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Seed Dispersal as a Maternally Influenced Character: Mechanistic Basis of Maternal Effects and Selection on Maternal Characters in an Annual Plant

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ABSTRACT: Maternal influences on progeny characters affect phenotypic correlations between characters expressed in maternal and progeny generations and consequently influence evolutionary responses to selection. Net selection on maternally influenced characters depends on selection both on the progeny character and on the maternal characters that influence it. I used seed dispersal in *Cakile edentula* as a system in which to identify the mechanisms of environmentally mediated maternal effects and to determine how selection on maternal characters alters the adaptive value of dispersal. In *C. edentula*, maternal morphology responds to conspecific density experienced by the mother. Maternal morphology in turn affects offspring (seed) dispersal and density and thereby offspring morphology and fitness. I estimated the magnitude of density-mediated maternal effects on dispersal and identified their mechanism by characterizing the plasticity of maternal morphology to density. I also measured density-dependent selection on maternal characters that influence dispersal. Maternal plasticity to density was caused by both allometric and nonallometric variation in morphology, and this plasticity resulted in a negative correlation between maternal and progeny density. Such negative maternal effects are expected to retard responses to selection. Maternal morphology influenced maternal fitness, in part through the relationship of fitness to maternal plant size and in part through size-independent fitness effects. Maternal phenotypes that promote dispersal, and thereby increase progeny fitness, were associated with decreased maternal fitness. Selection on dispersal at the level of progeny favors increased dispersal; maternal influences on dispersal, however, not only cause a greatly reduced adaptive value of dispersal but lead to the prediction of a slower response to selection.

Keywords: dispersal, maternal effects, maternal environmental effects, phenotypic selection, plasticity, seed dispersal.

Maternal inheritance occurs when a maternal trait affects the phenotype of progeny by non-Mendelian mechanisms (Kirkpatrick and Lande 1989; Wade 1998). A maternal effect, as defined by Kirkpatrick and Lande (1989), is the strength of the effect of a mother's phenotype on the phenotype of her offspring or the partial regression coefficient of the offspring's phenotype on the mother's phenotype, while controlling for Mendelian inheritance. Positive maternal effects lead to accelerated responses to selection, while negative maternal effects lead to retarded, or even negative, responses to selection in the short term. For example, if large parents have small offspring because of maternal effects, selection for large parents can result in small, not large, offspring in the following generation (Falconer 1965). Maternal effects can also cause evolutionary time lags, oscillatory evolutionary trajectories, maladaptive evolution, and evolutionary momentum whereby evolution continues even after selection has ceased (Kirkpatrick and Lande 1989). A maternal trait can influence a progeny trait both directly and indirectly through its correlations with other traits and with maternal and progeny environment. Such correlations result in a network, or matrix, of maternal effects on progeny characters that lead to the unique evolutionary dynamics of maternally influenced characters (Kirkpatrick and Lande 1989).

What is the mechanism by which maternal effects are transmitted across generations? Maternal effects have been considered to be a form of cross-generational phenotypic plasticity whereby the maternal environment influences the phenotype of progeny (Schmitt 1995; Bernardo 1996; Mousseau and Fox 1998). Two different conceptions of

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maternal effects exist in the literature. In most theoretical formulations (e.g., Kirkpatrick and Lande 1989; Wade 1998), the environment experienced by offspring is the maternal phenotype (fig. 1*A*). For example, the mother's size or nutritional state is considered to be the environment in which progeny develop. In many empirical studies, however, the environment of interest is the ecological environment experienced by the mother (e.g., Alexander and Wulff 1985; Mousseau and Dingle 1991; Lacey 1996; Donohue and Schmitt 1998 and references therein; Mazer and Wolfe 1998; fig. 1*B*). Both have been referred to as maternal effects. I will refer to the former as maternal phenotypic effects and the latter as maternal environmental effects.

The ecological environment influences both sorts of maternal effects. It can determine the maternal phenotype, which in turn influences the progeny phenotype, or it can influence the progeny phenotype directly. The environment experienced by parents and offspring is itself often influenced by maternal or progeny characters, and this reciprocity can lead to more complex paths of maternal effects (fig. 1*C*). For example, maternal characters strongly influence progeny environment (competitive, nutritional, etc.) by such means as oviposition site preference in insects or seed dispersal in plants. The environment itself is thereby an important element in the maternal effects matrix and consequently can influence the magnitude of maternal effects.

Explicit inclusion of the ecological environment within paths of maternal effects clarifies the manner by which non-Mendelian mechanisms contribute to phenotypic correlations between generations. For example, if the ecological environment is constant and influences maternal and progeny phenotypes in the same manner, a positive covariance between maternal and offspring characters may result. However, if the environment influences the maternal and progeny characters differently, or if the environment varies in a systematic manner between generations, then the covariance between maternal and offspring generations could be rendered negative. Because the stability or variability of the environment can be determined by phenotypes (fig. 1*C*), the covariance between maternal and offspring environments can influence the magnitude and direction of maternal effects (Lacey 1998). In this sense, the external environment plays a role in determining the non-Mendelian component of correlations between generations for the maternally influenced character. Its role is defined by the reciprocal interaction of phenotypes with the environment.

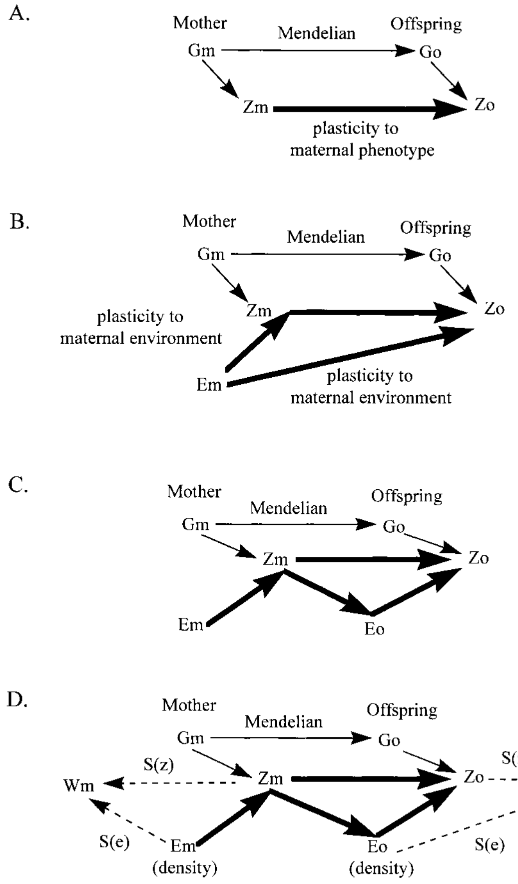

Figure 1: Mechanisms of maternal effects. Heavy lines indicate paths of maternal influence, and light lines indicate Mendelian transmission. *Z* represents a phenotype, *G* represents a genotype, and *E* represents the environment. Subscript *m* refers to the maternal parent, and subscript *o* refers to the offspring. *A*, Maternal phenotypic effect. The progeny character responds directly to the maternal phenotype, leading to a maternal effect. *B*, Maternal environmental effect. A maternal character responds to the maternal environment and then influences a progeny character, leading to an effect of the maternal environment. The progeny character can also respond to the maternal environment directly. *C*, Complex maternal phenotypic/environmental effects. Phenotype influences the environment experienced by progeny, and the environment influences phenotypic expression. Through the reciprocal interaction between phenotype and environment, the environment becomes an element within the paths of maternal effects. *D*, Selection on maternally influenced characters. Dashed lines indicate paths of selection; *W* represents fitness; *S*(*m*) represents the strength of selection on morphology or the magnitude of the effect of morphology on fitness; *S*(*e*) represents the magnitude of the effect of the environment on fitness. In the case of seed dispersal, dispersal is measured as density after dispersal. Therefore, *S*(*e*) represents the magnitude of the effect of dispersal, or density, on fitness.

