

DENSITY-DEPENDENT PROCESSES INFLUENCING THE EVOLUTIONARY DYNAMICS OF DISPERSAL: A FUNCTIONAL ANALYSIS OF SEED DISPERSAL IN *ARABIDOPSIS THALIANA* (BRASSICACEAE)¹

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We conducted a functional analysis of seed dispersal and its plasticity in response to density in *Arabidopsis thaliana* by growing morphologically diverse ecotypes under high and low density and measuring seed dispersion patterns under controlled conditions. Maternal plant architectural traits such as height and branching, and fruit traits such as dehiscence and silique length influenced various measures of seed dispersion patterns, including the average dispersal distance, kurtosis of the seed dispersion pattern, and post-dispersal seed density. The density at which plants grew determined which traits influenced dispersal. A change in density would therefore change which maternal characters would be subjected to natural selection through selection on dispersal. Density-mediated maternal effects on dispersal contributed to a negative correlation between parents and offspring for sibling density after dispersal, which could impede the response to selection on post-dispersal sibling density. Plant traits that influenced dispersal also influenced maternal fitness—sometimes opposing selection on dispersal and sometimes augmenting it—and the direction of the relationship sometimes depended on density. These density-dependent relationships between plant traits, dispersal, and maternal fitness can increase or reduce evolutionary constraints on dispersal, depending on the trait and depending on post-dispersal density itself.

Key words: *Arabidopsis thaliana*; Brassicaceae; dispersal; maternal effects; niche construction; plasticity; seed dispersal.

Dispersal influences evolutionary rates and outcomes (Fisher, 1930; Wright, 1931), geographic distributions of species (Primack and Miao, 1992; Matlack, 1994; Clark, 1998; Bossuyt et al., 1999; Cain et al., 2000; McKenna and Houle, 2000), population demographic dynamics (Roff, 1975; Horvitz and Schemske, 1986; Martinez-Ramos and Alvarez-Buylla, 1995; Caswell et al., 2003), and community associations (Platt, 1975, 1976; Tilman, 1997). It contributes to weedy and invasive habits (Tilman, 1997; Vila and D'Antonia, 1998; Marco et al., 2002), and the dispersal of seeds in addition to pollen can pose a risk of escape of genetically modified genotypes (Arnaud et al., 2003). In many ecological and population-genetic investigations of the consequences of dispersal, dispersal is a fixed parameter rather than an evolving one. However, because dispersal is determined in large measure by attributes of organisms, dispersal ability can evolve. The evolutionary potential of dispersal and the evolutionary constraints on it need to be characterized in order to predict its future contribution to ecological dynamics.

In plants, the evolvable component of seed dispersal is controlled primarily by the maternal parent rather than by the dispersing propagule itself (McCanny and Cavers, 1989; Do-

nohue, 1999). Characteristics of maternal plant architecture (Rabinowitz and Rapp, 1981; McCanny and Cavers, 1989; Sinha and Davidar, 1992; Thiede and Augspurger, 1996; Donohue, 1998), seed size, pericarp or achene structure, and fruit dehiscence patterns (Casper, 1982; Collins and Uno, 1985; Augspurger, 1986; McEvoy and Cox, 1988; Andersen, 1993; Lisci and Pacini, 1997; Jongejans and Telenius, 2001; Nathan et al., 2003) strongly determine seed dispersion patterns. All these traits are determined by the genotype of the maternal parent, since fruit, pericarp, and integument tissue are all maternal in origin (Westoby and Rice, 1982; Roach and Wulff, 1987).

Maternal determination of seed dispersal has important evolutionary and demographic consequences. First, the maternal determination of progeny characters can cause non-Mendelian contributions to correlations between maternal and offspring characters (Falconer, 1965; Kirkpatrick and Lande, 1989; Wade, 1998). While Mendelian inheritance is expected to cause positive correlations between maternal parents and offspring due to shared nuclear genes, maternal inheritance—especially through environmental mechanisms of progeny responses to maternal phenotypes—can alter intergenerational correlations between parents and offspring in ways that can qualitatively alter evolutionary responses to selection on progeny characters. For example, in a classic study, Falconer (1965) found that large mice tended to have large litters of small mice (because competition for milk among members of the larger litter caused slower growth rates and consequently smaller adult sizes) and that these small mice tended to have small litters of larger mice. This dynamic led to negative correlations between generations for body and litter size, and also led to a negative response to selection on body size; selection for larger mice actually resulted in smaller mice in the next generation. A similar negative maternal effect was found for

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seed dispersion patterns in the annual plant *Cakile edentula* (Brassicaceae), in which large plants had many seeds that were dispersed to high post-dispersal densities, and those seeds grew into small plants that dispersed seeds to low densities (Donohue, 1999).

Maternal determination of progeny characters can impose additional evolutionary constraints when a trait under selection in the offspring also influences the fitness of the maternal parent (Kirkpatrick and Lande, 1989; Wade, 1998; Wolf and Wade, 2001). That is, a maternal trait can directly influence maternal fitness, but it can also influence progeny fitness by altering the progeny's phenotype, which in turn influences progeny fitness. Correlated selection acting through both maternal parents and through progeny can impose constraints on the evolution of such maternal characters. For example, in *Cakile edentula*, traits that enhanced seed dispersal and thereby increased progeny fitness also reduced maternal fitness (Donohue, 1997, 1999). The evolution of these dispersal-enhancing traits would therefore be constrained by correlated selection acting through the maternal parent.

To predict the evolutionary dynamics of seed dispersal, explicit functional studies are necessary. It is the specific nature of the correlations among characters, both within and across generations, that determines the evolutionary constraints and the dynamics of maternally determined characters (Kirkpatrick and Lande, 1989). First, particular maternal traits need to be identified in order to assess their evolutionary potential. Second, their pleiotropic effects on other traits, including maternal fitness, need to be quantified. Third, the responses of these traits to environmental factors (Peroni, 1994; Donohue, 1999; Imbert and Ronce, 2001; Mazer and Lowry, 2003)—especially those factors, such as density, that are predicted to vary with dispersal itself—also need to be characterized. Combined, this information enables predictions of the evolutionary dynamics of dispersal by providing estimates of the across-generation correlations for dispersal and by revealing potential selective constraints on its evolution.

