch pot, surrounded by 19 yellow-seeded, "transparent testa" mutants ("ttg" stock no. CS3128 on a Landsberg ecotype background). Seeds from the nonmutant ecotype could be distinguished from seeds from the neighboring mutants so we could characterize the seed dispersion pattern of a specific individual within a matrix of common competitors. Plants in high density flower sooner, so they were planted 1 month later than plants at low density to enable all plants to flower within the same span of time.

Plants were grown in a Conviron E7/2 growth chamber in a randomized block design on a 12L : 12D photoperiod of full-spectrum light at 22°C. All plants received a 7-week vernalization period at 4°C to synchronize flowering. After vernalization, plants were grown in a randomized block design in a greenhouse with a 12L : 12D photoperiod at 22°C.

To minimize variance in the developmental state of plants during dispersal trials, the flowering date of each individual was recorded, and dispersal trials were conducted an average of 51 days after the day of first flowering. After that interval, most siliques were mature, and some had already dehisced. To standardize any variation in hydration across plants, each plant was dried, undisturbed in the pot, by withholding water for 10 days before the dispersal trial.

At the time of the dispersal trials, architectural traits of each plant and fruit characters were measured. See Wender et al. (2005) for a complete list of the measured traits. Based on that phenotypic study, we identified several plant characters that significantly influenced different compo-

nents of seed dispersion patterns. These characters were: the total number of fruits produced; the height of the primary stem; the total number of branches; the length of the longest branch off the primary stem (branch length); the average angle between the main stem and the adaxial surface of three inflorescence branches if they existed (branch angle); the average silique length, based on a subset of 10 siliques randomly located on each plant (silique length); and the total proportion of mature fruits that had dehisced during the dispersal trail (proportion dehisced; this does not include those that dehisced before the dispersal trial).

We conducted the dispersal trials in a wind tunnel at a mean wind speed of 4.9 m/s (SD = 0.09). The wind speed is a realistic estimate of wind speed during summer dispersal season, and the speed minimized dispersal beyond the length of seed collection in the wind tunnel (10 m long). We also imposed a standardized mechanical disturbance to facilitate dehiscence during the trial. A wooden dowel passed through the plant, in an arc from the base of one side of the plant to the top of the other side, at a constant speed one minute after the plant had been placed in the wind tunnel, and the plant remained in the wind tunnel for four minutes after the disturbance. This sequence was repeated once. This routine was established during preliminary trials that quantified the proportion of siliques that had dehisced during the trial, and our goal was to estimate the dispersion pattern of at least 25% of the siliques on the plant. The method frequently exceeded this goal.

The wind tunnel was lined with gridded sheets covered with petroleum jelly. The petroleum jelly prevented further movement of the seeds after they reached the base of the tunnel, enabling accurate assessment of primary dispersal. We quantified seed dispersion patterns of individual plants by recording the position of each seed on the sheet, based on the printed grid of 0.25 cm × 0.25 cm. Subsampling was necessary for some plants that dispersed a large number of seeds (more than 4,000 seeds, in many cases). When subsampling, we recorded the position of all seeds in every other 2.5-cm strip extending the length of the seed sheets.

We calculated six measurements of dispersal for each plant: the average distance dispersed, the standard deviation of that distance, the kurtosis of the distribution, the average density of seeds measured on two scales, and the proportion of seeds dispersed beyond recovery. The first density scale (small-scale density) was that of the 0.25 × 0.25-cm grid marks, representing the spatial scale of interactions between individual germinants. The second scale (large-scale density) was that of a 2.5 × 2.5-cm area, which represents a spatial scale of interaction among adult plants and approximates the scale that we used when we imposed different densities at the pot level. Density was measured as the "mean crowding index" or the mean number of neighbors a seed had within each unit area (Lloyd 1967). For the high-density plants, we estimated dispersal based only on seeds from the focal ecotypes, not those from the yellow-seeded mutants (but see Wender et al. 2005 for measures of background dispersal by the yellow-seeded mutants); the background density would be similar across all ecotypes because the same genotype was used as the competitor for all focal ecotypes. Consequently, the postdispersal density measurements estimate sibling density, not total density, and we thereby investigated the component of progeny density that is determined by the traits of the focal maternal plant. Most seeds were dispersed within 2 m of the maternal plant, and the detailed quantifications of dispersal just described were based on those seeds. To quantify the proportion of seeds that was dispersed beyond this distance, we first counted the number of siliques that dehisced during the dispersal trial and multiplied that number by 36.9 (seeds per silique; SD = 5.9) for plants grown in low density and 29.3 (seeds per silique; SD = 8.7) for plants grown at high density. The estimates of seeds per silique were based on a sample of 10 siliques from 10 plants from each density treatment (100 siliques total per treatment). The estimated proportion of seeds dispersed beyond recovery (percent beyond) was 1− [(the total number of seeds recovered)/(estimated number of seeds dispersed)].