The interaction between phenotype and environment, or phenotypic plasticity, is the primary mechanism of maternal effects in the preceding formulation. Plasticity, not only of the offspring but also of the maternal parent, determines the direction and magnitude of maternal effects.

In the formulation of Kirkpatrick and Lande, plastic responses that determine maternal effects are implicitly incorporated within the magnitude of the maternal effect, *m*, a fixed parameter that does not evolve. In contrast, many recent studies on the evolution of plasticity have determined that genetic variation for plasticity is common and that plastic responses often have fitness consequences. These results lead to the conclusion that plasticity itself, and maternal effects in particular, can evolve (e.g., Mousseau and Fox 1998; Schlichting and Pigliucci 1998) and that the evolution of maternal effects should be addressed within the context of the evolution of plasticity itself.

Both selection and response to selection can be altered by maternal influences. The magnitude and direction of maternal effects alter evolutionary responses to selection by influencing phenotypic correlations between generations, as discussed earlier. In addition, net selection on maternally influenced characters depends on the strength of selection in both maternal and progeny generations.

Selection on maternally influenced characters can act both on the progeny character and on the maternal characters that influence it (fig. 1*D*). Fitness consequences of both the progeny and maternal traits are incorporated into theoretical formulations of the evolution of maternally influenced characters (Kirkpatrick and Lande 1989; Wade 1998) since the vector of selection gradients includes selection on maternal and progeny characters. They are less frequently included in empirical investigations of the adaptive value of maternally influenced characters (Donohue and Schmitt 1998), with the exception of explicit investigations of parent-offspring conflict in behavioral studies (e.g., Alexander 1974; Wesneat and Sargent 1996) and studies concerned with trade-offs between offspring size and number (Smith and Fretwell 1974; Lloyd 1987; Haig and Westoby 1988). If a maternal effect results in an advantageous progeny phenotype but has negative fitness consequences for the mother, net selection favoring the progeny phenotype would be weaker owing to correlated selection on the maternal character.

Seed Dispersal as a Maternally Influenced Character

Seed dispersion patterns in many species are characterized by a high density of seeds within the vicinity of the maternal plant and decreasing density at greater distances (e.g., Rabinowitz and Rapp 1981; Howe and Smallwood 1982; Augspurger 1983*a*, 1983*b*; McEvoy and Cox 1988; Theide and Augspurger 1996). One question of interest is whether such a seed dispersion pattern is adaptive. Many studies on the selective consequences of seed dispersal suggest that it is not—that, in fact, the progeny would have much higher fitness if they were dispersed farther and to lower densities (Janzen 1972; Liew and Wong 1973; Burdon and Chilvers 1975; Augspurger 1983*b*; Donohue 1997). If this seed dispersion pattern is actually maladaptive, why then is it so common?

Dispersal, or dispersability, is here considered a progeny character because it is the progeny that are selected according to their position within a seed dispersion pattern. Previous studies of the adaptive value of seed dispersal have gone far in determining how dispersal influences the fitness of progeny. Absent from most of these studies, however, is the recognition that seed dispersal is maternally determined and that its evolution is therefore subject to the dynamics of maternally influenced characters (but see Roach and Wulff 1987; Theide and Augspurger 1996; Donohue 1998; Donohue and Schmitt 1998). Consequently, such studies are limited in their ability to estimate the net selective consequences of dispersal and to predict evolutionary responses to selection on dispersal.

Seed dispersal is much more strongly determined by the maternal phenotype than it is by the progeny's genotype. Dispersal is influenced by characteristics of seeds and fruits (e.g., Casper 1982; Venable and Levin 1985; Augspurger and Franson 1987; Andersen 1993) and by architectural traits of the maternal plant (e.g., McCanny and Cavers 1989; Shipley and Dion 1992; Theide and Augspurger 1996; Donohue 1998). Plant architectural traits are unambiguously traits of the maternal plant. Seed or fruit traits are determined by the seed coat, pericarp, or allocation of resources to endosperm, all of which are maternally determined (Roach and Wulff 1987).

Although numerous studies document fitness consequences of seed dispersal for progeny (reviewed in Howe and Smallwood 1982), no studies have investigated the fitness consequences to the mother of traits affecting seed dispersal. Some characters that influence seed dispersal, such as branch placement, fruit placement, and height, are associated with maternal resource acquisition ability or allocation strategies (Ballaré et al. 1989; Geber 1990; Weiner and Thomas 1992; Smith and Jordan 1994). Other characters, such as branch production and reproductive output, are directly associated with maternal vigor. Therefore, there is a strong indication that maternal traits that influence progeny dispersal may also influence maternal fitness. Net selection on dispersal includes selection on the maternal characters that determine dispersal.

Because seed dispersal is maternally determined, maternal effects are expected to influence its evolution. Maternal phenotypic effects, whereby maternal tissue influences progeny dispersal, have been documented abundantly, as just discussed. Direct evidence of maternal environmental effects on seed dispersion patterns is scarce (but see Lacey 1980; Peroni 1994; Theide and Augspurger 1996), but indirect evidence is abundant (reviewed in Donohue and Schmitt 1998). Environmental conditions often influence plant architecture, either through allometric relationships with size (Gerakis et al. 1975; Silander 1978; Thompson and Beattie 1981; Smith 1983; Huber and Stuefer 1997) or through a response to some cue, as in the case of photomorphogenic shade avoidance (Ballaré et al. 1987; Berntson and Weiner 1991; Schmitt and Wulff 1993; Smith and Jordan 1994). Plant architectural traits such as height, branchiness, or fruit abundance in turn often influence seed dispersion patterns (McCanny and Cavers 1989; Shipley and Dion 1992; Theide and Augspurger 1996; Donohue 1998). Consequently, the maternal environment is expected to influence seed dispersal through its influence on maternal plant morphology, and such maternal environmental effects on dispersal could be common.