In this study, we identified plant traits that influence dispersal under controlled conditions and examined their interaction with one important environmental factor: conspecific density. We focused on density because dispersal determines sibling density in many species (Howe and Smallwood, 1982), and many plant traits are known to be highly plastic in response to density (reviewed in Donohue and Schmitt, 1998; Donohue, 2003). Thus, dispersal in one generation can influence dispersal in the next generation through density-mediated maternal effects on plant traits.

We measured seed dispersion patterns of *Arabidopsis thaliana* (L.) Heynh. (Brassicaceae) grown at high and low density under controlled conditions. Studies under controlled conditions enabled us to manipulate density to determine its effect on specific plant characters and on seed dispersion patterns themselves. Such studies would have been prohibitively difficult in the field because the seeds of *A. thaliana* are tiny, making their recovery 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 the first necessary step towards identifying relevant mechanisms of dis-

persal variation in *A. thaliana* for future studies under more ecologically realistic environments.

We asked the following questions: (1) What maternal plant traits determine seed dispersion patterns, and are their effects on dispersal consistent across density environments? (2) Does dispersal itself respond to density, and if so, to what extent is its plasticity accounted for by plasticity of the measured maternal traits? (3) Do the maternal traits that influence dispersal also influence maternal fitness, and if so, does such selection on the maternal plants oppose or augment selection on dispersal acting through the progeny?

MATERIALS AND METHODS

The study system—*Arabidopsis thaliana* is a weedy mustard that typically displays a winter annual or spring annual life history (Napp-Zinn, 1976; Nordborg and Bergelson, 1999). It is native to Western Eurasia and 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. *Arabidopsis thaliana* is autogamous and has a high rate of self-fertilization in the field (Abbott and Gomes, 1989), resulting in high homozygosity (Todokoro et al., 1995; Berge et al., 1998; Bergelson et al., 1998).

We used 12 ecotypes of *A. thaliana* for this study. Five 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 from Rhode Island, Tennessee, and Michigan; two from Massachusetts and Kentucky; see Griffith et al., 2004, for more information on these populations). The ecotypes were chosen based on their variation in phenotypic characters hypothesized to be associated with dispersal ability, such as height, branching patterns, and silique morphology. 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.

Experimental design—We grew the 12 ecotypes at two densities and measured seed dispersion patterns of plants at a specific developmental stage under controlled conditions. 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 6.35 cm² pot. The high-density treatment consisted of a single plant of a given ecotype in a 6.35 cm² pot, surrounded by 19 yellow-seeded, "transparent testa" mutants ("ttg" stock # CS3128 on a Landsberg ecotype background). Seeds from the nonmutant ecotype could be distinguished from seeds of 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 were planted 1 month after plants at low density because they flower approximately 1 month sooner. This enabled plants in high and low density 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 12-h 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 12-h 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 first day of 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, fruit characters and architectural traits of each plant were measured. We measured the height of the primary stem, the

total number of branches, and the total number of mature and immature fruits. To characterize fruit placement, we recorded the proportion of fruits that was on the primary stem, the secondary inflorescence stem, and on basal branches. We measured the angle of attachment (the angle between the main stem and the adaxial surface of the branch) of three random branches on the main inflorescence if they existed, and we recorded the length of the average silique, based on a subset of 10 siliques randomly located on each plant. To estimate the propensity for siliques to dehisce, we calculated the total proportion of mature siliques that had dehisced during the dispersal trial (not including those that dehisced before the 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 1 min after the plant had been placed in the wind tunnel, and the plant remained in the wind tunnel for 4 min 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 4000 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. Even using subsampling techniques, the data set included the individual positions of over 250 000 seeds. To estimate background dispersal of neighboring plants grown in high density, we recorded the seed dispersion patterns of the yellow-seeded mutants based on 12 pots sampled across the ecotypes.

We calculated six measures 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 was that of the 0.25 × 0.25 cm grid marks, which represents the spatial scale of interactions between individual germinants. The second scale was that of a 2.5 × 2.5 cm area, which represents a spatial scale of interactions among adult plants and is approximately half the dimension 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 (although we provide measures of background dispersal by the yellow-seeded mutants as well); the background density would be similar across all ecotypes since the same genotype was used as competitors for all focal ecotypes. Consequently, post-dispersal density measures sibling density, not total density. 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 (again, not including those that dehisced prior to the 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 estimate of seeds per silique was based on a sample of 10 siliques from 10 plants sampled across ecotypes from each density treatment (100 siliques total per treatment). The estimated proportion of seeds dispersed beyond recovery ("% Beyond") was $1 - [(\text{the total number of seeds recovered}) / (\text{estimated number of seeds dispersed})]$.

Statistical analysis—We first tested for potential experimental artifacts by regressing our measurements of dispersal on flowering time and the interval (in days) between each plant's flowering and dispersal trial (a measurement of plant development at the time of dispersal) using PROC GLM in SAS (1990). To identify maternal traits to be used in the analysis, we calculated the Pearson correlations between all maternal characters (results are not presented for traits that were not chosen for further analysis). If characters were highly correlated, only one was chosen as a trait to be used in the analysis to avoid problems of collinearity. Based on the correlations, we chose the following characters for further analysis: total number of fruits produced, total number of branches, height of the primary stem, longest inflorescence branch length, average branch angle, average silique length (natural log transformed to normality), and propensity of fruit dehiscence (proportion of fruits dehisced during the trial, arcsine square-root transformed to normality). We used measurements of inflorescence branch traits instead of basal branch traits because most plants in high density did not produce basal branches, preventing comparisons between density treatments. We did not use characters of fruit placement because they were strongly correlated with number of branches. We also calculated Spearman correlations among all dispersal measurements.