To determine the degree of genetic variation observed within a single population for traits that influence seed dispersion patterns, we grew 10 replicates of 16 genotypes, collected from a single natural population, at high and low density using the same design and growing protocols as described above. Seeds were collected as open-pollinated (and presumably highly selfed) sibships from random plants in the field from a population in Montague, Massachusetts. Each sibship was grown in a greenhouse for two generations before the experiment, with selfed seeds being collected from one individual of each original sibship (i.e., single-seed descent). Seeds were collected from the second-generation plants, and 10 seeds of each inbred line were planted in high and low density, as described above. The same plant characters were measured at the same developmental stage as was used for the diverse ecotypes.

Statistical Analysis

To test for significant effects of density, ecotype, and the interaction between density and ecotype on maternal characters and dispersal measures, a MANOVA (Proc GLM in SAS; SAS 1999) was performed for maternal traits and for dispersal measures. Variables were transformed to normality when appropriate. Density was a fixed factor, eco-

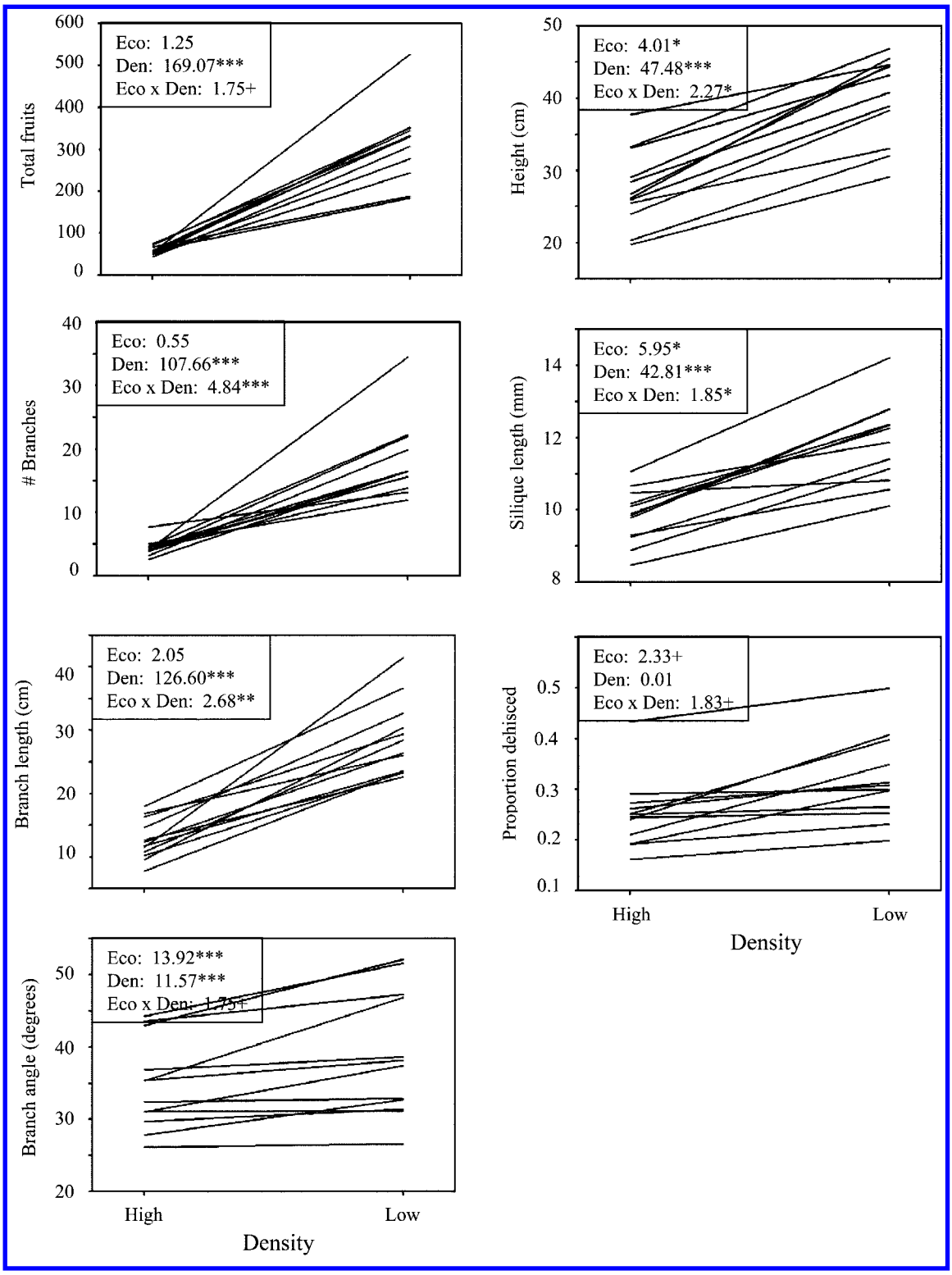

Figure 1: Ecotypic means of maternal plant traits at high and low density. Each line connects the mean value of an ecotype at each density. Boxes present the *F* ratios and significance levels of the effects based on mixed-model ANOVA, as described in "Methods." *Plus sign*, $P < .1$; *one asterisk*, $P < .05$; *two asterisks*, $P < .01$; *three asterisks*, $P < .001$.