Maternal morphology influences progeny dispersal, and dispersal in turn influences the expression of maternal morphological characters. In this manner, environmentally induced intergenerational phenotypic correlations, or maternal effects, can act on morphological characters (*m*[*m1*] and *m*[*m2*] in fig. 2) as well as on the progeny character, dispersal (*m*[*d*] in fig. 2). The direction and magnitude of these correlations depend on both the influence of maternal morphology on progeny dispersal and the plasticity of the morphological characters to the environment after dispersal. Such correlations create cycles of maternal effects that produce the unusual evolutionary dynamics of maternally influenced characters mentioned previously.

In this formulation, dispersal is both a progeny character and the progeny environment. Such a characterization of dispersal has many precedents. In theoretical models and empirical studies of the evolution of dispersal, dispersal is favored or disfavored depending on the environment to which progeny are dispersed. As such, dispersal is equated with the environment after dispersal. This somewhat solipsistic perspective makes explicit the components of the intergenerational correlations: plasticity of maternal morphology and the influence of maternal morphology on dispersal, or progeny environment.

In this study, I considered seed dispersal in *Cakile edentula* var. *lacustris* as a maternally influenced character and used this system to characterize the mechanism of maternal effects on seed dispersal and to determine how selection on maternal characters alters the adaptive value of dispersal. In *C. edentula*, density decreases with increased dispersal distance (Donohue 1998), whereas other environmental variables that influence progeny fitness do not (Donohue 1997). Consequently, selection on dispersal acts through density rather than through dispersal distance per se (Donohue 1997). The progeny character, dispersal, was therefore measured as progeny density after dispersal (or more specifically, mean crowding index as defined in Lloyd 1967). Maternal morphology influences progeny density after dispersal (Donohue 1998). I therefore studied the mechanistic basis of density-mediated maternal effects on dispersal by characterizing the plasticity of maternal morphology to density, and I measured selection on maternal morphological characters across a range of density environments.

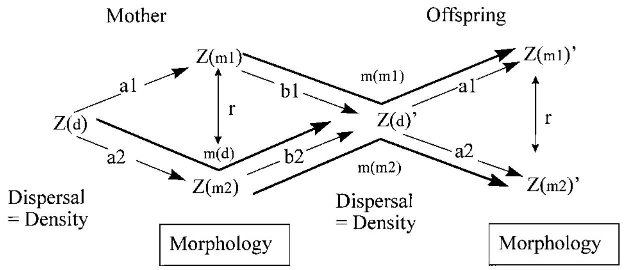

Figure 2: Path analysis to estimate environmentally induced correlations between generations (magnitude of maternal effects) for morphology and dispersal (density) when more than one maternal character influences a progeny character. Paths of Mendelian influence are not shown. The maternal effect of the phenotype of maternal trait 1 in the maternal generation, $Z(m1)$, on the same trait in the offspring generation, $Z(m1)'$, as mediated by density, $Z(d)'$, is denoted $m(m1)$. For a second character, the maternal effect of the phenotype in the maternal generation, $Z(m2)$, on that in the offspring generation, $Z(m2)'$, is $m(m2)$. Density in the maternal generation, $Z(d)$, influences density in the offspring generation $Z(d)'$, as mediated by morphology $Z(m1)$ and $Z(m2)$. The strength of this maternal effect is denoted $m(d)$. Path coefficients for the effects of density on morphology are represented as *a*'s, and *b*'s represent path coefficients for the effects of morphology on dispersal (density), estimated from multiple regression. Correlations among morphological characters are represented by *r*'s. See "Data Analysis" for details.

To characterize the mechanistic basis of density-mediated maternal effects on dispersal, I asked, first, How does density in the maternal generation influence the phenotypic expression of maternal morphological traits that affect seed dispersal, and what are the possible paths of indirect density effects through correlated characters? Second, Is plasticity of maternal characters attributable solely to allometric relationships of these characters with size, or can the characters respond to density independently of size? Finally, What are the magnitude and direction of density-mediated maternal effects on dispersal caused by plasticity of maternal morphological characters? By estimating the magnitude and direction of density-mediated maternal effects on dispersal, we can predict whether such maternal effects will enhance or retard the response to selection on dispersal.

To measure selection on maternal characters that influence progeny dispersal, I asked, Are morphological characters that influence seed dispersal associated with the fitness of the maternal parent? Does the nature of this association vary with density? To what extent are relationships between maternal morphology and fitness the result of their relationships with size as opposed to direct selection on the characters while controlling for size? The combined goals address both selection on dispersal and predicted evolutionary responses to selection (fig. 1*D*).

Methods

Biology of the Great Lakes Sea Rocket

Cakile edentula var. *lacustris* (Brassicaceae), or the Great Lakes sea rocket, is a highly selfing (Rodman 1974) annual plant that grows along the shores of the Great Lakes. Seed dispersal is by wind and water (Payne and Maun 1981; Donohue 1998). It has segmented fruits with a (usually) single-seeded deciduous distal segment that detaches easily from the proximal segment and can be dispersed independently from it. The proximal segment (also usually single seeded) often, but not always, remains attached to the dead maternal plant through germination. Even detached seeds, however, become entrapped by sand and branches of the maternal plant. Consequently, one often sees very high density clumps of seedlings near the dead and buried maternal plant as well as scattered individuals that germinated from proximal and distal segments that were dispersed by wind or water.

Density ranges enormously in the field, from individuals whose nearest neighbor is more than 20 m away to 200 individuals in a 100-cm^2 area (K. Donohue, personal observation). Plant morphology also varies substantially. A previous study showed that increased height, decreased spacing between branches, increased placement of fruits on the primary branch, and increased fruit production result in higher seed density after dispersal (Donohue 1998). These maternal morphological characters are the focus of this study. In addition, maternal site variables such as slope of the dune, distance from the water, and depth of burial of the maternal plant were shown to influence dispersal (Donohue 1998). These site variables were used in one analysis in this study (see "Data Analysis") to determine how variation in field environments influences maternal effects.

Greenhouse Experiment

To characterize density-mediated plasticity of maternal traits that influence dispersal and to measure selection on these maternal traits, seeds were collected from 45 plants along a 1/4-km transect at Mount Baldy in the National Lakeshore of the Indiana Dunes. One hundred twenty randomly selected seeds were used as focal individuals, and remaining seeds were used as competitors. Seeds were forced to germinate by removing the pericarp, scarifying the seed coat, and soaking the seeds in water for 24 h. Seed coats were removed as the seeds were planted into 3/4-inch plug trays containing Pro-Mix (Premier Brands; an artificial soil). During the first 2 wk, after cotyledons were open but before leaves began to develop, the seedlings were transplanted into one of four density treatments in Terra-green (Oil-Dry; baked clay). In 4 1/2-inch circular clay pots, one, eight, 15, and 30 seedlings were planted. After transplantation, plants were top watered as needed and fertilized twice a week with 50 ppm Peter's 20 : 10 : 20 NPK fertilizer.