To identify maternal traits associated with dispersal, we performed a multiple regression using the measurements of dispersal as the dependent variables and the maternal traits as the predictor variables. Maternal traits were standardized to have a mean of zero and SD of one in each treatment so that the relative effect of each trait could be compared within and across density treatments. We performed the regression on plants grown in high and low density separately. For some measures of dispersal, the residuals of these analyses were not always normally distributed so standard errors were based on jackknife resampling using the software *Freestat* (Mitchell-Olds, 1987). ANCOVA, pooled across both densities and with density as a fixed factor, tested for significant interactions between maternal traits and density, with significant interactions indicating that the effect of the maternal trait on dispersal differed between density treatments. This analysis also tested for residual effects of density after controlling for the effects of density on maternal traits.

To test for plasticity in maternal characters and dispersal, we performed an ANOVA on maternal characters and dispersal measures, using density (fixed), ecotype (random), and the interaction of density and ecotype as factors in the model. See Donohue et al. (2005) for further genetic analyses.

To quantify the association between maternal plant traits and maternal fitness, we conducted a phenotypic selection analysis (Lande and Arnold, 1983; Arnold and Wade, 1984; Mitchell-Olds and Shaw, 1987) of maternal plant traits on maternal fitness in each density treatment. Maternal fitness was estimated as the total number of fruits produced by the maternal plant. Maternal traits were standardized within each treatment to have a mean of zero and SD of one. Relative fitness was calculated in each treatment by dividing the number of fruits produced by an individual plant by the mean number of fruits produced by all plants in each density. The strength of direct selection (β), while controlling for correlations among characters, was estimated through multiple regression of all maternal traits on maternal fitness. Linear and quadratic selection coefficients were calculated to estimate directional and nonlinear (stabilizing or disruptive) selection respectively. Quadratic selection was not detected, so these results are not presented. To determine whether selection on maternal traits differed significantly between density treatments, we conducted an ANCOVA of fitness, with density and its interactions with maternal traits as factors. Significant interactions between density and a maternal trait would indicate that the strength of selection on that trait differed with density.

To summarize the correlations across generations for post-dispersal density, we calculated the Spearman correlation between maternal density and post-dispersal sibling and total density at the 2.5 × 2.5 cm spatial scale, which approximates half the dimension of the pots we used.

RESULTS

Effects of experimental artifacts—The mean estimated recovery rates of seeds that were dispersed during the trials were

TABLE 1. Pearson correlations among maternal plant characters. Correlations for plants grown at high density are shown above the diagonal, and correlations for plants grown at low density are shown below the diagonal. Significance based on Bonferroni corrections for multiple comparisons are indicated in boldface. $N = 116$ plants for high density, $N = 111$ plants for low density. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	Fruits	Branches	Height	Br. length	Br. angle	Silique length	Dehisc.	Flowering date
Fruits		0.62***	0.63***	0.59***	0.10	0.72***	0.00	-0.05
Branches	0.56***		0.42***	0.45***	-0.11	0.47***	0.06	-0.07
Height	0.23*	-0.06		0.50***	0.38***	0.51***	0.28**	-0.35***
Br. length	0.34***	-0.01	0.51***		0.12	0.31***	0.10	0.00
Br. angle	-0.23*	-0.20	0.39***	0.19		0.39***	-0.04	-0.41***
Sil. length	0.05	-0.05	0.44***	0.38***	0.62***		-0.18	-0.29**
Dehiscence	-0.06	-0.19	0.24*	0.14	0.10	-0.08		0.19*
Flowering	-0.12	0.01	-0.43***	-0.60***	-0.44***	-0.54***	0.02	

82.3% for low-density plants and 85.2% for high-density plants. The interval between flowering and the dispersal trial did not significantly influence any measure of dispersal. Plants that flowered later had slightly higher kurtosis ($\beta = 0.01$, $P < 0.05$). Flowering date was therefore included in subsequent analyses in order to control for possible effects of development time on the dispersal measurements.

Wind speed did not differ significantly among ecotypes ($P \gg 0.05$) or density treatments ($P \gg 0.05$). Wind direction slightly skewed all seed shadows to the left. The magnitude of the shift differed somewhat by trial, but it did not differ with ecotype or density. Therefore, these wind factors it did not affect our analysis of the influence of ecotype or density on dispersal.

The influence of maternal traits on dispersal—At both densities, plants that produced more fruits were taller, produced more branches, and had longer branches (Table 1). At high density, additional size (or elongation) traits were positively correlated, such that taller plants had more and longer branches with more oblique branching angles, longer siliques, and a higher propensity for silique dehiscence. Plants that flowered later at high density were shorter and had more acute branching angles. Silique length was positively associated with all other characters except propensity for dehiscence, with which it was not significantly correlated. Correlations among characters were similar at low density, except that branch number did not predict other size traits: plants with more branches were not taller, did not have longer branches, and did not have longer siliques. Plants that flowered later at low density had shorter branches, but otherwise the relationship between flowering date and the other traits resembled those at high density.

Some dispersal measures were significantly correlated, but the strength of the correlations indicated that the measures were not redundant to each other (Table 2). At both densities,

higher kurtosis was associated with shorter dispersal distances and smaller SDs in dispersal distance. Unexpectedly, sibling density was not correlated with local dispersal distance at either maternal density, but plants with denser seed dispersion patterns dispersed fewer seeds beyond 2 m. The two estimates of density were positively correlated at both densities. For plants grown at high density, high post-dispersal density was associated with lower SD and higher kurtosis, and plants that dispersed seeds farther also had higher SDs in dispersal distance.

Distance—In high density, taller plants dispersed seeds farther, and the effect of height on dispersal distance was significantly stronger for plants in high density (Table 3a). In low density, plants with fewer branches dispersed seeds farther, suggesting that branches impeded dispersal.

Standard deviation of distance—At high density, plants with more branches and smaller siliques had larger SDs of dispersal distance, indicating that spreading seeds among siliques and branches tended to increase the variance in dispersal distance (Table 3b). At low density, plants with an intermediate number of branches and branching angles, larger siliques and more silique dehiscence had larger SDs of dispersal distance. The effect of all these traits significantly differed between density treatments. In addition, plants at low density tended to have a larger SD in dispersal distance if they had fewer fruits, and this relationship was nonlinear (the relationship had a stronger effect when fruit number was larger). At low density, therefore, a larger variance in dispersal distance resulted from packaging fewer total seeds in more discrete units (i.e., more seeds within siliques and fewer siliques among branches).