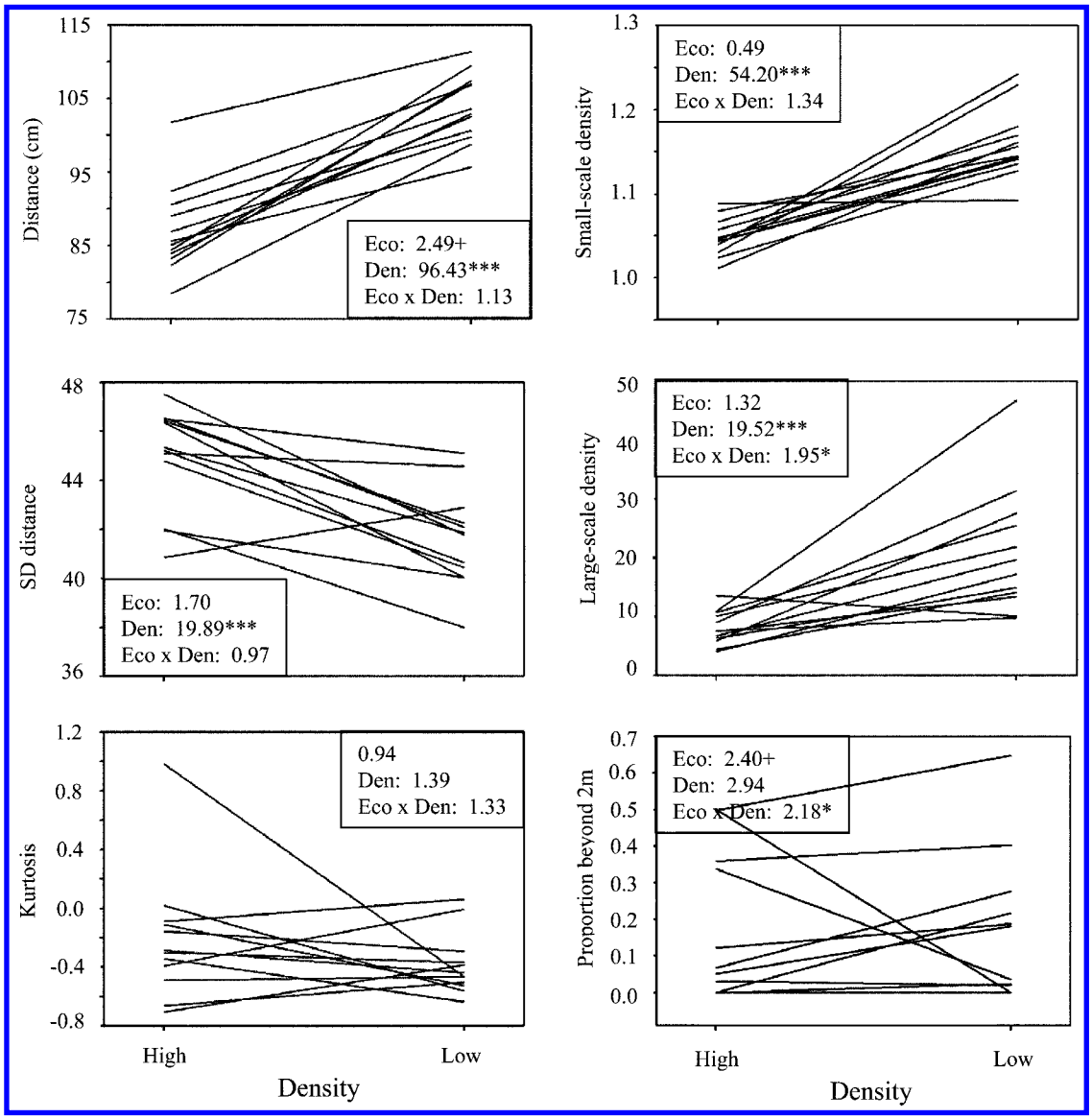

Figure 2: Ecotypic means of dispersal measures at high and low density. Each line connects the mean value of an ecotype at each density. "Small-scale density" indicates the postdispersal mean crowding index at the 0.25 × 0.25-cm scale. "Large-scale density" indicates the postdispersal mean crowding index at the 2.5 × 2.5-cm scale. Boxes present the *F* ratios and significance levels of the effects based on mixed-model ANOVA. *Plus sign*, $P < .1$; *one asterisk*, $P < .05$; *three asterisks*, $P < .001$.

type was a random factor, and ecotype and density effects were tested over the interaction term. Individual ANOVAs (Proc GLM in SAS) using the same model structure were then performed on each trait and dispersal measure separately. We also quantified ecotypic differences in maternal traits and dispersal measures within each density. Most residuals were normally distributed, but residuals for some dispersal measures were slightly leptokurtic. Therefore, Kruskal-Wallis tests also tested for ecotypic differences within each density for some measures of dispersal.