A fungal pathogen, probably present on the seed coat, caused mortality of many seedlings before and immediately after transplantation. Heavily infected individuals and pots were discarded. Approximately 1 wk after transplanting, after transplant shock and mortality caused by the fungal pathogen had occurred, the number of competitors remaining in the pots was counted. If the focal individual had died, a new focal individual was randomly selected from the pot. Previous competitive interactions with the now dead seedlings were assumed to be negligible, so the number of competitors remaining at this stage was used as a continuous variable in analyses rather than the initial number of competitors. For some analyses, pots were reclassified into three density classes: no competitors, 5–10 competitors, and 11–30 competitors. Classification intervals were chosen to result in nearly equal numbers of plants in the two higher-density classes.

After senescence, traits known to influence seed dispersal were measured on focal plants: number of fruit segments produced (number of fruits); height; number of secondary branches (branches growing directly from the primary stem) per centimeter of primary stem (branches/cm), used as a measure of the compactness of the branches (its inverse being a measure of the space between branches); and the percentage of fruits that grew directly from the primary stem (percentage primary fruits), used as a measure of fruit placement.

Field Observations

To supplement the greenhouse study, I conducted an observational field study of plants growing in a range of natural densities. The density of greenhouse-grown plants was necessarily lower than the density of naturally occurring clumps. Moreover, competition at any given density was likely to be less extreme in the greenhouse than in the field since greenhouse plants were watered and fertilized. However, environmental conditions in the field could cause mortality of many individuals, regardless of the density at which they grow. Consequently, the interactions among density, maternal morphology, and maternal fitness in the field may differ from those observed in the greenhouse.

The same morphological traits measured in the greenhouse were measured in single and clumped individuals in the field at the Indiana Dunes National Lakeshore. Plants were measured in late July, before complete fruit maturation and dispersal, so that accurate fruit counts could be obtained. I identified clumps of plants that had unambiguously grown from a buried maternal plant and that represented the center of a seed shadow of one plant. Clumps were chosen to be >25 m from each other. Five random individuals were sampled within each clump, and the five nearest singly occurring plants were sampled as well. I sampled 120 plants distributed among 12 clumps.

Data Analysis

The Mechanistic Basis of Density-Mediated Maternal Effects. To characterize the direction and magnitude of plasticity of maternal morphological traits to density, regression analysis of normalized morphological traits was performed on greenhouse-grown plants, with density as the independent variable. Despite the overrepresentation of single plants in the sample, residuals were normally distributed. Quadratic terms were tested but were not significant. To measure morphological differences between single and clumped plants in the field, mean values of the five clumped and of the five single nearest neighbors of each clump were calculated for each plant trait and compared with paired *t*-tests. Mean values for each group were used to avoid pseudoreplication since clumps were likely to be composed of related individuals and plants within a clump and their nearest neighbors were likely to experience similar microenvironments. To characterize indirect paths of maternal density effects, Pearson correlations among morphological characters were calculated.

To test whether plasticity of morphological characters was simply caused by allometric variation with density-dependent size, the relationship between morphological characters and a measure of plant size, total number of branches (secondary plus higher level branches), was compared across density treatments using log- (base 10) transformed data. Branch number was used because some of the morphological traits (branches/cm and percentage primary fruits in particular) are expected to vary allometrically with branch number. For example, the number of secondary branches/cm can indicate either the spacing of branches along the primary stem or simply the number of branches on the plant. Similarly, percentage primary fruits can reflect either selective fruit placement or simply the number of branches available to place fruits on; if few or no branches exist, then most or all of the fruits will be on the primary stem. The relationship between branch number and height is not presented because branches/cm is a function of height and number of branches, and consequently its analysis is redundant to the analysis of height (and gave similar results). ANCOVA was performed, with branch number as the independent variable, other morphological characters as dependent variables, and density class as a class variable. A significant interaction between branch number and density class indicated that the allometric relationship between the two characters differed with density treatment. This analysis was performed on greenhouse-grown plants by comparing the relationship between characters among the three density classes and on field plants by comparing the relationship between characters of single and clumped plants.

Estimating the Magnitude of Density-Mediated Maternal Effects. The magnitude and direction of density-mediated maternal effects on morphological characters and on dispersal were estimated using a modified path analysis of greenhouse-grown plants (fig. 2). Greenhouse plants were used because they provided a much more even distribution of density than did the field plants. They also more effectively controlled for genetic correlations between maternal and offspring traits. In the greenhouse study, genetic correlations between maternal and offspring characters are necessarily zero since different random samples were used in maternal and offspring generations and density (the progeny character) was experimentally manipulated to be random with respect to genotype. Consequently, the estimated correlations between generations are environmentally induced rather than genetically induced, and they therefore are proportional to the magnitude of the maternal effect.

The density-mediated maternal effect of a maternal morphological trait on the same trait in progeny was estimated for each trait. I estimated both total and direct maternal effects. A direct maternal effect is the maternal effect that would occur if indirect paths of maternal influence did not occur through correlations among maternal traits. Thus, direct maternal effects provide detail on the architecture of the maternal effects matrix that, in sum, influences evolutionary responses to selection. Total maternal effects were estimated as follows: the total predictive effect of density on a plant morphological trait was estimated as the standardized simple regression coefficient. The total effect of plant phenotype on seed density was estimated as the standardized simple regression coefficient in a previous study (Donohue 1998). The total maternal effect of a maternal trait on the same progeny trait is the product of the two standardized simple regression coefficients since they include paths of indirect influence. Direct maternal effects were estimated as follows: direct predictive effects of density on each morphological trait while controlling for correlations among plant traits (*a*'s in fig. 2) were estimated using multiple regression in which all plant traits except the dependent variable were included with density in the regression model. Direct effects of plant phenotype on seed density (*b*'s in fig. 2) were estimated as standardized multiple-regression coefficients in a previous study (Donohue 1998). The direct maternal effect of a maternal trait on the same trait in the progeny (effect of $Z[m1]$ on $Z[m1]'$ in fig. 2) was estimated as the product of the two standardized multiple-regression coefficients ($m[m1] = b1 \times a1$ for maternal trait 1 in fig. 2).

The maternal effect of dispersal (density) on itself was estimated as the effect of density in one generation on density in the next generation, as mediated by these morphological traits (effect of $Z[d]$ on $Z[d]'$ in fig. 2). In the notation of figure 2, the total maternal effect of $Z(d)$ on $Z(d)'$, as mediated by maternal traits $Z(m1)$ and $Z(m2)$, is

$$m(d) = a1(b1 + rb2) + a2(b2 + rb1), \tag{1}$$

where $(b1 + rb2)$ is the standardized simple regression coefficient for the effect of maternal character $Z(m_1)$ on dispersal, and $(b2 + rb1)$ is the standardized simple-regression coefficient of the effect of maternal character $Z(m_2)$ on dispersal. Consequently, the total maternal effect was estimated as the sum of the products of the direct effect of density on morphology (*a*'s) and the total effect of morphology on density. Maternal effects controlling for correlations among maternal characters were estimated as the sum of the products of the multiple-regression coefficients ($a1 \times b1 + a2 \times b2$). In a final path analysis, I used path coefficients that were estimated from a multiple regression that measured the effect of morphology on dispersal and that included maternal site variables (beach width, dune slope, depth of burial) and another plant trait: percentage detachment (not measured in this study but measured in a different field study; Donohue 1998). Therefore, this final path analysis controlled not only for correlations among maternal plant morphological characters but also for relationships between these characters and maternal site characters in the field.