Kurtosis—At high density, shorter plants had more leptokurtic seed distributions (longer tails), and the influence of

TABLE 2. Spearman rank correlations among measures of dispersal. Correlations for plants grown at high density are shown above the diagonal, and correlations for plants grown at low density are shown below the diagonal. Significance based on Bonferroni corrections for multiple comparisons are indicated in boldface. “MCI at 0.25 cm” = Mean crowding index at the small spatial scale (seeds/0.25 cm × 0.25 cm). “MCI at 2.5 cm” = Mean crowding index at the larger spatial scale (seeds/2.5 cm × 2.5 cm). $N = 116$ plants for high density, $N = 111$ plants for low density. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	Distance	SD distance	Kurtosis	MCI at 0.25 cm	MCI at 2.5 cm	% Beyond
Distance		0.32***	-0.55***	-0.08	-0.05	0.09
SD distance	0.13		-0.72***	-0.25**	-0.58***	0.16
Kurtosis	-0.25**	-0.69***		0.18	0.38***	-0.11
MCI at 0.25 cm	-0.17	0.02	0.02		0.53***	-0.30**
MCI at 2.5 cm	-0.16	-0.02	0.15	0.67***		-0.21*
% Beyond	0.08	0.00	-0.06	-0.45***	-0.24*	

TABLE 3. Results of multiple regression of standardized plant traits on measures of dispersal. β = the linear regression coefficient. γ = the quadratic regression coefficient, when significant. "F-inter" refers to the *F*-ratio of the interaction between the traits and density, which tests for significant differences in the effects of plant traits on dispersal in high and low density. *N* = 116 plants for high density, *N* = 111 plants for low density. Boldface indicates significance according to a Bonferroni criterion that corrects for multiple tests across all six measure of dispersal. * *P* < 0.05, ** *P* < 0.01, *** *P* < 0.001.

TABLE 3A. Distance. Parametric standard errors are given.

Trait	High density		Low density		F-inter
	β	SE	β	SE	
Fruits	-0.62	2.91	-0.05	1.49	0.03
Branches	-2.72	2.93	-3.78**	1.36	0.12
Height	10.49***	2.64	1.35	1.41	10.31**
Branch length	-1.61	1.98	2.63	1.48	2.96
Branch angle	-0.06	1.81	-0.38	1.46	0.02
Silique length	-4.44	2.53	-1.03	1.59	1.38
Dehiscence	-0.94	1.73	-2.30	1.42	0.36
Flowering	0.27	1.90	-0.78	1.62	0.17
<i>R</i> ²	0.27		0.17		

TABLE 3B. SD distance. Jackknife standard errors are given.

Trait	High density		Low density		F-inter
	β	SE	β	SE	
Fruits	-1.37	1.33	-0.93 ($\gamma = 0.70^*$)	0.66 (0.27)	0.28
Branches	3.32*	1.34	-0.54 ($\gamma = -0.82^*$)	0.46 (0.37)	8.40**
Height	-0.60	1.21	0.40	0.46	1.07
Branch length	0.10	0.91	-0.21	0.48	0.01
Branch angle	1.08	0.83	-0.75 ($\gamma = -0.74^*$)	0.48 (0.32)	4.02*
Silique length	-2.24*	1.16	1.83***	0.53	9.86**
Dehiscence	-0.59	0.79	1.34**	0.46	4.81*
Flowering	-0.58	0.87	0.68	0.53	1.07
<i>R</i> ²	0.23		0.48		

TABLE 3C. Kurtosis. Jackknife standard errors are given.

Trait	High density		Low density		F-inter
	β	SE	β	SE	
Fruits	-0.22	0.31	0.12**	0.04	1.73
Branches	0.01	0.31	-0.02	0.04	0.01
Height	-0.82**	0.28	-0.04	0.04	9.72**
Branch length	0.13	0.21	0.01	0.04	0.41
Branch angle	0.35	0.19	-0.04 ($\gamma = 0.08^{**}$)	0.04 (0.03)	3.43
Silique length	0.33	0.27	-0.12**	0.04	2.92
Dehiscence	0.11	0.18	-0.09*	0.04	1.24
Flowering	-0.21	0.20	-0.05	0.04	0.73
<i>R</i> ²	0.23		0.42		

TABLE 3D. Mean crowding index at the small spatial scale (seeds/0.25 cm \times 0.25 cm). Jackknife standard errors are given.

Trait	High density		Low density		F-inter
	β	SE	β	SE	
Fruits	0.00	0.01	0.02**	0.01	3.86
Branches	0.00	0.01	0.00	0.01	0.00
Height	0.01	0.01	0.01	0.01	0.50
Branch length	0.00	0.01	-0.01	0.01	1.43
Branch angle	0.00	0.01	-0.02*	0.01	2.58
Silique length	0.00	0.01	0.02	0.01	2.09
Dehiscence	0.00	0.01	0.02**	0.01	8.15**
Flowering	0.00	0.01	0.01	0.01	0.36
<i>R</i> ²	0.07		0.35		

TABLE 3E. Mean crowding index at the larger spatial scale (seeds/2.5 cm × 2.5 cm). Parametric standard errors are given. + = $P < 0.06$.

Trait	High density		Low density		F-inter
	β	SE	β	SE	
Fruits	0.46*** ($\gamma = 0.20^{**}$)	0.09 (0.06)	0.67***	0.10	1.27
Branches	-0.24*	0.09	-0.14*	0.09	0.00
Height	-0.20*	0.09	0.04	0.10	1.12
Branch length	-0.04	0.06	-0.16	0.10	0.38
Branch angle	0.09 ($\gamma = -0.07^{*}$)	0.06 (0.03)	-0.17**	0.10	4.44*
Silique length	0.21*	0.08	0.19**	0.10	0.53
Dehiscence	0.39*** ($\gamma = -0.06^{**}$)	0.06 (0.02)	0.32**	0.10	0.08
Flowering	0.13*	0.06	0.05	0.11	0.02
R^2	0.69		0.77		

TABLE 3F. Proportion of seeds dispersed beyond recovery. Parametric standard errors are given.