We estimated genetic and environmental variance components and tested for significant differences in genetic and environmental variances in high and low density using restricted maximum likelihood (REML) analysis (Proc Mixed in SAS). Differences between the −2Log residual likelihood between the unconstrained model and the models in which the genetic or environmental variances were constrained to be equal were compared with a χ^2 distribution with one degree of freedom. We also computed the correlation between the trait when expressed in high and

Table 1: Ecotypic-level genetic and environmental variances of maternal traits in high and low density

Character	High density			Low density							
	V_{GH}	V_{EH}	H_H^2	V_{GL}	V_{EL}	H_L^2	$r_{(H, L)}$	$V_{GH} = V_{GL}$	$V_{EH} = V_{EL}$	$H_H^2 = H_L^2$	$G \times E$
Fruits	.0007	.83	.00	.082	1.07	.07*	−1.00	NS	*	+	+
	(.006)	(.11)	(.02)	(.083)	(.15)	(.04)	(NE)				
Branches	.022	.297	.07	.064	.119	.35*	−.39	NS	***	*	***
	(.022)	(.041)	(.10)	(.032)	(.017)	(.17)	(.48)				
Height	20.85	65.70	.24***	29.67	58.01	.33*	.99[a]	NS	NS	NS	*
	(11.87)	(9.25)	(.08)	(15.45)	(8.54)	(.11)	(.13)				
Branch length	6.18	34.78	.15*	31.68	30.03	.54***	.41[b]	**	NS	**	**
	(4.28)	(4.94)	(.07)	(14.92)	(4.23)	(.15)	(.35)				
Branch angle	30.81	37.92	.48***	72.27	27.87	.73***	1.00[a]	***	NS	**	+
	(15.41)	(5.85)	(.10)	(32.19)	(4.19)	(.09)	(.00)				
Silique length	.27	4.18	.06	1.24	.45	.73***	1.00[a]	NS	***	***	*
	(.24)	(.56)	(.06)	(.55)	(.07)	(.13)	(.00)				
Proportion dehisced	.006	.034	.14*	.008	.028	.23***	.63	NS	NS	NS	+
	(.004)	(.005)	(.07)	(.005)	(.004)	(.12)	(.35)				

Note: V_{GH} = genetic variance at high density; V_{EH} = environmental variance at high density; V_{GL} = genetic variance at low density; V_{EL} = environmental variance at low density; H_H^2 = ecotypic-level broad-sense heritability at high density; H_L^2 = ecotypic-level broad-sense heritability at low density; $r_{(H,L)}$ = genetic correlation across density. Standard errors of the variance component estimates and correlations are given in parentheses; $V_{GH} = V_{GL}$ tests for a significant departure from the null hypothesis that the genetic variances are equal in the two densities; $V_{EH} = V_{EL}$ tests for a significant departure from the null hypothesis that the environmental variances are equal in the two densities; $H_H^2 = H_L^2$ tests for a significant departure from the null hypothesis that the heritabilities are equal in the two densities, based on jackknife standard errors; $G \times E$ tests for genotype by environment interactions that indicate either that the heritabilities differ across density or that reaction norms cross. $N = 236$. Significance levels of the heritability estimates are based on the significance of ecotype main effects in ANOVA. NS = not significant; NE = nonestimable because of negative variance components.

[a] Significantly different from model in which the correlation across environments is constrained to be 0.

[b] Significantly different from model in which the correlation across environments is constrained to be 1.

+ $P < .1$.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

low density and tested for significant differences from 0 or 1 using REML and comparing likelihoods between the unconstrained model and those in which the correlation was constrained to be either 0 or 1, as just described. These tests were verified with jackknife standard errors of the variance component estimates. Broad-sense heritabilities were estimated within each environment as the genetic variance divided by the total phenotypic variance (genetic plus environmental variance). Their significance was assessed based on the ecotype effect in the ANOVA analysis conducted within each density previously described (Fry 1992), and results were verified by computing jackknife standard errors. A significant ecotype-by-density interaction in the ANOVA would indicate that the heritabilities differed significantly between densities and/or that the ecotypes exhibited crossing reaction norms (Fry 1992). Jackknife standard errors distinguished between these possibilities.

At each density, we computed genetic correlations among maternal traits and between maternal traits and dispersal measures based on genetic variance and covariance components using the Free-stat statistical package (Mitchell-Olds 1989). Free-stat calculates genetic variances based on variance components and tests their significance with permutation tests. Common principal component analysis tested whether the structure of the genetic covariance matrix of maternal morphological traits differed between density treatments (Phillips 1998; Phillips and Arnold 1999).