Fitness Consequences of Maternal Characters That Influence Dispersal. To determine how maternal morphological characters covaried with maternal fitness, phenotypic selection analysis (Lande and Arnold 1983) was performed on the morphological variables (height, branches/cm, and percentage primary fruits). Morphological variables were transformed to normality for all analyses, using natural-log transformation (height and branches/cm) or arcsine-square root transformation (percentage primary fruits). Total fruit segment production was used as an estimate of fitness. Because fruit segments are almost always single seeded, and because *C. edentula* is highly selfing, the number of fruit segments is an accurate estimate of total lifetime fitness. Residuals from all selection analyses were normally distributed. Selection differentials (s), or the strength of total selection, were estimated as the regression coefficient of relative fitness against standardized morphological traits in a simple regression. Selection gradients (β), or the strength of direct selection, were estimated as the regression coefficient obtained from a multiple regression that included the three characters. Stabilizing or disruptive selection was estimated as the regression coefficients of quadratic terms from univariate- (g) and multivariate- (γ) regression analysis. No correlational selection was detected in any analysis, so interactions among morphological characters were not included in the selection analyses reported. Because morphology and fitness can covary with the number of competitors (Rausher 1992), the aforementioned selection coefficients were estimated by regressing relative fitness against standardized morphological traits and the number of competitors (continuous variable) to determine the effect of morphology while controlling for the number of competitors. To determine whether the strength of selection varied with density, interactions between plant traits and density were estimated in an additional analysis like the one already described but that included an interaction term between the variables and density. Selection sometimes varied with density (see "Results"). To determine how selection varied with density, separate selection coefficients were estimated within each density class, using variables that were standardized within each density class.

The strong associations of plant traits with fitness detected in the selection analysis just described could be because of relationships between plant traits and plant size or because of selection on plant traits independent of plant size. To distinguish between these two possibilities, a principal components analysis was performed. Plant size was the first principal component, and the next two principal components reflected plant morphology independent from plant size. Phenotypic selection analysis was performed on these principal components as described earlier.

A similar selection analysis was conducted on the field plants, but identity of the clump and its nearest neighbors was used as a class variable in the analysis. Clump identity was included because clumps and their nearest neighbors are likely to experience similar microenvironments. An analysis that does not control for direct effects of microenvironment could artificially strengthen the relationship between phenotype and fitness if individuals of like phenotype also have like fitness, owing to their similar location (Rausher 1992).

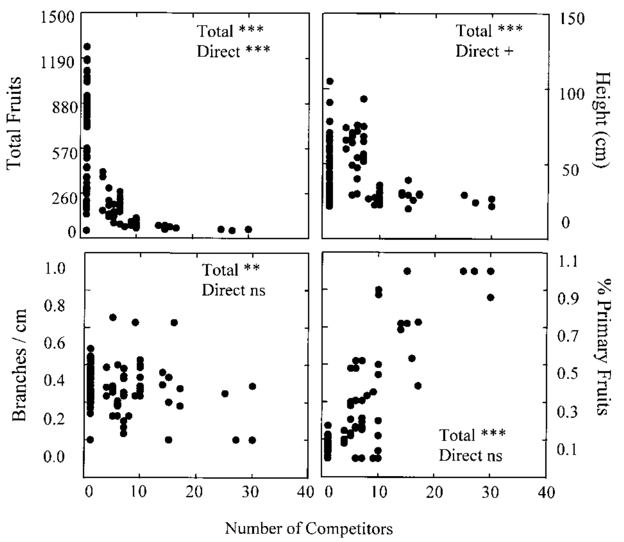

Figure 3: Scatter plots of density against untransformed morphological traits of plants grown in the greenhouse. *Total* refers to the total effect of density on the trait, and *direct* refers to the effect of density while controlling for correlations among characters. The magnitude of the effect of density on these traits is shown in table 2. +, $P < .1$; *, $P < .5$; **, $P < .01$; ***, $P < .001$.

Results

The Mechanistic Basis of Maternal Effects on Dispersal

Plant morphological traits varied strongly with density both in the greenhouse (fig. 3) and in the field (fig. 4). In both field and greenhouse samples, high density resulted in lower fruit production, reduced height (significant in the greenhouse), fewer branches/cm, and a greater percentage of fruits located on the primary stem (significant in the greenhouse).

Indirect paths of maternal effects may be strong since many characters were highly correlated, especially in the field (table 1). Percentage primary fruits was negatively correlated with the other characters, while the other characters were positively correlated with each other.

Plasticity to density appears not to be a result simply of allometric variation of all characters with size since the allometric relationship between morphological characters and branch number sometimes changed significantly with density. The positive relationship (coefficient = 0.14) between branches/cm and number of branches did not change significantly with density in the greenhouse (F interaction = 0.78, $P = .46$), but it did vary significantly between clumped and single plants in the field (F interaction = 7.00, $P = .009$; single coefficient = 0.09, clumped coefficient = 0.13). In the field, plants with few branches had greater spacing between branches at high density than at low density, and plants with many branches had less space between branches at high density than at low density. This indicates that branch spacing varied more at high density than at low density. Consequently, density-dependent variation in branch spacing cannot be attributed entirely to variation in branch number.

The relationship between percentage primary fruits and number of branches differed among density treatments in the greenhouse (F interaction = 8.50, $P = 0.0004$) but not in the field (F interaction = 2.40, $P = 0.125$; coefficient = −0.67). In the field, more fruits were placed on the primary stem as branch number decreased. In the greenhouse, the relationship was positive at low density (coefficient = 0.61) but strongly negative at high density (intermediate-density coefficient = −0.12, high-density coefficient = −0.93). This result suggests a nonallometric increase in the placement of fruits on the primary stem by small plants (with few branches) at high density compared with those at low density in the greenhouse.