Trait	High density		Low density		F-inter
	β	SE	β	SE	
Fruits	0.24*** ($\gamma = -0.25^{***}$)	0.09 (0.05)	-0.11**	0.04	14.53***
Branches	0.07	0.09	0.07*	0.04	0.01
Height	-0.07	0.08	0.01	0.04	0.85
Branch length	0.03	0.06	0.12**	0.04	1.55
Branch angle	-0.04	0.06	0.11**	0.04	4.44*
Silique length	-0.04	0.08	-0.12**	0.04	0.75
Dehiscence	0.25***	0.05	0.12**	0.04	3.21
Flowering	-0.06	0.06	0.12**	0.05	5.67*
R^2	0.33		0.35		

height was significantly stronger at high density (Table 3c). At low density, plants with more fruits, shorter siliques, and less dehiscence had more leptokurtic distributions, and plants with intermediate branch angles had more platykurtic distributions. The effect of these characters did not differ significantly across density, although their effects were not significant at high density.

Post-dispersal sibling density—No plant characters significantly predicted post-dispersal sibling density at the scale of interactions among seedlings (0.25 × 0.25 cm) when plants were grown at high density (Table 3d). Plant characters accounted for substantially more of the variance in small-scale seed density when plants were grown at low density. These plants had higher post-dispersal densities if they had more fruits, had more acute branching angles, and dehisced more fruits (significantly stronger at low density).

Plant traits accounted for much of the variation in post-dispersal seed density at the larger spatial scale (Table 3e). Plants had higher post-dispersal density if they produced more fruits (with a stronger effect of fruit number at higher values when plants were grown at high density), had fewer branches (nearly significant), were shorter (nearly significant at high density only), had longer siliques, and had dehisced more fruits (with a stronger effect of dehiscence at lower values when plants were grown at high density). Intermediate branch angle (high density) or more acute branch angle (low density) was associated with high post-dispersal density (significantly stronger at low density). As was observed for density at the smaller spatial scale, higher density resulted from more seeds being dispersed and from the seeds not being distributed across the plant (i.e., among branches or among siliques).

Dispersal beyond 2 m—At high density, plants with an intermediate number of fruits and greater dehiscence dispersed

more seeds beyond recovery (Table 3f). At low density, plants dispersed a higher proportion of seeds beyond 2 m if they had fewer fruits (significantly different across density treatments) but more dehiscence of those fruits (nearly significant), more and longer branches with more oblique branching angles (significantly different across density treatments), shorter siliques, and if they flowered later (nearly significant). Plant traits therefore influenced short-distance dispersion patterns (“average distance” less than 2 m) differently from longer distance (beyond 2 m) dispersal ability.

In summary, the number of seeds dispersed and the distribution of those seeds among siliques and branches influenced multiple aspects of seed dispersion patterns. Different traits, however, influenced different components of seed dispersion patterns. In addition, the effect of a given plant trait on dispersal frequently depended on the density in which the plant grew.

Plasticity of maternal traits and dispersal—Density significantly altered maternal plant morphology (Fig. 1; MANOVA: F [Wilk's λ] = 35.83, $P < 0.001$). Plants grown at high density were shorter, produced fewer branches, had shorter branches with more acute angles, had shorter siliques (with fewer seeds; 292.8, SE = 24.2 vs. 369.2, SE = 15.2 at low density), and flowered approximately 3 days later than plants grown in low density. The propensity to dehiscence did not differ significantly between density treatments.

Dispersal differed significantly between plants grown at low and high density (Fig. 2; MANOVA: F [Wilk's λ] = 73.73, $P < 0.001$). Plants grown at high density dispersed their seeds shorter distances, had a higher SD in dispersal distance, and had lower sibling density at both spatial scales after dispersal. Kurtosis and the percentage of fruits dispersed beyond recovery did not differ between density treatments. For plants at high density, background dispersal resulted in shorter dispersal