To determine how much of the observed ecotypic difference in dispersal measures was caused by ecotypic differences in the maternal characters, we compared the ecotype effect on dispersal, with (ANCOVA) and without (ANOVA) the maternal traits mentioned above. For dispersal measures that gave nonnormal residuals, we first calculated the residual variation in dispersal after factoring out effects caused by maternal traits using ANCOVA, and we then analyzed the dispersal measures and the residuals of dispersal measures using Kruskal-Wallis tests.

We calculated genetic and environmental variances, heritabilities, and genotype-by-environment interactions of the maternal traits within the single natural population using the same methods as described above.

Table 2: Ecotypic-level genetic and environmental variances of dispersal measures in high and low density

Character	High density			Low density							
	V_{GH}	V_{EH}	H^2_H	V_{GL}	V_{EL}	H^2_L	$r_{(H, L)}$	$V_{GH} = V_{GL}$	$V_{EH} = V_{EL}$	$H^2_H = H^2_L$	$G \times E$
Distance	16.27	194.13	.08*	11.987	92.25	.14**	.86	NS	***	NS	NS
	(15.58)	(26.92)	(.08)	(10.62)	(13.13)	(.08)	(.46)				
SD distance	.35	53.26	.01	3.60	13.39	.21**	1.00	NS	***	**	NS
	(.94)	(7.03)	(.04)	(2.16)	(1.90)	(.08)	(.00)				
Kurtosis	.024	1.68	.01	.038	.067	.36***	−.13	NS	***	***	NS
	(.09)	(.23)	(.04)	(.02)	(.01)	(.12)	(.947)				
Small-scale density	.0001	.0005	.17**	.00	.0037	.00	.00	NS	***	**	NS
	(.0003)	(.0002)	(.08)	(.00)	(.003)	(.03)	(.00)				
Large-scale density	4.93	28.31	.15***	58.45	483.45	.11	.49	NS	***	NS	*
	(3.44)	(3.94)	(.06)	(48.23)	(68.80)	(.06)	(.48)				
% beyond	.013	.048	.22*	.023	.050	.32***	.56	NS	NS	NS	*
	(.009)	(.008)	(.05)	(.013)	(.009)	(.12)	(.34)				

Note: Column headings and statistical tests are as in table 1. $N = 236$. Significance levels of the heritability estimates are based on the significance of ecotype main effects in ANOVA for "Large-scale density" and "% beyond" and on Kruskal-Wallis analysis for the other nonnormal measures. NS = not significant.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

Results

Plasticity of Maternal Traits and Dispersal

Ecotype, density, and their interaction influenced plant traits significantly (MANOVA, factor [nnf, ddf]; Wilks's λ, ecotype [77, 37], $\lambda = 2.55$, $P < .005$; density [7, 5], $\lambda = 35.83$, $P < .001$; density × ecotype [77, 900], $\lambda = 2.47$, $P < .001$; $N = 239$). High density resulted in shorter plants with fewer fruits and branches, shorter and more acute branches, and shorter siliques (fig. 1). The ecotypes responded differently to density for most characters, as indicated by the significant ecotype-by-density interactions (nearly significant for fruit number, branch angle, and dehiscence).

Density significantly influenced dispersal measures (MANOVA, factor [nnf, ddf]; Wilks's λ, ecotype [66, 38], $\lambda = 1.57$, $P = .06$; density [6, 6], $\lambda = 27.29$, $P < .001$; density × ecotype [66, 696], $\lambda = 1.01$, $P > .05$; $N = 239$), with high density being associated with shorter dispersal distances, higher SD of dispersal distance, and lower postdispersal sibling (but not total) density at both spatial scales (fig. 2). See Wender et al. (2005) for more discussion on the plasticity of the maternal traits and dispersal measures.

Genetic Variation for Maternal Traits and Dispersal

We detected no significant genetic variation for any maternal trait within the natural population, except for height at low density (appendix table A1). In contrast, significant ecotypic variation was detected for all maternal characters at low density (table 1; fig. 1). Fruit production, branch number, and silique length did not express significant genetic variation at high density. Genetic variances and heritabilities were significantly greater at low density for branch length and branch angle. The heritability of number of branches and silique length was also higher at low density, in part because of a reduction of environmental variance at low density. A significant genotype-by-density interaction caused by crossing reaction norms was detected for height. Height, branch angle, and silique length were significantly correlated across density environments, indicating that evolution of these traits in one density would cause correlated evolution of the trait expressed in the other density.