Plants with few branches had significantly more fruits at high density than at low density in the greenhouse (F interaction = 18.18, $P = .0001$), indicating a nonallometric increase in fruit production of small plants at high density (low-density coefficient = 1.98, intermediate-density coefficient = 0.83, high-density coefficient = 1.05). The number of fruits varied allometrically with density in the field (F interaction = 6.74, $P = .012$; coefficient =

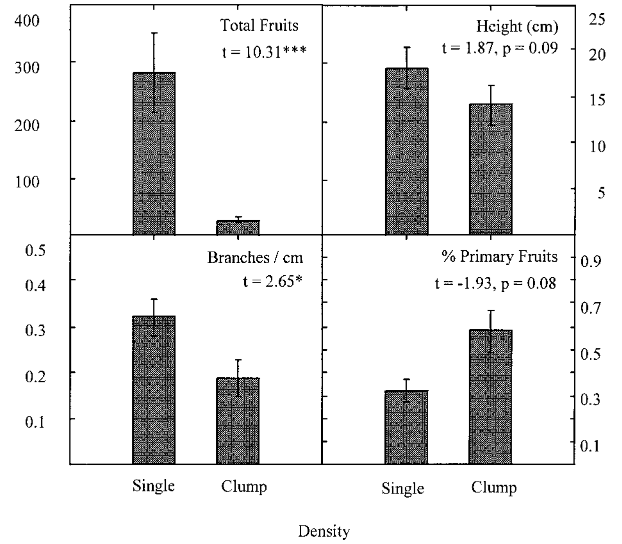

Figure 4: Means and SEs of plant morphological traits for plants growing singly and in high-density clumps in the field. Values of t are given based on paired t-tests. Average number of plants per clump = 28, SD = 42; $N = 12$ clumps. +, $P < .1$; *, $P < .5$; **, $P < .01$; ***, $P < .001$.

Table 1: Pearson correlation coefficients for plants grown in the greenhouse (above diagonal) and in the field (below diagonal)

	Height	Branches/cm	Percentage primary fruits	Total fruits
Height		.06	$-.43^{***}$	$.61^{***}$
Branches/cm	$.70^{***}$		$-.25^{**}$	Ψ $.22^{*}$
Percentage primary fruits	$-.68^{***}$	$-.77^{***}$		$-.53^{***}$
Total fruits	$.89^{***}$	$.76^{***}$	$-.72^{***}$	

Note: Ψ not significant with sequential Bonferroni correction.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

1.16) such that plants with more branches had more fruits at both densities.

The Magnitude of Density-Mediated Maternal Effects

The total estimated maternal effect of a character on itself was negative for total fruit production and height, and it was close to zero for branches/cm and percentage primary fruits (table 2). Therefore, tall maternal plants with many fruits are predicted to produce short offspring with few fruits because of density-mediated maternal effects. When correlations among traits were controlled for, the effect of density on phenotypic expression led to negative direct maternal effects on fruit production, height, and branches/cm. When site variables that were associated with the location of the maternal plant in the field were also controlled for, the negative maternal effects became even more negative. The predicted maternal effect of density on itself was negative whether or not correlations among traits were controlled for, and it was strongest when correlations among characters and site variables were controlled for. Therefore, a maternal plant that grew in high density is predicted to have progeny that grow in low density, and vice versa.

Fitness Consequences of Maternal Characters That Influence Dispersal

In the greenhouse, plants with higher fitness were taller (coefficients controlling for density: $s = 0.30$, $P < .001$; $\beta = 0.22$, $P < .001$), had more branches/cm ($s = 0.17$, $P < .01$; $\beta = 0.02$, $P > .05$), and had a smaller percentage primary fruits ($s = -0.23$, $P < .001$; $\beta = -0.31$, $P < .001$). Significant stabilizing selection was detected on percentage primary fruits such that plants that placed most but not all of their fruits on higher-level branches had highest fitness (univariate $= -0.18$, $P < .001$; multivariate $= -0.09$, $P < .05$). Selection did not vary across density treatments for any character.

The principal components analysis of greenhouse-grown plants (table 3) identified three principal components. The first principal component (size) reflects plant

Table 2: Estimates of maternal effects on morphology and dispersal (measured as density)

	Ψ Morphology → dispersal (density)			Density → morphology		Maternal effect		
Trait	Total	Direct	Direct field	Total	Direct	Total	Direct	Direct field
Total fruits	$.36^{*}$	$.38^{*}$	$.82^{***}$	$-.88^{***}$	$-.48^{***}$	$-.31$	$-.18$	$-.39$
Height	$.37^{*}$	$.62^{*}$	$.66^{***}$	$-.75^{***}$	$-.34^{\dagger}$	$-.28$	$-.21$	$-.22$
Branches/cm	$-.14$	.36	$.49^{*}$	$-.36^{**}$	$-.28$	.05	$-.10$	$-.14$
Percentage primary fruits	.08	.13	.09	$.78^{***}$	.25	.06	.03	.02
Maternal effect on dispersal (density)	...	...	...	...	...	$-.24$	$-.46$	$-.73$

Note: "Direct field" refers to path coefficients estimated from a multiple regression that included field site variables. See "Data Analysis" for explanation of coefficients and calculation of maternal effects. Ψ data from Donohue 1998.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

† $P < .1$.

Table 3: Principal components analysis of plant morphological traits (PC1, PC2, PC3) for greenhouse-grown plants and plants in the field

	PC1	PC2	PC3
Greenhouse-grown plants:			
Height	.61	.49	.62
Number of branches/cm	.39	−.87	.31
Percentage primary fruits	−.69	−.06	.72
Percentage variance explained	50.9	31.7	17.4
Plants in the field:			
Height	.56	.82	.10
Number of branches/cm	.58	−.48	.66
Percentage primary fruits	−.59	.31	.75
Percentage variance explained	80.0	12.3	7.7

size since height and branches/cm loaded positively and percentage primary fruits loaded negatively (indicating that most fruits were not on the primary stem but rather on higher-level branches, which are abundant on larger plants). The second principal component (elongation) reflects elongation since height loaded positively and branches/cm loaded negatively. A plant with a large positive score for this component would be tall with its branches spaced far apart. The third principal component (fruit placement) indicates the degree of fruit placement on the primary stem. Plants that had a high positive score were taller with more branches, but they had a large proportion of fruits on the primary stem. Principal components analysis of field plants gave similar results (table 3), and the components can be interpreted similarly.

As expected, large size was associated with increased fitness in all density classes in the greenhouse (table 4, A), but direct selection was significantly weaker at high density (table 4, B). Stabilizing selection on size was detected at low density, accounting for the nearly significant stabilizing selection overall (table 4, C). However, a fitness optimum was not observed within the range of the phenotypic variation in this sample. Hence, the significant stabilizing selection coefficient reflects a nonlinear but monotonic increase in fitness with increasing size.

Direct selection favored increased elongation at low density in the greenhouse (table 4, B). Otherwise, directional selection was neutral regarding elongation (table 4, A, B). Disruptive selection on elongation was detected in the univariate analysis (table 4, C), but it was significant only at low density. The fitness minimum was not within the range of phenotypic variation in this sample, however, indicating a nonlinear but monotonic increase of fitness with increased elongation.