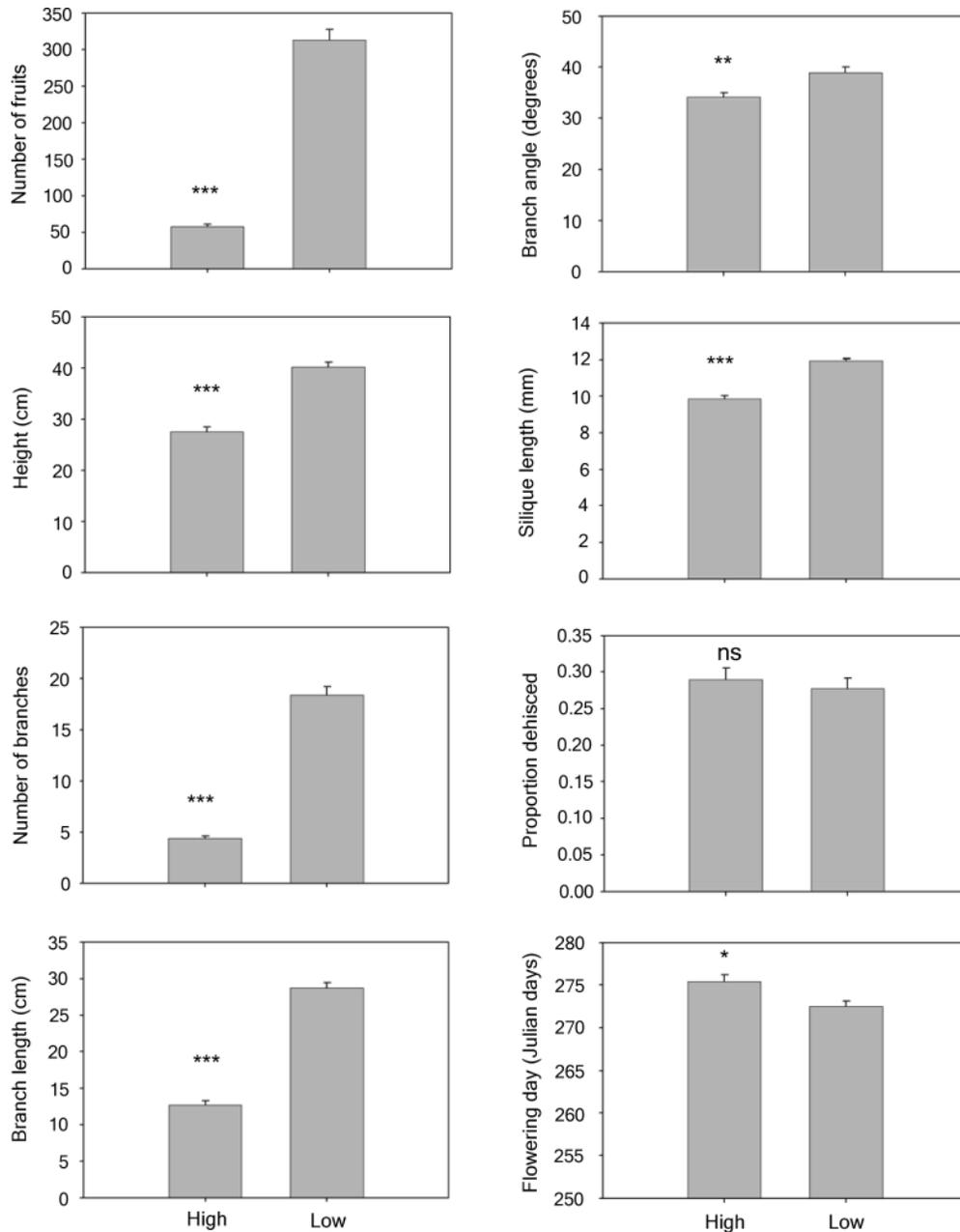


Fig. 1. Means and standard errors of maternal plant traits of *Arabidopsis thaliana* when plants were grown at high and low density. Significance levels indicate significant differences between density treatments. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns = not significant.

distances of the total sample of seeds than at low density, a lower SD, and a more leptokurtic seed shadow. Total density (including background seeds) was higher at both spatial scales for plants grown at high density than at low density.

Density significantly ($P < 0.001$) influenced all measures of dispersal that differed between density treatments even after controlling for the plasticity of characters to density. Therefore either interference by neighbors inhibited dispersal, or density altered the expression of unmeasured maternal traits that influence dispersal.

Plasticity of plant traits and dispersal influenced their predicted correlations across generations (Table 4). The correlation in fitness (number of fruits) across generations is expected

to be negative; high fruit production by maternal plants (i.e., high fitness of maternal plants) was associated with higher sibling density (Tables 3d and e), but this higher density caused plants to produce fewer fruits (lower fitness; Fig.1). The correlation between generations for silique length is also predicted to be negative. In contrast, the correlations across generations for the number and angle of branches and for height are predicted to be positive. At high density, a constant background seed shadow would weaken the correlations, however.

The correlation between the density of maternal plants and their seeds was -0.47 ($P < 0.001$). Therefore, plants growing in high density are predicted to have progeny with lower sib-

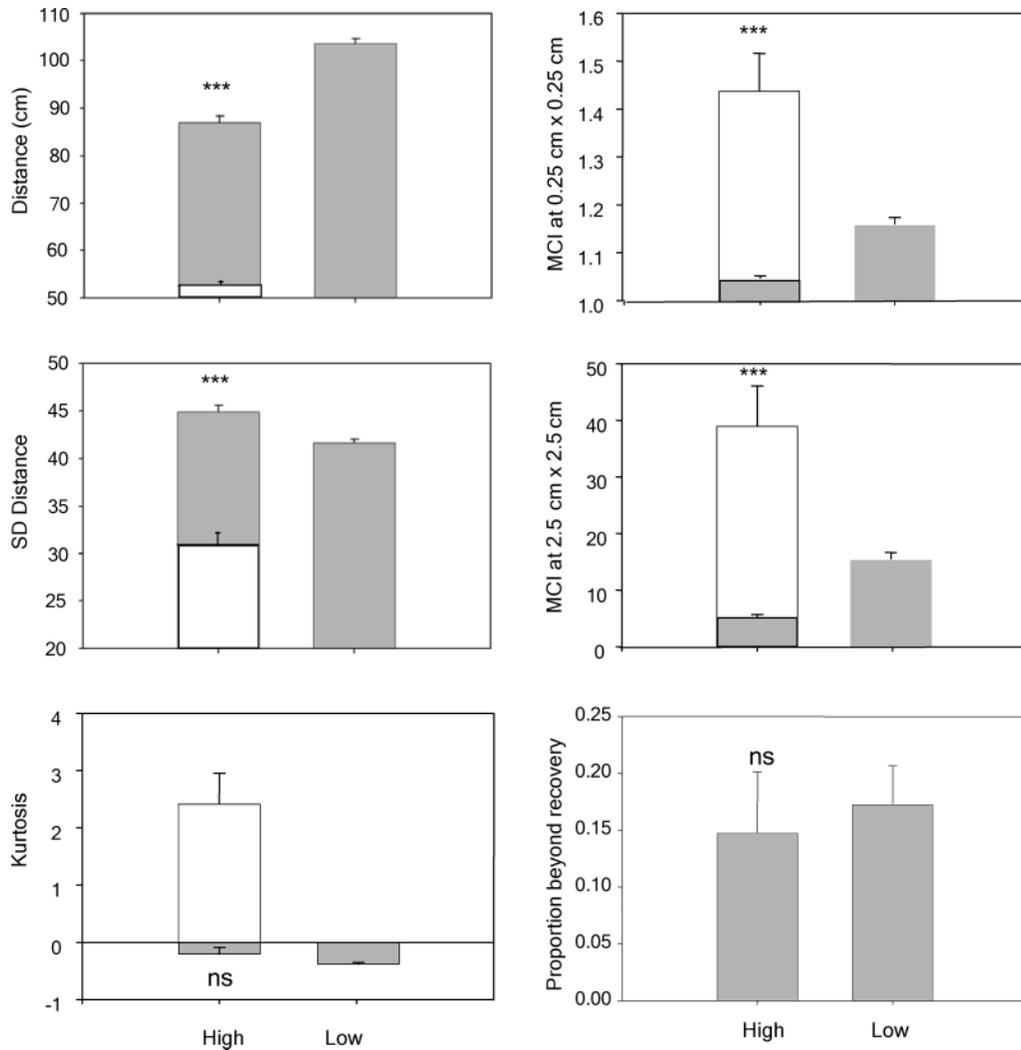


Fig. 2. Means and standard errors of dispersal measures of *Arabidopsis thaliana* when maternal plants were grown at high and low density. White bars at high density indicate the seed dispersion patterns of the background yellow-seeded mutants. Significance levels indicate significant differences between density treatments for focal seeds. Background dispersal at high density differed significantly ($P < 0.001$) from dispersal at low density for all measures. *** $P < 0.001$, ns = not significant.

ling densities. However, their progeny would nevertheless experience higher total density because of the high background density of seeds dispersed by neighbors ($r = 0.66, P < 0.01$).