Significant ecotypic variation was detected for seed dispersion patterns (table 2; fig. 2), and the degree of ecotypic differences in some measures depended on density. Significant ecotypic variation for dispersal distance and the proportion of seeds dispersed beyond 2 m was detected at both densities. Significant ecotypic variation for the SD of dispersal distance and kurtosis was detected only at low density, and significant ecotypic variation for postdispersal sibling density at both spatial scales was detected only at high density. While the genetic variance components did not differ significantly across density treatment for any measure, changes in the environmental variance were pronounced. In particular, for most cases in which the heritability estimate was greater at low density, the environmental variance component was smaller at low density, causing larger heritabilities. For the proportion of seeds dispersed beyond 2 m, however, the genetic component

Table 3: Ecotypic-level genetic correlations among maternal traits at high (above diagonal) and low (below diagonal) density

	Fruits	Branches	Height	Branch length	Branch angle	Silique length	Proportion dehisced
Fruits		NE	NE	NE	NE	NE	NE
Branches	.94***		**−.05**	**.46***	−.11	−.73	.06
Height	−.55***	**−.32****		.90***	.55***	**−.25**	.57*
Branch length	−.07	**−.30*****	.74***		.11	−.36	1.00***
Branch angle	−.59***	−.35***	.65***	.43***		.51**	.23*
Silique length	−.39***	−.32***	**.80*****	.47***	.80***		−.58
Proportion dehisced	−.14	−.17	.57***	.60***	.21*	.18+	

Note: NE = nonestimable because of negative variance components. Boldface indicates correlations are significantly different across density. Covariance matrices are not equivalent ($\chi^2 = 48.33$, df = 28, $P = .010$), they are not proportional ($\chi^2 = 43.07$, df = 27, $P = .026$), they do not share all principal components ($\chi^2 = 33.01$, df = 21, $P = .05$), but they share five out of six, based on the "jump-up" test of Phillips and Arnold (1999).

+ $P < .1$.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

of variance was higher at low density (not significantly), causing slightly higher heritability. The significant ecotypic variation for postdispersal sibling density at the small spatial scale, detected only at high density, was because of higher genetic variance (not significant) and lower environmental variance at high density. The significant heritability of postdispersal sibling density at the large spatial scale, also detected only at high density, was due entirely to a lower environmental variance at high density because the genetic variance was actually lower (but not significantly) at high density. Correlations across density were not significantly different from 0 or 1 because of high environmental variation.

In summary, density frequently altered the evolutionary potential (heritability) of plant traits and of different components of dispersal ability. It did so by influencing the expression of both genetic and environmental variance components.

Genetic Correlations among Characters

Genetic correlations among several maternal characters tended to be more strongly significant at low density than at high density, and some correlations changed direction in high density (table 3). Branch number and branch length were positively correlated at high density but negatively correlated at low density. Silique length was positively correlated with height and branch length at low density but (nonsignificantly) negatively correlated at high density. In general, ecotypes with more branches were shorter, had shorter siliques, and had shorter branches with more acute branch angles. Taller ecotypes had longer siliques and branches with more oblique angles and greater dehiscence.

Some plant traits were significantly genetically correlated to measures of dispersal at high density (table 4, upper half). Ecotypes with fewer branches and more oblique branching angles dispersed seeds farther. Shorter ecotypes with acute branch angles, shorter siliques, and greater dehiscence had higher postdispersal sibling densities at both spatial scales. Greater dehiscence was also associated with increased dispersal beyond 2 m.

At low density, many maternal characters were significantly genetically correlated to dispersal measures (table 4, lower half). Taller ecotypes with fewer fruits and fewer but longer branches with oblique branching angles, longer siliques, and greater dehiscence had longer dispersal distances, greater SD of dispersal distance, and less kurtosis. Branch number and angle were associated with dispersal distance in a similar manner at high and low density. Ecotypes with higher postdispersal sibling density also were shorter, with more and shorter branches with acute branch angles and shorter siliques. With the exception of branch length, the maternal characters were associated with postdispersal density in a similar manner at both densities.

Role of Maternal Traits in Ecotypic Differentiation of Dispersal

At low density, the ecotypic differences in maternal characters appear to have accounted for the ecotypic differences in dispersal because inclusion of maternal traits left no residual differences among ecotypes in dispersal (table 5). At high density, however, significant ecotypic differentiation remained for dispersal distance and postdispersal sibling density at the larger spatial scale, even after inclusion of maternal traits. In fact, ecotypic differences in the maternal traits may have obscured ecotypic differences in

Table 4: Ecotypic-level genetic correlations between maternal traits and dispersal measures at high (upper) and low (lower) density

	Distance	SD distance	Kurtosis	Small-scale density	Large-scale density	% beyond
High density:						
Fruits	NE	NE	NE	NE	NE	NE
Branches	−1.00***	NE	−.76	.21	−.40^{+}	.68
Height	.47	NE	−.31	−.37^{+}	−.55***	.17
Branch length	.12	NE	−.50	.36	.14	.77
Branch angle	.52**	NE	.20	−.86**	−.48***	.17
Silique length	−1.00	NE	1.00	−1.00*	−1.00**	−.21
Proportion dehisced	.25	NE	.22	.99**	.62**	.94*
Low density:						
Fruits	−.61**	−.55**	.70***	NE	.34	NE
Branches	−.75***	−.87***	.81***	1.00**	.17	NE
Height	.15	.74***	−.82***	−.96	−.62**	NE
Branch length	.42**	.68***	−.77***	−1.00**	−.50**	NE
Branch angle	.22^{+}	.36*	−.69***	−1.00**	−.89***	−.41
Silique length	.17	.76***	−.82***	−.62*	−.44**	NE
Proportion dehisced	.58**	.46*	−.45***	.32	.30	NE

Note: Jackknife estimates and standard errors are available on request. NE = nonestimable because of negative variance component.