Total selection favored placing fruits on the primary stem at high density in the greenhouse but disfavored it at low density (table 4, A). Direct selection favored placing fruits on the primary stem only at low density (table 4, B), and it was not significant overall when controlling for density. Stabilizing selection on fruit placement was detected for plants grown at intermediate density (table 4, C, D), and an intermediate fitness optimum was within the range of phenotypic variation present in the sample. Plants that distributed their fruits among primary and higher-level branches, therefore, had the highest fitness. Stabilizing selection was not significant, but nearly so, when controlling for density.

Directional selection in the field was generally stronger than in the greenhouse. The direction of selection was similar to that in the greenhouse for all morphological characters (coefficients with density: height $s = 0.79$, $P < .001$; $\beta = 0.74$, $P < .05$; branches/cm $s = 0.44$, $P < .05$; $\beta = -0.23$, $P > .05$; percentage primary fruits $s = -0.61$, $P < .01$; $\beta = -0.37$, $P > .05$). Selection on height was significantly stronger at high density (F univariate $= 5.95$, $P < .05$; F multivariate $= 3.19$, $P < .1$). Unlike the results from plants grown in the greenhouse, disruptive selection was observed on height in the field ($g = 0.66$, $P < 0.001$; $\gamma = 0.71$, $P < .001$), and it was significantly stronger at high density (F univariate $= 7.36$, $P < .01$; F multivariate $=$ 3.55, $P < .1$). In both single and clumped plants, the tallest plants had the highest fitness, but the shortest plants did not have the lowest fitness. Disruptive selection was also detected in the univariate analysis of percentage primary fruits ($g = 0.43$, $P < .05$). Plants with a greater than average percentage primary fruits were most strongly selected against, but plants with all primary fruits did not have the lowest fitness.

Most of the association of plant morphological traits with fitness in the field can be attributed to the relationship between plant size and fitness (table 5). Large plants were favored more strongly at high density. Although plants with the highest fitness were the largest plants (table 5, A, B), some of the smallest plants at both low and high density had higher fitness than plants that were slightly larger, as indicated by significant disruptive selection on size (table 5, C, D). Increased elongation was favored in the field, as it was at low density in the greenhouse (table 5, A, B). Clumped plants that placed fruits on the primary stem had higher fitness (table 5, A), and nearly significant ($P = .08$) stabilizing selection was observed in these plants (table 5, C). However, selection on fruit placement was not significant when controlling for density.

Discussion

Mechanism and Magnitude of Density-Mediated Maternal Effects

Plant morphological traits varied strongly with density, both in the greenhouse and in the field. The response, in

Table 4: Directional (A–B) and stabilizing-disruptive (C–D) selection analysis of principal components of plants grown in the greenhouse

Trait	Coefficient with density	F interact with density	1 plant/ pot	5–10 plants/ pot	11–30 plants/ pot
A. Total selection, s:					
Size	.40***	.29	.40***	.39***	.45***
Elongation	−.07	.03	−.03	.09	−.10
Fruit placement	−.12*	18.49***	−.36***	−.07	.43***
B. Direct selection, β:					
Size	.42**	4.73*	1.15***	.40***	.30
Elongation	.08	2.95†	.29***	−.03	−.03
Fruit placement	.04	.13	.65**	−.02	.18
C. Total stabilizing-disruptive selection, g:					
Size	−.03†	.48	−.06*	.02	−.06
Elongation	.05*	3.22†	.13***	−.08	−.15
Fruit placement	.00	.23	−.02	−.20*	.06
D. Direct stabilizing-disruptive selection, γ:					
Size	.01	.71	.15	−.00	−.26
Elongation	.00	.34	.01	−.04	−.04
Fruit placement	−.08†	.31	−.11	−.16*	.16

Note: Selection differentials (s), selection gradients (β), univariate stabilizing-disruptive selection coefficients (g), and multivariate stabilizing-disruptive selection coefficients (γ) are shown for each density class. "Coefficient with density" is the coefficient from an analysis that controls for density. "F interact with density" is the F ratio for the interaction of the trait with density as a continuous variable.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

† $P < .1$.

general, was such that plants growing at high density expressed traits that would enhance dispersal (Donohue 1998). Plasticity in the field was caused by a nonallometric increase in branch spacing by small plants at high density and allometric variation in fruit placement and fruit production. Small plants showed nonallometric placement of fruits on the primary stem and increased fruit production rather than branch production at high density in the greenhouse.

The plastic responses of maternal plant traits to density resulted in negative maternal effects on most traits that influence dispersal and an overall negative maternal effect on dispersal or density. Correlations among characters reduced maternal effects, as did variation in site variables in the field. These negative maternal effects were the result of interactions among maternal morphological characters and density. The cycles necessary to produce the unique evolutionary dynamics of maternally influenced characters referred to by Kirkpatrick and Lande (1989) were effected in this system by the influence of maternal morphology on dispersal, the correspondence between dispersal and density, and the plastic responses of morphological characters to density.

Although these estimated phenotypic correlations between generations do not include any genetic component, the fact that most environmentally induced correlations were negative suggests that the response to selection on dispersal may be retarded or rendered negative (Kirkpatrick and Lande 1989). In a field study in which density was measured in the maternal and progeny generations, the correlation between generations for density after dispersal was very close to zero (Donohue 1998). Although this result is, in part, likely to be because of a lack of statistical power in a field study with much environmental variance, it also suggests that negative maternal effects on density occur in the field. Such maternal effects would operate in the opposite direction and may have canceled out genetically based positive correlations that may have been present in the sample of plants in the field study. Thus, the observed maternal effects lead to the prediction of a slower response to selection on dispersal.

Selection on Maternal Morphological Characters

Maternal morphology was strongly associated with maternal plant fitness. This association was in part because of the relationship of morphology with size; larger plants had higher fitness. However, elongation and fruit placement were under selection independently of plant size, both in the field and in the greenhouse. Selection favored increased elongation, possibly because increased spacing of branches reduces self shading or breakage (which is

Table 5: Directional (A–B) and stabilizing-disruptive (C–D) selection analysis of principal components of single and clumped plants in the field

Trait	Coefficient with density	*F* interact with density	Single	Clumped
A. Total selection, *s*:				
Size	.73***	3.45†	.36	.81*
Elongation	.32†	1.23	.14	.40†
Fruit placement	−.30	.09	−.02	.45*
B. Direct selection, β:				
Size	.72***	3.93*	.43	.65†
Elongation	.33*	1.58	.21	.36†
Fruit placement	−.17	.11	−.03	.36
C. Total stabilizing-disruptive selection, *g*:				
Size	.86***	1.48	.39†	1.30***
Elongation	.04	.35	−.07	.17
Fruit placement	−.10	.00	−.06	−.13†
D. Direct stabilizing-disruptive selection, γ:				
Size	1.04***	2.71	.58*	1.45***
Elongation	.19†	.08	.09	.19†
Fruit placement	−.16	.57	−.06	−.05

Note: See table 4 for explanation of terms.

* $P < .05$.