Selection on dispersal and maternal traits—High density was associated with lower fruit production in maternal plants

TABLE 4. Summary of the directions of the effects of maternal traits on post-dispersal density and the effects of density on maternal traits. The last column shows the direction of the predicted correlation between maternal traits and traits of progeny, as estimated by the product of the two coefficients.

Maternal trait	Increase in maternal trait → Post-dispersal density	High density → Maternal trait	Correlation across generations
Fruits	+	–	–
No. of branches	–	–	+
Height	–	–	+
Branch angle	–	–	+
Silique length	+	–	–
Dehiscence	+	0	0

(Fig. 1), with plants grown in low density having up to six times more fruits than plants grown in high density. Therefore, dispersal to lower density would be favored by selection, all else being equal.

Maternal plant traits also influenced maternal fruit production (Table 5). In plants grown at high density, plants produced more fruits if they were taller, had longer, more acute branches, had longer siliques and flowered later. All plant characters influenced fruit production in a similar manner at low density, except that the effect of silique length was not significant and was significantly weaker at low density. The effect of branch production was significant for plants grown at low density but not for plants grown at high density, although the effect of this trait did not differ significantly between density treatments. The effect of dehiscence differed significantly across treatments, but its effect was not significant in either density.

Some maternal plant characters that were associated with high maternal fitness were also associated with higher progeny densities and therefore lower progeny fitness (Table 6). This was the case for fruit production, branch angle (at low den-

TABLE 5. Results of selection analysis of standardized plant traits on relative maternal fitness in two density treatments. " β " measures the strength of direct selection. " F -interaction" refers to the F -ratio of the interaction between the plant trait and density in order to test for differences in the strength of selection in high and low density. $N = 116$ plants for high density, $N = 111$ plants for low density. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Trait	β High (SE)	β Low (SE)	F -interaction
Branches	0.16 (0.09)	0.28 (0.04)***	1.89
Height	0.24 (0.07)**	0.10 (0.04)*	2.88
Branch length	0.15 (0.06)**	0.10 (0.05)*	0.52
Branch angle	-0.12 (0.05)*	-0.13 (0.04)**	0.01
Silique length	0.27 (0.06)***	0.02 (0.05)	10.12**
Dehiscence	-0.09 (0.05)	0.07 (0.04)	6.17*
Flowering day	0.01 (0.01)*	0.02 (0.01)*	0.07

sity), and silique length. In contrast, increased height and number of branches would increase fitness in both generations, while selection on dehiscence would occur only through selection on dispersal because it did not influence maternal fitness.

DISCUSSION

Several plant characters influenced dispersal, but the magnitude of their effect depended on the density in which the maternal plant was growing. Therefore, as dispersal evolves in response to natural selection, altering post-dispersal densities, the plant traits that would contribute to the further evolution of dispersal are expected to change. The nature of the interactions between post-dispersal density and maternal plant traits led to the prediction of negative correlations between maternal and progeny generations for sibling density, fitness, and some morphological traits, but positive correlations between generations for total density and other traits. Such correlations are predicted to alter the evolutionary trajectories of these traits, causing accelerated (if positive) or retarded (if negative) responses to selection (Kirkpatrick and Lande, 1989). Some traits were associated with high maternal fitness but low progeny fitness, while others influenced the fitness of maternal plants and progeny in the same manner. Opposing fitness effects in maternal and progeny generations would constrain the adaptive evolution of the plant traits and dispersal.

Density-dependent effects of maternal plant characters on dispersal—Density significantly influenced dispersal, both directly and indirectly. Neighboring plants physically impeded dispersal (see also Telenius, 1992; Thiede and Augspurger, 1996), but indirect effects of density, operating through its influence on the expression of maternal plant traits, were also strong. Such plasticity of maternal characters in response to density caused the influence of maternal characters on dispersal to change with density.

For example, the effect of branch characters on dispersal changed with density. Fewer branches with more acute branching angles resulted in shorter dispersal distances (branch number only), less variance in dispersal distance (branch number only), higher post-dispersal sibling density, and less dispersal beyond 2 m. The stronger effect of branch number on the SD of dispersal distance at high density is likely to be because several plants at high density had no or very few branches. A lack of branches at high density limited the variation in fruit placement, while a small number of branches was highly ef-

TABLE 6. Summary of the effects of maternal traits on predicted progeny fitness (operating through effects on dispersal) and on maternal fitness. If the direction of the effect differs between maternal plants and offspring, then a conflict on the effect of the trait on maternal and progeny fitness exists between the two generations. ¹ At high density, more oblique angles increased density and lowered progeny fitness, and at low density more acute angles increased density and lowered progeny fitness. ² Effect significant only at low density. ³ Effect significant only at high density.

Maternal trait	Increase in maternal trait \rightarrow progeny fitness (via low density)	Increase in maternal trait \rightarrow maternal fitness	Conflict?
Fruits	-	+	Y
No. of branches	+	+ ²	N
Height	+	+	N
Branch angle	+ ¹	-	Y
Silique length	-	+ ³	Y
Dehiscence	-	0	N

fective at redistributing fruits and increasing the variation in dispersal distance. In low density, in contrast, all plants had several branches, so the effect of adding additional branches on fruit distribution was not as effective. This interpretation is consistent with the nonlinear effect of branch number on the SD of dispersal distance at low density. Likewise, the stronger effect of branch angle on post-dispersal density and dispersal beyond 2 m at low density is likely to be because plants in low density had longer branches and more oblique branch angles than those at high density. Oblique angles of long branches effectively placed siliques away from those on the primary stem, decongesting fruits and decreasing progeny density while dispersing more seeds longer distances. In contrast, branches were not long enough in high density for branch angle to influence dispersal strongly.