$^{+}$ $P < .1$.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

large-scale postdispersal sibling density because ecotypic differences were more pronounced after factoring out their contribution. Therefore, the measured maternal traits accounted for less ecotypic variation in dispersal at high density than at low density.

Discussion

Ecotypes differed genetically in maternal traits that influence seed dispersal, and they differed in their seed dispersion patterns themselves. Heritability and ecotypic variance of several of the maternal traits were higher when plants were grown at low density, and genetic correlations between maternal traits and dispersal distance, SD of dispersal distance, and kurtosis were also strong at low density. This contributed to higher heritabilities of these dispersal measures at low density. Indeed, ecotypic differences in maternal traits appeared to account fully for the ecotypic differences in dispersal observed at low density (table 5).

In contrast, ecotypic variation for postdispersal seedling density was detected only at high density. Some genetic correlations between maternal traits and postdispersal density were stronger at high density, while others were stronger at low density. While ecotypic differences in maternal traits did account for ecotypic differences in "% beyond" and postdispersal density at the small spatial scale, they did not account for ecotypic differences in the other dispersal measures. In fact, they even may have obscured ecotypic differences in postdispersal sibling density at the larger spatial scale because ecotypic differences in this measure were more apparent after factoring out ecotypic variation in maternal traits. At high density, therefore, plant traits not measured in this study also contributed to genetically based differences in dispersal.

Thus, the degree of genetic variation for dispersal that is expressed at each density depended in large part on the density-dependent expression of genetic and environmental variation for maternal traits that determine dispersal and on the strength of the associations of those traits with different measures of dispersal. Density-dependent genetic variation has been documented for many plant characters (Mazer and Wolfe 1992; Dorn et al. 2000; Munir et al. 2001), so this result is likely to be quite general. In addition, the effect of maternal characters on dispersal ability has been shown to be context dependent in a few studies (Telenius 1992; Theide and Augspurger 1996; Wender et al. 2005), and while this phenomenon is not widely documented, it too is likely to be common because the ecological mechanisms that cause it, such as neighbor interference and phenotypic plasticity, are quite intuitive.

The result that seed dispersal has a detectable genetic basis at all means that the postdispersal environment, which typically has been considered to be purely ecological, has evolutionary potential and can evolve in response to

Table 5: Contribution of maternal characters to ecotypic differences in dispersal measures

	High density with no traits	High density with traits	Low density with no traits	Low density with traits
Distance	21.50*	19.65*	26.71**	16.81
SD distance	12.28	8.75	29.44**	12.42
Kurtosis	12.43	18.95 $^{+}$	38.80***	14.56
Small-scale density	30.59**	10.77	6.44	11.92
Large-scale density	2.01*	3.18**	1.53	1.75
% beyond	2.99**	1.38	4.03***	1.58

Note: The F ratios ("Large-scale density" and "% beyond") or χ^2 (other measures) for ecotype main effects are given for models that do not include maternal traits (ANOVA or Kruskal-Wallis) and for those that do (ANCOVA or Kruskal-Wallis on residuals). The χ^2 values for effects of ecotype after factoring out the influence of maternal characters were obtained by performing Kruskal-Wallis tests on the residual variation from an ANOVA that modeled the effect of maternal plant traits on nonnormal dispersal measurements. $N = 212$.

$^{+}$ $P < .1$.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

natural selection. The genetic component of postdispersal sibling density is especially noteworthy. Countless studies have demonstrated that conspecific density strongly influences plant fitness. Natural selection on postdispersal sibling density is strong in many species, typically favoring lower density (e.g., Augspurger and Kitajima 1992; Donohue 1997). In *Arabidopsis thaliana*, high density has been shown to lower fitness as well (e.g., Dorn et al. 2000; Wender et al. 2005). This study shows that plants have the genetic potential to respond to such selection evolutionarily. In addition, the density-dependent genetic variation of plant morphological traits indicates that the evolutionary potential of these traits will change as dispersal (i.e., postdispersal density) evolves.

The context dependency of genetic variation for dispersal ability is important because it can lead to novel plasticity-imposed constraints on the evolution of dispersal. For example, plants growing at high density express significant genetic variation for the ability to disperse to lower density. If natural selection favors lower postdispersal density, then the population is expected to respond to such selection, giving lower postdispersal density in subsequent generations. At lower density, however, the genetic variation for postdispersal density is no longer expressed because of phenotypic plasticity. Therefore, the evolution of the environment-determining character can constrain its own further evolution because of its environment-dependent genetic expression. While it has long been appreciated that character evolution can be genetically constrained over time because of depletion of genetic variation by natural selection, the process just described can operate even without any significant depletion of genetic variation; plasticity alone can prevent the expression of genetic variation, even among the exact same genotypes. This genetic constraint results from the evolution of the environment that the organism experiences.