*** $P < .001$.

† $P < .1$.

common in the field). Selection on fruit placement varied with density under some conditions and reflected potential allocational trade-offs that could vary with density. Allocation of meristems to reproductive structures precludes further vegetative growth from the meristem (Diggle 1994; Stafstrom 1995). Early meristem allocation to vegetative structures can enhance resource acquisition ability and thereby increase total reproduction if conditions are favorable (Watson 1984; Geber 1990; Watson et al. 1997). Under such favorable conditions, selection would favor meristem allocation to branches rather than to fruits and consequently favor the placement of fruits on branches rather than on the primary stem. Such selection was observed at low density in the greenhouse—the condition that was most favorable. However, this selection can be attributed to indirect selection through plant size rather than direct selection on fruit placement. At high density, selection favored placing fruits on the primary stem rather than on branches, possibly reflecting the expense of creating a branch to put fruits on under more competitive conditions. The observed nonallometric increase in the placement of fruits on the primary stem at high density supports this interpretation. Moreover, size itself was under disruptive selection in the field; small plants with a few branches had lower fitness than the smallest plants with no branches and all fruits on the primary stem. This result also supports the interpretation that branch formation is costly under competitive conditions.

Whether the traits themselves were under selection, or whether they merely reflected maternal vigor, the association between maternal traits that influence dispersal and maternal fitness will influence the net selective value of dispersal. In short, maternal plant traits and their response to density influence progeny fitness through their influence on dispersal, yet they also influence the fitness of the maternal plant. Characters that were associated with an increase in maternal plant fitness tended to impede dispersal and thereby decrease progeny fitness (table 6; Donohue 1997).

The Adaptive Value of Plasticity to Density

The strength of selection on maternal plant characters sometimes changed with density. Such density-dependent selection would determine whether the plastic responses of maternal morphology would increase or decrease maternal plant fitness (Schmitt et al. 1995; Dudley and Schmitt 1996). For example, the observed plastic response of height to density would result in a tall plant at low density, which would increase maternal fitness at low density. However, shorter plants grew at high density, and short plants were even more strongly selected against at high density in the field than at low density. Therefore, the plastic response of height—namely, decreasing height at high density—would not increase maternal plant fitness under field conditions. Selection on the number of branches/cm and percentage primary fruits did not vary with density in the field. Because plants at low density had

Table 6: Summary of effects of plant traits on maternal and progeny fitness (net selection) through the influence on dispersal (measured as seed density after dispersal)

Trait	Maternal fitness	Density after dispersal	Progeny fitness
Total fruits	Positive	Increased	Negative
Height	Positive	Increased	Negative
Branches/cm	Positive	Neutral/ increased	Neutral/negative
Percentage primary fruits	Negative	Increased/ neutral	Negative/ neutral

Note: The table shows the effects of an increase in the plant trait. When two effects are shown, the left-hand side indicates the total effect of an increased in the trait and the right-hand side indicates the direct effect of an increase in the trait.

more branches/cm and a smaller percentage of primary fruits, the plastic response would increase maternal plant fitness at low density but decrease it at high density. Again, it appears that the plastic response of these traits would not increase maternal plant fitness under field conditions. Rather than being adaptive responses to the density environment, the observed plastic responses of these characters may be explained by resource limitation or developmental constraints despite the fact that the responses are not strictly allometric. It appears that the nonallometric responses do not fully compensate for the allometric constraints on these characters. Genetic constraints on the responses may also prevent them from being adaptive. Thus, selection is expected to favor decreased plasticity of these characters, which would likely lead to weaker maternal effects.

Evolving Environments

In this study of *Cakile edentula*, not only did maternal plasticity to density influence progeny dispersal, and consequently progeny fitness, but it also affected the selective environment experienced by the progeny—namely, the density environment. Because selection was shown to be density dependent on some characters, the maternal response to density can influence how the response will be selected by determining not only the phenotype expressed in an environment but also the selective environment itself. Plastic responses—particularly maternally controlled responses—often influence the selective environment experienced by a genotype, and examples of this can be found in very different taxa. In butterflies (Rausher 1981) and bruchid beetles (Fox 1993), the maternal response to host plant chemistry, host nutritional quality, or egg abundance (Rausher 1979) influences oviposition site preference and, consequently, influences the nutritional and competitive environment experienced by offspring. Frogs also respond to conspecific egg densities when choosing egg-laying sites and thereby influence the competitive environment of their offspring (Resitarits and Wilbur 1989). In mice, the availability of milk when young influences the litter size maintained by the mother, which in turn influences the competitive environment (and milk availability) of her offspring (Falconer 1965). In the annual plant *Arabidopsis thaliana* (Hayes and Klein 1974), the red : far red ratio of light wavelengths experienced by a maternal plant during seed maturation acts as a cue of competitive conditions (Ballaré et al. 1987), and it can influence whether its seeds require light (or an open canopy, indicative of noncompetitive conditions) before they can germinate (Hayes and Klein 1974). In that example, the maternal light environment influences germination behavior and consequently the light (and possibly competitive) environment of the offspring. Finally, as in this study, the response of the maternal plant to its density environment influences dispersal and, consequently, the density environment experienced by the progeny. In all of these examples, the response of the maternal parent to its environment influences the selective environment experienced by the progeny. As a result, the maternal response will influence how that response itself is selected. These examples demonstrate that the environment—as experienced by organisms—is not necessarily fixed by external conditions; rather, it is in large part biologically determined. If environments are biologically determined, they can evolve. The evolution of dispersal is an example of the evolution of environments experienced by organisms.

Plastic maternal responses, such as those in the examples just described, influence the variation in selective environments between generations and thereby influence the frequency of selective environments experienced by a genotype. The frequency of environments strongly influences the evolution of specialists versus generalists, including phenotypically plastic generalists (Via and Lande 1985; Van Tienderen 1991); if the selective environment does not vary, plasticity will not be favored over specialization. Therefore, when a plastic response determines the selective environment—and the variation in selective environments—experienced by a genotype, it can influence its own evolution. This sort of coevolution of characters with their environment has only very recently been incorporated into theoretical or empirical frameworks (Evans and Cabin 1995; Moore et al. 1997, 1998; Wolf et al. 1998), but it is likely to be important in understanding the evolution of plastic characters and parental effects.

Conclusion

Plasticity of maternal morphology to density resulted in negative maternal effects on dispersal. In addition, selection on maternal morphology that influences dispersal was strong. In this example, a response that increased progeny fitness through increasing dispersal was most often associated with greatly reduced maternal fitness. Therefore, selection operates in opposite directions on mothers and offspring. By considering only the fitness of progeny under different dispersion patterns, one would have predicted a rapid evolution toward increasing dispersal ability. This cannot explain the presence of the high-density clumps of seedlings so common on the beach. Nor does such an approach alone have promise for explaining the ubiquity of underdispersal in so many diverse systems. By considering dispersal as a maternally influenced character, with maternal plants under selection as well as progeny, we predict not only a dramatically reduced selective advantage to dispersal but also a slower or even negative response to selection.

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