Height influenced dispersal distance and kurtosis at high density but not at low density. Height relative to neighbors appears to be most important at determining dispersal efficiency at high density; if plants were taller than their neighbors, dispersal was more efficient.

Plants with efficient silique dehiscence had larger SDs of dispersal distance and more platykurtic seed shadows. The effect was stronger at low density at which the range of plant size was much greater. In addition, longer siliques decreased the SD of distance and increased post-dispersal sibling density at high density, but they increased the SD and caused more platykurtic distributions at low density. At high density, larger siliques could result in less even distribution of fruits across the plant and consequently cause higher density at longer distances and thereby less variable dispersal distance. At low density, large siliques located on branches (which are more abundant at low density) might enable a large number of seeds to be dispersed to intermediate distances, decreasing kurtosis. The relationship between silique length, distribution of silique size among branches, and seed mass (i.e., larger seeds within longer siliques) should also be investigated in order to determine the mechanism through which silique length influences dispersal.

The changing influence of plant traits on dispersal at different densities indicates that different plant traits would be more important at determining seed dispersion patterns as dispersal evolves. For example, if natural selection were to favor more efficient dispersal to lower density, selection would first favor taller plants with extreme branch angles when post-dis-

persal densities were still high. As dispersal evolved to result in lower post-dispersal density, further selection on dispersal would favor more oblique branch angles. A change in the importance of different plant traits at different post-dispersal densities could alleviate the requirement for abundant genetic variation in a single character for the further evolution of dispersal; as dispersal evolves, different characters, not previously subjected to selection, can contribute to evolutionary responses to selection. Conversely, a change in the direction of selection on a trait as dispersal evolves, as is expected for branch angle, could impose a genetic constraint if genetic variation has been depleted by previous selection in the opposite direction.

Density as an evolving environment—The plasticity of maternal plant traits to density caused plasticity in dispersal itself. Plants growing at low density dispersed seeds to high sibling densities, and plants growing at high density dispersed seeds to lower sibling densities, although total density was higher. Consequently, effects of density contributed to a negative correlation between generations for post-dispersal sibling density and a positive correlation between generations for total density. Because sibling density is under the control of the maternal plant, such negative maternal effects on sibling density can impede the response to selection on post-dispersal density (Kirkpatrick and Lande, 1989; Donohue, 1999). The effect of background dispersal by neighbors would dampen correlations at high density, so the evolutionary dynamics will also depend on whether the background matrix of competitors is also evolving.

The ability of genetically based maternal characters to influence post-dispersal density makes the density environment itself a potentially evolving character (Wenny, 2001). Most plant morphological traits such as those measured in this study are known to have a genetic basis (Donohue et al., 2005). Even the plastic responses of such traits are known to have a genetic basis (reviewed in Donohue and Schmitt, 1998). Therefore, variation in dispersal itself is likely to have a genetic basis (Venable and Burquez, 1989; Kelman and Culvenor, 2003). In addition, dispersal is known to be under strong natural selection (e.g., Burdon and Chilvers, 1976; Augspurger, 1983; Howe and Smallwood, 1982; Donohue, 1997). Therefore, the post-dispersal environment is highly likely to be an evolving character. This study shows that dispersal has the potential to influence its own evolutionary dynamics by determining which maternal traits are subject to selection on dispersal and by influencing the correlation between generations for dispersal properties.

Selection on maternal characters—Maternal traits that influenced dispersal also influenced maternal fitness. Selection acting in the maternal generation sometimes augmented selection on dispersal. For example, plants with more branches had high fitness and also had lower post-dispersal density, which would increase progeny fitness. Such complementary selection can accelerate the evolution of dispersal. Selection acting through maternal fitness can also oppose selection on dispersal. For example, plants with more fruits and longer siliques had higher fitness but also higher post-dispersal density, which would decrease progeny fitness. Such conflicting selection acting on maternal plants and progeny can retard or even potentially reverse the evolution of dispersal. Other characters, such as percentage fruit dehiscence, significantly influenced dis-

persal but did not influence maternal fitness. Such characters can therefore respond to selection on dispersal without being constrained by selection on the maternal plants. The general result of plant architectural traits influencing maternal plant fitness is quite common (reviewed in Donohue and Schmitt, 1998), so the selective constraints on dispersal identified here are likely to be common in plants. How constrained the evolution of dispersal will be due to opposing selection acting through maternal fitness therefore will depend on which traits determine dispersal and the conditions under which they do so.

The relationship between plant traits and maternal fitness sometimes depended on density, as did the relationship between plant traits and dispersal. Consequently, as dispersal evolves and density changes, the relationship between selection on maternal traits acting through maternal fitness and through progeny dispersal also changes. For example, plants with larger siliques (which caused higher post-dispersal density) had higher fitness at high density but not at low density. If density evolved to be lower, then opposing selection acting through maternal fitness would disappear. Thus density-dependent effects of plant traits on both dispersal and maternal fitness can cause complex evolutionary dynamics of dispersal.

Conclusions—This functional analysis of seed dispersal identified several plant characters that influence seed dispersal under controlled conditions and characterized important density-dependent processes that can influence the evolution of dispersal. First, the density in which plants grew determined which plant characters influenced dispersal. Consequently, a change in density will change which maternal characters are subject to selection through selection on dispersal. Second, density-mediated maternal effects contributed to a negative correlation between generations for sibling density after dispersal. Such environmentally induced correlations between generations can impede responses to selection on dispersal. Finally, plant traits that influenced dispersal also influenced maternal fitness—sometimes augmenting selection on dispersal and sometimes opposing it—and the direction of the relationship sometimes depended on density. These density-dependent relationships between plant traits, dispersal, and maternal fitness can increase or reduce evolutionary constraints on dispersal, depending on the trait and depending on dispersal itself. Thus dispersal, by determining density, can influence its own evolution through density-dependent processes.

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