It should be noted, as well, that the dynamics just described need not cause evolutionary constraints but could conceivably facilitate evolutionary responses, depending on the patterns of plasticity. That is, if low density had increased the expression of genetic variation for postdispersal density (instead of decreasing it), then one would expect that as dispersal evolved to give lower postdispersal densities, the amount of genetic variation for dispersal ability could actually increase, facilitating its further evolution. Thus the ability of organisms to alter the environment they experience, and the environment-dependent genetic variation for that ability, can cause novel evolutionary dynamics that can either constrain or facilitate the evolution of such characters.

These dynamics will also depend on several ecological factors not investigated in this study. For example, the identity of the competitors, specifically whether competitive conditions are imposed by conspecific plants, related genotypes, or dissimilar genotypes, could be important because dispersal ability at high density is likely to depend on attributes of plants relative to their neighbors (Telenius 1992; Theide and Augspurger 1996; Wender et al. 2005). Furthermore, when dispersal does not effect a change in the density experienced by seeds, as in the case of a continuous con- or heterospecific stand of competitors, then such feedback dynamics would not occur. Nevertheless, effects of competitors still may alter the expression of genetic variation for dispersal and influence its evolutionary dynamics. A continuous high-density stand, for instance, could consistently constrain the evolution of kurtosis and the SD of the dispersion pattern because the heritability for those measures was lower at high density.

Finally, while we detected genetic differences among ecotypes in their dispersal ability, we detected almost no genetic variation within a population for traits associated with dispersal. Importantly, the stocks used for this portion of the study were collected from the field, and distinct genotypes were preserved during culturing through single-seed descent. The lack of genetic variation observed here is therefore not a culturing artifact and represents a true lack of genetic variation expressed under the conditions of the experiment. Because the ecotypic variance for maternal characters was more easily detected than the ecotypic differences in dispersal measures, this result indicates that genetic variation for dispersal is likely to be undetectable within this natural population. This is especially true for plants in low density, where genetic variation in the traits fully accounted for genetic variation in dispersal. The lack of genetic variation within a single population is not surprising because populations of *Arabidopsis thaliana* are known not only to be highly homozygous but also to be not genetically variable at the molecular level (Todokoro et al. 1995; Bergelson et al. 1998), although some studies have detected significant genetic variation for quantitative traits within natural populations (Dorn et al. 2000).

The lack of genetic variation within populations and the presence of genetic variation between populations for characters associated with population processes, such as dispersal and colonization, are noteworthy. The results suggest extremely limited evolutionary potential for local dispersal ability on the spatial scale of interacting genotypes within a population but significant evolutionary potential for dispersal through higher-level selection processes such as differences between populations in their colonization frequency after long-distance dispersal. It is perhaps the case that evolutionary responses to selection on dispersal in some species can occur only through higher-level, interdemic selection as opposed to individual mass selection operating within populations. Much more research is needed to investigate how small-scale dispersal patterns of genotypes reflect their long-distance dispersal ability. Indeed, this is likely to be one of the most important questions concerning the evolution of dispersal, namely, to determine how the evolutionary dynamics of local dispersal within populations influences the evolution of long-distance dispersal and colonization ability of different populations.

In conclusion, we found a significant genetic basis of seed dispersion patterns that depended on the postdispersal environment. Dispersal, therefore, not only can evolve in response to natural selection, but its evolution will influence the phenotypic expression and evolutionary potential of plant morphology and of dispersal itself. The evolutionary potential of niche-constructing characters has the potential to facilitate or constrain evolutionary responses in a general manner.

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APPENDIX

Table A1: Within-population genetic and environmental variances of maternal traits in high and low density

Character	V_{GH}	V_{EH}	H^2_H	V_{GL}	V_{EL}	H^2_L	$r_{(H, L)}$	$V_{GH} = V_{GL}$	$V_{EH} = V_{EL}$	$G \times E$
Fruits	.025	.339	.07	.00	.066	.00	.00	NS	***	NS
Branches	.00	.257	.00	.00	.046	.00	.00	NS	***	NS
Height	1.06	27.62	.04	.225	3.95	.05*	−1.00	NS	***	+
Branch length	.00	8.13	.00	.00	7.98	.00	−1.00	NS	NS	NS
Branch angle	.006	.190	.03	.0006	.039	.02	1.00	NS	***	NS
Silique length	NE	4.98	NE	NE	.621	NE	.16	NE	NE	NS
Proportion dehisced	.0016	.033	.05+	.0002	.0084	.02	.095	NS	***	+

Note: See legend of table 1 for explanation of the column headings and statistical procedures. $N = 236$. No heritability estimates differed significantly across density treatments. NE = nonestimable because of negative variance component.

+ $P < .1$.

* $P < .05$.

*** $P < .001$.

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